LETTER

A general theory of avian migratory connectivity

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Abstract

Birds exhibit a remarkable array of seasonal migrations. Despite much research describing migratory behaviour, the underlying forces driving how a species' breeding and wintering populations redistribute each year, that is, migratory connectivity, remain largely unknown. Here, we test the hypothesis that birds migrate in a way that minimises energy expenditure while considering intraspecific competition for energy acquisition, by developing a modelling framework that simulates an optimal redistribution of individuals between breeding and wintering areas. Using 25 species across the Americas, we find that the model accurately predicts empirical migration patterns, and thus offers a general explanation for migratory connectivity based on first ecological and energetic principles. Our model provides a strong basis for exploring additional processes underlying the ecology and evolution of migration, but also a framework for predicting how migration impacts local adaptation across seasons and how environmental change may affect population dynamics in migratory species.

KEYWORDS

cost of migration, eBird, genoscape, ideal free distribution, Migratory connectivity, optimal migration

INTRODUCTION

Birds exhibit a wide diversity of seasonal migration patterns (Newton, 2008). Some birds undertake extraordinary journeys across continents while others only migrate short distances and many others do not migrate at all (Newton, 2008). Using novel technologies, substantial research has been conducted to document differences in migratory behaviour and map geographic patterns of how individuals redistribute between the seasonal grounds of migratory species (Faaborg et al., 2010; Finch et al., 2017; Ruegg et al., 2014; Ruegg & Smith, 2002; Webster et al., 2002). Migratory connectivity, the

spatiotemporal linkages of individuals and populations between seasons stemming from migratory movements (Webster et al., 2002), has important consequences for the biology of migratory animals, as it can affect short-term population dynamics and long-term evolutionary responses (Taylor & Norris, 2010; Webster & Marra, 2005). It is also a critical aspect to consider for developing sound conservation strategies to stem the rapid decline of the migratory avifauna (Rosenberg et al., 2019; Webster & Marra, 2005).

Previous research on avian migratory connectivity has almost exclusively focused on describing the geographic patterns of connections between breeding and wintering

populations (e.g. Knight et al., 2018; Kramer et al., 2018; Ruegg et al., 2014; Trierweiler et al., 2014) and/or exploring the consequences of migratory connectivity, particularly for population dynamics (Dolman & Sutherland, 1994; Taylor & Norris, 2010; Taylor & Stutchbury, 2016). The few studies that investigated the causes of migratory connectivity found that drivers include minimising energetic costs of migration given environmental conditions en route (Norevik et al., 2020), cultural transmission of migratory behaviour (Harrison et al., 2010), land availability (Finch et al., 2017) and natal dispersal and density-dependent population regulations (Taylor, 2019). However, these studies were largely species specific or only used theoretical simulations. Therefore, despite the increasingly large amount of migration data available and the ecological significance of seasonal migration, we still lack a general, unified understanding of the ecological and evolutionary processes underlying avian migratory connectivity. With population declines expected to accelerate under global change (Zurell et al., 2018), there is an urgent need to develop a framework to understand not just where birds migrate but also the fundamental forces driving these patterns.

Density dependence, particularly related to intraspecific competition for resource consumption, has been shown to shape connectivity patterns in simulated migration networks (Taylor, 2019). In particular, costs associated with mutual interference (Goss-Custard, 1980; Somveille et al., 2018), increasing search time (Pawar et al., 2012) and territorial defence (Greenberg et al., 2010), are likely to negatively affect the density dependence of energy intake in migratory birds. The ideal free distribution (IFD) is a standard ecological model of competitive equilibrium, which predicts the density-dependent distribution of individuals within a species that maximises energy intake given the spatial distribution of resources (Fretwell & Lucas, 1970). Therefore, the IFD can in principle be used to better understand how migratory species distribute in seasonal environments and explain migratory connectivity. However, for migratory species, in addition to the process of competitive interactions for maximising energy intake, the cost of relocating between seasonal grounds must be taken into account as it has been shown to have a strong influence on migratory behaviour (Alerstam, 2011; Amélineau et al., 2018; Flack et al., 2016; Norevik et al., 2020). We call *energy efficiency* the mechanism of optimising both energy expenditure and energy acquisition from the environment together. We propose that individuals within migratory species migrate in the most energy efficient way and follow an *ideal optimal redistribution*, which shapes patterns of species-level migratory connectivity. Similar to the IFD, this proposed hypothesis assumes that individuals have complete knowledge of resource quality in the environment (i.e. they are *ideal*) and compete for access to energy supply, but also that, in addition to intraspecific competition, energetic costs are minimised when individuals relocate between breeding and wintering grounds.
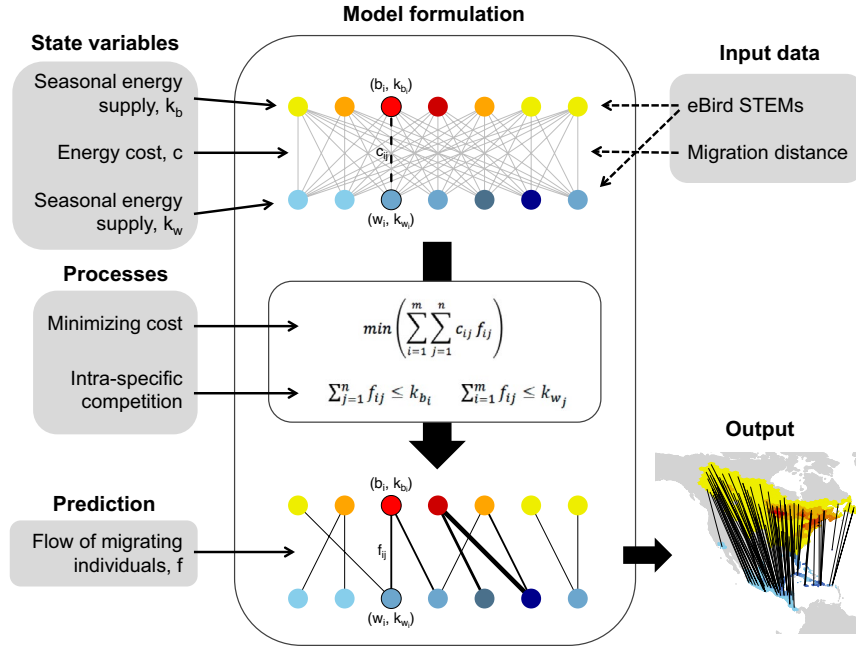
The aim of this study is to investigate whether patterns of seasonal redistribution of individuals within migratory species are driven by energy efficiency. To do so, we developed a modelling framework that simulates the optimal redistribution of ideal individuals within a migratory species. For each species investigated, the model uses linear optimisation to simulate optimal migratory connectivity between the species' seasonal distributions (see Material and Methods; Figure 1). We used spatio-temporal exploratory models based on observation data from the eBird citizen-science program (Fink et al., 2020b) to calibrate the distribution of energy supply across species' seasonal ranges, and model predictions were validated using migratory movement data for 7145 individuals belonging to 25 species of North American migratory birds, pooling together data from electronic tracking devices, banding recoveries and high-resolution genetic markers to map migratory connectivity.

