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João L. Guilherme*[1,2], Victoria R. Jones[2], Inês Catry[3,4,5], Martin Beal[2,6], Maria P. Dias[2,7], Steffen Oppel[8], Juliet A. Vickery[8,9,10], Chris M. Hewson[9], Stuart H. M. Butchart[2,10] and Ana S. L. Rodrigues[1]

1. CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France.
2. BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge, CB2 3QZ, United Kingdom.
3. CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão, 4485–601 Vairão, Portugal.
4. CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Instituto Superior de Agronomia, Laboratório Associado, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal.
5. BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal
6. MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, Lisboa, Portugal.
7. Centre for Ecology, Evolution and Environmental Changes, cE3c & Department of Animal Biology, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal
8. Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, United Kingdom.
9. British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom.
10. Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, United Kingdom.

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*corresponding author: Address: CEFE UMR5175 - Campus du CNRS - 1919, route de Mende - 34293 Montpellier 5 - France; email: joaolguilherme@gmail.com; ORCID: https://orcid.org/0000-0003-4542-589X

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Article impact statement: Understanding how migratory birds link countries is key for flyway conservation. Tracking data can unveil these dynamics but gaps remain.

Abstract

The conservation of long-distance migratory birds requires coordination between the multiple countries connected by the movements of these species. The recent expansion of tracking studies is shedding new light on these movements, but much of this information is fragmented and inaccessible to conservation practitioners and policy decision-makers. Here, we synthesize current knowledge on the connectivity established between countries by landbirds and raptors migrating along the African-Eurasian flyway. We reviewed tracking studies to compile migration records for 1229 individual birds, from which we derived 544 migratory links, each link corresponding to a species' connection between a breeding country in Europe and a non-breeding country in sub-Saharan Africa. We used these migratory links to analyse trends in knowledge over time, as well as spatial patterns of connectivity per country (across species), per species (across countries) and at the flyway scale (across all countries and all species). We found the taxonomic coverage of existing tracking data to be highly incomplete, with, to date, an average of just 7.5% of migratory landbird species and 14.6% of raptor species tracked per country. Furthermore, existing data are biased towards more westerly countries and larger bodied species. Despite these limitations, existing data can already inform conservation efforts, and we provide species- and country-level syntheses of the migratory links we identified (involving 123 populations of 43 species, migrating between 28 European and 43 African countries). Finally, we highlight countries (e.g., Spain, Poland, Ethiopia, Democratic Republic of Congo) that are strategic priorities for future tracking studies to complement existing data, particularly on landbirds. Our data and analyses can inform discussions under two key policy instruments at the flyway scale: the African-Eurasian Migratory Landbirds Action Plan, and the Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia.

Introduction

Migratory birds undertake spectacular movements across continents and oceans, coupling distant ecosystems (Bauer & Hoye, 2014) and linking multiple political jurisdictions (Harrison et al., 2018; Beal et al., 2021a; Morrick et al., 2021). Over two billion landbirds (Hahn et al., 2009) and millions of raptors (Verhelst et al., 2011; Miller et al., 2016) migrate seasonally across the African-Eurasian flyway, one of the largest avian migratory systems in the world (Newton, 2008). Throughout their annual cycles migratory birds face a suite of threats, including agricultural intensification on the breeding grounds (Reif & Vermouzek, 2019), energy infrastructure development along migratory routes (Marques et al., 2020), illegal taking at stopover sites (Brochet et al., 2016), habitat degradation in non-breeding grounds (Zwarts et al., 2018), and climate change across their ranges (Zurell et al., 2018). As a result, many populations of African-Eurasian migrants are declining (Sanderson et al., 2006; Vickery et al., 2014).

The conservation of migratory birds is a challenge requiring concerted efforts among the multiple countries connected by the movements of these birds. In the African-Eurasian flyway, two policy instruments are focused on the conservation of migratory landbirds and raptors: the African-Eurasian Migratory Landbirds Action Plan (AEMLAP; UNEP/CMS, 2014) and the Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia (Raptors MOU; UNEP/CMS, 2008). These agreements were adopted under the United Nations Convention on Migratory Species and provide frameworks for cooperation between governments and with other key stakeholders (including non-governmental organizations, industry and funding agencies), fostering collective action in tackling the conservation needs of migratory species, and guiding decision making (Baldwin, 2011; Hensz & Soberón, 2018). To be effective, however, such conservation efforts require a sound understanding of the spatial and temporal distributions of different migratory bird populations.

