

ECOGRAPHY

Research

The influence of seasonal migration on range size in temperate North American passerines

Teresa M. Pegan and Benjamin M. Winger

T. M. Pegan (https://orcid.org/0000-0002-0990-815X) ✉ (tmpegan@umich.edu) and B. M. Winger (https://orcid.org/0000-0002-2095-2020), Museum of Zoology and Dept of Ecology and Evolutionary Biology, Univ. of Michigan, Ann Arbor, MI, USA.

Ecography

43: 1–12, 2020

doi: 10.1111/ecog.05070

Subject Editor: Morgan Tingley

Editor-in-Chief: Miguel Araújo

Accepted 31 March 2020



Seasonal migration has been alternately proposed to promote geographic range size in some contexts and to constrain it in others, but it remains unclear if migratory behavior has a general effect on range size. Because migration involves movement, most hypotheses about the relationship between migration and range size invoke an influence of migration on the process of dispersal-mediated range expansion. Intuitively, a positive relationship between migratory behavior and dispersal ability could bolster range expansion among migratory species, yet some biogeographic patterns suggest that long-distance migration may instead impede range expansion, especially in the temperate zone. We conducted a comparative analysis of the relationship between migratory behavior and range size by testing the effect of migratory status, migration distance and morphological dispersal ability on breeding range size among all temperate North American passerines. Further, we assessed whether these traits affect range expansion into suitable habitat by analyzing their relationship with range filling (the proportion of climatically-suitable area occupied, or 'filled' by a species). Contrary to previous studies, we found migration and dispersal ability to be poor predictors of range size and range filling in North America. Rather, most variation in range size is explained by latitude. Our results suggest that migratory behavior does not affect range size within the scale of a continent, and furthermore, that temperate North American passerines' breeding ranges are not influenced by their dispersal abilities. To better understand why migratory behavior appears to promote range size in some contexts and constrain it in others, future studies should investigate how migratory behavior affects dispersal at the individual level, as well as the relationship between the evolution of migratory behavior and the breadth of species' climatic niches.

Keywords: dispersal ability, migration, passerine, range filling, range size, species distribution modeling

Introduction

The geographic range boundaries of species are determined by numerous biotic, abiotic and historical factors (Angert 2009, Price and Kirkpatrick 2009, Sexton et al. 2009). Among species occupying seasonal temperate latitudes, specialized adaptations for severe fluctuations in climate and resources are necessary for the persistence or



www.ecography.org

© 2020 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Table 1. A summary of 20 studies assessing the effect of migration on a property of geographic range. For each study, 'Migration' column indicates how migration behavior was classified; 'Range' column indicates what type of range variable was analyzed; 'Phylogeny' column indicates whether the study tested for or accounted for phylogenetic relatedness; 'Latitude' column indicates whether the study tested for an effect of latitude on range; and 'Effect' column indicates how migration affected range in the study. These studies analyze breeding range and/or resident range, not wintering range, unless otherwise noted. These studies show no consistent relationship between migration and geographic range, but they also vary widely in purpose, method of analysis and geographic and taxonomic scope. Most of these studies focus on a variety of traits, including migration, to identify traits related to the geographic range variable in question, but some specifically focus on migration (Böhning-Gaese et al. 1998, Bensch 1999, Thorup 2006, Henningson and Alerstam 2008, Toews 2017).

Ref	Main question	Range	Migration	Geographic scale	Species	Phylogeny	Latitude	Effect
Gaston and Blackburn 1996	What affects range size?	Range size	Non/short/long	Worldwide	158 Anseriformes (Aves)	Yes	Yes	+
Blackburn and Gaston 1996	What affects range size?	Range size	Nonmigratory/Migratory	Western hemisphere	3906 birds	Yes	Yes	+
Böhning-Gaese et al. 1998	Does migration affect colonization?	Longitudinal colonization between continents	Non/short/long	North America and Europe	526 land birds, 460 nonvolant mammals	Yes	No	-
Bensch 1999	Testing hypotheses of Böhning-Gaese et al. 1998	Longitudinal colonization within continent	Nonmigratory/migratory	Scandinavia and Siberia	Land birds: 153 Scandinavian, 187 Siberian	No	Yes	-
Forsyth et al. 2004	What affects invasion success?	Invasion success within continent	Nonmigratory/migratory	Australia	40 introduced mammals	Yes	No	-
Böhning-Gaese et al. 2006	What affects range size?	Range size	Migration distance	Eastern Hemisphere	26 <i>Sylvia</i> (Aves: Sylviidae)	Yes	Yes	+
Thorup 2006	Testing hypotheses of Böhning-Gaese et al. 1998, Bensch 1999	Number of continents comprising wintering range	Non/short/long	South America, India, Africa	5662 Non-pelagic birds	No	No	+
Henningson and Alerstam 2008	Testing hypotheses of Böhning-Gaese et al. 1998, Bensch 1999	Range size	Non/short/long	Arctic region	208 birds	Yes	No	- in terrestrial birds; + in pelagic birds
Brommer 2008	What affects range shifts?	Range shift in recent time	Non/short/long/irruptive/partial	Finland	116 birds	No	No	No effect
Zuckerberg et al. 2009	What affects range shifts?	Range shift in recent time	Non/short/long	New York	129 birds whose ranges shifted	No	No	- for elevation shifts; no effect on latitude shifts
Brommer and Møller 2010	Extension of Brommer 2008	Range shift in recent time	Non/short/long/irruptive/partial	Finland and Britain	138 birds	No	No	+, but partial migrants shifted more than obligate migrants
Angert et al. 2011	What affects range shifts?	Range shift in recent time	Nonmigratory/migratory	North America and Britain	245 North American birds, 24 British odonates	Yes	Yes	No effect
Tingley et al. 2012	What affects range shifts?	Elevational range shift in recent time	Non/short/long	Sierra Nevada Mountains	99 birds	No	No	- long distance migrants less likely to shift in elevation
Laube et al. 2013a	What affects range size?	Range size	Non/short/long/facultative/obligate	Europe	165 passerines	Yes	No	+

(Continued)

Table 1. (Continued)

Ref	Main question	Geographic scale				Effect
		Range	Migration	Species	Phylogeny	
Lees and Gilroy 2014	What affects island colonization?	Colonization of islands	Nonmigratory/migratory	Worldwide	Yes	+ in temperate zone only
Engler et al. 2014	What affects range limits in Citril Finch?	Range filling	NA: not comparative	Europe	NA	No statistical comparison; negative effect suggested
Pigot and Tobias 2015	What affects whether sister species are sympatric?	Whether sister species are sympatric	Non/short/long	Worldwide	Yes	+
Toews 2017	Do migratory warblers have unoccupied suitable habitat in the western boreal forest?	Range filling	NA: not comparative	Boreal forest of North America	No	No statistical comparison; negative effect suggested
Estrada et al. 2018	What affects range filling?	Range filling	Nonmigratory/migratory	Europe	Yes	No effect
Outomuro and Johansson 2019	What affects range size?	Range size	Nonmigratory/migratory	North America	Yes	+

expansion of geographic range. Some species have adaptations to survive seasonality in situ (e.g. hibernation), but a wide variety of animals, including birds, fish, mammals and insects, have independently evolved an alternative strategy: seasonal migration. This annual round-trip journey facilitates persistence by letting animals temporarily escape their breeding locations when climate becomes harsh and resources scarce. Migration therefore carries an important consequence for biogeography: the breeding ranges of migratory species are seasonally ephemeral, arising annually as the result of the site fidelity that drives them to return after traveling sometimes thousands of kilometers away (Winger et al. 2019). Here, we aim to understand how seasonal migration, a common life history adaptation among birds breeding at high latitudes, influences the size and extent of birds' breeding ranges at a continental scale.