MATERIAL AND METHODS

Model description

We developed a modelling framework to simulate species' migratory connectivity that follows an ideal optimal redistribution of individuals between the breeding and wintering grounds. This model – called the Optimal Redistribution Simulator (ORSIM) – is based on energy optimisation. It is structured as a bipartite network with nodes representing seasonally occupied sites of two types: departing sites, from which individuals start their migration, and destination sites, where individuals end their migration. Each node, of either type, has a seasonal energy supply, and each pair of departing–destination nodes is connected by an edge representing the energetic cost of relocating between them (Figure 1). In addition to available energy supply at seasonal sites and energetic cost of seasonal relocation, individuals have a seasonal energy demand that corresponds to the energy that they need to survive the season spent at the destination sites. The model uses optimal transport theory to predict the flow of migrating individuals between sites seasonally occupied by a species, capturing two processes: minimising energetic costs associated with relocating between seasonal grounds, and intraspecific competition for access to energy supply (Figure 1). In particular, we used a solution to the Monge–Kantorovich transportation problem (Hitchcock, 1941; Rachev, 1984), which, applied to a migratory species, can be formalised with linear programming as follows:

Let $B = \left\{ \left(b_1, k_{b_1} \right), \cdots, \left(b_m, k_{b_m} \right) \right\}$ be the distribution of energy supply during the breeding season, with m breeding sites, where b_i is breeding site i and k_{b_i} is the weight of this site, which corresponds to the energy available

Model formulation

State variables

Seasonal energy supply, k_b

Energy cost, c

Seasonal energy supply, k_w

(b_i, k_{b_i})

c_{ij}

(w_i, k_{w_i})

Input data

eBird STEMs

Migration distance

Processes

Minimizing cost

Intra-specific competition

$$min\left(\sum_{i=1}^{m}\sum_{j=1}^{n}c_{ij}f_{ij}\right)$$

$$\sum_{j=1}^{n}f_{ij}\leq k_{b_i} \qquad \sum_{i=1}^{m}f_{ij}\leq k_{w_j}$$

Prediction

Flow of migrating individuals, f

(b_i, k_{b_i})

f_{ij}

(w_i, k_{w_i})

Output

FIGURE 1 The Optimal Redistribution Simulator, ORSIM. The model is structured as a bipartite graph between seasonal grounds. Nodes and edges on the graph represent different state variables. Each breeding site b_i is characterised by an energy supply k_{b_i} that limits the number of migratory individuals departing; each wintering site w_j is characterised by an energy supply k_{w_j} that limits the number of migratory individuals it can accommodate; and each edge between a pair of breeding–wintering sites is characterised by the energy cost of relocating between these two sites c_{ij}. On this graph, ORSIM simulates the processes of minimising energetic costs while considering intraspecific competition. It uses a solution to the transportation problem from linear optimisation (see Methods for details) to find the flows f_{ij} of migrating individuals between each departing site, here b_i, and each destination site, here w_j. Input data for model calibration include spatiotemporal exploratory models (STEMs), which estimate relative abundance using citizen-science data from eBird (Fink et al., 2020b) and were converted into values onto a grid of hexagons covering the Americas (see Material and Methods), to calibrate the seasonal distribution of energy supply. The energetic costs associated with relocating between seasonal grounds were calibrated using the cost of migratory movement based on the distance separating the breeding and wintering sites. The output of the calibrated model is the simulated migratory connectivity that follows an ideal optimal redistribution of the species

