



## Research

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# Migratory connectivity then and now: a northward shift in breeding origins of a long-distance migratory bird wintering in the tropics

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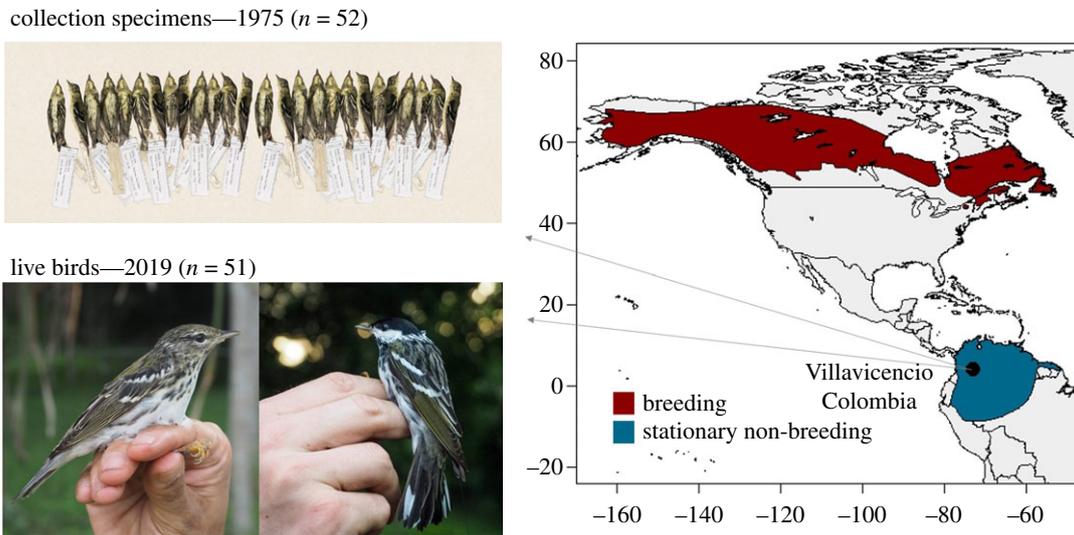
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Temporal variation in the connectivity of populations of migratory animals has not been widely documented, despite having important repercussions for population ecology and conservation. Because the long-distance movements of migratory animals link ecologically distinct and geographically distant areas of the world, changes in the abundance and migratory patterns of species may reflect differential drivers of demographic trends acting over various spatial scales. Using stable hydrogen isotope analyses ( $\delta^2\text{H}$ ) of feathers from historical museum specimens and contemporary samples obtained in the field, we provide evidence for an approximately 600 km northward shift over 45 years in the breeding origin of a species of songbird of major conservation concern (blackpoll warbler, *Setophaga striata*) wintering in the foothills of the eastern Andes of Colombia. Our finding mirrors predictions of range shifts for boreal-breeding species under warming climate scenarios and habitat loss in the temperate zone, and underscores likely drivers of widespread declines in populations of migratory birds. Our work also highlights the value of natural history collections to document the effects of global change on biodiversity.

## 1. Introduction

Migratory species link geographical areas separated by distances reaching thousands of kilometres on an annual basis [1,2]. The degree of linkage, or migratory connectivity, can vary across species or across populations within a single species, depending on whether most or few individuals from a population spend time in the same or different geographical areas throughout the annual cycle. The strength of migratory connectivity can determine the effect of seasonal interactions between periods of the annual cycle, and these in turn can influence population dynamics and the evolution of life-history and migratory strategies [1,2]. Understanding migratory connectivity is, therefore, central to advancing knowledge of migratory species' ecology and conservation.

A challenge to understanding migratory connectivity is that the geographical ranges of migratory species are dynamic in space and time [3]. Not only do the



**Figure 1.** Blackpoll warbler feathers were sampled from individuals captured on their non-breeding grounds in the foothills of the eastern Andes, near the town of Villavicencio, Colombia (red dot on the map) with approximately 45 years of difference. The species breeds in boreal forests from Alaska to Newfoundland and winters in northern South America. Range map recreated using © BirdLife distribution shapefiles [29]. Specimen illustration © Carolina Rojas Céspedes (c.rojas209@uniandes.edu.co), live bird photos © Paula Cardozo, left—female, right—male blackpoll warbler. (Online version in colour.)

ranges of migrants change seasonally, as populations of a species move from breeding to non-breeding grounds, but they have also changed historically, responding to biotic and abiotic factors as diverse as interactions with other species and climate change [4–6]. Although many recent studies describe patterns of present-day migratory connectivity (reviewed in [7]), very little work has been directed at assessing the temporal stability of these patterns or at determining how temporal changes in connectivity could help understand geographical variation in population trends within species [4,8–10].

