Why do birds migrate?
A macroecological perspective

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ABSTRACT

Aim Bird migration poses a challenge to macroecology, because with one in five species moving twice yearly between breeding and non-breeding grounds, macroecological patterns in birds are dynamic rather than static. But migration is also a natural experiment for testing hypotheses about the ecological mechanisms driving species distributions. Here, we use macroecological patterns of migratory bird diversity to test whether seasonality, winter harshness and the cost of migration drive the global distribution of migratory birds.

Location Global.

Methods We used data on the distribution of the world’s bird species to derive global empirical patterns of: the number of breeding migrants, the number of non-breeding migrants and the difference in seasonal diversity. We built statistical models with ecologically meaningful predictors related to each of the hypotheses and investigated if they can significantly explain global empirical patterns of migratory bird diversity. We formally tested these models by training on one hemisphere (Western or Eastern) to predict the other hemisphere in turn. Model predictions were assessed in terms of match to the empirical data and their ability to predict the spatial features of patterns.

Results We found strong support for the hypotheses that birds move to breeding grounds to exploit a surplus in resources, preferring areas with harsh winters (presumably to avoid competition). In contrast, distribution during the non-breeding season seems driven by avoidance of harsh winters and connectivity to breeding grounds. Models integrating these hypotheses explain well the observed variance in the empirical patterns and reproduce key spatial features, even when models trained in one hemisphere are used to predict another.

Main conclusions The strong predictive power of the models suggests that we have captured the main mechanisms that drive global patterns in bird migration. The fact that the models perform well despite being applied to species with very different ecologies suggests general mechanisms driving migration across taxa.

Keywords Bird migration, bird species richness, cost of migration, dynamic pattern, macroecology, seasonality.
Bird migration, involving almost 20% of the world’s nearly 10,000 species (Kirby et al., 2008), is ‘a seasonal ecological adjustment on a gigantic scale’ (Moreau, 1952), a redistribution of bird diversity that radically changes community composition world-wide (Somveille et al., 2013). It therefore poses a particular challenge to macroecology, as patterns of diversity in birds are dynamic rather than static. But migration is also an extraordinary opportunity, as a natural experiment for testing hypotheses of the mechanisms driving the spatial distribution of species (H-Acevedo & Currie, 2003; Hurlbert & Haskell, 2003; Boucher-Lalonde et al., 2014; Dalby et al., 2014).

In a previous study (Somveille et al., 2013), we mapped patterns of diversity in migratory birds at the global scale. We found that despite the great biological and ecological diversity in migratory birds, strong spatial patterns emerge when they are all pooled together, suggesting common underlying ecological drivers to which migratory birds respond. Understanding what drives these patterns can bring insights into the old question of why birds migrate.

Scientists have been trying to explain the spatial distribution of migratory birds for millennia. In his Historia Animalium, Aristotle proposed that birds ‘[quit] the cold countries after the autumnal equinox to avoid the approaching winter, and after the spring equinox [migrate] from warm lands to cool lands to avoid the coming heat’ (Aristotle, Book VIII, section 12; written 350 BCE and translated by Thompson, 1907). MacArthur (1959) was the first to tackle migration quantitatively in a spatial way, by measuring the proportion of breeding individuals in North American communities that migrate into the Neotropics for winter, hypothesizing seasonality in food supply as the most reasonable explanation for the observed variation. Seasonality in climate and in resource availability were therefore put forward early on as the key drivers of bird migration. Many subsequent studies investigated spatial patterns of migratory bird diversity as tools to advance understanding of bird migration, either by explicitly testing hypotheses or (more frequently) by deriving post-hoc explanations from observed spatial patterns. From these studies, three mechanisms have been hypothesized as the main drivers of bird migration.