at this site; and $W=\left\{\left(w_1, k_{w_1}\right), \cdots, \left(w_n, k_{w_n}\right)\right\}$ be the distribution of energy supply during the wintering season, with n wintering sites, where w_j is wintering site j and k_{w_j} is the weight of this site, which corresponds to the energy available at this site (Figure 1). We want to find a global flow of migrating individuals $F=\left[f_{ij}\right]$, with f_{ij} representing the flow of individuals between departing site b_i and destination site w_j, that minimises the overall cost:

$$C(B, W, F)=\sum_{i=1}^{m}\sum_{j=1}^{n}c_{ij}f_{ij}$$

where c_{ij} is the energetic cost associated with individuals relocating between sites b_i and w_j. This function is subject to the following constraints:

$$f_{ij}\geq 0 \qquad 1\leq i\leq m, \qquad 1\leq j\leq n \qquad (1)$$

$$\sum_{j=1}^{n}f_{ij}\leq k_{b_i} \quad 1\leq i\leq m \qquad (2)$$

$$\sum_{i=1}^{m}f_{ij}\leq k_{w_j} \quad 1\leq j\leq n \qquad (3)$$

$$\sum_{i=1}^{m}\sum_{j=1}^{n}f_{ij}=\min\left(\sum_{i=1}^{m}k_{b_i}, \sum_{j=1}^{n}k_{w_j}\right) \qquad (4)$$

Constraint (1) allows individuals to move from B to W and not vice versa (but the model would generate the same results if it was set up so that individuals would move from W to B). Constraint (2) limits the number of individuals departing the breeding sites in B so that the population-level energy demand (i.e. the sum of energy demand across all individuals in a population) at a breeding site before migration is not higher than the seasonal energy supply at that breeding site. Constraint (3) limits the wintering sites in W to receive no more individuals than can be accommodated given the energy supply in these sites. Finally, constraint (4) specifies that the combined energy demand of all the individuals in the system must be equal to either the total energy supply of breeding sites or the total energy supply of wintering sites, whichever one is the smallest, thus forcing to move the maximum number of individuals possible.

This modelling approach assumes that individuals are energetically equivalent, that is, they all have the same energy demand and cost function, and the same

competitive ability. Population-level energy demand is, therefore, proportional to the number of individuals in the population. These individuals are also ideal, that is, with perfect knowledge of how energy supply is distributed in the environment. This assumption of omniscience about the environment has been used often in ecology (e.g. the ideal free distribution is a classic model; Fretwell & Lucas, 1970) and in migration modelling (Bauer & Klaassen, 2013; Revell & Somveille, 2017). In our model, since energy supply is entirely used by the individuals exploiting it (see constraints in the model formulation) and all individuals are identical and gain identical shares of the energy supply, then, similarly to the Ideal Free Distribution (Fretwell & Lucas, 1970), the predicted distribution of individuals at each season is proportional to the amount of energy available. Thus, the constraints in the model implicitly consider the competitive equilibrium expected under the IFD when minimising energy cost associated with seasonal relocation. Migratory connectivity is then predicted by the model as the pattern of inter-seasonal flow of migrating individuals (Figure 1).

A solution to the transportation problem from linear optimisation is implemented in the Earth Mover's Distance (EMD) algorithm (Rubner et al., 2000), which uses the transportation-simplex method (Hillier & Lieberman, 1990). To simulate migratory connectivity, we used the FastEMD algorithm (Pele & Werman, 2008, 2009), which is implemented in the Python wrapper PyEMD. No distance threshold was used when running FastEMD.

Model calibration

To calibrate the seasonal distribution of energy supply when applying ORSIM to avian species, we used predictions from spatiotemporal exploratory models (STEMs) that estimate species distribution and abundance across continental extents and throughout the full annual cycle (Fink et al., 2020b). We assume that the distribution of relative abundance predicted by STEMs, which correlates bird observation data and information on habitat quality, reflects the distribution of energy available to the species across their seasonal ranges (Figure 1). STEMs are based on observation data from eBird citizen-science program (Sullivan et al., 2014), which has a particularly good survey completeness in North and Central America (La Sorte & Somveille, 2020) where most of the species analysed here are located (Figure S1). STEMs use land cover descriptors from remote-sensing data to capture associations of birds with a variety of habitat and topography across continents, and it accounts for biases (1) due to heterogeneous and imperfect observation processes and (2) in the spatiotemporal distribution of survey effort (Fink et al., 2020b). Estimates of relative abundance for the breeding and wintering seasons were

obtained from eBird Status and Trends products (Fink et al., 2020a), and were downloaded through the R package *ebirdst*.

We aggregated relative abundance estimates within equal-area hexagons (ISEA3H resolution 7; hexagons centres separated by ~165 km) of a hexagon grid covering the Americas (Sahr et al., 2003). For each hexagon, we obtained an estimate of relative abundance by averaging the relative abundance values (i.e. pixels in the raster) contained in that hexagon. For each season, we then standardised the relative abundance distribution across the entire hexagon grid so that its total sum is equal to 1. Thereafter, we consider the breeding sites of a given species to be the hexagons in the grid for which relative abundance of that species during the breeding season is greater than 0, and wintering sites to be the hexagons for which relative abundance of that species during the wintering season is greater than 0. Note that a hexagon can be both a breeding and a wintering site for a given species.