Previous studies have shown conflicting evidence as to whether migratory behavior generally promotes or constrains range size (Table 1). Some studies have found migratory behavior to be associated with increased range size (Blackburn and Gaston 1996, Gaston and Blackburn 1996, Böhning-Gaese et al. 2006, Laube et al. 2013a, Pigot and Tobias 2015, Outomuro and Johansson 2019) or increased likelihood of colonizing islands (Lees and Gilroy 2014) or continents (Thorup 2006). These studies have typically interpreted the elevated range size of migratory species to reflect a positive effect of migratory movements on the dispersal-mediated process of range expansion. Dispersal, the one-way movement of an individual from a natal location to a breeding location or from one breeding site to another (in contrast to the round trip of seasonal migration), may occur at higher rates or over longer distances in species with high morphological and physical capacities for movement (dispersal ability), potentially facilitating range expansion in these species (Dytham 2009, Cain et al. 2000, Kubisch et al. 2014). Indeed, dispersal ability has been shown to be positively associated with range size in a variety of volant animals including birds, dragonflies and bats (Böhning-Gaese et al. 2006, Rundle et al. 2007, Laube et al. 2013a, White 2016, Luo et al. 2019). Owing to their capacity for long distance flights, migratory birds have inherently high dispersal ability (Bowlin and Wikelski 2008, Phillips et al. 2018). Migratory behavior could also promote range expansion through a tendency of migratory animals to become 'lost' and subsequently breed far from where they were born (Lees and Gilroy 2014) as a direct consequence of the migratory journey.

However, other studies have revealed biogeographic patterns suggesting that migratory behavior, particularly long-distance migration, constrains breeding range expansion. These studies have focused on temperate bird communities whose constituent species are predominately migratory. For example, Böhning-Gaese et al. (1998) demonstrated that long-distance migratory birds in the Northern Hemisphere are less likely than short-distance or non-migratory taxa to have colonized multiple continents to become Holarctic in distribution. At a smaller geographic scale, Bensch (1999) and Henningson and Alerstam (2008) found that long-distance

migrants were less likely than short-distance migrants or non-migrants to occupy a large breeding range in the Eurasian boreal forest and in terrestrial arctic regions, respectively. More recently, species distribution modeling (SDM) studies of migratory species have interpreted the presence of apparently suitable habitat outside of the occupied breeding range to reflect a constraint of migratory behavior on range expansion (Engler et al. 2014, Toews 2017). Authors of these studies note that migratory taxa may experience strong selection against dispersal into novel regions if such range expansions are incongruous with their finely tuned migratory routes or timing (Böhning-Gaese et al. 1998, Bensch 1999, Engler et al. 2014, Toews 2017). Migratory routes are thought to have a strong genetic component (Berthold and Querner 1981, Helbig 1991, Delmore and Irwin 2014), such that individuals dispersing to locations outside their normal range may fail to establish a persistent population if their innate migration route leads to unsuitable areas when undertaken from the novel region. That is, failure to adapt migratory routes to new geographic settings could limit range expansion.

As diverse as these hypothesized processes are, all of them suggest migration influences range size through an effect on range expansion – either by promoting or constraining it. These hypotheses assume that unoccupied suitable habitat exists outside of many species' breeding ranges (i.e. that they show range boundary disequilibrium: Sexton et al. 2009, Peterson et al. 2011). However, the relationship between migratory behavior and the extent to which species occupy suitable habitat has not been investigated at a broad taxonomic scale in a phylogenetic comparative framework.

Here we use the entire passerine fauna of temperate North America to investigate the relationship between seasonal migration and range size. Further, to understand whether seasonal migration influences range size through an effect on the process of range expansion, we test whether migratory behavior is correlated with the amount of climatically suitable habitat each species occupies (a metric called 'range filling', assessed with species distribution modeling, Laube et al. 2013b, Boucher-Lalonde and Currie 2016, Estrada et al. 2018). Previous studies have not produced a clear general prediction for how migration affects range size (Table 1), but studies focusing on terrestrial temperate species have tended to find evidence that long-distance migration constrains range expansion, perhaps reflecting the difficulty of adapting the precise timing and direction of long-distance migratory movements to new locations (Böhning-Gaese et al. 1998, Bensch 1999, Henningsson and Alerstam 2008, Toews 2017). As such, we predict that after controlling for latitudinal effects on range size (Stevens 1989, Blackburn and Gaston 1996, Gaston et al. 1998, Hawkins and Felizola Diniz-Filho 2006, Orme et al. 2006), migratory species in temperate North America should have smaller ranges than sedentary species, and migration distance should correlate negatively with range size.

Likewise, we further predict that long-distance migration constrains range filling in temperate North American species,

which would be evidence that migration constrains these species' range size specifically through its influence on the process of range expansion (Engler et al. 2014, Toews 2017). Analyzing range filling allows us to assess whether a relationship between migration and range size is mediated by the tendency of species to occupy all area available to them within their climatic niche (sensu Hutchinson 1957). If migratory behavior constrains range expansion, we predict that migratory species should show more unoccupied suitable habitat (i.e. lower range filling) than nonmigrants and that migration distance should correlate negatively with range filling.

Given the positive relationship between migratory behavior and movement capacity, we also analyze whether dispersal ability (as measured by wing shape) predicts range size and range filling in temperate North America. However, we predict that morphological dispersal ability is not an important determinant of passerine breeding range size in a temperate continental context. Although the high dispersal ability associated with migration may generally promote range expansion when taxa are compared at a global scale (Pigot and Tobias 2015), temperate bird species tend to show high dispersal ability relative to tropical species regardless of whether they migrate (Moore et al. 2008, Salisbury et al. 2012). That is, we expect that all North American birds are sufficiently vagile that their dispersal ability should not impose a constraint on range size.