Many migratory animals have experienced significant population declines over recent decades [11–13]. Declines are not only worrying owing to the intrinsic value of migratory species but because migration influences ecosystem function through massive transport of nutrients and trophic interactions at a global scale [14]. However, declines of migrants are not uniform throughout geography or across species; while some populations of a species may be declining drastically, others may be thriving and even increasing [11,15]. It is likely that factors driving differential population declines in migratory species are linked to their patterns of migratory connectivity [16,17]. For example, global warming could be driving some population declines [18], whereas habitat loss [19], regional weather patterns [10] or biotic interactions [4,20] may be responsible for others. Therefore, any evidence of temporal changes in migratory behaviour or in links among populations can have important repercussions for conservation and other aspects of migratory species biology [21–23].

Stable isotope analyses of inert tissues have been widely used to assess present-day migratory connectivity patterns in various animals [24]. Feathers, hairs or claws retain the isotopic values of the geographical region where they grew and can, therefore, be traced back to those regions by relating them to known spatial variation in isotopic values or isoscapes [25]. Patterns of migratory connectivity revealed through stable isotope analysis have been assumed to be static in time. However, temporal changes in isotopic signature could also reveal temporal changes in migratory connectivity if populations of a species shifted their range to an isotopically distinct region (e.g. they moved higher or lower in latitude or elevation), or

if populations were lost or declined in abundance in a given region (e.g. through habitat loss). However, temporal variation in isotopic composition fixed in animal tissues could also be observed in the absence of changes in species' distributions owing to shifts in the isotopic baseline of foodwebs underlying isoscapes [26]. The idea that migratory connectivity is dynamic over time could profoundly alter our understanding of population change, yet such dynamics have not previously been demonstrated for any species.

By comparing individual tissue samples from different time periods, it should be feasible to evaluate whether changes in isotopic values have taken place, and if so, make inferences about potential drivers underlying them. Museum specimens preserve a snapshot of abiotic conditions at the time of their collection [8,27] and, therefore, provide unique opportunities to observe temporal changes in organisms and their environments. However, surprisingly few studies have used comparative stable isotope analyses of historical and contemporary specimens to test hypotheses about the temporal dynamics of migratory connectivity [8,10,28]. In this paper, we provide one of the first applications of this comparative approach to document temporal changes in connectivity in a steeply declining migratory songbird, the blackpoll warbler (*Setophaga striata*).

The blackpoll warbler breeds in the northern temperate zone across boreal forests of Canada, Alaska and the north-eastern USA, and overwinters in northern South America (figure 1). Despite weighing only *ca* 12 g, blackpoll warblers engage in extremely long-distance (greater than 2500 km) migratory flights while crossing the Atlantic Ocean and the Caribbean Sea back and forth between North and South America, and may move over 20 000 km in a single year [30–32]. Recent work revealed that a wintering site in eastern Colombia may contribute over half of the energy required to fuel spring migration in individuals of this species, highlighting the importance of links between areas where migrants spend different parts of their annual cycle [31].

Blackpoll warblers have experienced staggering breeding population declines in the last 50 years [11,33,34]. Although long-term trends have high uncertainty because vast expanses of the species' range have not been surveyed owing to its

remoteness and difficult access, patterns seem to vary spatially, with southern and eastern populations showing steeper declines than northern and western ones [34–36]. Understanding such precipitous declines and their causes requires a full annual cycle and temporal perspective, where connections between breeding and wintering populations are established [37]. Information from light-level geolocators and automated VHF tracking has revealed parts of the present-day migratory connectivity in blackpoll warblers, suggesting that individuals wintering in eastern Colombia originate from breeding populations mostly in the eastern boreal region of the USA and Canada [31,32]—including those showing the steepest declines.

