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thesis abstract

# The global ecology of bird migration: patterns and processes

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**Abstract.** Nearly 20% of bird species are migratory, their seasonal movements causing a redistribution of bird diversity that radically changes avian community composition worldwide. And yet, bird migration has been largely ignored in studies of global avian biodiversity. My thesis is the first global macroecological analysis of bird migration. Using a dataset on the geographical distributions of the world's birds, I mapped global patterns of migratory bird diversity, revealing strong spatial features. I then used these patterns to test hypotheses exploring the ecological processes driving bird distributions in space and time. From these results, I developed the first mechanistic, process-based model of bird migration at the global scale. From first principles – converting key ecological processes into a common currency of energy – this model successfully explains the global patterns previously described. My research provides a better understanding of why birds migrate and opens new research avenues on this remarkable phenomenon.

**Keywords.** Bird migration, macroecology, ecological process, mechanistic model, seasonality

## Introduction

Animal migration is one of the most remarkable phenomena in nature, generating important, regular redistributions of organisms in space and time. In particular, birds, being highly mobile organisms, have evolved an impressive migration system composed of hundreds of species. Migratory birds range from nectarivorous hummingbirds weighing only a couple of grams to carnivorous raptors up to 3 orders of magnitude heavier, some travelling short distances while others undertake extraordinary journeys across continents (Greenberg and Marra 2005; Newton 2008). Bird migration is defined as the "*regular, seasonal, large-scale, long-distance movement of a population twice a year between a fixed breeding and a fixed non-breeding area*" (Lack 1968), and is a flexible, adaptive behaviour that evolves as a function of environmental conditions (Lack 1954, 1968, Sutherland 1998, Alerstam et al. 2003, Greenberg and Marra 2005). Nearly one in five bird species is migratory (Kirby et al. 2008) and considering the enormous number of individuals involved (e.g. about 5000 million birds enter sub-Saharan Africa in Autumn from the Palaearctic; Moreau 1972), it is clear that migration dramatically rearranges avian communities across the world every season, leading Moreau (1952) to describe it as "*a seasonal ecological adjustment on a gigantic scale*". Yet, despite its ecological importance and global extent, and although the migratory behaviour itself has received a great deal of attention, bird migration has been mostly ignored in previous studies of global avian biodiversity.

The scientific study of large-scale biodiversity patterns has deep roots in ecology (e.g. Wallace 1876, Arrhenius 1920), but it has received increasing attention since the concept of 'macroecology' was formalized 25 years ago (Brown and Maurer 1989). The macroecological approach uses 'macroscopes' (in reference to the use of microscopes by other fields of biology, Brown 1995) to step away from local ecological interactions and reveal the general mechanisms that shape ecological systems (Brown 1995, Gaston and Blackburn 2000). As one of the better-studied taxonomic groups, birds have had a key role in the development of macroecology (Jetz et al. 2004, Orme et al. 2005, 2006, Davies et al. 2007, Storch et al. 2006, Gaston et al. 2007, Olson et al. 2009). However, despite this extensive body of work, most macroecological studies considered bird species only on their breeding grounds. Very few have addressed one of the most striking features of avian biogeography: the fact that, for a substantial proportion of the species, distributions vary seasonally, and accordingly so do macroecological patterns. I conducted an extensive literature review on bird migration from a macroecological perspective that confirmed the paucity of studies that have analyzed bird migration at a regional or global scale and involved suites of species (chapter 1 in Somveille 2015, Somveille et al. 2013). These studies focused mainly on Europe and North America, none was global in scale and only two spanned the equator. They also often analyzed just a subset of the local bird community (e.g. only breeding species). In addition, only some of these studies used environmental variables in an attempt to infer the processes from the patterns, and only using verbal and correlative statistical approaches.

Bird migration poses a particular challenge to macroecology, because bird diversity patterns are dynamic (i.e. they fluctuate seasonally) rather than static. However, it is also an extraordinary opportunity as a natural experiment for testing hypotheses on the mechanisms driving the spatial distribution of species (H-Acevedo and Currie 2003, Hurlbert and Haskell 2003, Boucher-Lalonde et al. 2014, Dalby et al. 2014). A macroecological perspective applied to bird migration can also provide valuable insights into the ecology and evolution of this remarkable phenomenon. Because we still lack a mechanistic understanding of what shapes the global bird migration system, which impedes predictions of the impact of environmental changes, such investigations are timely and important.

The overall aim of my PhD thesis (Somveille 2015) was to use a macroecological approach to study the global bird migration system in its entirety for the first time. I used patterns of migratory bird diversity to test hypotheses about the ecological processes driving bird distributions in space and time. Ultimately, my goal was to explain the distribution of migratory bird species across the world from first ecological principles.