Clarifying the relationship between migration, dispersal and range size is an important step for understanding the evolution and biogeography of birds in temperate latitudes where migration is prevalent. The life history and ecology of migratory species are strongly shaped by their migrations (Berthold et al. 2003). If the effects of migratory behavior extend to geographic range size, then migration could also influence range-mediated macroevolutionary and macroecological processes such as extinction (Lawton 1993, Jablonski 2005), speciation (Mayr 1942, Kisel and Barraclough 2010) and community assembly (Arita and Rodríguez 2002, Graves and Rahbek 2005). Yet seasonal migration is only one of numerous factors that can influence range size and it is unclear whether its hypothesized effects should produce a general trend in range size among migratory birds with diverse biogeographic and life histories. Our study, using the entire passerine avifauna of North America, represents the most comprehensive analysis to date of whether migration shows an emergent effect on range size and range filling in temperate birds.

Methods

Species and geographic area covered by analyses

For the purposes of our analyses, we defined the southern edge of temperate North America as 23° latitude, which coincides with a recognized transition zone between a primarily sedentary and a primarily migratory avifauna

(Cox 1985) and a major biogeographic transition zone more generally (Morrone 2015, White et al. 2019). We included all passerine species whose breeding ranges exist entirely or partially above 23° latitude in continental North America, except four species of Eurasian passerines with small portions of breeding range at the margins of arctic North America (*Phylloscopus borealis*, *Motacilla tschutschensis*, *Oenanthe oenanthe*, *Cyanecula svecica*), and two species for which we did not have access to specimens to measure wing morphology (*Melospiza aberti*, *Polioptila nigriceps*). Our study includes 306 species, of which 228 are migratory and 78 are nonmigratory. A list of species used in our analyses can be found in the Supplementary material Appendix 1.

Some species in our study have breeding ranges extending south of 23° or to the eastern hemisphere, but we include only the portion of the range that exists within North America above 23°. Although limiting the geographic scope of our analyses requires us to draw an artificial boundary to the continent and to species' ranges, it allows us to test our hypotheses within a specific, highly seasonal geographic context with a high proportion of migratory species. Furthermore, bird species in tropical regions show different range size patterns than temperate species (Hawkins and Felizola Diniz-Filho 2006, Orme et al. 2006), and including tropical species or tropical portions of species' ranges would complicate our ability to interpret results. To test whether using 23° latitude as a boundary for the study biases our results, we also repeated our analyses using only species endemic to higher latitudes (i.e. those whose ranges did not have an artificial boundary at 23° latitude) and report the results of these analyses in the Supplementary material Appendix 5.

Calculating response variables: range size and range filling

We calculated range size using BirdLife International polygons (BirdLife International 2015) with Lambert azimuthal equal area projection using the R package 'rgeos' (Bivand and Rundel 2019). We calculated range filling using species distribution models (see Supplementary material Appendix 3 for details). Briefly, we calculated species distribution models (SDMs) using Maxent as implemented in the R package 'maxnet' (Phillips 2017). Presence points came from the citizen science database eBird (Sullivan et al. 2009). We spatially thinned the presence points to reduce sampling bias (Kramer-Schadt et al. 2013, Boria et al. 2014). We sampled 100 000 background points from across North America. Points were sampled randomly but the probability that a background point existed on a particular raster cell was proportional to the number of eBird checklists within that cell (this subjects background points to the same effort biases as the presence points). Our model predictors were all 19 WorldClim bioclimatic variables (Fick and Hijmans 2017); elevation data; and NDVI data from 2010 to 2012 and 2014 to 2015 obtained with the R package gimms (Pinzon and Tucker 2014, Detsch 2018). After running an SDM, we made a raster of climatically suitable habitat using the function 'threshold' (from

the R package 'dismo'; Hijmans et al. 2017). This function counts a cell as suitable if its predicted suitability value is as high or higher than the suitability value with the highest sum of sensitivity (proportion of correctly-predicted presences) and specificity (proportion of correctly-predicted absences) for that model. Then, using Lambert azimuthal equal area projection, we calculated the total area predicted to be suitable and compared it to the suitable area within the BirdLife International polygon to calculate range filling (Fig. 1).

Calculating predictors: migratory status and distance, wing shape, mass and breeding range latitude

We characterized variation in migratory behavior using two metrics: a binary variable indicating whether or not a species is migratory (hereafter, 'migratory status'), and a continuous estimate of migration distance. We measured migration distance as the distance between the centroid of a species' breeding range and the centroid of its wintering range. Similarly, we defined migratory status based on whether the distance between the centroid of species' breeding and wintering ranges was greater than 10 km (migratory) or not (nonmigratory). Distances were calculated in a latitude/longitude projection using the function 'distGeo', which accounts for the curvature of the earth, from the R package 'geosphere' (Hijmans 2019). Species range shapefiles, including breeding, resident (year-round) and nonbreeding ranges, were downloaded from BirdLife International (2015). For partially migratory species (i.e. species in which some populations migrate and others do not), the resident range where individuals are present year-round was included as part of both the breeding and wintering range when range centroids were calculated.

Variation in morphological dispersal ability in birds is best captured by wing shape (Claramunt and Wright 2017), which is related to flight efficiency (Bowlin and Wikelski 2008). We measured wing shape using a metric of wingtip pointedness called hand-wing index (HWI; Claramunt and Wright 2017). High HWI indicates a pointed wingtip suited for long-distance flight while low HWI indicates a rounded, less-efficient wingtip. We used calipers to measure two museum specimens for each species from the Univ. of Michigan Museum of Zoology. We use mass as a covariate in all models with wing shape. Mass data were obtained from the CRC handbook of avian body masses (Dunning 1992). For species not included in the CRC handbook, we obtained mass data from Birds of North America online (Rodewald 2015).

In all of our analyses, we include latitude as a covariate. With increasing latitude, migratory behavior becomes increasingly prevalent and migration distances increase (Newton and Dale 1996, Somveille et al. 2015; Supplementary material Appendix 2 Fig. A1). Latitudinal gradients in other factors that affect range – such as climatic tolerance, habitat size, biogeographic history or species richness – may lead to a positive relationship between range size and latitude

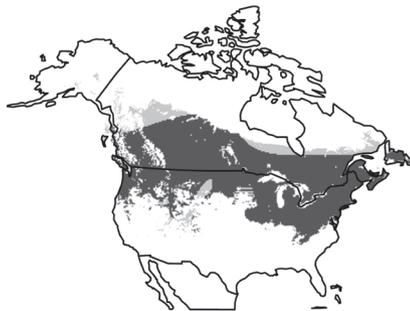
(a) *Bombycilla garrulus*
 Range filling = 0.41
 Suitable area = 7 million km²