The most frequently proposed mechanism is that birds migrate to benefit from a seasonal availability of resources. This explanation has been put forward to explain observed positive correlations between latitude and either the percentage (Herrera, 1978; Newton & Dale, 1996a,b) or the absolute numbers of breeding migrants (Barcena et al., 2004; Carnicer & Diaz-Delgado, 2008), assuming latitude to be a surrogate for seasonality in resources. Other studies investigated more direct measures of resource availability. H-Acevedo & Currie (2003) showed that climate variables (temperature and precipitation) and seasonality in productivity (as measured by the normalized difference vegetation index, or NDVI, a remote sensing measure of greenness) explain the distribution and differences of overall species richness between breeding and non-breeding seasons (including migrants and residents), suggesting that birds track environmental conditions throughout the year. Similarly, Hurlbert & Haskell (2003) and Boucher-Lalonde et al. (2014) found that the relationship between avian richness and temperature and productivity was consistent between seasons. Dalby et al. (2014), however, proposed an important refinement to this hypothesis. Investigating global patterns in the diversity of waterfowl (Anseriformes, most of which are migratory), they found that richness in breeding birds is better predicted by variability in NDVI across seasons rather than NDVI in the breeding season. They deduced that breeding migrants respond not so much to the total amount of resources available locally in the breeding season but more to the surplus of resources not exploited by year-round residents, and thus available to be exploited by incoming migrants. However, they found that in the non-breeding season diversity was related to productivity in that season rather than to the surplus in resources. Few other studies have addressed patterns in the non-breeding season, but Newton & Dale (1996a,b) found that the percentage of non-breeding migrants in local communities in North America and Europe was inversely (rather than positively) related to latitude.

The second main mechanism proposed in the literature is that birds migrate to avoid harsh winters. Winter harshness was found to be positively associated with the percentage and number of breeding migrants (Herrera, 1978; Newton & Dale, 1996a; Lemoine & Boëning-Gaese, 2003; Carnicer & Diaz-Delgado, 2008; Schaefer et al., 2008), explained in terms of reduced competition with resident birds. Hence, in areas of harsh winters, most food becomes seasonally unavailable (‘locked by ice in soils and water’; Newton & Dale, 1996a, p. 144), limiting the number of species able to stay as residents, and freeing more resources for incoming breeding migrants (Herrera, 1978; Fretwell, 1980; Newton & Dale, 1996a). Accordingly, Hurlbert & Haskell (2003) found that areas with lower winter productivity (lower minimum annual NDVI) had fewer residents. The effect of winter harshness on non-breeding migrants is expected to be the opposite, with regions with milder winters receiving more species during the non-breeding season. That was indeed what was observed for birds in Europe (Newton & Dale, 1996a), North America (Newton & Dale, 1996b), sub-Saharan Africa (Wisz et al., 2007) and for waterfowl across the world (Dalby et al., 2014).

The third mechanism proposed in the literature is that birds avoid migrating too far because migration is costly, given the energetic costs of flying (Wikelski et al., 2003) and increasing mortality during displacement (Newton, 2008). In an early study comparing the number of non-breeding migrants across major tropical regions, Karr (1980) suggested that ‘survivorship of migrants may decline with length of migration’. Newton (1995) proposed that ‘species move to whatever suitable region in Africa is nearest to their breeding area’ to justify a general north-eastern gradient in the richness of non-breeding migrants in Africa. Hockey (2000) and Wisz et al. (2007) also proposed this mechanism to explain a decreasing richness in non-breeding sub-Saharan migrants with distance to the Sahara (and
therefore to Europe). Whereas the previous two mechanisms attempt to explain local diversity of migratory species using local environmental conditions, this third mechanism acknowledges the fact that, for any given species, breeding and non-breeding ranges are necessarily connected. Yet, this mechanism has received little consideration in the literature, possibly because it is less straightforward to incorporate into statistical models.

In summary, previous macroecological studies highlighted three plausible mechanisms to explain bird migration, with variable degrees of support by formal testing of predictions. Yet, no single study has attempted to integrate all three into a coherent understanding of the migration phenomenon. Studies have focused mainly on breeding migrants, with much less attention afforded to their whereabouts in the non-breeding season, and even less to how the two might be connected. All studies were done at regional scales, with the exception of that of Dalby et al. (2014), which was global but covered only 169 species of waterfowl. Fifty-five years after MacArthur’s (1959) hypothesis, and 25 years after the term macroecology was coined (Brown & Maurer, 1989), our understanding of the drivers of bird migration and its effects on the global distribution of birds across the seasons remains patchy and largely based on verbal models.