## Methods

Using a newly released dataset of digital distribution maps for the world's birds, distinguishing breeding and non-breeding ranges of migratory species (Birdlife International and NatureServe 2012), I first mapped global diversity patterns associated with bird migration (chapter 2; Somveille et al. 2013). For operational purposes, I defined migratory species as those mapped with at least one part of their entire geographical distribution coded as breeding or non-breeding only. Hence, my analyses focused on species whose annual movements result in predictable, large-scale changes in bird diversity. I also concentrated on geographical patterns over land and therefore marine species were excluded from the analyses (but the terrestrial part of coastal species' distributions was included). Range maps represent coarse generalizations of species' distributions that potentially overestimate the species' true area of occupancy. However, given the coarse spatial resolution of the analyses – the spatial units employed were equal-area hexagons of ~23,322 km$^2$ (Sahr et al. 2003) – such limitations are not expected to significantly affect the global patterns obtained (Hurlbert and Jetz 2007). In addition, this dataset compiled distributional information in a consistent manner for all species globally, thus minimizing the degree to which variations in data quality affect the spatial patterns. I mapped global spatial patterns in the seasonal variation in avian species richness due to migration, the richness in migratory species during both the breeding and non-breeding seasons, and the contribution of migratory birds to local bird diversity, investigating whether the regional patterns described in previous studies using a small number of species can generalize to the global scale and to all bird species.

In chapter 3 (Somveille et al. 2015), I then used these global empirical spatial patterns of migratory bird diversity to test hypotheses for the ecological processes driving bird distributions in space and time. In particular, I investigated whether birds move to breeding grounds to exploit a surplus in resources and then avoid harsh winters by redistributing to the nearest suitable non-breeding grounds (Herrera 1978, Karr 1980, Newton 1995, Hockey 2000, Hurlbert and Haskell 2003, Wisz et al. 2007). To do so, I built statistical models – ordinary least-squares regression models and simultaneous autoregressive models introducing an autoregressive process in the error term to account for spatial autocorrelation – that were 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. The quality of the models was evaluated in terms of the proportion of observed variance that they explained as well as their ability to predict the qualitative features of spatial patterns.

These statistical analyses focused on explaining spatial variation in migrant bird communities but could not explain the great diversity of breeding and non-breeding destinations chosen by migratory species. In chapter 4 (Somveille et al. in review), I therefore searched for the general mechanisms that could explain the specific choice of breeding and non-breeding grounds made by each migratory species. I first tested the hypothesis that migration allows each species to track its climatic niche throughout the year more than if it had stayed year-round in either its breeding or non-breeding ground. I then investigated whether the cost of migration was compensated for by an increased seasonal availability of resources, measured using seasonal variations in the Normalized Difference Vegetation Index (NDVI). Finally, I simulated alternative realistic migration options (i.e. combinations of breeding and non-breeding ranges) and investigated how favourable the observed migration is, compared with what the species could potentially do given its geographical location – based on access to resources, climatic niche tracking and geographical distance.

These analyses (chapters 3–4), however, were limited by their correlative nature, a problem particularly exacerbated by the dynamic nature of the migration phenomenon. In the last chapter of my thesis (chapter 5; Somveille et al. in prep), I developed a spatially explicit, process-based mechanistic model of bird distributions in space and time. It was built from first ecological principles, making no direct use of data on the observed geographical distributions of species. I converted each of the processes highlighted by the previous statistical analyses into the same unit – species' energy use throughout the year – thus being able to integrate them into the same model. To take into account the spatial distribution of energy supply in the environment, I used NDVI as an indicator of the energy resources available to birds in each site at each season. I then simulated the breeding and non-breeding distributions of virtual species, considering the energetic requirements of each one of them based on the four processes. This mechanistic model explicitly takes into account the effect of competition with other species (both residents and migrants) to determine the choice of breeding and non-breeding destinations of any given species (i.e. the most energy-efficient option), and allows for the integration of the processes throughout the year and their effects on the breeding and non-breeding distributions of species simultaneously. The model was as simple as possible, and based on simple rules, in order to capture the essence of the underlying mechanisms. This approach allowed the global spatial patterns to emerge from first ecological principles and only driven by the processes included.