We capitalized on the rare opportunity of comparing the geographical origins of blackpoll warblers from our study site in the foothills of the eastern Andes of Colombia with those of individuals in a historical collection of specimens made nearly 50 years ago at a nearby site. We used stable hydrogen isotope ( $\delta^2\text{H}$ ) analyses of feathers [38] from museum specimens collected during the non-breeding seasons of 1972–1975 and from live birds captured on similar dates in 2018–2019 to infer geographical areas of likely breeding origin of over-wintering individuals. These data allowed us to not only describe past and present patterns of migratory connectivity in blackpoll warblers but to highlight potential drivers that may be underlying observed changes in connectivity. Because the blackpoll warbler is one of several boreal species showing precipitous population declines over large spatial scales [11,39–41], our work more broadly serves to document patterns and to identify potential causes of salient phenomena in global change biology.

## 2. Methods

The foothills of the eastern Andes of Colombia, in and around the town of Villavicencio, are part of the core winter range of the blackpoll warbler in South America (figure 1) [42,43]. We selected a study site in that area, which provided a unique opportunity to compare birds wintering at adjacent locations in the 1970s and in the late 2010s. We sampled the tip of the innermost primary feather (P1) from 103 individuals to measure their stable hydrogen isotope abundance ( $\delta^2\text{H}$ ). Because P1 is the first feather to be moulted during the pre-basic moult after the breeding season, it reflects the isotopic value most closely associated with the breeding grounds [44]. Fifty-two individuals comprised the entirety of the specimens housed in the Museo de Historia Natural Cornelis Marinkelle at Universidad de los Andes (ANDES) in Bogotá, which were collected during the winters of 1972–1975 in the Finca El Buque, Villavicencio (4.08 N, –73.39 W) [45]. The remaining 51 individuals were captured using passive mist netting during the winter of 2018–2019 at two banding stations near Villavicencio, one on the campus of Universidad de los Llanos (4.0733 N, –73.5813 W) [31] and the other in Agrosavia (4.0606 N, –73.4639 W). Historical and current sampling locations are less than 15 km apart.

Feathers were cleaned of debris and stored in paper envelopes prior to laboratory analyses. Stable isotope analyses were carried out at the LSIS-AFAR stable isotope laboratory, Western University—London, Canada, and are fully described in [38]. Measurements of  $\delta^2\text{H}$  in feathers were those of the non-exchangeable fraction of feathers obtained through continuous-flow isotope-ratio mass spectrometry following the ‘comparative equilibration’ method which uses calibrated keratin reference materials Caribou Hoof Standard (–197‰) and Kudu Horn Standard (–54‰) to correct for exchangeable hydrogen [46]. We report stable hydrogen

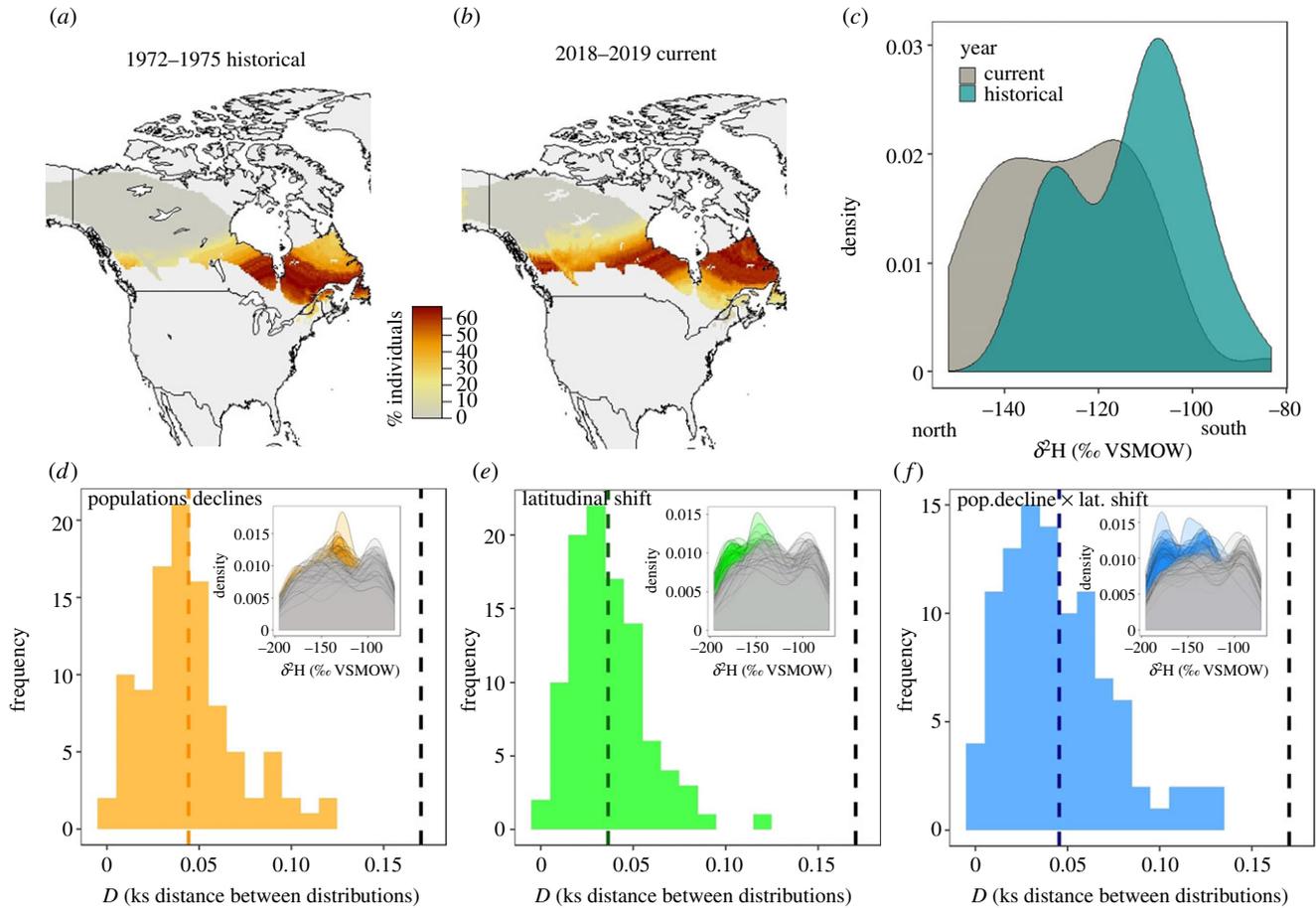
isotope ratios in standard delta ( $\delta$ ) notation, in parts per thousand (‰) relative to Vienna Standard Mean Ocean Water (VSMOW). Based on within-run replicates ( $n = 5$ ) of calibration standards, we estimate analytical error to be in the order of  $\pm 2\text{‰}$ .

