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Short communication

Genetic analysis of museum samples suggests temporal stability in the Mexican nonbreeding distribution of a neotropical migrant

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Seasonal migration is highly labile from an evolutionary perspective and known to rapidly evolve in response to selective pressures. However, long-distance migratory birds rely partially on innate genetic programs and may be constrained in their ability to alter their migratory behavior. We take advantage of recent advances in our ability to genotype historical DNA samples to examine the temporal stability of migratory connections between breeding and nonbreeding populations (i.e. migratory connectivity) and population-level nonbreeding distributions in the Wilson's warbler *Cardellina pusilla*, a long-distance migratory songbird. By assigning historical and contemporary samples collected across the nonbreeding range to genetically distinct breeding clusters, we suggest that broad-scale population-level nonbreeding distributions within this species have remained largely consistent within Mexico from the mid-1900s to the present day. These findings support the idea that the nonbreeding distributions of long-distance migrants may remain stable over long time scales, even in the face of rapid environmental change.

Keywords: *Cardellina pusilla*, historical DNA, migratory connectivity, seasonal migration

Introduction

Seasonal migration between breeding and nonbreeding locations is a widespread phenomenon that allows organisms to take advantage of resources that vary in space and time. These annual movements have long-term impacts on ecosystem processes occurring at a global scale, including trophic interactions and nutrient cycling (Bauer and Hoye 2014). According to studies across multiple taxa, migratory behavior is highly

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labile and can rapidly change in response to selection (Pulido 2007). For example, migratory lineages have repeatedly evolved from sedentary populations (La Sorte and Thompson 2007, Pulido 2007). In addition, selection for shorter migratory distances due to anthropogenic environmental change has led to poleward shifts in the nonbreeding ranges of many migratory taxa and the loss of migratory behavior over the past century (La Sorte and Thompson 2007, Visser et al. 2009). In one of the most striking examples illustrating the flexibility of migratory behavior, Eurasian blackcaps *Sylvia atricapilla* breeding in central Europe have evolved a novel northwestern migratory route since the 1950s that takes them to overwintering grounds in the UK rather than the Iberian Peninsula (Berthold et al. 1992).

Despite the demonstrated evolutionary flexibility of seasonal migration, particularly for short-distance migrants like the Eurasian blackcap, long-distance migratory birds appear relatively constrained in their ability to alter their migratory patterns and establish new nonbreeding grounds (Sutherland 1998, Alerstam et al. 2003). It is well known that many long-distance migrants follow seemingly sub-optimal migratory trajectories that retrace ancestral routes of colonization (Sutherland 1998, Ruegg and Smith 2002, Bairlein et al. 2012). This evolutionary inertia associated with the genetic inheritance of migratory behavior has been invoked to explain why long-distance migratory birds have been less successful at colonizing different sides of the Eurasian continent (Bensch 1999) and both North America and Eurasia (Böhning-Gaese et al. 1998) when compared to sedentary species (Bensch et al. 2023). In addition, several studies comparing the breeding and nonbreeding ranges of Palearctic long-distance migrants over time have found that nonbreeding distributions during the last glacial maximum (21 000 years before present) were surprisingly similar to those of the present day (Ponti et al. 2020, Thorup et al. 2021). Given these patterns, we might expect the nonbreeding ranges of long-distance migratory birds to be spatially stable over long time periods, even in the face of environmental change. However, few studies have examined the temporal stability of migratory connections between breeding and nonbreeding areas (i.e. migratory connectivity) in long-distance migrants (Gómez et al. 2021), particularly at the population level.

We leverage single nucleotide polymorphism (SNP) genotyping data from historical and contemporary samples of the Wilson's warbler *Cardellina pusilla*, a long-distance migratory bird that breeds throughout the western USA and Canada and overwinters in Mexico and Central America (Ammon and Gilbert 2020), to reconstruct past and present patterns of migratory connectivity (Bay et al. 2021, Ruegg et al. 2021). Previous research on contemporary samples of the Wilson's warbler identified geographically linked genetic variation within the species and used this variation to assign nonbreeding populations of unknown breeding origin to six breeding clusters (Western Boreal, Pacific Northwest, Coastal California, California Sierra, Basin Rockies, and Eastern Boreal) (Ruegg et al. 2014, 2020). Using these geographically informative loci, we determine the breeding origin of historical Wilson's warblers overwintering in Mexico from 1934 to 1964 and compare the resulting assignments to those of contemporary nonbreeding individuals sampled across the same sites from 1994 to 2020. Where possible, we also include contemporary birds from additional sites across Mexico and Central America to advance our understanding of migratory connectivity in the Wilson's warbler.