(c) *Spizella pusilla*
 Range filling = 0.94
 Suitable area = 3 million km²



(b) *Bombycilla cedrorum*
 Range filling = 0.86
 Suitable area = 7 million km²



(d) *Passerculus sandwichensis*
 Range filling = 0.94
 Suitable area = 12 million km²

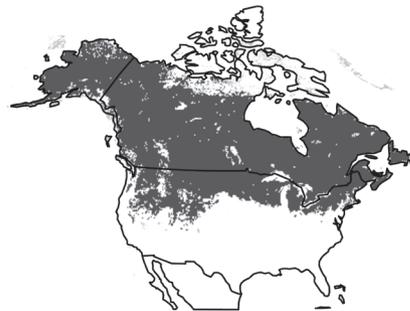


Figure 1. Example maps of range filling demonstrate that range size (dark gray) is affected by both suitable habitat area (light gray) and range filling (proportion of suitable habitat covered by range). On the left side of the figure are maps for two species of waxwings which have a similar amount of climatically suitable habitat but different range filling values. *Bombycilla garrulus* (a) has lower range filling than *Bombycilla cedrorum* (b), so it has a smaller range. The substantial range boundary disequilibrium demonstrated by *Bombycilla garrulus* suggests that this species could be constrained from expanding its range by a dispersal limitation or by a biotic factor such as the presence of a competitor. On the right side of the figure are maps for two species of sparrows that show little range boundary disequilibrium: both species occupy almost the entirety of their suitable habitat. However, their ranges are different in size because *Spizella pusilla* (c) has less suitable habitat than *Passerculus sandwichensis* (d). Because little climatically suitable habitat exists outside of the range of either of these species, the difference in range size between them is not likely attributable to dispersal or migration-related constraints on range expansion.

(Stevens 1989, Hawkins and Felizola Diniz-Filho 2006, Orme et al. 2006). In addition to the possible biotic effects of latitude on range size, the geographically bounded nature of our study results in a strong hump-shaped relationship between latitude and the maximum possible range size at that latitude (Supplementary material Appendix 2 Fig. A2). We measured the latitudinal midpoint of each species' North American breeding range in maps with a latitude/longitude projection. For species whose ranges extend south of 23° latitude, we used 23° latitude as the southern range limit in these calculations. We use latitudinal midpoint as a quadratic term in our models of range size because of the relationship between latitude and maximum range size. The maximum possible range filling for every species is 1.0, regardless of range size, so this metric is not affected by continental bounds

and we include latitude as a linear predictor in models with range filling as the response variable. We hereafter refer to this predictor simply as 'latitude'.

Hypothesis testing

We used R (ver. 3.5.2, R Core Team) to explore our data (following recommendations of Zuur et al. 2010) and to fit generalized linear models assessing the influence of migratory status, migration distance and morphological dispersal ability on range size and range filling. Range size shows a positive skewed distribution, so we used Gamma regression with a log link for models with these response variables. Range filling is a proportion, so for models of range filling we used beta regression (Cribari-Neto and Zeileis 2010). Our predictors

span several orders of magnitude, so we centered and standardized all predictors such that the mean was 0 and the standard deviation was 1. We rescaled range size to between 1 and 10 to improve model fitting.

Species with shared evolutionary history are not independent of each other, so it is necessary to consider phylogenetic relationships when comparing traits among many species (Felsenstein 1985). However, unlike methods such as phylogenetic generalized least squares that incorporate phylogenetic relatedness into regression frameworks directly, few methods are available to control for phylogenetic relatedness with gamma and beta regression. Therefore, we tested whether phylogenetic relatedness had an influence on our model results by fitting a full model (i.e. with all predictors) with a phylogenetic covariance matrix and a full model without the matrix using the Bayesian R package ‘brms’ (Bürkner 2017) and comparing the results. We downloaded phylogenetic data for all of our species from birdtree.org (Jetz et al. 2012, ‘Hackett all species’ dataset) as a sample of 2000 phylogenetic trees. We calculated a consensus tree from these data using the SumTrees program in the ‘DendroPy’ python package (Sukumaran and Holder 2010) and used the R packages ‘ape’ (Paradis and Schleip 2018) and ‘phytools’ (Revell 2012) to manipulate phylogenetic data in R.

Our results indicated that the phylogenetic covariance matrix did not influence model results (Supplementary material Appendix 4 Table A2, A3). Therefore, we carried out the remainder of our analyses using functions from R’s default ‘stats’ package and from ‘betareg’ (Cribari-Neto and Zeileis 2010).

After fitting a full model for each response variable, we used the package ‘MuMIn’ (Bartón 2019) to compare the AICc of the full model with that of three reduced models (one model using only migration predictors, one using only wing shape and mass, and one using only breeding latitude) to test for overfitting of the full model.

Finally, we repeated our analyses on two subset datasets (Supplementary material Appendix 5). First, to test whether cropping ranges at 23° latitude influenced our results, we fit models using only the 161 species whose entire range is north of 23° latitude. Second, to test whether wing shape shows a relationship with range size among less-mobile species, we next repeated our analyses on a dataset including only 78 non-migratory species. Models including non-migrants did not include migration-related predictors.

Results

Species distribution models

The average AUC (a measure of model fit) for our species distribution models was 0.91 (range 0.61–1), indicating that our models generally performed much better than a random null model (which would produce AUC = 0.5; Phillips 2010). AUC values are expected to correlate with species range size (Phillips 2010), which we observed in our data: models

with low AUC tend to come from species with large ranges (Supplementary material Appendix 1 Table A1).

Do migration and wing shape influence range size in North American passerines?

Migration and wing shape are significant predictors of range size in a model with no other predictors, but in our best-fit model predicting range size, which included latitude as a quadratic predictor, no predictors were significant other than latitude (latitude $\beta = 7.18$, SE = 0.51, $p < 0.0001$; latitude² $\beta = -3.90$, SE = 0.43, $p < 0.0001$; migratory status $\beta = 0.017$; SE = 0.070; $p = 0.81$; migration distance $\beta = 0.0068$; SE = 0.033; $p = 0.83$; wing shape $\beta = 0.051$; SE = 0.03; $p = 0.076$; mass $\beta = 0.046$; SE = 0.026; $p = 0.079$). When latitude is included in the model, migratory status, migration distance and wing shape do not significantly contribute to explaining variation in range size (Fig. 2, Supplementary material Appendix 4 Table A4).

Do migration and wing shape influence range filling in North American passerines?

The best-fit model for range filling included only migratory status and migration distance as predictors, but these predictors were not significant (migratory status $\beta = 0.12$, SE = 0.14, $p = 0.36$; migration distance $\beta = 0.059$, SE = 0.060, $p = 0.33$) and the pseudo-R² of this model was low (0.013). None of the predictor variables were significant in any of the models of range filling (Fig. 2, Supplementary material Appendix 4 Table A5).