The collection dates of specimens and live birds differed slightly, with specimens from 1972 to 1975 mostly collected during late November when some blackpoll warblers may still be migrating through Villavicencio, whereas in 2018–2019, birds were captured mostly during December and January and so presumably comprised mostly stationary individuals (electronic supplementary material, figure S1). Comparing such samples to assess potential changes in migratory connectivity over time would be problematic if migrating individuals belonged to different wintering populations. Nonetheless, because collection date was unrelated to  $\delta^2\text{H}$  values within the historic and contemporary samples in a linear model ( $R^2 = 0.01$ ,  $\beta_{\text{day}} = 0.014$ ,  $p = 0.20$ ), samples were comparable regardless of differences in the date of collection.

We carried out geographical assignments based on  $\delta^2\text{H}$  values in feathers, restricting our inference of origins to the estimated area of occurrence of blackpoll warblers during the breeding season [29]. However, we excluded Alaska because evidence from 16 tracked birds suggests that blackpoll warblers wintering in our study area are eastern in origin [31], and because birds from Alaska have longer wings on average (mean  $\pm$  s.d. =  $75 \pm 2.1$  mm [47,48]) than those at our study site (mean  $\pm$  s.d. =  $71 \pm 2.1$  mm; electronic supplementary material, figure S2). We used the precipitation  $\delta^2\text{H}$  database based on the International Atomic Energy Agency Global Network of Isotopes in Precipitation [49] to derive an amount-weighted mean growing-season precipitation  $\delta^2\text{H}$  ( $\delta^2\text{H}_p$ ) map from 1960 to 2019. We then transformed this isoscape into an expected feather  $\delta^2\text{H}$  ( $\delta^2\text{H}_f$ ) surface using the calibration equation estimated for feathers of canopy-foraging Neotropical migrants [50]:  $\delta^2\text{H}_f = -17.57 + 0.95 (\delta^2\text{H}_p)$ . We followed a likelihood framework for geographical assignment extensively used for Neotropical migratory birds [50–52] and obtained a cumulative surface of likely breeding origins for every individual from each time period. Briefly, this procedure involves obtaining likelihoods of each individual belonging to a given  $30 \times 30$  km cell on the breeding grounds and then transforming them to a probability surface by dividing by the total sum of likelihoods [50,53]. The upper 67% of probabilities were defined as the likely origin of each bird [50,53] and we overlaid all individuals by time period to obtain cumulative surfaces [25].