To calibrate the energetic cost associated with relocating between breeding and wintering grounds, we used migration distance, as the cost of migratory movement has been shown to be a key factor influencing migratory behaviour (Alerstam, 2011; Amélineau et al., 2018; Flack et al., 2016; Norevik et al., 2020). We assume that individuals migrate along the shortest path between breeding and wintering sites. This assumption has been used in previous studies investigating the factors explaining migratory destinations at species level (Somveille et al., 2018, 2019). In addition, we assume that the cost of migration is a linear function of the length of the migratory path, which is supported by empirical results obtained by Wikelski et al., (2003), showing a linear relationship between flight duration and energy expenditure, under the assumption that birds fly at a relatively constant cruise speed.

Model validation

To validate predictions from ORSIM, we assessed the extent to which the predicted migratory connectivity captures empirical patterns. We mapped empirical migratory connectivity for 25 species of North American migratory birds (i.e. species for which the breeding distribution is mostly in North America and the wintering distribution can be located anywhere across the Americas; Table 1, Figure S1), belonging to 13 different avian families. These species have a wide range of migration patterns (Figure S1), including short-distance migrants (e.g. Brown Thrasher), long-distance migrants (e.g. Swainson's Thrush) and partial migrants (e.g. Red-winged Blackbird), as well as a wide distribution of range size, including restricted range species (e.g. Blue-winged Warbler) and widespread species (e.g. American Kestrel). These species were selected because estimates of relative abundance from eBird data were available for model calibration and sufficient individual-level

migration data were available (i.e. 10 or more individuals; Table 1) from multiple sites across the species' distribution. For these species, we obtained data on migratory movement for a total of 7145 individuals from three sources: (a) banding recoveries, (b) tracking data and (c) genetic data. These different data types were pooled together to map empirical migratory connectivity. Details regarding how we obtained and processed the validation data sets are available in the *model validation* section in Supplementary Material. Information regarding data types and number of individuals available for each species is shown in Table 1.

To quantify the extent to which ORSIM captures empirical migratory connectivity, we computed the Mantel correlation coefficient (r_M; Mantel, 1967) between the matrix of empirical distances between migration start and end points and the matrix of equivalent distances simulated by ORSIM. This validation metric (r_M) varies between −1 and 1, with 1 being a perfect positive correlation between the empirical and simulated geographical distributions of migration destinations (Fig. S3), and 0 corresponding to no association. This measure is sensitive to both the distance and direction of simulated migrations (Fig. S4). A full description of the validation procedure is available in the *model validation* section in Supplementary Material.

We also estimated the strength of migratory connectivity (MC) by computing the Mantel correlation coefficient between the matrices of breeding distances (i.e. pairwise distances between the sets of breeding grounds) and wintering distances (i.e. pairwise distances between the sets of wintering grounds) for both the empirical data set and the ORSIM simulations (see Supplementary Material for details). MC varies between −1 and 1, with 1 being a perfect positive correlation between the distributions of breeding and wintering sites, thus indicating the strongest migratory connectivity possible.

Null models

To investigate the contribution of the two key processes, that is, minimising the energetic cost of seasonal

TABLE 1 Empirical data on individual-level migratory movements

Species	Banding data (# individuals)	Tracking data (# individuals)	Genetic data (# individuals)	Total # individuals
Wood Thrush	7	102	–	102
Swainson's Thrush	3	35	–	22
Hermit Thrush	7	5	–	10
American Robin	928	–	–	872
Red-winged Blackbird	528	–	–	482
Yellow Warbler	–	–	186	178
Common Yellowthroat	–	–	96	91
Wilson's Warbler	–	–	241	232
Blue-winged Warbler	–	25	–	17
Ovenbird	5	52	–	53
Willow Flycatcher	–	–	334	261
Grasshopper Sparrow	–	33	–	15
White-throated Sparrow	24	–	–	19
American Goldfinch	238	–	–	211
Purple Finch	404	–	–	358
Common Loon	149	–	–	82
Brown Thrasher	106	–	–	94
Gray Catbird	42	6	–	29
Brown-headed Cowbird	595	–	–	530
Common Grackle	2843	–	–	2737
Tree Swallow	25	–	–	19
Barn Swallow	3	25	–	26
American Kestrel	317	–	–	278
Burrowing Owl	32	–	–	14
Osprey	698	71	–	413

For each species included in the analysis, this table shows the number of individuals for which data were obtained from the different sources as well as the total number of individuals used in the analysis after removing data falling outside the relative abundance distribution of species.

relocation and intraspecific competition, in ORSIM's performance, we assessed whether the model performed better than three different null models at capturing the empirical migratory connectivity.

Null model 1: The null expectation for migratory connectivity is obtained by randomising migratory destinations, that is, randomly pairing breeding and wintering sites across the seasonal distributions of species. This model nullifies both key processes in ORSIM, that is, competition for energy acquisition and minimising the energetic cost of seasonal relocation. It thus corresponds to individuals migrating completely freely without any constraint other than spending the winter within the species' wintering range.