Bird migrations have fascinated people for millennia, but it was only with the development of ringing programs in the 20th century that the precise movements of individual birds started to become clearer (Bairlein, 2001), including their migratory connectivity patterns at the scale of the flyway (Spina et al., 2022). More recently, the developments in tracking technologies (e.g., light-level geolocators [or Global Location Sensors; GLS], satellite transmitters [also known as Platform Transmitter Terminals; PTT], and Global Positioning System [GPS] devices; Bridge et al., 2011) are making it possible to follow birds with unprecedented detail, and understand how long they stay at each location throughout their annual cycles. The resulting increase in bird tracking studies is revealing a progressively more detailed picture of the migratory behavior and connectivity patterns of many bird populations (e.g., Finch et al., 2015; Buechley et al., 2021). New opportunities are thus emerging for targeted international cooperation, wherein tracking data can play an important role in informing where and when conservation action for different populations might be most effective (e.g., Hewson et al., 2016; Knight et al., 2021).

Despite these advances, tracking studies are still far from realizing their potential to inform flyway-scale conservation of migratory birds, including in terrestrial environments (Katzner & Arlettaz, 2020). First, and despite the increasing recognition of the utility of global data repositories such as

MOVEBANK (Kays et al., 2021), much of the existing data are fragmented and confined to the academic literature (Fraser et al., 2018), and remain difficult to find and access (Davidson et al., 2020). Second, given that tracking studies are initiated with different underlying motivations (e.g., scientific, conservation) and their feasibility is constrained by a diversity of considerations (e.g., technology, species' ecology, access to funding), existing data tend to be biased towards particular regions and species (Bernard et al., 2021). Even so, as the volume of data increases, it becomes progressively more important to bring them together, synthesize them into formats that are accessible to scientists and conservation practitioners, and translate their results into policy-relevant scientific evidence (Dunn et al., 2019).

In the African-Eurasian flyway, previous studies integrating tracking records for multiple species have described general spatial and temporal patterns of migration (e.g., Strandberg et al., 2009; Briedis et al., 2020), connectivity (e.g., Finch et al., 2017), and mortality (e.g., Klaassen et al., 2014), as well as the potential impacts of threats on population dynamics (e.g., Cresswell et al., 2020). However, no study has attempted to bring together all the available tracking data in a format that can be useful to guide international cooperation at the flyway scale, namely through the AEMLAP and the Raptors MOU. From a policy perspective, countries are the key spatial unit of analysis given that the implementation of policies steered in international fora is dependent upon the decision-making processes of each country (Dallimer & Strange, 2015), their national conservation priorities, and their differing capacities for implementation (Boardman, 2006). Understanding how migratory bird populations link countries throughout their annual cycle is thus key to highlighting shared conservation priorities across countries, and guide effective, targeted and equitable international cooperation efforts for their long-term conservation.

Here, we review the tracking literature to assess the state of knowledge on the connectivity established among countries by birds migrating along the African-Eurasian migration flyway, as a contribution to supporting international agreements for the conservation of migratory landbirds and raptors in this region (AEMLAP and Raptors MOU). For this purpose, we compiled all available tracking data on the links between countries created by landbirds and raptors as they migrate from breeding to non-breeding grounds. We then synthesized the current knowledge regarding these connections at the level of individual countries, individual species, and at the flyway scale. Finally, we evaluated the extent of the remaining gaps in knowledge, proposing priorities for future bird tracking studies that can strategically reduce those gaps.