Wilson's warblers inhabit forested areas throughout the annual cycle and defend territories during both breeding and nonbreeding seasons (Hutto 1981, Ruiz-Sánchez et al. 2017). During the nonbreeding period, the species has been described as a habitat generalist (Ammon and Gilbert 2020), occupying a broad range of vegetation types ranging from mangroves and tropical evergreen forest in the coastal lowlands to high-elevation cloud forest (Hutto 1981, 2020). Nonetheless, some habitats are likely higher quality than others, and sexes may segregate by habitat in certain areas (Rappole 1988). For example, Wilson's warblers overwintering in southeastern Mexico are present at higher densities and hold smaller territories in conserved cloud forest than disturbed sites with reduced forest cover, suggesting that mature cloud forest provides high-quality habitat for the species (Ruiz-Sánchez et al. 2017). In addition, previous research has demonstrated that genetically distinct breeding groups of the Wilson's warbler likely occupy distinct ecological niches, with eastern breeding birds occurring in areas with higher precipitation and lower temperature during the nonbreeding season than other genetic groups (Ruiz-Sánchez et al. 2015). In the highlands of Veracruz, Mexico, forested areas containing montane cloud forest have been logged over the past few decades to make way for cattle ranching and coffee and sugar cane plantations (Williams-Linera 2007, Muñoz-Villers and López-Blanco 2008). Additionally, Mexico has lost over 10% of its mangrove forest cover since 1970 due to conversion for agriculture (Valderrama et al. 2014), impacting the amount and quality of nonbreeding and migratory habitat available for the species. Examining how nonbreeding distributions at the population level have shifted over a 50+ year timespan will provide insight into the temporal stability of migratory connections in long-distance migrants faced with rapid environmental change.

Material and methods

Sample collection and DNA extraction

We acquired toepads from 49 Wilson's warbler individuals that were collected in Mexico from 1934 to 1964, prior to significant global land use change (Winkler et al. 2021), and stored as study skins in the Moore Lab of Zoology at Occidental College in Los Angeles, California and the Instituto de Biología at the Universidad Nacional Autónoma de México (UNAM) in Mexico City (Table 1). According to early bulletins and eBird records, the nonbreeding distribution of the Wilson's warbler was known to extend throughout

Table 1. Number of nonbreeding Wilson's warblers included in the historical (n=49) and contemporary (n=370) datasets and their corresponding sampling locations. Successfully genotyped samples that were collected in close geographic proximity were merged on the map in Fig. 2.

Country	State/Department	Latitude	Longitude	n
Historical				
Mexico	Chiapas	16°39'36''N	92°33'36''W	5
	Colima	19°14'24''N	103°37'12''W	1
	Durango	25°8'24''N	106°14'24''W	4
	Guanajuato	20°40'48''N	101°20'60''W	3
	Guerrero	16°28'12''N	98°24'36''W	1
	Hidalgo	20°20'24''N	98°35'60''W	3
	Jalisco	19°41'60''N	103°27'36''W	2
	Mexico City	19°20'24''N	99°20'24''W	2
	Michoacán	18°59'24''N	101°58'48''W	9
	Morelos	18°43'12''N	99°16'48''W	2
	Oaxaca	17°11'60''N	95°45'0''W	7
	Puebla	19°31'12''N	97°5'60''W	4
	Querétaro	20°26'24''N	100°4'12''W	2
	Sinaloa	24°24'36''N	106°55'48''W	4
Contemporary				
Belize	Cayo	17°5'24''N	89°4'12''W	1
Costa Rica	Puntarenas	8°48'0''N	82°57'36''W	21
	Guanacaste	10°18'36''N	84°49'48''W	9
El Salvador	San Salvador	13°41'60''N	89°12'0''W	12
	Santa Ana	14°24'0''N	89°21'36''W	23
	Sonsonate	13°49'12''N	89°39'0''W	18
Honduras	Yoro	15°9'0''N	87°28'12''W	77
	Francisco Morazán	14°5'60''N	87°13'12''W	26
Mexico	Baja California Sur	23°16'12''N	109°57'0''W	18
	Chiapas	16°45'0''N	93°7'12''W	1
	Guerrero	17°35'24''N	100°28'12''W	4
	Jalisco	19°43'12''N	104°17'60''W	31
	Mexico City	19°18'36''N	99°10'48''W	9
	Oaxaca	16°41'60''N	96°50'24''W	33
	Sinaloa	24°14'24''N	106°43'48''W	29
	Tamaulipas	23°0'0''N	99°5'60''W	15
	Veracruz	19°8'60''N	96°24'36''W	29
Nicaragua	Granada	11°49'48''N	86°0'36''W	2
	Jinotega	13°13'48''N	86°2'60''W	12