Null model 2: The null expectation for migratory connectivity is obtained by selecting migratory destinations solely based on minimising the energetic cost of seasonal relocation. For a given breeding site b, a migratory connection is obtained by sampling a wintering site w within the set of sites across the wintering distribution (W) with probability $P_w = (c_{bw})^{-1} / \sum_{i=1}^{W} (c_{bi})^{-1}$, with c the energetic cost of seasonal relocation, which is here estimated using the great circle distance separating a breeding site and wintering site. This model nullifies one of the key processes in ORSIM, that is, competition for energy acquisition, while keeping the other key process, that is, minimising the energetic cost of seasonal relocation, at play.

Null model 3: The null expectation for migratory connectivity is obtained by selecting migratory destinations solely based on the competitive equilibrium for energy acquisition. For a given breeding site b, a migratory connection is obtained by sampling a wintering site w within the set of sites across the wintering distribution (W) with probability $P_w = k_w / \sum_{i=1}^{W} k_i$, with k the energy available in a wintering site. This model nullifies one of the key processes in ORSIM, that is, minimising the energetic cost of seasonal relocation, while keeping the other key process, that is, competition for energy acquisition, at play.

We ran each null model 1000 times and each time we followed the same validation procedure described in the *model validation* section in Supplementary Material to obtain a Mantel correlation coefficient (r_M) between the matrices of empirical distances and distances simulated by the null model. To assess statistical significance, we investigated whether ORSIM is performing better than each null model by comparing r_M values and assessing whether the r_M of ORSIM is higher than 95% of the r_M of the null model. We also measured effect size as $E = r_M^{ORSIM} - mean(r_M^{NULL})$, where r_M^{ORSIM} is the validation metric (Mantel correlation) for ORSIM and r_M^{NULL} is the set of Mantel correlations for null models.
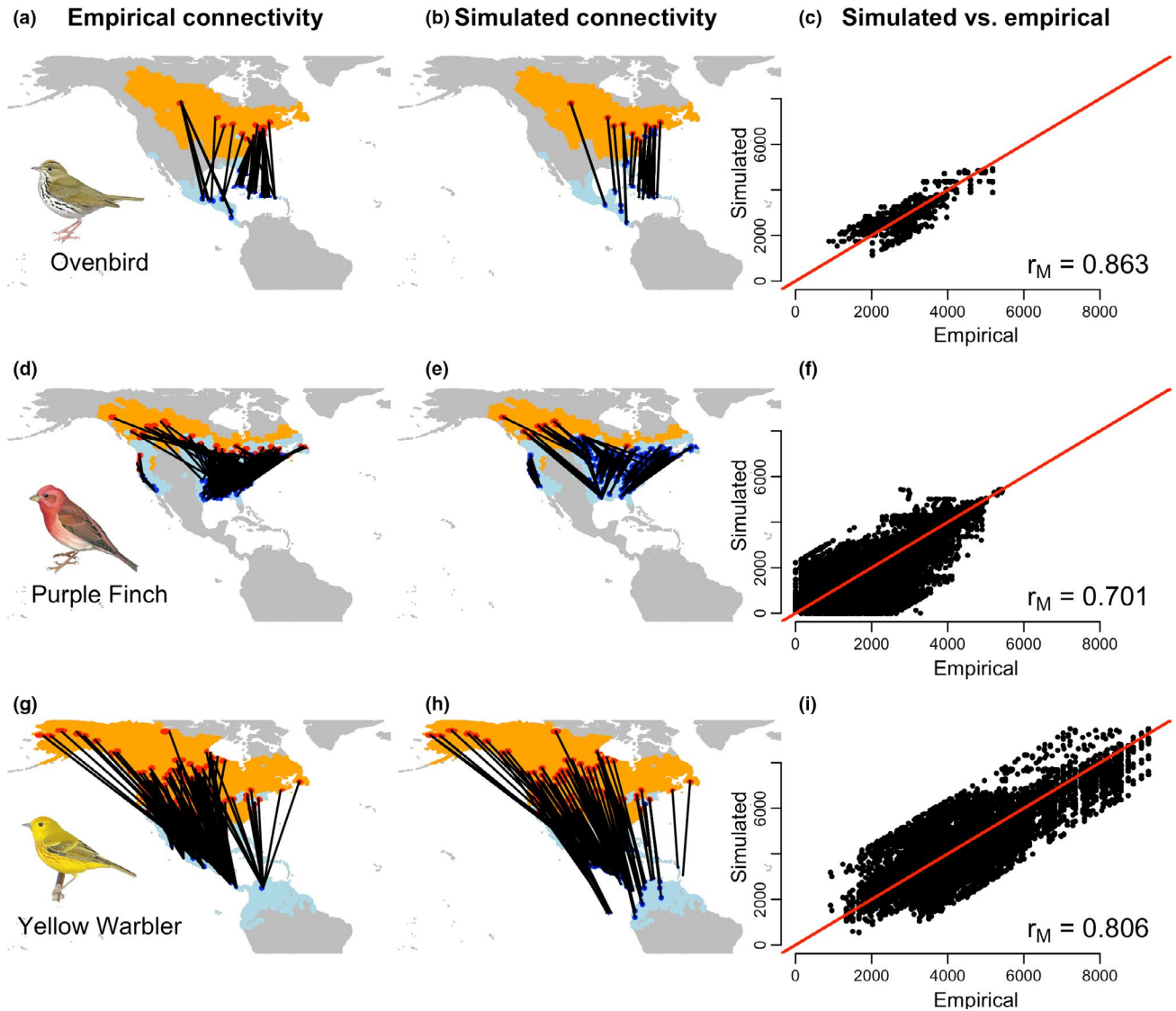
RESULTS