Methods

Study region

Our broad study region is the African-Eurasian migratory flyway. Within this, we focused on breeding grounds in Europe (including Turkey and excluding Russia) and on non-breeding grounds in sub-Saharan Africa (i.e., excluding Morocco, Western Sahara, Algeria, Tunisia, Libya and Egypt; Appendix S1). We did not include European Russia and Asian countries within the flyway because a preliminary scoping of the literature (Finch et al., 2017; Briedis et al., 2019, 2020; Brlík et al., 2020; Cresswell et al., 2020) revealed very few studies for this region. We grouped countries into sub-regions: four in

Europe (western Europe, central Europe, northern Europe, and eastern Europe) and four in sub-Saharan Africa (western Africa, central Africa, southern Africa and eastern Africa) (Appendix S1).

Species and populations

We analyzed 118 long-distance migratory bird species (including 91 landbirds covered by the AEMLAP and 27 raptors covered by the Raptors MOU), all breeding in Europe and spending the non-breeding season in sub-Saharan Africa (Appendix S2). We used the distribution maps from (BirdLife International and Handbook of the Birds of the World, 2018) to identify species' breeding ranges in Europe and non-breeding ranges in sub-Saharan Africa.

We defined a 'population' as the set of individuals of the same species that breed in a given European country (hence, when used alone, the term 'population' refers to a single species in a single country). We use national boundaries to define populations because our aim is to characterize links between countries. Although these national populations are not ecologically isolated, patterns of natal and breeding dispersal are likely negligible at this scale of analysis (Paradis et al., 1998; Fandos et al., 2021).

We also use the terms 'European population' (all individuals of a species that breed across Europe) and 'sub-regional population' (all individuals of a species in a given European or African sub-region). Each of the analyzed species therefore has one or more (country-level) populations, a single European population and one or more European and African sub-populations.

We used the European Red List of Birds (BirdLife International, 2021), to obtain European-level population trends (Appendix S2), the list of species (among those analyzed) per European country, and the respective country-level population size estimates. We used the latter to calculate European and sub-regional populations' sizes, from where we estimated the percentage of each species' European or sub-regional populations in each country. We could not follow the same approach for sub-Saharan countries, as no country-level population size estimates were available. Instead, we used the above-mentioned distribution maps to obtain the list of migratory species per country, and then to calculate for each of these species the percentage of their (sub-Saharan) non-breeding range or sub-regional ranges within each country.

Definition of migratory link

An individual migratory bird typically crosses the borders of multiple countries during its annual cycle, including where it breeds, stops over during migration, and spends the non-breeding season. Here, we focused on just two countries per individual: the one where it breeds (hereafter 'breeding country'); and the one where it spends the most time during the non-breeding season ('non-breeding country'). As we extracted data from available studies rather than from raw tracking data (see below), we were unable to extract finer details (e.g., on stopover sites) across all individuals.

We define a 'migratory link' as the connection between two countries established by birds from a population as they migrate from a European breeding country to a sub-Saharan African non-breeding country. We define the strength of each migratory link as the proportion of individuals in the population that spend the non-breeding season in a given country in sub-Saharan Africa. Hence, if all individuals of a given population (breeding in a given European country) migrate to the same

African country, they establish a single migratory link of 100% strength. If instead the birds spread across multiple African countries, they establish multiple links of lower strength. This measure of strength is directional (e.g., Morrick et al., 2021): it reflects the degree of importance of an African country to the population breeding in a European country. We did not calculate the reverse (the extent to which the European country is important to the non-breeding population of the African country) because tracking studies were initiated in Europe and representativeness of African countries' non-breeding populations is therefore too low for broad inference.

Compiling migration records from studies

We focused on tracking data obtained from birds fitted with GLS, PTT or GPS devices, aiming to obtain as many migration records as possible for the analyzed species. A 'migration record' corresponds to the minimum information needed to identify a migratory link, i.e., evidence that an individual of a given species migrated from its breeding country in Europe to its non-breeding country in sub-Saharan Africa. Although ringing data can provide robust insights on migratory connectivity (Ambrosini et al., 2009), we did not attempt to incorporate these data in our analysis because ring recoveries do not provide information on how long the individual spent at a given location. Indeed, ringing recoveries provide location information for single points in time and often only one recovery location is available for each individual (e.g., Strandberg et al., 2009), making it impossible to determine if it corresponds to the main non-breeding country (as defined above).