Central America to Panama in the 1960s (Bent 1953). However, very few historical museum specimens were collected from the southern half of their nonbreeding range in Central America. As a result, we focused on samples collected within Mexico, which provided us with the best opportunity to examine the stability of population-level nonbreeding distributions over time.

DNA was extracted using a phenol-chloroform protocol to maximize DNA yield from historical specimens (Billerman and Walsh 2019, Tsai et al. 2020, Raxworthy and Smith 2021). In addition, we acquired blood (n=23), feather (n=90), and liver (n=18) samples from 131 contemporary individuals collected from 1998 to 2020 across Mexico and Honduras. The liver samples were taken from museum specimens stored in the Museum of Zoology 'Alfonso L. Herrera' at the Universidad Nacional Autónoma de México (UNAM), while the blood and feather samples were compiled from field collections. We extracted DNA from the contemporary samples using the Qiagen DNeasy Blood (Qiagen, Netherlands) and Tissue Kit. Once extracted, we quantified DNA from both historical and contemporary individuals using a fluorometer (Qubit dsDNA HS Assay Kit; Thermo Fisher Scientific, USA). All contemporary and historical birds were captured during the nonbreeding period from 15 November to 28 February.

SNP genotyping

Samples were genotyped using SNPtype Assays (Fluidigm Inc.) on a FluidigmTM 96.96 IFC controller at a panel of 96 loci that were previously identified by Ruegg et al. (2014) as being highly correlated with breeding location. We ran three plates of contemporary samples and one plate of historical individuals, including 14 contemporary samples in duplicate across contemporary and historical plates to check for potential plate effects. We used an EP1 Array Reader (Fluidigm Inc.) to image the plates and automatically called genotypes using the Fluidigm Genotyping Analysis Software (Fluidigm Inc.). We then visually inspected the SNP results to verify the automatic calls.

Principal component analysis

We converted the SNP genotyping data from the historical and contemporary samples to pedigree (.ped) format and ran a principal component analysis (PCA) using the --pca command in plink 1.9 (Purcell et al. 2007). We plotted the first two principal components for the historical and contemporary datasets using R ver. 4.1.2 (www.r-project.org) to compare patterns of genomic differentiation between the two time periods.

Population assignment

We supplemented our SNP genotyping data from 131 contemporary samples with previously generated data from Ruegg et al. (2014), which contained 239 contemporary individuals sampled during the nonbreeding period (December–February) from 1994 to 2009 in Mexico, Nicaragua, El Salvador, Belize, Costa Rica, and Honduras to increase coverage of the nonbreeding range for the contemporary samples (Table 1). We used the 'rubias' R package to assign nonbreeding individuals in our historical and contemporary datasets to contemporary breeding clusters (Moran and Anderson 2019), including 407 birds with known breeding locations from previous genomic analyses (Ruegg et al. 2014) as reference samples within the program. Each nonbreeding individual was assigned to a breeding cluster if the sample had less than 6% missing data, a z-score between −2.5 and 2.5, and a probability of assignment (PofZ) greater than 0.8, as in Ruegg et al. (2014). To determine an appropriate z-score cutoff, we carried out leave-one-out self-assignment of reference samples within the 'rubias' package and examined the resulting distribution of z-scores for reference individuals that were assigned to the correct breeding cluster. A z-score considerably lower than the z-scores of the reference individuals may indicate that the nonbreeding bird does not belong to any of the populations included in the reference dataset (e.g. possibly due to admixture) (Fig. 1).