ORSIM, which is based on basic ecological processes – integrating the energetic cost associated with relocating

between seasonal grounds and intraspecific competition for access to energy supply – is able to capture very well empirical migratory connectivity patterns (mean Mantel correlation coefficient: $r_M = 0.721 \pm 0.156$; Table S1; Figures 2, 3a and S5–S9). These results were not affected by data type (i.e. whether empirical data are from electronic tracking, banding recoveries or high-resolution genetic markers; one-way ANOVA: $F = 0.576$, $p = 0.57$), or sample size (i.e. number of individuals included for mapping a species' migratory connectivity; Table 1; linear regression: $t = 0.157$, $p = 0.877$), or range size (breeding range: linear regression $t = -0.586$, $p = 0.564$; wintering range: $t = -0.904$, $p = 0.376$; seasonal difference in range size: $t = -0.626$, $p = 0.537$), or the degree of partial migration (i.e. seasonal range overlap; linear regression: $t = -0.215$, $p = 0.832$).

The strength of migratory connectivity in the empirical data sets varies greatly among species (Figure 3c), with some species exhibiting strong migratory connectivity, such as Red-winged Blackbird (empirical MC = 0.843; based on banding data), Barn Swallow (empirical MC =0.782; mostly based on tracking data) and Common Yellowthroat (empirical MC = 0.742; based on genetic data), while other species exhibit weak migratory connectivity, such as Blue-winged Warbler (empirical MC = −0.027; based on tracking data) and Wilson's Warbler (empirical MC = 0.159; based on genetic data). ORSIM is able to broadly capture this variation by simulating values for the strength of migratory connectivity that correlate with the empirical values ($r = 0.708$, $p < 0.001$; Figure 3c). However, ORSIM is generating strengths of migratory connectivity that are consistently higher than the empirical values (mean empirical MC = 0.555; mean simulated MC = 0.776; simulated MC is higher than empirical MC for 23 out of 25 species). In addition, we found no correlation between the strength of empirical migratory connectivity and the validation metric (r_M) assessing ORSIM's performance at capturing the empirical patterns (linear regression $t = 0.406$, $p = 0.689$), thus indicating that ORSIM's good performance is not biased towards species with strong or weak migratory connectivity.

ORSIM was able to capture migratory connectivity patterns better than null models, with effect sizes generally high (Figure 3b): null model 1 has median effect size = 0.529; null model 2 has median effect size = 0.915 and null model 3 has median effect size = 0.364. ORSIM performed significantly better than the null model randomising migratory destinations (null model 1) for 23 out of 25 species (except for Gray Catbird and Grasshopper Sparrow; Table S1), and the null model selecting migratory destinations solely based on minimising the energetic cost of seasonal relocation (null model 2) for all species (Table S1). When compared to the null model selecting migratory destinations solely based on competition for energy acquisition (null model 3), ORSIM performed significantly better for most species (80%

(a) Empirical connectivity **(b) Simulated connectivity** **(c) Simulated vs. empirical**

Ovenbird

$r_M = 0.863$

Purple Finch

$r_M = 0.701$

Yellow Warbler

$r_M = 0.806$

FIGURE 2 ORSIM is capturing empirical migratory connectivity patterns. Three species are presented here: (a–c) Ovenbird, *Seiurus aurocapilla*, for which the empirical pattern was mapped using mostly tracking data; (d–f) Purple Finch, *Haemorhous purpureus*, for which the empirical pattern was mapped using banding data and (g–i) Yellow Warbler, *Setophaga petechia*, for which the empirical pattern was mapped using genetic data. For each species, the empirical migratory connectivity (using empirical data; a, d and g) and the simulated migratory connectivity (from ORSIM; b, e and h) are mapped. On the maps, in orange is the breeding distribution and in blue is the wintering distribution. Plots of simulated versus empirical (c, f and i) indicate the relationship between empirical and simulated pairwise distances between breeding and wintering grounds (see Figure S3), as well as the associated Mantel correlation coefficient (r_M). Red lines in (c, f and i) indicate the 1:1 relationships between empirical and simulated. Bird illustrations reproduced with permission from Lynx Edicions

of species), but not for Wood Thrush, Blue-winged Warbler, Tree Swallow and, as for the fully randomised null model, Gray Catbird and Grasshopper Sparrow (Table S1). After removing validation data located in the top quartile of abundance values (see details in Supplementary Material), analyses showed similar results, with ORSIM being able to capture well empirical migratory connectivity patterns (mean Mantel correlation coefficient: $r_M = 0.702 \pm 0.161$; Table S2) and performing significantly better than the null models (except only for ovenbird against null model 3; Table S2). Thus, the bias of validation data towards high abundance area (see Supplementary Material) does not appear to have

a significant effect on the results. Overall, these results indicate that the key processes included in ORSIM, that is, minimising energetic cost associated with seasonal re-location and intraspecific competition for access to energy supply, are both strongly contributing to the good performance of the model.