Here, as a contribution to understanding why birds migrate, we test whether the previously proposed mechanisms can explain empirical spatial patterns of migratory bird diversity at the global scale. We build statistical models that are ecologically plausible (based on meaningful variables related to the proposed mechanisms) and parsimonious (with as few assumptions as possible) to explain the spatial distribution of migrant birds, evaluating the quality of the models in terms of proportion of variance explained as well as their ability to predict the qualitative features of spatial patterns (e.g. asymmetry between hemispheres, regions of rapid transition). Using the results, we discuss the mechanisms driving bird migration.

**MATERIAL AND METHODS**

**Species distribution data**

This analysis focuses on spatial patterns of migratory species diversity, derived from a global dataset of the distribution of the world’s bird species (Birdlife International & NatureServe 2012). The data and their treatment for mapping patterns of bird diversity are described in detail in Somveille et al. (2013). Briefly, polygons representing the global distribution of 9783 non-marine bird species were obtained from BirdLife International and NatureServe (2012). For 1855 migratory species, breeding distributions (defined as polygons corresponding to the areas where they are present only during the breeding season) were analysed separately from non-breeding distributions (defined as polygons where they are present only during the non-breeding season). Spatial patterns were mapped using a hexagonal grid across the Earth’s surface (each hexagon c. 23,322 km²; Sahr et al., 2003). Hexagonal grids have equal-sized, equal-area, spatial units (therefore being more suitable for representing variation in global diversity than rectangular grids) and each cell is equidistant from all of its neighbours (therefore being more appropriate for analyses of connectivity; Birch et al., 2007). After removing hexagons that contained no land (and thus with no values for environmental variables), 7105 terrestrial hexagons remained. A species was assumed to occur in a given hexagon whenever its mapped range overlapped any part of the hexagon. Given the coarseness of the species distribution data this is not always true, but it is a good approximation of occurrence given the spatial resolution of the hexagons (Hurlbert & Jetz, 2007).

**Global patterns of migratory bird diversity**

We analysed three patterns of migratory bird diversity, quantified as follows for any given hexagon.

1. **Number of breeding migrants**: number of bird species present only in the breeding season.
2. **Number of non-breeding migrants**: number of bird species present only in the non-breeding season.
3. **Difference in seasonal diversity**: variation in bird diversity between the breeding and non-breeding seasons, calculated as the number of breeding migrants minus number of non-breeding migrants. This differs from Somveille et al. (2013), who quantified the difference between the species richness in July and in January (thus, the patterns are the same in the Northern Hemisphere but reversed below the equator compared with our earlier publication).

**Environmental predictors**

To represent the two extremes of seasonality in the year across most of the world, we concentrated on two time periods: from May to August (MJJA), and from November to February (NDJF), corresponding respectively to summer and winter in the Northern Hemisphere and to winter and summer in the Southern Hemisphere. We averaged environmental values across the four months of each of these two opposite seasons.

Based on previous studies, we predicted that migration into the breeding grounds is driven by seasonality in resources (e.g. Herrera, 1978; Newton & Dale, 1996a,b; Hurlbert & Haskell, 2003; Lemoine & Bohning-Gaese, 2003; Barcena et al., 2004; Carnicer & Díaz-Delgado, 2008; Schaefer et al., 2008). Building from the findings in Dalby et al. (2014), we focused on variables that reflect a surplus of resources available to incoming migrants, rather than measures of the absolute resource availability in the breeding season (which, being shared between resident breeding species and migrants, should be better predictors of overall diversity in the breeding season, as found by Hurlbert & Haskell, 2003). We considered two variables as indicators of this surplus:

- **ndviSeas**, NDVI seasonality (measured as the absolute difference between mean NDVI in NDJF and mean NDVI in MJJA), capturing the surplus in primary productivity during the most productive (i.e. the breeding) season.
- **tempSeas**, temperature seasonality (absolute difference between mean temperature in NDJF and mean temperature in
MJJA), capturing the surplus in environmental energy during the warmest (i.e. the breeding) season.

We also predicted that, as suggested by previous studies (Herrera, 1978; Newton & Dale, 1996a;b; Hurlbert & Haskell, 2003), winter harshness is likely to benefit breeding migrants by reducing competition with resident species. In contrast, areas with mild winters are expected to be preferred by non-breeding migrants because they will have conditions more favourable to the persistence of overwintering species (e.g. Newton & Dale, 1996a;b; Dalby et al., 2014). We considered two variables to reflect this:

• \( \text{minTemp} \), minimum temperature (mean temperature of the coldest season, i.e. NDJF in the Northern Hemisphere and MJJA in the Southern Hemisphere).