Results

We successfully assigned 46 of the 49 (94%) historical individuals and 328 of the 370 (89%) contemporary birds in the combined dataset to breeding groups, detecting all six genetic clusters in the contemporary dataset and four of the six contemporary genetic clusters in the historical dataset (Fig. 2). All contemporary samples that were run in duplicate across contemporary and historical plates were consistently assigned to the same genetic cluster regardless of plate type, indicating that plate effects were not a concern. The historical individuals had similar levels of missing data (1.2%) to the newly genotyped contemporary samples (0.9%). Two of the 49 historical birds, five of the 131 newly genotyped contemporary individuals, and 14 individuals from previously published data (Ruegg et al. 2014) had more than 6% missing data and/or a z-score less than −2.5 or greater than 2.5, and were therefore excluded from further analyses. However, we retained two historical samples with low z-scores (−2.92 and −3.15) that were assigned to the Eastern Boreal breeding cluster, as these samples possessed genotypic data for at least eight of the nine highly diagnostic SNPs that differentiate the Eastern Boreal cluster from the other five breeding groups. Finally, one historical bird and 23 contemporary birds from the combined dataset had a probability of assignment (PofZ) less than 0.8 and could not be confidently assigned to a breeding cluster. SNP genotyping data generated from the historical and contemporary samples were characterized by similar patterns of genomic differentiation (Fig. 1). A principal component analysis clearly differentiated individuals assigned to the 1) Western Boreal and Basin Rockies, 2) Pacific Northwest, Coastal California, and California Sierra, and 3) Eastern Boreal breeding clusters during both time periods (Fig. 1).

Historical individuals from the Western Boreal breeding cluster had a wide nonbreeding distribution that was consistent with the contemporary samples, overwintering from Durango in northern Mexico to Chiapas on the border with Guatemala (Fig. 2). However, we lacked historical

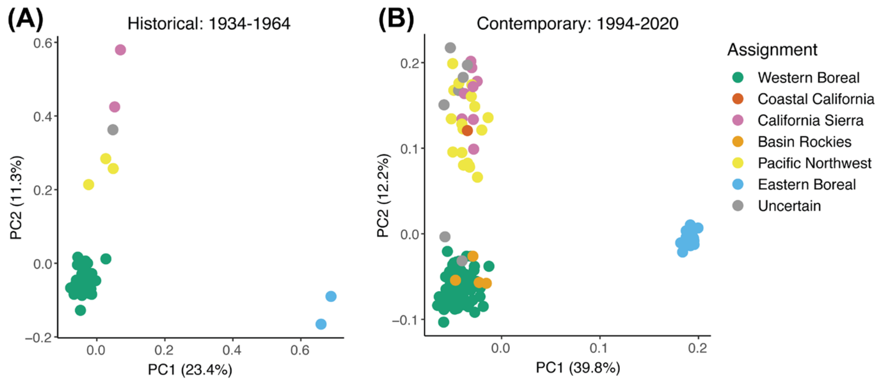

Figure 1. Principal component analysis illustrating patterns of genomic differentiation following filtering between Wilson's warblers in the (A) historical (n = 47) and (B) contemporary (n = 126) datasets. Individuals are colored by their assignment to genetically distinct breeding clusters. Individuals classified as uncertain had a probability of assignment (PofZ) less than 0.8 and could not be confidently assigned to a breeding cluster.