DISCUSSION

The modelling framework that we present is based on general principles of energetics and ecology and it can be used to predict the migratory connectivity of any animal
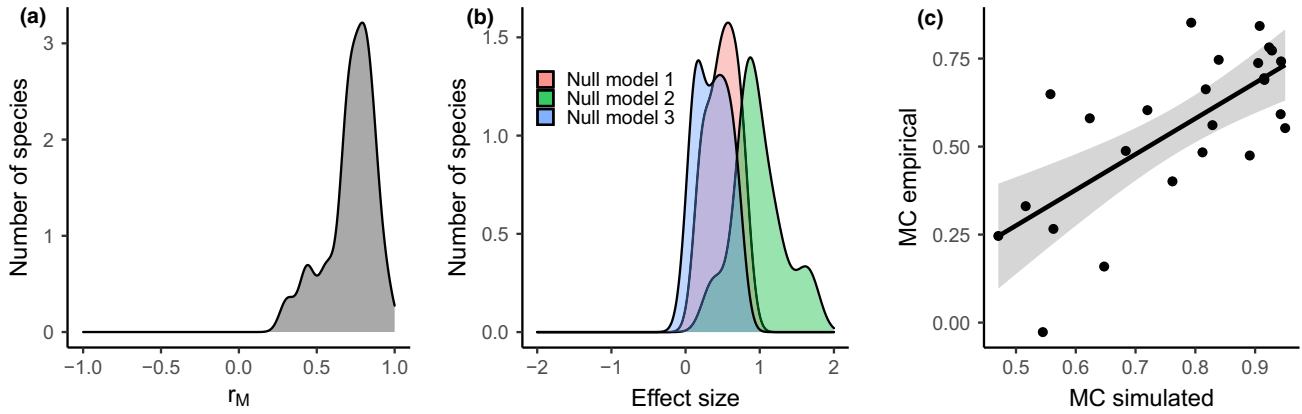
FIGURE 3 Energy efficiency drives the seasonal redistribution of individuals within migratory species. (a) Density plot of the validation metric (r_M) for the 25 species investigated; r_M varies between −1 and 1, with 1 being a perfect positive correlation between the empirical and simulated migration patterns (Figure S3), and 0 corresponding to no association. (b) Density plots of the effect sizes when comparing ORSIM to null models for the 25 species investigated; effect size was calculated as $r_M^{ORSIM} - mean(r_M^{NULL})$ and positive values indicate that ORSIM tend to perform well at capturing empirical migratory connectivity when compared to the null models. (c) Relationship between the strength of migratory connectivity (MC) simulated by ORSIM and calculated from empirical data

species performing seasonal migration. Here, we used data on 25 avian species to calibrate and validate the model. Our results indicate that individuals within migratory species tend to follow an ideal optimal redistribution across seasons, and suggest that energy efficiency explains much of the intraspecific variation in migratory destinations. Following previous work showing that the mechanism of energy efficiency explains bird migration well at the inter-specific level of the entire avifauna (Somveille et al., 2018), we show here that it is also able to explain this phenomenon at the intraspecific level. Thus, in combination with previous work, our results support the idea that energy efficiency provides a general explanation for bird migration across scales, from individual behaviour to global patterns. Further, these results support Lotka's maximum power principle (Lotka, 1922), which states that natural selection should favour organisms that best optimise energy acquisition from the environment and energy used for survival to allocate the surplus energy to growth and reproduction. Following such energetic definition of fitness (Brown et al., 1993), our results support the hypothesis that natural selection has shaped the behaviour of migratory birds to maximise net energy gains while competing with each other for seasonally available resources.

Our model, which generates patterns expected under an ideal optimal redistribution of migratory individuals, provides a strong theoretical basis for exploring additional processes underlying the ecology and evolution of migration, particularly since it is based on many simplifying assumptions. In particular, we assume that energetic costs associated with relocating between breeding and wintering grounds are solely based on migratory movement. However, other factors are likely to be at play, such as individual- and population-level seasonal tracking of habitat and climatic conditions (Ramos et al., 2015; Ruegg et al., 2021). Integrating climate into ORSIM, in

particular through an energetic cost of switching climate (Somveille et al., 2019) that can be added to the energetic cost that is minimised in the model, would allow testing the general role of this mechanism in driving within-species migration patterns. In addition, we assume that birds migrate along a straight line between breeding and wintering sites and that the cost of migratory movement is a linear function of the length of this straight line. However, birds usually migrate following more complex routes, involving stop-overs and barrier avoidance (Cano et al., 2020; Delmore et al., 2012; Irwin & Irwin, 2005; Norevik et al., 2020; La Sorte et al., 2016), and are affected by environmental conditions along the way such as wind (Kranstauber et al., 2015; Norevik et al., 2020). These, in turn, might affect the energetic cost associated with relocating between seasonal grounds and therefore impact model predictions.