Results of analyses on subset datasets

Models fit with species whose ranges are entirely north of 23° latitude and models fit with only non-migrants produced results that are qualitatively similar to models fit with all species in our dataset: latitude is the strongest predictor of range size and filling, and the addition of other predictors (migratory status and distance, wing shape, mass) does not improve model fit (Supplementary material Appendix 5).

Discussion

Although the geographic location and interannual reappearance of migratory species’ breeding ranges depend on their migratory behavior, we found no evidence of an emergent effect of migration or dispersal ability (wing shape) on range size. Our analyses failed to reject the null hypotheses that range size is unrelated to migratory behavior or wing shape. Other possible causes of range size variation, such as latitudinal effects, climatic niche breadth or biotic factors may have stronger influence on range size in this avifauna. Indeed, we found evidence that latitude shows a strong relationship with range size (Table 2, Supplementary material Appendix 2 Fig. A3), and migratory behavior and wing shape were not

significant predictors of range size or range filling after controlling for latitude. However, our analyses were designed specifically to test the emergent influence of migration and wing shape on range size, rather than to parse which of many other biotic or abiotic factors most strongly influences range size, so we refrain from drawing conclusions about the dynamics that contribute most to range size variation among North American birds.

We also tested whether migration or wing shape influence range filling. Range filling represents the extent to which species occupy climatically-suitable area (as determined by their present distributions), so it allows us to test for an effect of migratory behavior or wing shape on range expansion even in circumstances where raw range size variation is more strongly influenced by climatic niche or other factors. Here, too, we did not reject the null hypotheses that there is neither a relationship between migration nor wing shape and range filling.

Our calculation of range filling comes with two caveats. First, our SDMs assessed only climatic suitability. Biotic interactions (such as the presence of competitors,

important resource species or predators and pathogens) also limit species' capacity to exist in climatically suitable areas (Peterson et al. 2011, Laube et al. 2013b, Sanín and Anderson 2018). Second, it is also possible that unoccupied 'climatically suitable' regions are not actually climatically suitable for the species, but instead represent a mismatch between the predictors we used to build our species distribution models and the factors that determine our species' range boundaries. Without knowledge of the proximate causes of a species' range boundary, it is difficult to assess whether a model is capturing information about what determines climatic suitability for that species (Boucher-Lalonde and Currie 2016, Moore et al. 2018). Nonetheless, the hypothesis that long-distance seasonal migration generally limits range filling in temperate birds (Engler et al. 2014, Toews 2017) is not supported by our results.

Our results add to a body of correlative studies that, when considered together, suggest that the apparent effects of migration and wing shape on biogeographic patterns depend on the geographic context and taxonomic scale of the analysis.

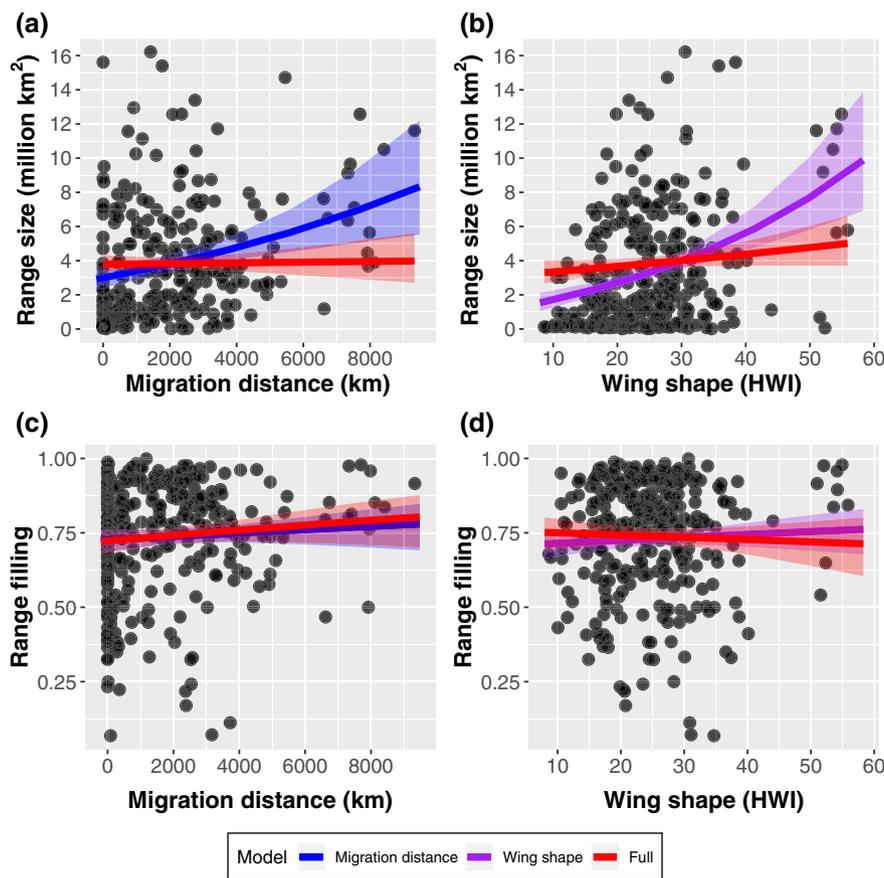


Figure 2. Range size increases slightly with migration distance and wing shape (a, b; blue and purple line, respectively), but these effects are not significant in models that include latitude as a predictor (a, b; red lines). Migration distance and wing shape show no significant relationship with range filling (c, d). Each point represents one species. Species with wing shape HWI values greater than 50 belong to the family Hirundinidae (swallows). Lines on plots show marginal effects (with confidence intervals) of migration distance on range size or range filling. Line color indicates which model (Table 2) the plotted migration distance marginal effect estimate comes from: blue lines are from a model with only migratory status and migration distance predictors; purple lines are from a model with only wing shape and mass predictors; and red lines are from a full model which includes all predictors, including latitude.

Past work on smaller groups of taxa has suggested that migration constrains breeding range expansion within the scale of a continent (Bensch 1999, Engler et al. 2014, Toews 2017), but we find that this is not a general pattern when considering the full set of North American passerines. However, it is worth noting that our data replicate the pattern described by Toews (2017): among the 17 parulid warbler species considered in that study, longer-distance migrants tend to have smaller ranges and lower range filling values (Supplementary material Appendix 1). Further, migration may still constrain colonization between continents (Böhning-Gaese et al. 1998), which could require a more abrupt and longer-distance geographic shift that species with inflexible migratory behavior may be unable to accommodate. The processes producing these varying patterns remain elusive.