• \( \text{minNDVI} \), minimum NDVI (mean NDVI of the least productive season, i.e. NDJF in the Northern Hemisphere and MJJA in the Southern Hemisphere), capturing the amount of resources available during the non-breeding season.

Monthly climate data were obtained from WorldClim (resolution 5°; Hijmans et al., 2005) and monthly estimates of NDVI from NASA’s Earth Observatory (resolution 0.1°; NASA’s Earth Observatory, 2014). Environmental values for each month were obtained by averaging the values from November 2000 to August 2010 (May 2003 was not included due to missing data for North America). Environmental values for each hexagon were obtained by averaging the values across the pixels within each hexagon. For NDVI data, values ranged between \(-0.1\) and \(0.9\) (the higher the value, the greener the land). Barren areas of rock, sand or snow (NDVI < 0), and areas above the Arctic Circle during the northern winter (No Data) were coded as 0 for analytical purposes (as in Hurlbert & Haskell, 2003).

Finally, we predicted that, given the costs of migration, the number of non-breeding migratory species would be affected by the proximity to the breeding grounds (as suggested by Newton, 1995; Hockey, 2000; Wisz et al., 2007), as well as by the size of the incoming migrants’ pool. To reflect this, we created a new variable:

• \( BG\text{connectivity} \), connectivity to the breeding grounds, with larger values for hexagons closer to large regions that are predicted to be rich in breeding migrants (see Appendix S1 in Supporting Information for the computation method).

Statistical models
We started by modelling relationships between the relevant environmental predictors and each of the elementary patterns of migratory species diversity, using ordinary least squares models (OLSs), to test whether empirical data support the hypothesis that each of the mechanisms investigated drives bird migration.

We first explored univariate models (Fig. 1, Table 1) and then computed multivariate models (see Appendix S2), allowing for quadratic terms when the relationships seemed nonlinear. For breeding migrants, we computed multivariate models with seasonality variables, winter harshness variables, and seasonality and winter harshness combined (Fig. S3 in Appendix S2). Predictors of seasonality as well as response variables were normal-
Global patterns of breeding migrants

The number of breeding migrants was strongly and positively associated with seasonality in temperature (tempSeas, $R^2 = 0.60$) and in NDVI (ndviSeas, $R^2 = 0.57$; Fig. 1, Table 1). Together, they explained 76% of the observed pattern (Fig. S3, Table S1 in Appendix S2), both being retained in the most informative full model (Table 1). Larger numbers of breeding migrants were associated with lower minimum annual temperature (minTemp, $R^2 = 0.67$; Fig. 1, Table 1). There was also a negative, but weaker, association with minimum annual NDVI (minNdvi, $R^2 = 0.24$; not significant in SAR model; Fig. 1, Table 1). minNdvi had a limited impact on the explanatory power of minTemp ($R^2 = 0.72$ instead of 0.67; Fig. S3, Table S1 in Appendix S2). Although both variables were retained in the most informative OLS and SAR models (Table 1), the direction of the relationship with minNdvi was not stable, possibly because minTemp and minNdvi are highly correlated ($r = 0.69, P < 0.001$).

A full model combining both seasonality and winter harshness had substantially higher explanatory power ($R^2 = 84\%$) than separate models. All four variables were retained in the most informative OLS and SAR models, with the directions of the effects the same as in the two intermediate multivariate models. The full model had small residuals in relation to the variability observed in the data (Fig. S3i in Appendix S2) and accurately predicted that breeding migrants occupy mainly a wide band across the Northern Hemisphere around latitude 50° N (Fig. 2a,b), being much rarer elsewhere including all over the Southern Hemisphere (Fig. 3a).