To evaluate whether there were differences in the geographical origins of birds from 1972 to 1975 and 2018 to 2019, we compared the probability distributions of  $\delta^2\text{H}_f$  values (an index of latitude of origin) between periods with a Kolmogorov–Smirnov test and estimated a Jaccard coefficient of similarity between the two predicted surfaces of the breeding origin. The Jaccard coefficient is equal to the intersection divided by the union of the surfaces under comparison ( $J = \text{intersection}/\text{union}$ ). A coefficient of 0 means complete dissimilarity, one of 0.5 means the surfaces share half of their area, whereas a coefficient of 1 means surfaces are identical.

To separate potential drivers of temporal change in migratory connectivity as inferred by stable isotopes, we used random samples of the  $\delta^2\text{H}_f$  isoscape to generate expected distributions of differences in isotopic values between historical and contemporary samples, given the alternative scenarios of: (i) breeding population declines, (ii) a northward shift in the geographical range of the species, and (iii) both factors combined. Information on blackpoll warbler population trends was obtained from data on bird conservation regions (BCR) throughout the breeding range [34,35]. We constructed a shapefile creating a 100 km radius buffer around each BCR centroid coordinate for which we had data on population trends. This scale was considered appropriate to sample enough variation in the feather  $\delta^2\text{H}$  isoscape from the boreal region, as well as to include a broader isotopic representation



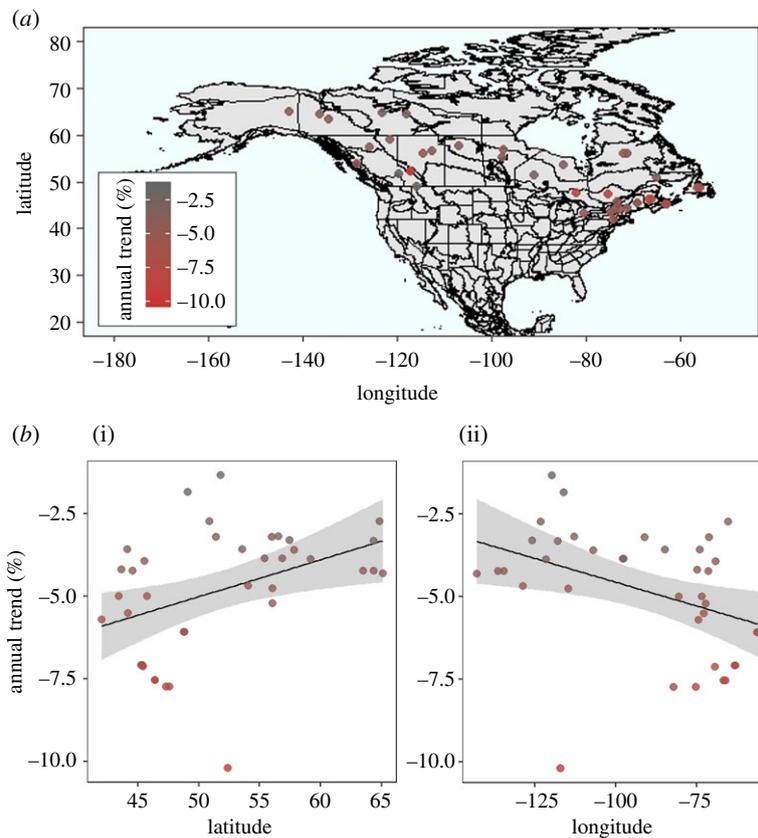
**Figure 2.** (a,b) We observed an isotopic shift in feather samples between time periods translating into an approximately 600 km northward change in the proportion of individuals originating from different regions of the blackpoll warbler breeding range (excluding Alaska). There are currently more northeastern and central-western birds that winter in the foothills of the eastern Andes of Colombia. (c) Density distributions of  $\delta^2\text{H}$  values from blackpoll warbler feathers collected on the wintering grounds in the historical sample of 1972–1975 ( $n = 52$ ), and the current sample of 2018–2019 ( $n = 51$ ) are significantly different ( $\delta^2\text{H}$  ks test:  $D = 0.17$ ,  $p < 0.0001$ ) with a shift from less negative  $\delta^2\text{H}$  values originating from more southern latitudes during the 1970s (mean =  $-113\text{‰}$ ) to more depleted  $\delta^2\text{H}$  values in the current sample (mean =  $-126\text{‰}$ ). (d–f) Histograms representing the distribution of distances between 100 curves of null models (insets) from the Kolmogorov–Smirnov tests. Differences between null model distributions were significantly lower than between our sample of historical and current blackpoll warblers ( $D = 0.17$ , black dashed vertical lines). Null models show expected shifts in isotopic distributions if (d) population declines (left), (e) latitudinal shifts (centre) or (f) both factors combined (right) were more likely driving changes in migratory connectivity between time periods. In all cases, a shift towards more negative values of  $\delta^2\text{H}$  is expected. Grey curves in the insets represent random samples and coloured curves represent samples with weighted probabilities. Dashed vertical lines show the mean value of  $D$  in the distributions. (Online version in colour.)