We also assume in our model that birds are ideal, that is, with complete knowledge of the environment, and free to choose the optimal migratory destinations. This assumption greatly simplifies the model, and it can be equivalent to assuming that over time (across many generations) birds will converge towards the optimal behaviour via natural selection, thus mimicking full knowledge of the environment while assuming the large-scale environment has been stable for long enough for natural selection to fully optimise. However, in reality, individuals are more likely to have restricted information about the quality of the environment at a large scale, and information about where to migrate is instead partially coded in genes (Liedvogel et al., 2011) and/or transferred culturally (Harrison et al., 2010). Consequently, migration patterns might deviate from optimality as they are in part shaped by historical legacy of how populations have shifted their distributions in response to past climate change (Ruegg & Smith, 2002; Winger et al., 2019). Integrating restrictions on knowledge of the environment

and heritable information about migratory behaviour into our modelling framework could, therefore, potentially help explain why some species in our analysis could not be well explained by ORSIM (Table S1) and yield new insights into the evolution of migration. For example, the serial residency hypothesis (Cresswell, 2014), which is based on differential survival of juveniles that are exploring different migration destinations, could be implemented in future development of our modelling framework to test it. It must also be noted that ORSIM is a deterministic model that does not consider the stochasticity inherent to seasonal destinations of migratory individuals. This could explain why the model currently overestimates the strength of migratory connectivity for example. Implementing a stochastic version of ORSIM would be another valuable future development of the model, and we expect that it would generate values for the strength of migratory connectivity that are more in line with the empirical ones.

Specific mismatches between model predictions and empirical patterns are apparent, and such differences highlight important areas for future research. In particular, ORSIM is highly efficient at capturing longitudinal patterns of migratory connectivity (Table S3), but less so at capturing latitudinal patterns (Table S4), indicating that additional processes are important for driving how individuals redistribute latitudinally. For example, life-history strategies have been shown to influence differential migration in birds (Gow & Wiebe, 2014), and intraspecific trait variation that affect climate tolerance could affect the energetic cost associated with relocating between seasonal sites. We expect that adding traits related to migratory performance and climate tolerance, but also competitive ability, such as age and size, as well as taking into account environmental factors en route, such as wind and barriers, will improve the ability of the model to capture latitudinal patterns, and better explain migratory patterns more generally.

The explanatory capacity of ORSIM is tied to the data sets used to calibrate and validate it. For calibration, we used here seasonal relative abundance predicted by STEMs, which correlate eBird data and information on habitat quality, to estimate the distribution of energy available to the species across their seasonal ranges. However, other types of data could be used for species for which STEMs are not available, such as using proxies for resource availability for these species. To validate model predictions, we used a combination of banding, tracking and genetic data. These data sets have specific biases, such as a bias towards areas of high human density for band retrieval or variable accuracy for the breeding destinations with genetic data and for the wintering destinations with tacking data. However, we found no effect of data type on the validation results of ORSIM, thus suggesting that sampling biases might not be a significant problem for our validation analysis. In addition, while we selected data sets with at least 10 individuals

available per species, some species still have a relatively small amount of data points (e.g. Hermit Thrush, Burrowing Owl; Table 1). This is a limitation because these smaller data sets might not cover a wide range of migration strategies, and using small data sets hinders the power of comparing ORSIM predictions to null models. However, we found that the validation results were not affected by sample size, which indicates that the data sets that we used were not inadequately small. It would still be important and useful to expand these data sets, particularly obtaining migration data from individuals located in informative locations (i.e. areas of the range currently lacking data; areas where individuals are expected to use several different migration strategies), to confirm the results obtained in this study.

Our model provides, for the first time, quantitative predictions of migratory connectivity based on first ecological and energetic principles. The strong predictive ability for populations with empirical data suggests that ORSIM could be used for mapping the migration patterns of populations for which movement data are not yet available. Thus, further test of the modelling framework could be done by collecting data from new sites across species' seasonal ranges for which ORSIM's prediction is not what would be expected based on other models or current knowledge, which could be particularly useful for local populations undergoing rapid decline. Through manipulating the distribution of energy in the environment, ORSIM predictions could also inform how migratory networks respond to environmental change, particularly habitat loss, and ultimately how this affects population dynamics (Dolman & Sutherland, 1994; Taylor & Norris, 2010; Taylor & Stutchbury, 2016). In addition, our modelling framework can predict the behaviour of sedentary individuals within partially migratory species, and therefore it could be applied to species with validation data sets that include both migrant and sedentary individuals to predict patterns of partial migration and better understand this phenomenon. Overall, our finding that migratory birds tend to follow an ideal optimal redistribution between seasons opens the door for a better understanding of the evolutionary causes and consequences of migration patterns as well as a strong framework for understanding how seasonal migrations may change amidst future rapid environmental change.

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AUTHORSHIP

M.S. conceived and designed the model, performed the analysis with support from R.A.B. and K.C.R. and drafted the manuscript. All authors contributed critical input to the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The eBird Status and Trends data products are open access and free to use for research, and are downloadable through the R package *ebirdst*. The banding recoveries data are publically available upon request from the USGS Bird Banding Lab (https://www.usgs.gov/centers/pwrc/science/bird-banding-laboratory?qt-science_center_objects=4#qt-science_center_objects). The tracking data are available in the supplementary materials of Finch et al., (2017), Kramer et al., (2018) and Hill & Renfrew (2019). The genomics data products are available in a public repository on figshare at https://doi.org/10.6084/m9.figshare.c.5420643. The computer code used for this study is available on GitHub: https://github.com/msomveille/optimal-redistribution-simulator.git.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.