We conducted a review of published articles in ISI Web of Science core collection (https://www.webofknowledge.com/) and Google Scholar (https://scholar.google.com/), complemented by additional studies (details in Appendix S3).

From each selected study, we extracted as many migration records as possible, each record corresponding to an individual bird for which we obtained: the species, the breeding-country (in Europe), and the non-breeding country (i.e., where the bird stayed the longest in sub-Saharan African) (details in Appendix S4, including how we dealt with highly mobile species).

For four species in our dataset – European nightjar (*Caprimulgus europaeus*), Eurasian bee-eater (*Merops apiaster*), barn swallow (*Hirundo rustica*), and collared flycatcher (*Ficedula albicollis*) – the tracking data revealed non-breeding ranges covering more countries than those identified by (BirdLife International and Handbook of the Birds of the World, 2018). Therefore, we updated these ranges (details in Appendices S5 & S6) before using them in our analyses.

Observed and inferred migratory links

We grouped all migration records by population (i.e., conspecifics breeding in the same European country), and excluded from further analysis any populations with fewer than three migration records. For each population, we then identified one or more migratory links (between a European and a sub-Saharan country). Given the incompleteness of our dataset, these 'observed links' (derived from the migration records) certainly underestimate the true number existing for each population. Nevertheless, some missing links are predictable and can be inferred through interpolation between known links. For example, if for a given population breeding in European country A the migration records show connections to two African countries, B and C (through observed links A-B and A-C);

and if there is a third country D spatially located between B and C that is also within the species' non-breeding range; then link A-D likely also exists and, in such cases, we inferred that the population also migrates to country D (see Appendix S7 for details on the inference method; inferred links made up only 16% of all the links we analyzed and they had a negligible effect on the results).

Estimating the strength of migratory links

Assuming tagged birds are representative of their populations, the strength of a migratory link can be estimated from the distribution of migration records among the migratory links in a population (akin to van Wijk et al., 2018; Morrick et al., 2021). Calculating this requires estimating the number of expected records for any inferred links, which we did by interpolating from number of observed migration records in neighboring countries (details in Appendix S7). We thus estimated the strength of migratory links in each population as the percentage of migration records (observed or interpolated) occurring in each country over the sum of all records across all migratory links (observed or inferred).

State of knowledge on migratory connectivity along the African-Eurasian flyway

We analyzed the dataset to synthesize current knowledge on patterns of connectivity in the African-Eurasian flyway, including trends over time, and spatial syntheses per country (across species), per species (across countries), and at the flyway scale (across all countries and all species). We analyzed data for landbirds and raptors separately.

Trends in knowledge

We plotted the cumulative number of studies and migratory links (observed and inferred) over time, as indicators of trends in knowledge on migratory connectivity between countries along the African-Eurasian flyway.

Tracking effort per population

We plotted the relationship between the number of migration records per population and number of migratory links to investigate if tracking effort per population appears sufficient.

Country-level connectivity

For each of the analyzed countries (European or African) we synthesized connectivity with other countries by plotting all the corresponding migratory links according to strength.

Species-level connectivity

For each of the species in our dataset, we synthesized the connectivity between breeding and non-breeding countries by plotting all migratory links for each population and estimating how representative each link is of the species' overall European population by weighting its strength relative to the percentage of the total European population breeding in each country. We then quantified the importance of each sub-Saharan country as a non-breeding destination for that particular species by summing the weighted values across all migratory links to each African country.

Flyway-level connectivity

We synthesized current knowledge on spatial patterns of connectivity between countries in the flyway by generating three maps. First, a map plotting the known migratory links across all species.

Second, a map with the number of migratory links per country. Third, a map of the number of tracked species per country.

Knowledge gaps

Gaps per country

For each country in Europe or in sub-Saharan Africa, we quantified the extent of knowledge gaps by calculating the percentage of long-distance migratory species per country present in the country but for which we did not find migratory links. This value varies between 0% (no gaps) and 100% (all species missing).