## Results

My analyses revealed that despite the great biological and ecological diversity among migratory birds, strong spatial patterns emerge when they are all pooled together. This suggests common underlying ecological drivers to which migratory birds respond. In particular, I found a striking asymmetry between the northern and southern Hemispheres in all the patterns investigated, migration being much stronger in the former at similar latitudes (chapter 2). Another interesting feature is a clear transition, around 35°N latitude, from avian communities to the south that are net senders of breeding migrants to avian communities to the north that are net receivers of breeding migrants, with no equivalent in the southern Hemisphere (chapter 2). These patterns had not been readily apparent from the combined results of previous regional-scale studies, highlighting the importance of a global perspective. The statistical models then strongly supported the hypotheses that birds move to breeding grounds to exploit a surplus in resources, preferring areas where the winter is harsh, presumably to avoid competition with resident species (chapter 3). In contrast, distribution during the non-breeding season seems driven by avoidance of both harsh winters and migrating too far from breeding grounds (chapter 3). In addition, I found that underneath their great diversity of breeding and non-breeding destinations, migratory birds appear to follow a common strategy of tracking their climatic niche year-round, presumably to keep thermoregulation costs low. This climatic niche tracking was observed within the context of a broader trade-off between the costs of migration and the benefits of better access to resources (chapter 4). Each species' migration (i.e. combination of breeding and non-breeding grounds) also tends to be one of the most favourable (considering access to resources, climatic niche and geographical distance) among the alternative migration options that are available given the species' geographical location (chapter 4). These correlative analyses shed light on the main processes, namely thermoregulation, competition for accessing resources, migration cost and reproduction, which together appear to be shaping the global bird migration system. Building on these results, my mechanistic model – framing the processes in terms of energy use and relating them to the energy supply in the environment – was able to successfully generate all the previously described global patterns associated with bird migration (chapter 5). It strongly indicates that the four processes considered are together sufficient to explain the spatio-temporal distribution of bird species across the globe.

## Discussion

My results indicate that seasonality is the main force driving bird migration worldwide. They suggest that migration is a behavioural response to this seasonality that keeps migratory species in a more favourable energy balance throughout the year. It is mainly a Northern Hemisphere phenomenon because seasonality is more pronounced than in the Southern Hemisphere, as the latter benefits from the buffering effect of the oceans on their smaller landmasses. The northern landmasses also extend to higher latitude, creating vast areas with a large summer surplus in resources that attract more species from less seasonal areas at lower latitudes. Migration being a costly activity, these species then mostly relocate to the nearest suitable areas in the southern part of the Northern Hemisphere (i.e., Central America, India, South-east Asia, the Mediterranean Basin and sub-Saharan Africa north of the equator) during the non-breeding season, with few species crossing the equator. In turn, many species that breed in these regions find themselves in a situation where it is a better strategy to migrate slightly further south over winter than to endure the increased competition with these wintering visitors. The Southern Hemisphere, without large landmasses of high seasonality, does not generate many internal breeding migrants and hence is mainly visited by non-breeding migrants arriving from the Northern Hemisphere.

The mechanistic model also provides an explanation for the neat transition from avian communities that are net senders and those that are net receivers of breeding migrants observed in the Northern Hemisphere at *ca*. 35°N latitude. It answers the puzzling question initially raised by the existence of this turnover zone: if species richness is the same year-round, why are the species here not all residents? I show that it emerges because this corresponds to a location with intermediate seasonality that receives wintering visitors from the high-seasonality areas further north with similar summer climate, but also receives breeding migrants from areas further south attracted by the proximity and similarity in climate to their winter grounds as well as the room left by the migrants that moved back further north for the breeding season.

Overall, my PhD thesis has provided, for the first time, a mechanistic understanding of bird migration at the global scale within one quantitative modelling framework. However, the inferences were constrained by the use of range maps, which did not provide information on the geographic linkage of migrating individuals or populations across the annual cycle, or on the trajectory, timing and magnitude of movements of migratory populations. The growing wealth of data from tracking devices (e.g. movebank), band returns (e.g. North American Bird Banding Laboratory), radar (Kelly and Horton 2016) and citizen science programs (eBird, La Sorte et al. 2016), provide exciting opportunities to advance the mechanistic explanation developed in my thesis – for example, by improving estimates of the cost of migration and climatic niche tracking as well as assessing factors associated with partial migration.

Mechanistic explanations of Nature's phenomena, grounded on first principles and simple rules, are important because they provide a predictive capacity that promotes better extrapolation and generalization to new conditions. With bird migration, this may include predictions on how the seasonal distributions of migratory bird populations are likely to respond to global environmental change. It can also allow extrapolation into other migration systems such as plankton (Lampert 1989), insects (Chapman et al. 2011) or large marine predators (Block et al. 2011). Lastly, understanding how patterns emerge from first principles promotes a better connection between phenomena and disciplines, which will advance the development of general theories in biodiversity science (McGill and Nekola 2010, Marquet et al. 2014).

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