Global patterns of non-breeding migrants

The diversity of non-breeding migrants was positively related to minTemp ($R^2 = 0.52$) and to minNdvi ($R^2 = 0.49$; Fig. 1, Table 1).
Model (two columns to the right), we present the model, whichever gave a better fit based on the Akaike information criterion). For each multivariate variable, we only present information for either the linear or quadratic (including the linear term). Breeding migratory species $R^2 = 0.84$

Non-breeding migratory species

<table>
<thead>
<tr>
<th>Variables</th>
<th>Univariate models</th>
<th>Multivariate models</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OLS</td>
<td>SAR</td>
</tr>
<tr>
<td>tempSeas</td>
<td>254.0</td>
<td>102.6***</td>
</tr>
<tr>
<td>tempSeas$^2$</td>
<td>22.9</td>
<td>9.3***</td>
</tr>
<tr>
<td>ndviSeas</td>
<td>243.1</td>
<td>94.6***</td>
</tr>
<tr>
<td>ndviSeas$^2$</td>
<td>50.1</td>
<td>19.5***</td>
</tr>
<tr>
<td>minTemp</td>
<td>–240.6</td>
<td>–107.0***</td>
</tr>
<tr>
<td>minTemp$^2$</td>
<td>–121.6</td>
<td>–54.1***</td>
</tr>
<tr>
<td>minNdvi</td>
<td>–156.6</td>
<td>–45.9***</td>
</tr>
<tr>
<td>minNdvi$^2$</td>
<td>–38.4</td>
<td>–11.2***</td>
</tr>
</tbody>
</table>

Combining both winter harshness variables explained 59% of the variation in observed values (Fig. S4, Table S1 in Appendix S2). However, this model strongly underestimated diversity in the southern part of the Northern Hemisphere (particularly in Central America and Southeast Asia) while overestimating values in regions in the Southern Hemisphere (South America, Madagascar, Australia; Fig. S4c in Appendix S2).

On its own, the measure of proximity to breeding grounds, $BGconnectivity$, had moderate explanatory power ($R^2 = 0.32$; Table 1), but it substantially improved the explanatory power of the model with winter harshness variables only (full model: $R^2 = 0.72$; Table 1). Furthermore, adding $BGconnectivity$ markedly improved the match to the observed spatial pattern (Fig. 2e–f), generally reducing the residuals between predicted and observed values (Fig. S4i in Appendix S2). The most informative full model captured well the peak of diversity in non-breeding migrants around latitudes 35°N (Fig. 3b), particularly in Central America and southern Asia (Fig. 2e–f). However, it continued to underestimate diversity in these regions, particularly in coastal areas.

Global variation in the seasonal difference in bird diversity

The composite model of difference in seasonal diversity explained 87% of the observed variation (Table 1). Furthermore, it captured very well the transition zone in the observed pattern of null or low difference, at about 30–40° N, separating northern areas where diversity is higher in the breeding season from southern areas where diversity is higher in the non-breeding season (Figs 2i–j & 3c, Fig. S5 in Appendix S2).

Cross-hemisphere predictions

Models trained on Eastern Hemisphere data predicted 83% of the diversity in breeding migrants, 59% of the diversity in the non-breeding migrants and 84% of the difference in seasonal diversity observed in the Western Hemisphere. Conversely, data from the Western Hemisphere predicted 80, 42 and 80% of the diversity in breeding migrants and 84% of the difference in seasonal diversity observed in the Western Hemisphere.