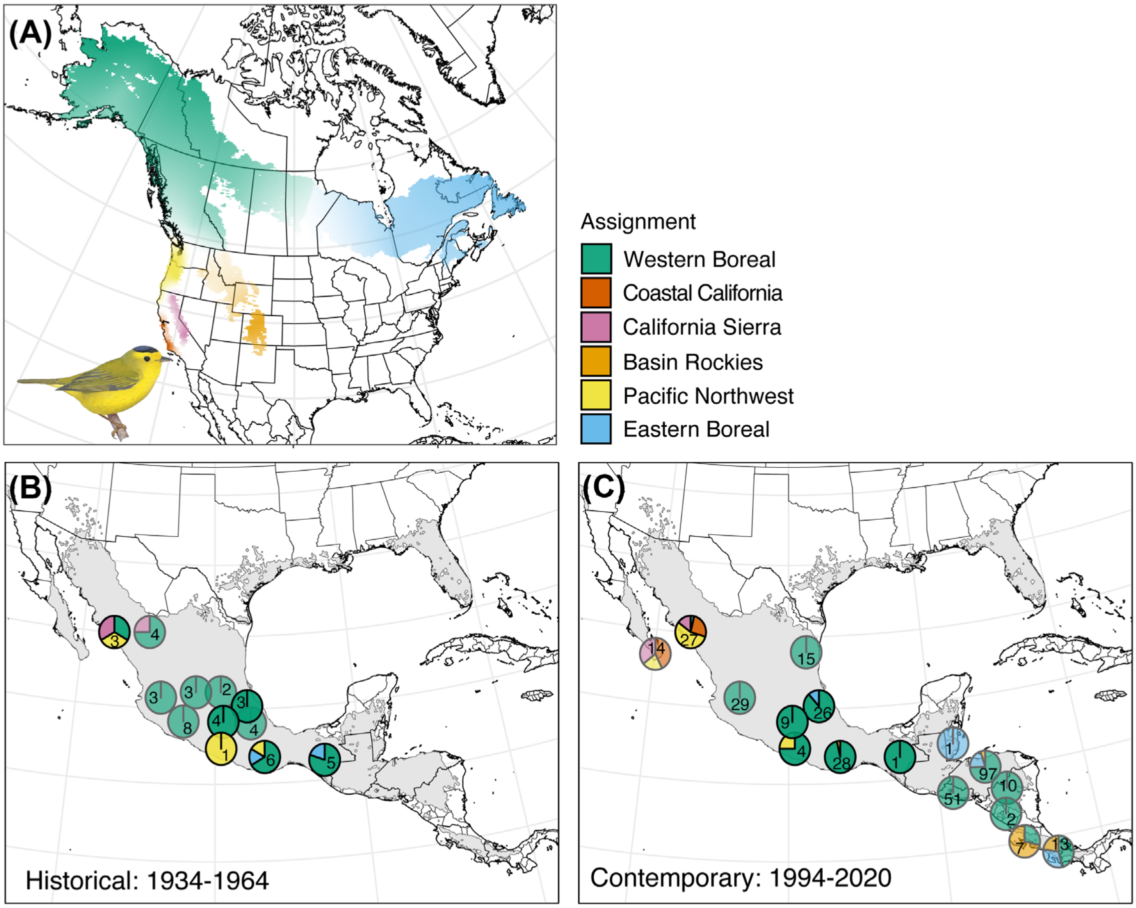

Figure 2. Past and present patterns of migratory connectivity in the Wilson's warbler assessed using SNP genotyping. (A) The six contemporary breeding clusters identified from Ruegg et al. (2014). (B) Assignment of historical individuals collected from 1934 to 1964 on the nonbreeding grounds in Mexico to breeding clusters in A (n = 46). Pie charts indicate the proportion of individuals assigned to each breeding cluster, with the total number of birds shown within each pie. Pies outlined in black indicate sampling sites that overlapped between historical and contemporary datasets, while those with reduced transparency and outlined in gray depict sites that differed between the two time periods. (C) Assignment of contemporary nonbreeding individuals captured from Mexico to Costa Rica from 1994 to 2020 to breeding clusters in A (n = 328).

data from the southern half of the species' nonbreeding range in Central America. The distribution of historical birds from the California Sierra, Pacific Northwest, and Eastern Boreal breeding clusters also largely mirrored their nonbreeding ranges in the contemporary dataset (Fig. 2). We were unable to analyze shifts in the nonbreeding ranges of the Coastal California or Basin Rockies breeding clusters, as we did not detect these breeding groups in the historical data. Nonetheless, the Coastal California breeding group appeared to be quite rare in the contemporary dataset, comprising fewer than 4% of sampled individuals, while the Basin Rockies cluster was detected further south than the distribution of our historical samples.

The newly genotyped contemporary samples provided additional resolution on the genomic makeup of individuals overwintering in Honduras, as well as in northwestern and southwestern Mexico. For example, in contrast to Ruegg et al. (2014), we detected the Coastal California breeding cluster in Baja California, the Western Boreal cluster in Sinaloa, and the Basin Rockies cluster in Oaxaca, Mexico and in Yoro, Honduras with our increased sample size.