Priorities for tracking

We recommend that any flyway-wide strategy for tracking long-distance migratory birds to fill knowledge gaps should: (i) prioritize species with decreasing populations (as per the European Red List of Birds; 38 species, 31 landbirds, 7 raptors; Appendix S2); (ii) prioritize the countries across the flyway holding the largest fractions of the population for which no migratory links are known; and (iii) aim to spread tracking effort across species' ranges (i.e., across all sub-regions in both continents), to ensure new tracking data captures the main ecological gradients and a range of migratory strategies. Based on these premises, we identified for each species with decreasing European population, in each sub-region (Appendix S1), a set of priority countries for future tracking, defined as those needed to complement existing studies to ensure that there will be records representative of at least 50% of the overall population of the sub-region (Appendix S2). For example, the European turtle dove (*Streptopelia turtur*) breeds in Western Europe, with the sub-regional population distributed across seven countries: Spain (73.8%), France (24.9%), Portugal (0.9%), UK (0.2%), Belgium (0.2%), the Netherlands (<0.1%) and Luxemburg (<0.1%). Our dataset includes migratory links for France and the UK (25.1% of the sub-regional population), so we highlight the turtle dove in Spain as a priority for future tracking. Through this process, we obtained a set of unique species-country combinations, each highlighting a particular species that we consider a priority for tracking in a particular country, which we synthesized into a list to support future tracking initiatives in each country.

Software

All analyzes were conducted in R (R Core Team, 2021), using a base world map at 1:50 m scale (https://www.naturalearthdata.com/) in the *sf* package (Pebesma, 2018). All figures were produced in *ggplot2* (Wickham, 2009), using a base map at 1:110 m scale in orthographic projection.

Results

Tracking studies, migration records and migratory links

From an initial set of 1496 unique studies found through Web of Science (776) and/or Google Scholar (928), plus 51 obtained through complementary searches, we retained a final list of 132, from which we gathered 1282 migration records (Appendices S3 & S4). The final dataset analyzed (excluding populations with < 3 migration records), comprised 1229 migration records covering 43

bird species (29 landbirds, 14 raptors), representing 123 populations, of which 361 records (38 populations) for Western Europe, 470 records (42 populations) for Central Europe, 264 records (26 populations) for Northern Europe, and 134 records (17 populations) for Eastern Europe (Appendix S8). When translated into geopolitical space, the migration records revealed 544 migratory links (458 observed, 86 inferred; Appendix S9).

Trends in knowledge

The first study (and thus migratory link) in our dataset dates from 1996 and the cumulative number of studies and links has increased steadily since (Fig. 1). Studies up to 2010 focused almost exclusively on raptors, yet studies on landbirds have had a strong increase since 2010, corresponding to 48.7% of the studies we analyzed (Fig. 1a) and to 57.2% of all links (Fig. 1b).

Tracking effort per population

The number of migratory links per population tends to increase with the number of migratory records, even if there is substantial variation around this trend (Fig. 1c). The increase is faster for landbirds than for raptors, with none of the curves having yet reached an asymptote.

Country-level connectivity

Mapping migratory links per country reveals their connections to other countries through the long-distance migrations of bird populations – e.g., Spain (Fig. 2a). We found migratory links between 28 European countries and 43 sub-Saharan African countries, with substantial variation in the number of links and species tracked per country. On average, each of the European countries analyzed had 19.4 (range 1 - 63) migratory links, established by 4.4 (1 – 14) species, linking them to 12.5 (1 - 27) countries in sub-Saharan Africa. Conversely, each of the African countries had on average 14.7 (1 - 47) migratory links, established by 8.6 (1-21) species, linking them to 9.5 (1-17) European countries (Table 1; Appendix S10).

Species-level connectivity

The number of migratory links per species varied substantially, being generally higher for raptors (average 16.6) than for landbirds (10.7; Table 1). Each species was tracked on average in 2.8 (1 – 7) populations (i.e., countries) across its European breeding range, with migratory records revealing non-breeding grounds in 7.4 (1 - 27) African countries (Table 1). On average, across all populations of all species analyzed, we found 4.4 (1 – 12) migratory links per population. Mapping the migratory links for each population of each species separately – e.g., lesser kestrel (*Falco naumanni*) (Fig. 3a-f) – reveals how they connect to countries in sub-Saharan Africa (Appendix 11).