Table 1 Statistical tests of the effect of environmental predictors.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Slope</th>
<th>$t$-value</th>
<th>$R^2$</th>
<th>Slope</th>
<th>$z$-value</th>
<th>$t$-value</th>
<th>$z$-value</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding species</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>tempSeas</td>
<td>254.0</td>
<td>102.6***</td>
<td>–</td>
<td>117.1</td>
<td>20.3***</td>
<td>43***</td>
<td>16***</td>
<td>0.84</td>
</tr>
<tr>
<td>tempSeas$^2$</td>
<td>22.9</td>
<td>9.3***</td>
<td>0.60</td>
<td>19.0</td>
<td>6.4***</td>
<td>–</td>
<td>24***</td>
<td>8***</td>
</tr>
<tr>
<td>ndviSeas</td>
<td>243.1</td>
<td>94.6***</td>
<td>–</td>
<td>13.9</td>
<td>6.6***</td>
<td>–</td>
<td>45***</td>
<td>6***</td>
</tr>
<tr>
<td>ndviSeas$^2$</td>
<td>50.1</td>
<td>19.5***</td>
<td>0.57</td>
<td>3.9</td>
<td>3.4***</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>minTemp</td>
<td>–240.6</td>
<td>–107.0***</td>
<td>–</td>
<td>–71.5</td>
<td>–140.0***</td>
<td>–5***</td>
<td>–7***</td>
<td>0.72</td>
</tr>
<tr>
<td>minTemp$^2$</td>
<td>–121.6</td>
<td>–54.1***</td>
<td>0.67</td>
<td>–16.5</td>
<td>–5.6***</td>
<td>–49***</td>
<td>–7***</td>
<td></td>
</tr>
<tr>
<td>minNdvi</td>
<td>–156.6</td>
<td>–45.9***</td>
<td>–</td>
<td>–0.07</td>
<td>–0.8</td>
<td>17***</td>
<td>6***</td>
<td></td>
</tr>
<tr>
<td>minNdvi$^2$</td>
<td>–38.4</td>
<td>–11.2***</td>
<td>0.24</td>
<td>–</td>
<td>–</td>
<td>–16***</td>
<td>–4***</td>
<td></td>
</tr>
<tr>
<td>BGconnectivity</td>
<td>$2.0 \times 10^{-4}$</td>
<td>57.2***</td>
<td>0.32</td>
<td>$1.6 \times 10^{-4}$</td>
<td>16.6***</td>
<td>56***</td>
<td>14***</td>
<td></td>
</tr>
</tbody>
</table>
As with the global models, the hemisphere models performed less well at predicting the diversity of non-breeding migrants, with particularly poor predictive power for the desert regions of the Sahara and the Middle East. To investigate this further, we also tested the performance of models separating the Eastern Hemisphere into two flyways (large regions including the breeding, non-breeding and migratory grounds for a group of species): the African–Eurasian flyway in the west and the Asian–Australasian flyway in the east (see Appendix S3 for more details). We found excellent cross-flyway predictive power for the number of breeding migrants ($R^2 = 73$–$85\%$; Table S5 in Appendix S3). For the number of non-breeding migrants, the Western Hemisphere (i.e. the Americas flyway) and the Asian–Australasian flyway predicted each other quite well ($R^2 = 67$ and 64$\%$), but models trained on either of these regions had poor predictive ability for the African–Eurasian flyway ($R^2 = 0.09$ and 0.31; Table S5 in Appendix S3), strongly overpredicting the desert regions (Figs S7 & S8 in Appendix S3).
Migrants are found in the southern latitudes of the Northern Hemisphere, rather than being distributed across other areas of mild climate across the tropics and in the Southern Hemisphere (Fig. 2e). Our analyses therefore support the hypothesis that the cost of migration affects the distance birds are willing to travel between their breeding and non-breeding grounds (Wikelski et al., 2003; Newton, 2008).

These results suggest that birds are particularly demanding about local resource availability during the breeding season (perhaps as a result of higher energetic requirements associated with reproduction; Moreau, 1972, p. 258), subsequently selecting their non-breeding grounds as a compromise solution between local suitability and accessibility to the breeding grounds. There is, however, a conceptually different (but not mutually exclusive) explanation for the same results: rather than convenient destinations for birds leaving their breeding areas, non-breeding grounds can be seen as strategically placed sources of breeding migrants. In other words, the regions at lower latitudes in the Northern Hemisphere where non-breeding migrants concentrate might correspond less to refuges for birds moving southwards to escape the harsh winters, and more to well-placed areas from where birds can easily access the surplus of resources seasonally available further north. Accordingly, we found that the observed latitudinal peak in the richness of breeding migrants is located further south (c. 50° N) than the peak predicted from seasonality and winter harshness (c. 55° N; Figs 2 & 3), consistent with the hypothesis that breeding grounds are not only influenced by local conditions but also by the proximity to non-breeding source areas.