of extensive BCR regions which are probably not fully represented isotopically by values too close to their coordinate centroid alone. We then randomly sampled the  $\delta^2\text{H}_f$  isoscape within these 100 km buffers to generate null distributions where 50 values were extracted at random (i.e. every population had equal probability of being sampled) and then 50 values were extracted with a weighted probability inverse to the population trends for each region (i.e. regions with higher declines were less likely to be sampled). For scenario (ii), 50 additional values were extracted with a weighted probability inverse to the latitude of the BCR coordinate (i.e. northernmost latitudes were more likely to be sampled, thus reflecting a northward latitudinal range shift). Finally, for scenario (iii), 50 values were extracted from layers by multiplying the weighted population trend and latitude rasters. We repeated this procedure 100 times for each scenario and then compared the null distributions with the weighted distributions using the Kolmogorov–Smirnov tests. We then compared the direction and magnitude of the differences between the null and weighted distributions with those found between our two time periods to determine the extent to which observed patterns reflected those expected given alternative drivers of temporal changes. We also assessed whether population trends within BCR regions varied

by longitude and latitude by running simple linear models. All analyses were carried out using the R statistical software [54].

### 3. Results

Stable isotope data revealed that blackpoll warblers wintering in the foothills of the eastern Andes of Colombia probably originate from regions in the southern and northeastern portions of the species' boreal-breeding range, and possibly from portions of the central Canadian boreal region (figure 2a,b). The distribution of  $\delta^2\text{H}_f$  values of birds wintering in our study site was significantly different between time periods (figure 2c; Kolmogorov–Smirnov test  $D = 0.17$ ,  $p < 0.0001$ , 95% confidence interval (CI) = 0.14–0.2). Values of  $\delta^2\text{H}_f$  from 2018 to 2019 were on average more negative (mean =  $-126\text{‰}$ ) than those from 1972 to 1975 (mean =  $-113\text{‰}$ ). This resulted in a significant difference between the predicted breeding origins for blackpoll warblers wintering in Colombia during the 1970s and the present (Jaccard coefficient of similarity



**Figure 3.** Between 1970 and 2017, southeastern populations of blackpoll warbler in North America have experienced steeper annual declines, than northern or western populations. (a) Annual trends of blackpoll warblers in Canada and the USA between 1970 and 2017 [34,35]. Dots are centroids of bird conservation regions and colour intensity depicts the magnitude of population declines. (b) Linear models with 95% confidence intervals showing population declines are steeper at lower latitudes ((i)  $R^2 = 0.16$ ,  $\beta = 0.11$ ,  $p = 0.01$ ) and at eastern longitudes ((ii)  $R^2 = 0.16$ ,  $\beta = -0.03$ ,  $p = 0.01$ ). (Online version in colour.)

$J = 0.51$ , i.e. surfaces were 49% different), with the most recent sample showing a northern shift. Close to 60% of the individuals from the 1970s had probable origins in eastern Ontario, southern Quebec and eastern Newfoundland (figure 2a), whereas the origins of birds sampled in the late 2010s were centred in areas located approximately 600 km to the north in Quebec and Labrador and also in northwestern Ontario and Manitoba (figure 2b).