Discussion

The decline of North American migratory birds over the past half century highlights the need for information regarding the flexibility of migratory routes over different time scales. Here, we used SNP genotyping to determine the breeding origin of historical and contemporary nonbreeding individuals of the Wilson's warbler and examine how nonbreeding ranges and patterns of migratory connectivity have shifted from the mid-1900s to the present day. Our data indicate that the nonbreeding distributions of genetically distinct breeding clusters have remained largely consistent over the past 50+ years. These results support the findings of previous studies indicating that the nonbreeding ranges of long-distance migratory birds can remain stable over remarkably long time periods (even from the last glacial maximum to the present day) (Ponti et al. 2020, Thorup et al. 2021). Despite little evidence for broad-scale shifts in the nonbreeding distributions of the Wilson's warbler, we identified subtle population-level differences between the contemporary and historical datasets that could be attributed to low sample size, habitat differences between sampling sites, small-scale range shifts, or a combination of factors. For example, in Oaxaca, Mexico, we did not identify any contemporary individuals from the Pacific Northwest or Eastern Boreal breeding clusters despite a higher sample size in the contemporary (n = 28) than the historical (n = 6) data. We acknowledge that our findings are limited by the availability of historical museum specimens, and additional sampling may reveal subtle shifts in the population-level nonbreeding distributions of the Wilson's warbler.

Few studies have leveraged historical DNA to examine past migratory patterns in long-distance migrants. Despite DNA degradation and higher rates of missing data in historical DNA, we managed to confidently assign 94% of our historical individuals to contemporary breeding clusters, illustrating the utility of historical DNA for population assignment. The low rates of missing data observed in our historical samples and similar patterns of genomic differentiation between the historical and contemporary datasets suggest that shifts in allele frequencies over time at the geographically informative loci identified from contemporary data did not hinder our ability to accurately assign individuals to breeding clusters. Museum specimens can provide a historical baseline with which to interpret current migratory patterns in order to examine the flexibility of migratory strategies in response to anthropogenic change (Billerman and Walsh 2019).

An estimated three billion birds in North America have been lost since 1970, with 12 avian families, including warblers (Parulidae), making up 90% of that decline (Rosenberg et al. 2019). Wilson's warbler populations have declined by approximately 60% since 1966 (Sauer et al. 2017), and the California Sierra, Basin Rockies, and Coastal California breeding clusters have been identified as particularly vulnerable to population decline based on predictive models (Ruegg et al. 2020). Migratory birds face numerous challenges along their annual journeys, including habitat degradation and fragmentation, predation, collisions with buildings and wind turbines, and the effects of global climate change on both their breeding and nonbreeding grounds (Robbins et al. 1989, Both et al. 2006, Loss et al. 2013, 2014, Bairlein 2016). Long-distance migratory songbirds are thought to rely in part on innate genetic programs to carry out their seasonal movements (Liedvogel et al. 2011) and may lack the evolutionary flexibility to shift their nonbreeding distributions in the face of habitat loss and climate change. While the habitat requirements of Wilson's warblers vary across their nonbreeding distribution (Ammon and Gilbert 2020), montane cloud forest, which is thought to constitute high-quality habitat during the nonbreeding season (Ruiz-Sánchez et al. 2017), has been subject to drastic land use change within Mexico over the past century (Williams-Linera 2007, Muñoz-Villers and López-Blanco 2008). Although additional research is needed to investigate the flexibility of migratory strategies in long-distance migratory species, the fact that we observed largely consistent patterns of migratory connectivity within Mexico from the mid-1900s to the present day supports the idea that long-distance migrants may be constrained in their ability to alter their nonbreeding distributions to track rapid environmental shifts (Sutherland 1998, Alerstam et al. 2003). A better understanding of the flexibility of migratory strategies in long-distance migratory taxa will improve our ability to predict how species will respond to future stressors in a changing world.

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Author contributions

Sheela P. Turbek: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Supervision (lead); Visualization (equal); Writing – original draft (lead). **Alexandria Polich**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Visualization (equal); Writing – review and editing (equal). **Christen M. Bossu**: Formal analysis (supporting); Writing – review and editing (supporting). **Christine Rayne**: Data curation (supporting); Writing – review and editing (supporting). **Amanda Carpenter**: Data curation (supporting); Writing – review and editing (supporting). **Genaro Rodríguez Otero**: Data curation (supporting); Formal analysis (supporting); Writing – review and editing (supporting). **Sergio Gómez Villaverde**: Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Fabiola Rodríguez Vásquez**: Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Blanca E. Hernández-Baños**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **John McCormack**: Data curation (supporting); Resources (supporting); Writing – review and editing (supporting). **Kristen Ruegg**: Conceptualization (supporting); Funding acquisition (supporting); Project administration (supporting); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data are available in the Supporting information and the Dryad Digital Repository (https://doi.org/10.5061/dryad.w3r2280xw) (Turbek et al. 2024). Code can be accessed on GitHub (https://github.com/sturbek/WIWA-Population-Assignment).

Supporting information

The Supporting information associated with this article is available with the online version.

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