Our results also contrast with those of other authors who found positive relationships between migration or wing shape and range size even among highly volant taxa (Blackburn and Gaston 1996, Gaston and Blackburn 1996, Böhning-Gaese et al. 2006, Laube et al. 2013a, b, Pigot and Tobias 2015, White 2016, Luo et al. 2019, Outomuro and Johansson 2019). Unlike our study, most of these other studies include both temperate and tropical fauna. Tropical organisms, including birds and flying insects, are known to be poorer dispersers than their temperate counterparts (Moore et al. 2008, Salisbury et al. 2012, Polato et al. 2018). Our results suggest that temperate passerines are generally mobile enough that dispersal limitation does not affect their ability to expand their ranges. Even nonmigratory members of this avifauna show no relationship between wing shape and range size (Supplementary material Appendix 5). As such, relationships between dispersal ability and range size in volant organisms that are apparent at a global scale, such as those found by Blackburn and Gaston (1996), Gaston and Blackburn (1996), Pigot and Tobias (2015) and Luo et al. (2019), are likely not maintained when poorly-dispersing tropical species are excluded. Although Laube et al. (2013a) found a positive effect of dispersal ability on range size in temperate European passerines (including migratory species), this analysis did not control for breeding latitude and thus is difficult to compare with our results.

Migratory behavior could also affect range size if it is correlated with other determinants of range size that are not directly related to movement (Stevens 1989, Blackburn and Gaston 1996, Gaston and Blackburn 1996). For example, migratory birds may be less ecologically specialized than sedentary birds (Gómez et al. 2016; but see Martin and Fahrig 2018) and as such their suitable habitat area may be larger. Migration also allows birds to breed at high latitudes, where range sizes tend to be larger than they are in the tropics (Blackburn and Gaston 1996, Hawkins and Felizola Diniz-Filho 2006, Orme et al. 2006), while avoiding the harshest climatic conditions associated with these latitudes (Winger et al. 2019). The ability to discern the processes underlying variation in the relationship between migratory behavior and range size across studies is limited because traits and biogeographic patterns can be spatially autocorrelated: an apparent relationship between a trait and a biogeographic pattern does not necessarily imply that the pattern is caused by the trait, even when there is a putative biological mechanism (Gove et al. 2009, Warren et al. 2014).

To better understand what factors constrain or promote range size in migratory animals, it will be useful to investigate how range boundaries are formed in these species. For example, the processes affecting range size in species whose range boundaries reflect the limits of their climatic niche are different from those of species showing range boundary disequilibrium (Sexton et al. 2009, Hargreaves et al. 2014). In cases when range boundaries are proximately determined by climatic niche (Fig. 1c–d) and the species has nowhere to expand without broadening its niche, traits such as migratory behavior may be less likely to influence range expansion. The relationship between species' migratory behavior and the breadth of their climatic niches has been a topic of increasing interest in recent years (Gómez et al. 2016, Reif et al. 2016, Martin and Fahrig 2018, Ponti et al. 2019) and results of further such studies will contribute to our understanding of the biogeography of migratory taxa.

We will also gain insight into the processes affecting range boundaries in migratory animals by tracking the fate of individual dispersers, especially near range edges. For example, recent studies tracking migratory godwits

Table 2. Models predicting range size and range filling. Migratory status and migratory distance are not significant predictors of range size in the best-fit model (see also Supplementary material Appendix 4 Table A4). None of our predictors showed a significant relationship with range filling (see also Supplementary material Appendix 4 Table A5). Model coefficients were calculated with centered/standardized predictors with mean=0 and SD=1. Range size is rescaled to be between 1 and 10 and range filling is a proportion. R² shown for models of range size are trigamma estimates calculated using the R package 'MuMIn'. For models of range filling, we show pseudo R² calculated by the R package 'betareg'.

Response	Migratory status	Migration distance	Wing shape	Mass	Latitude	Latitude ²	logLik	AICc	Delta	Weight	R ²
Range size	0.017	0.0068	0.051	0.046	7.18	-3.90	-431.1	878.8	0	0.78	0.58
Range size	-	-	-	-	7.67	-3.97	-436.6	881.3	2.58	0.22	0.58
Range size	0.37	0.15	-	-	-	-	-530.4	1069.0	190.2	0	0.19
Range size	-	-	0.21	0.017	-	-	-544.3	1096.7	217.9	0	0.11
Range filling	0.12	0.059	-	-	-	-	122.7	-237.3	0	0.49	0.013
Range filling	-	-	-	-	0.05	-	121.2	-236.3	0.93	0.31	0.002
Range filling	-	-	0.042	0.031	-	-	121.5	-234.8	2.49	0.14	0.004
Range filling	0.18	0.092	-0.033	0.078	-0.028	-	123.7	-233.1	4.18	0.06	0.02

Limosa limosa have demonstrated that shifts in geographic range and migratory routes are driven by dispersal of young individuals, while adults remain site faithful throughout their lives (Verhoeven et al. 2018, Gill et al. 2019). However, more generally, the relationship between migratory behavior and dispersal is poorly understood. The extent to which dispersal patterns in migratory birds are dictated by exploration of and settlement in novel environments versus site fidelity and natal philopatry – attempting to return to a previous territory or a habitat similar to where an individual was born – has implications for how the breeding ranges of these species have evolved and how they respond to environmental change (Davis and Stamps 2004, Canestrelli et al. 2016, Jönsson et al. 2016).

Data availability statement

Data are provided in the Supplementary material Appendix 1–5.

Acknowledgements – We thank Brian Weeks, Eric Gulson-Castillo, Susanna Campbell, Shane DuBay, Marketa Zimova, Kristen Wacker, Rachel Wadleigh, Daniel Rabosky, Lacey Knowles, and Andrew Marshall for helpful discussion. Janet Hinshaw and Brett Benz facilitated access to specimens at the Univ. of Michigan Museum of Zoology. Vera Ting, Charles Kotila and Kaia Newman assisted with wing shape measurements.

Funding – Vera Ting and Charles Kotila were supported by the Univ. of Michigan Undergraduate Research Opportunity Program. This research was supported in part through computational resources and services provided by Advanced Research Computing at the Univ. of Michigan, Ann Arbor. TP was supported by a National Science Foundation Graduate Research Fellowship (DGE 1256260, Fellow ID 2018240490).