We evaluated two potential drivers of the observed temporal change in isotopic values for birds wintering in Colombia: population declines (figure 2d) and latitudinal range shifts (figure 2e), and the combination of both factors (figure 2f). A change in underlying isotopic variation was discarded because under that scenario,  $\delta^2\text{H}_f$  values of contemporary individuals were expected to be less negative than those from the historical sample [26], which was the opposite of what we found. Null models representing expectations of change owing to population declines, latitudinal shifts and both combined all generated trends towards more negative  $\delta^2\text{H}_f$  values (figure 2d–f), so we could not determine which of the factors was a more likely driver of the pattern in our observations. However, although the magnitude of the differences between all the null models were lower than what we obtained from our empirical sample, the combined model (figure 2f; scenario c) is the one that most closely approached our empirical observation, suggesting that both factors may be playing a role. Finally, population trends of blackpoll warbler varied significantly as a function of latitude and longitude, with southern and eastern populations showing the highest declines since 1970 (figure 3;  $R^2_{\text{latitude}} = 0.16$ ,  $\beta = 0.11$ ,  $p = 0.01$ ;  $R^2_{\text{longitude}} = 0.16$ ,  $\beta = -0.03$ ,  $p = 0.01$ ).

## 4. Discussion

Our study is among the first to document a temporal change in patterns of migratory connectivity of a migratory species [8,10]. Comparison of  $\delta^2\text{H}_f$  from two time periods spanning 45 years (1975–2019) provide evidence for an approximately 600 km northward shift in the breeding origin of blackpoll warblers wintering in the foothills of the eastern Andes of Colombia. Our finding is consistent with predictions of changes in the geographical range of this and other species caused by warming climate scenarios [18,55] and habitat loss in the southern boreal forest [56], and signals likely contributing factors to the declines we are witnessing in the blackpoll warbler and other boreal birds [8,57,58].

Previous work showing evidence for both southern population declines [34,35] and northern latitudinal shifts [18,20] are consistent with our results, showing that a larger proportion of the blackpoll warblers that winter in eastern Colombia currently come from areas hundreds of kilometres to the north and west of where they did 45 years ago. Given the latitudinal trend in population declines of blackpoll warbler, the predictions from our null models did not enable us to fully differentiate between the effect of declining populations or latitudinal shifts on the observed changes in migratory connectivity. However, given that the magnitude of the difference in the combined null model (scenario (iii)) most closely approached our empirical observation, we believe both factors are probably playing a role. A recent study [18] found that various Neotropical migrants are experiencing range contractions as a result of climate warming, with populations at the southern edges of breeding

ranges shifting north and northern populations remaining static. This could well be the case for blackpoll warblers because between the 1970s and 2010s, warming temperatures in the boreal forest have pushed some populations up in elevation [41] (although not others [59]), and southern populations have declined drastically [35]. However, there are also reports of a northern range expansion of blackpoll warblers in the Torngat Mountains of northern Labrador [20], one of the regions our isotope data highlight for potential breeding provenance. Because vast expanses of the northern portion of the blackpoll warbler's range remain unsurveyed owing to their remoteness, confirming whether northern shifts or elevation movements are widespread is still necessary.

We think a northward range shift coupled with declining southern-breeding populations are the most plausible causes of our observed change in breeding origins of blackpoll warbler wintering in eastern Colombia, similar to what has been reported for other Neotropical migrants such as the golden-winged warbler (*Vermivora chrysoptera*) [4]. However, we cannot rule out alternative explanations. For instance, shifts in the wintering range of southeastern-breeding birds away from our study sites could create the same observed effect, as could a shift in the winter range of northern-breeding populations such that they increased at our study sites. Rapid changes in over-wintering range are not unprecedented, with Rufous and Anna's hummingbirds (*Selasphorus rufus*, *Calypte anna*), and European blackcaps (*Sylvia atricapilla*) being examples of birds adapting to new wintering areas over the course of decades [60–63]. However, in those examples, novel conditions in the winter (i.e. increased supplementary feeding in the case of blackcaps), and not in the breeding range, promoted the observed shifts [60–63]. Because we are not aware of any consistent changes in land use or food availability within the foothills of eastern Colombia [64,65] that could have caused the pattern we observed in the blackpoll warbler, it is more likely that changes in the breeding range are driving the northwestward shift in breeding origins we documented. Our approach also assumes that any long-term variations in the amount-weighted average value of growing-season precipitation  $\delta^2\text{H}$  ( $\delta^2\text{H}_p$ ) has not influenced our interpretation of the data. Indeed, underlying trends of long-term variation in isotopic values of  $\delta^{18}\text{O}$  (which are correlated to  $\delta^2\text{H}$  through the meteoric water line [66]) are spatially variable, and in the few cases where there is a directional trend such as in Ottawa, it is opposite to what we observed (i.e. isotopic values of amount-weighted mean precipitation  $\delta^2\text{H}$  in Ottawa are expected to be approx. 17.2‰ less negative than 45 years ago) [26].