However, the patterns of residuals in the models for non-breeding migrants (Figs S4 in Appendix S2 & S6 in Appendix S3) suggest some possible limitations of our analysis. First, the models correctly predict concentrations of non-breeding migrants in Central America and southern Asia but underestimate diversity. This might be because the models do not take into account the shape of the continents: these are both narrow regions south of wide breeding grounds which might create a ‘funnel’ effect concentrating migratory species in higher densities than expected (Terborgh, 1980). Secondly, the tendency of the model to underestimate coastal regions in particular might reflect a limitation in our measure of connectivity to the breeding grounds. Indeed, we measured the shortest arc distance, but migratory birds sometimes follow less direct routes, including along coastlines (e.g. because of favourable atmospheric conditions, to facilitate orientation, or to benefit from refuelling habitats such as wetlands; Newton, 2008). Some coastal areas might therefore be better connected to breeding grounds than expected from simple distance. In contrast, the models overestimate numbers of non-breeding migrants in desert regions such as the Sahara, the Arabian Peninsula and the Tibetan Plateau, all of which have low observed numbers of migrants, despite being well connected to breeding grounds and having favourable temperatures (Figs S4 in Appendix S2 & S6d in Appendix S3). This suggests that a region’s overall productivity (and not just in the non-breeding season) affects its suitability as a destination for non-breeding migrants. Overall, the patterns of residuals in our models indicate that other geographic factors...
Besides those captured in our models influence the distribution of migratory birds, particularly in their non-breeding ranges. Other ecological processes not included in our analysis and that may influence bird migration (and hence contribute to the unexplained variance in our models) include nest predation (e.g. selection of nesting regions with lower predation risk; Fretwell, 1980; McKinnon et al., 2010) and site dominance (e.g. if residents have an advantage over migrants, impacting the number and proportion of migrants in a community; Fretwell, 1980).

Despite these limitations, our approach correctly predicts the main features of the global patterns of migratory bird diversity, and furthermore offers plausible ecological explanations for them. We were able to replicate very well the asymmetries between the Northern and Southern Hemispheres observed for all patterns (Figs 2 & 3). Our results suggest that they are caused by the unequal distribution of landmasses across hemispheres, through two interlinked mechanisms. First, the large continental areas across Eurasia and North America have very high seasonality and harsh winters, and hence a high diversity of breeding migrants, whereas for equivalent latitudes southern South America, southern Africa and Australia have milder climates thanks to the buffering effect of the oceans, and consequently few breeding migrants. Secondly, non-breeding migrants tend to concentrate in suitable areas closer to the breeding grounds. Hence, both breeding and non-breeding migrants are mainly found in the Northern Hemisphere (Fig. 2a,e), and migration is mainly a northern phenomenon.

Our model also correctly predicts the location of a transition area at about 30–40° N, separating areas of high seasonality and harsh winters to the north, where bird diversity is higher during the breeding season, from areas of mild winters to the south, with more species during the non-breeding season (Fig. 2i–l). This seems to be somewhat related to the position of the 0 °C isocline in the northern winter, north of which the ground and water remain frozen during the winter. If so, this might correspond to an ecological threshold for many species in terms of their ability to persist in an area during winter, and a major determinant of spatial patterns of bird migration. We predict that as global climate change affects the location of this isocline (IPCC, 2013), global patterns in migratory bird diversity will respond accordingly.

In conclusion, we have demonstrated that globally consistent models based on just a few, but ecologically plausible, environmental variables can successfully explain macroecological patterns of bird migration. The good predictive power of these models strongly supports the underlying hypotheses upon which they have been built: that migration is driven by seasonality and by winter harshness, and that its costs increase with distance. The fact that the models perform well despite being applied to very different parts of the world and to species with very different ecologies (from small insectivore warblers, to medium-sized aquatic waders, to large carnivorous raptors) suggests general mechanisms driving migration across regions and across taxa. This assertion is further supported by the good predictive power across hemispheres, which shows that the effectiveness of the models is not simply due to over-fitting the data.

Our analysis provides a first attempt to analyse migration as a dynamic phenomenon at the global scale, by relating breeding and non-breeding grounds temporally and spatially. But we also demonstrate the limits of doing so through a correlational approach, highlighting the need for mechanistic models. The study of bird migration therefore provides both a challenge and an opportunity for macroecology as the field is steering towards a more mechanistically explicit understanding of large-scale patterns.

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**REFERENCES**


**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

**Appendix S1** Supporting methods: calculating the connectivity to the breeding grounds (Figs S1 & S2).

**Appendix S2** Supporting results: global models (Tables S1, S2, S3; Figs S3, S4, S5).

**Appendix S3** Supporting results: cross-hemisphere and cross-flyway models (Tables S4, S5; Figs S6, S7, S8).

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