References

- Angert, A. L. 2009. The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. – *Proc. Natl Acad. Sci. USA* 106: 19693–19698.
- Angert, A. L. et al. 2011. Do species' traits predict recent shifts at expanding range edges? – *Ecol. Lett.* 14: 677–689.
- Arita, H. T. and Rodríguez, P. 2002. Geographic range, turnover rate and the scaling of species diversity. – *Ecography* 25: 541–550.
- Bartón, K. 2019. MuMIn: multi-model inference. – R package ver. 1.43.6, <<https://CRAN.R-project.org/package=MuMIn>>.
- Bensch, S. 1999. Is the range size of migratory birds constrained by their migratory program? – *J. Biogeogr.* 26: 1225–1235.
- Berthold, P. and Querner, U. 1981. Genetic basis of migratory behavior in European warblers. – *Science* 212: 77–79.
- Berthold, P. et al. 2003. Avian migration. – Springer.
- BirdLife International. 2015. IUCN Red List for birds. – <www.birdlife.org>, accessed 1 January 2015.
- Bivand, R. and Rundel, C. 2019. rgeos: interface to geometry engine – open source ('GEOS'). – R package ver. 0.4-3, <<https://CRAN.R-project.org/package=rgeos>>.
- Blackburn, T. M. and Gaston, K. J. 1996. Spatial patterns in the geographic range sizes of bird species in the New World. – *Phil. Trans. R. Soc. B* 351: 897–912.
- Böhning-Gaese, K. et al. 1998. Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. – *Evol. Ecol.* 12: 767–783.
- Böhning-Gaese, K. et al. 2006. Range size: disentangling current traits and phylogenetic and biogeographic factors. – *Am. Nat.* 167: 555–567.
- Boria, R. A. et al. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. – *Ecol. Model.* 275: 73–77.
- Boucher-Lalonde, V. and Currie, D. J. 2016. Spatial autocorrelation can generate stronger correlations between range size and climatic niches than the biological signal – a demonstration using bird and mammal range maps. – *PLoS One* 11: e0166243.
- Bowlin, M. S. and Wikelski, M. 2008. Pointed wings, low wing-loading and calm air reduce migratory flight costs in songbirds. – *PLoS One* 3: e2154
- Brommer, J. E. 2008. Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology. – *Ornis Fenn.* 85: 109–117.
- Brommer, J. E. and Møller, A. P. 2010. Range margin changes, life history and ecology. – In: Møller, A. P. et al. (eds), *Climate change and birds*. Oxford Univ. Press, pp. 249–274.
- Bürkner, P.-C. 2017. brms : an R package for Bayesian multilevel models using Stan. – *J. Stat. Softw.* 80: 1–28.
- Cain, M. L. et al. 2000. Long-distance seed dispersal in plant populations. – *Am. J. Bot.* 87: 1217–1227.
- Canestrelli, D. et al. 2016. Bolder takes all? The behavioral dimension of biogeography. – *Trends Ecol. Evol.* 31: 35–43.
- Caramant, S. and Wright, N. A. 2017. Using museum specimens to study flight and dispersal. – In: Webster, M. S. (ed.), *The extended specimen: emerging frontiers in collections-based ornithological research*. CRC Press, pp. 127–142.
- Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. – *Am. Nat.* 126: 451–474.
- Cribari-Neto, F. and Zeileis, A. 2010. Beta regression in R. – *J. Stat. Softw.* 34: 1–24.
- Davis, J. M. and Stamps, J. A. 2004. The effect of natal experience on habitat preferences. – *Trends Ecol. Evol.* 19: 411–416.
- Delmore, K. E. and Irwin, D. E. 2014. Hybrid songbirds employ intermediate routes in a migratory divide. – *Ecol. Lett.* 17: 1211–1218.
- Detsch, F. 2018. gimms: download and process GIMMS NDVI3g data. – R package ver. 1.1.1, <<https://CRAN.R-project.org/package=gimms>>.
- Dunning, J. B. J. 1992. CRC handbook of avian body masses. – CRC Press.
- Dytham, C. 2009. Evolved dispersal strategies at range margins. – *Proc. R. Soc. B* 276: 1407–1413.
- Engler, J. O. et al. 2014. Suitable, reachable but not colonised: seasonal niche duality in an endemic mountainous songbird. – *J. Ornithol.* 155: 657–669.
- Estrada, A. et al. 2018. Equipped to cope with climate change: traits associated with range filling across European taxa. – *Ecography* 41: 770–781.
- Felsenstein, J. 1985. Phylogenies and the comparative method. – *Am. Nat.* 125: 1–15.

- Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. – *Int. J. Climatol.* 37: 4302–4315.
- Forsyth, D. M. et al. 2004. Climatic suitability, life-history traits, introduction effort and the establishment and spread of introduced mammals in Australia. – *Conserv. Biol.* 18: 557–569.
- Gaston, K. J. and Blackburn, T. M. 1996. Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. – *J. Anim. Ecol.* 65: 701–714.
- Gaston, K. J. et al. 1998. Rapoport's rule: time for an epitaph? – *Trends Ecol. Evol.* 13: 70–74.
- Gill, J. A. et al. 2019. Mechanisms driving phenological and range change in migratory species. – *Phil. Trans. R. Soc. B* 374: 20180047.
- Gómez, C. et al. 2016. Niche-tracking migrants and niche-switching residents: evolution of climatic niches in new world warblers (Parulidae). – *Proc. R. Soc. B* 283: 1–9.
- Gove, A. D. et al. 2009. Dispersal traits linked to range size through range location, not dispersal ability, in Western Australian angiosperms. – *Global Ecol. Biogeogr.* 18: 596–606.
- Graves, G. R. and Rahbek, C. 2005. Source pool geometry and the assembly of continental avifaunas. – *Proc. Natl Acad. Sci. USA* 102: 7871–7876.
- Hargreaves, A. L. et al. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. – *Am. Nat.* 183: 157–173.
- Hawkins, B. A. and Felizola Diniz-Filho, J. A. 2006. Beyond Rapoport's rule: evaluating range size patterns of New World birds in a two-dimensional framework. – *Global Ecol. Biogeogr.* 15: 461–469.
- Helbig, A. J. 1991. SE- and SW-migrating blackcap (*Sylvia atricapilla*) populations in central Europe: orientation of birds in the contact zone. – *J. Evol. Biol.* 4: 657–670.
- Henningson, S. S. and Alerstam, T. 2008. Does migration promote or restrict circumpolar breeding ranges of arctic birds? – *J. Biogeogr.* 35: 78.
- Hijmans, R. J. 2019. geosphere: spherical trigonometry. – R package ver. 1.5-10, <<https://CRAN.R-project.org/package=geosphere>>.
- Hijmans, R. J. et al. 2017. dismo: species distribution modeling. – R package ver. 1.1-4, <<https://CRAN.R-project.org/package=dismo>>.
- Hutchinson, G. E. 1957. Concluding remarks: the demographic symposium as a heterogeneous unstable population. – *Cold Spring Harbor Symp. Quant. Biol.* 22: 415–427.
- Jablonski, D. 2005. Mass extinctions and macroevolution. – *Paleobiology* 31: 192–210.
- Jetz, W. et al. 2012. The global diversity of birds in space and time. – *Nature* 491: 444–448.
- Jönsson, K. A. et al. 2016. Tracking animal dispersal: from individual movement to community assembly and global range dynamics. – *Trends Ecol. Evol.* 31: 204–214.
- Kisel, Y. and Barraclough, T. G. 2010. Speciation has a spatial scale that depends on levels of gene flow. – *Am. Nat.* 175: 316–334.
- Kramer-Schadt, S. et al. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. – *Divers. Distrib.* 19: 1366–1379.
- Kubisch, A. et al. 2014. Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. – *Oikos* 123: 5–22.
- Laube, I. et al. 2013a. Towards a more mechanistic understanding of traits and range sizes. – *Global Ecol. Biogeogr.* 22: 233–241.
- Laube, I. et al. 2013b. Intra-generic species richness and dispersal ability interact to determine geographic ranges of birds. – *Global Ecol. Biogeogr.* 22: 223–232.
- Lawton, J. H. 1993. Population abundance and conservation. – *Trends Ecol. Evol.* 8: 409–413.
- Lees, A. C. and Gilroy, J. J. 2014. Vagrancy fails to predict colonization of oceanic islands. – *Global Ecol. Biogeogr.* 23: 405–413.
- Luo, B. et al. 2019. Wing morphology predicts geographic range size in vespertilionid bats. – *Sci. Rep.* 9: 4526.
- Martin, A. E. and Fahrig, L. 2018. Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. – *Ecology* 99: 2058–2066.
- Mayr, E. 1942. Systematics and the origin of species, from the viewpoint of a zoologist. – Columbia Univ. Press.
- Moore, R. P. et al. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. – *Ecol. Lett.* 11: 960–968.
- Moore, T. E. et al. 2018. Spatial autocorrelation inflates niche breadth–range size relationships. – *Global Ecol. Biogeogr.* 27: 1426–1436.
- Morrone, J. J. 2015. Halffter's Mexican transition zone (1962–2014), cenocrons and evolutionary biogeography. – *J. Zool. Syst. Evol. Res.* 53: 249–257.
- Newton, I. and Dale, L. C. 1996. Bird migration at different latitudes in eastern North America. – *Auk* 113: 626–635.
- Orme, C. D. L. et al. 2006. Global patterns of geographic range size in birds. – *PLoS Biol.* 4: 1276–1283.
- Outomuro, D. and Johansson, F. 2019. Wing morphology and migration status, but not body size, habitat or Rapoport's rule predict range size in North-American dragonflies (Odonata: Libellulidae). – *Ecography* 42: 309–320.
- Paradis, E. and Schliep, K. 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. – *Bioinformatics* 35: 526–528.
- Peterson, A. T. et al. 2011. Ecological niches and geographic distributions. – Princeton Univ. Press.
- Phillips, A. G. et al. 2018. Evidence for distinct evolutionary optima in the morphology of migratory and resident birds. – *J. Avian Biol.* 49: 1–12.
- Phillips, S. 2010. 'A brief tutorial on Maxent' in species distribution modeling for educators and practitioners. – *Lessons Conserv.* 3: 107–135.
- Phillips, S. J. 2017. maxnet: fitting 'Maxent' species distribution models with 'glmnet'. – R package ver. 0.1.2, <<https://CRAN.R-project.org/package=maxnet>>.
- Pigot, A. L. and Tobias, J. A. 2015. Dispersal and the transition to sympatry in vertebrates. – *Proc. R. Soc. B* 282: 20141929.
- Pinzon, J. E. and Tucker, C. J. 2014. A non-stationary 1981–2012 AVHRR NDVI3g time series. – *Remote Sens.* 6: 6929–6960.
- Polato, N. R. et al. 2018. Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. – *Proc. Natl Acad. Sci. USA* 115: 12471–12476.
- Ponti, R. et al. 2019. Seasonal climatic niches diverge in migratory birds. – *Ibis* 162: 318–330.
- Price, T. D. and Kirkpatrick, M. 2009. Evolutionarily stable range limits set by interspecific competition. – *Proc. R. Soc. B* 276: 1429–1434.
- Reif, J. et al. 2016. Linking habitat specialization with species' traits in European birds. – *Oikos* 125: 405–413.

- Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). – *Methods Ecol. Evol.* 3: 217–223.
- Rodewald, P. 2015. The birds of North America. – Cornell Lab of Ornithology, <<https://birdsna.org>>.
- Rundle, S. D. et al. 2007. Range size in North American *Enallagma* damselflies correlates with wing size. – *Freshwater Biol.* 52: 471–477.
- Salisbury, C. L. et al. 2012. The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. – *Ecol. Lett.* 15: 847–855.
- Sanín, C. and Anderson, R. P. 2018. A framework for simultaneous tests of abiotic, biotic and historical drivers of species distributions: empirical tests for north american wood warblers based on climate and pollen. – *Am. Nat.* 192: E48–E61.
- Sexton, J. P. et al. 2009. Evolution and ecology of species range limits. – *Annu. Rev. Ecol. Evol. Syst.* 40: 415–436.
- Somveille, M. et al. 2015. Why do birds migrate? A macroecological perspective. – *Global Ecol. Biogeogr.* 24: 664–674.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. – *Am. Nat.* 133: 240–256.
- Sukumaran, J. and Holder, M. T. 2010. DendroPy: a Python library for phylogenetic computing. – *Bioinformatics* 26: 1569–1571.
- Sullivan, B. L. et al. 2009. eBird: a citizen-based bird observation network in the biological sciences. – *Biol. Conserv.* 142: 2282–2292.
- Thorup, K. 2006. Does the migration programme constrain dispersal and range sizes of migratory birds? – *J. Biogeogr.* 33: 1166–1171.
- Tingley, M. W. et al. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. – *Global Change Biol.* 18: 3279–3290.
- Toews, D. P. L. 2017. Habitat suitability and the constraints of migration in New World warblers. – *J. Avian Biol.* 48: 1614–1623.
- Verhoeven, M. A. et al. 2018. Generational shift in spring staging site use by a long-distance migratory bird. – *Biol. Lett.* 14: 2009–2012.
- Warren, D. L. et al. 2014. Mistaking geography for biology: Inferring processes from species distributions. – *Trends Ecol. Evol.* 29: 572–580.
- White, A. E. 2016. Geographical barriers and dispersal propensity interact to limit range expansions of Himalayan birds. – *Am. Nat.* 188: 99–112.
- White, A. E. et al. 2019. Regional influences on community structure across the tropical-temperate divide. – *Nat. Commun.* 10: 1–8.
- Winger, B. M. et al. 2019. A long winter for the Red Queen: rethinking the evolution of seasonal migration. – *Biol. Rev.* 94: 737–752.
- Zuckerberg, B. et al. 2009. Poleward shifts in breeding bird distributions in New York State. – *Global Change Biol.* 15: 1866–1883.
- Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. – *Methods Ecol. Evol.* 1: 3–14.

Supplementary material (available online as Appendix ecog-05070 at <www.ecography.org/appendix/ecog-05070>). Appendix 1–5.