Because the negative shift in  $\delta^2\text{H}_f$  values we observed could not be attributed to a single driving force, we think a combination of factors acting in the same direction most likely produced the observed effect. In addition to population declines and northward latitudinal shifts, local variation in hydrological regimes, such as consistent variation in growing-season precipitation, can be responsible for significant fluctuations in  $\delta^2\text{H}$  concentration [67,68], but, as discussed, we think this unlikely. We cannot rule out that other factors throughout the complex annual cycle of this species may also be acting, for instance, local extirpations of populations not captured by long-term averages; however, future research should unveil the mechanisms that underlie our observations.

Boreal forests are particularly vulnerable to climate warming, and conversion to agriculture plus extensive timber and mineral extraction have promoted further modification to

this ecosystem and the biodiversity within, including loss of species and prolonged droughts [39,56,69]. Evidence suggests that the effects of environmental change are intensified on the edges of species ranges where individuals are already under pressure owing to habitat or ecological limits to their dispersal [70]. Therefore, boreal animal populations on the edge of their range are predicted to respond to environmental and ecological changes first [18,39,71]. The northward expansion of at least one population of blackpoll warbler into Arctic habitats [20], and steep declines of southern and eastern populations reflected in North American Breeding Bird Survey data and observed in other boreal birds [8,39,40], may be sounding an alarm pointing to additional negative changes that could occur if current climate warming trajectories and habitat transformation rates are maintained [71].

Scientific collections are treasure troves of knowledge and their potential to contribute to research and conservation is immense [72–74]. Here, we highlight the use of scientific collections to help understand the temporal dynamics of migratory connectivity. Our work on blackpoll warblers, a study on rusty blackbirds (*Euphagus carolinus*) [8] and one on monarch butterflies (*Danaus plexippus*) [10] are the only examples we know of examining long-term changes in migratory connectivity using historical collection specimens. However, unlike rusty blackbirds or monarch butterflies which showed little variation in migratory connectivity over time [8,10], blackpoll warblers that wintered in our study site in Colombia have made a significant northward shift in a shorter time period. This opens interesting questions for future research, such as whether these temporal dynamics in connectivity are widespread, and whether they can be detected for other populations of species for which we have long-term data. Expanding the types of analyses we carried out to a wide range of species, geographies and covering longer time frames is a promising avenue of research to unravel temporal changes in populations and connectivity of migratory animals.

These future avenues of research also point at caveats from our study which should be highlighted. For instance, our inference of geographical origins using a single stable isotope could be improved if several isotopes and other intrinsic markers were combined [75,76], and annual tracking of individuals from throughout the range would also improve our understanding of current links among populations [77]. Furthermore, our study comes from a single region, so until more work evaluates other cases, the extent to which our observations may apply more broadly will remain uncertain. Finally, understanding where individuals of the southern populations of blackpoll warbler are wintering currently is important to reverse the trends of these declining populations and to unveil more broadly which factors have driven the long-term changes in migratory connectivity we observed.

Migratory species are sentinels of global change [12,14,78]. Given their widespread populations, large-scale movements and the intimate relationship they hold with their environments, research on the ecology and behaviour of migratory species has provided important insight into the broad effects of environmental change on biodiversity [10,79–81]. The blackpoll warbler is an iconic migratory species, and the decline of its southern and eastern populations does not only risk the loss of a unique portion of the genetic diversity of the species, but also loss of an integral part of boreal [71,82] and tropical ecosystems [31]. Most importantly, the blackpoll warbler is not the only boreal species showing steep and worrying

declines [8,39,40], so it may be acting as a ‘canary in the coal-mine’ alerting to changes that could affect the integrity of the boreal ecosystem. Scientific collections provide opportunities to describe historical changes for which there is a strong need in the broader study of animal migration and generally for temporal comparisons of ecological change [74,83], and we hope this research will serve as a basis for more to come.

**Ethics.** All field and laboratory activities in this study were approved by Colombian law under research permit no. 00874.

**Data accessibility.** All data provided as electronic supplementary material.

**Authors’ contributions.** C.D.C. and C.G. designed the research, N.J.B., A.M.-R. and P.C. led fieldwork and feather sampling, K.A.H. carried out stable isotope analyses, C.G. led data analysis and manuscript writing, and all authors contributed to text editing and approved the final version.

**Competing interests.** We declare we have no competing interests.

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