Combining the information on the migratory links per population (including their strength) with the percentage of the breeding population in each European country reveals the relative importance of each country in sub-Saharan Africa as a non-breeding ground for each species – e.g., lesser kestrel (Fig. 3g). The corresponding patterns vary substantially across species. For example, great reed-warblers (*Acrocephalus arundinaceus*) from the five populations represented in our dataset spread across 21 African countries, estimated to receive between <1% (Liberia) and 9.3% (Sierra Leone) of the European population (Appendix S11). In turn, Montagu's harriers (*Circus pygargus*) from seven populations in Europe concentrate in nine African countries, estimated to receive between <1% (Ghana) and 23.9% (Niger) of the European population (Appendix S11).

Flyway-level connectivity

Mapping all known migratory links across species (Fig. 4a,d) reveals a complex network of ecological connectivity between European and African countries, created both by landbird (Fig. 4a) and raptor species (Fig. 4d). The number of migratory links (Fig. 4b,e) and of species tracked (Fig. 4c,f) varies substantially across countries. In Europe, four countries stand out both in number of links and of species tracked: Sweden (63 links; 11 species); Germany (56; 11); the Czech Republic (47; 8); and Spain (45; 14). For most Eastern European countries we found relatively few links and few species tracked.

In Africa, the western sub-region stands out in terms of the number of migratory links for both landbirds and raptors, in particular Mali (47 links; 21 species) but also Mauritania (33; 16), Nigeria (29; 16), and Burkina Faso (27; 15). Countries in central and southern Africa also stand out for links for landbirds (but not for raptors), in particular the Democratic Republic of Congo (26 links; 14 species), Angola (24; 11), Botswana (19; 8) and Namibia (17; 8). We found few links and few tracked species for countries in Eastern Africa (e.g., Somalia, Kenya).

Knowledge gaps

The vast majority of long-distance migratory bird species in each country have not been tracked (Fig. 5a,c; Appendix S12). Within Europe, the average percentage of gap species per country was 96.7% for landbirds (minimum 83.7% in Denmark; maximum 100% in 21 countries) and 90.4% for raptors (minimum 58.3% in Germany; maximum 100% in 19 countries). In Africa, there were on average 87.8% gap species per country for landbirds (minimum 76.6% in the Democratic Republic of the Congo; maximum 100% in three countries) and 79.7% for raptors (minimum 50% in Mauritania; maximum 100% in Eritrea and Lesotho).

Priorities for future tracking

We highlight 287 species-country combinations as priorities for future tracking (6.5% of the gaps; Appendix S12), mostly for landbirds (248; Fig. 5b) but also for raptors (39; Fig 5d). These are spread across the study region, within countries concentrating relatively large population numbers in each sub-region. In Europe, highlighted countries include: Poland (19 species) in central Europe; Spain (17) in western Europe; Turkey and Belarus in eastern Europe (13), and Sweden in northern Europe (12) (Fig 4b,d). In Africa: the Democratic Republic of Congo (15 species) in central Africa, Ethiopia (15) in eastern Africa, Nigeria (11) in western Africa, and Angola (9) in southern Africa (Fig 5b,d).

Discussion

A wealth of data on the African-Eurasian flyway

Our study sheds light on the wealth of data acquired from the tracking of thousands of African-Eurasian migratory landbirds and raptors from 1996 to 2021 (Appendix S4; Fig. 1a). Synthesized into migratory links, these data reveal how migratory birds connect countries in breeding areas in Europe and non-breeding grounds in sub-Saharan Africa. Further synthesized per country (Appendix S10), per species (Appendix S11) and at the flyway scale (Fig 4), these data can inform international

cooperation efforts for conserving migratory birds, particularly for well-studied species and for well-sampled countries, and they highlight potential priorities for future tracking efforts.

For example, existing data reveal how the Danish population of willow warblers (*Phylloscopus trochilus*) disperses across nine countries in western and central Africa (Lerche-Jørgensen et al., 2017), establishing migratory links of relatively low strength (average 11.1%), whereas European rollers (*Coracias garrulus*) tagged in six European countries establish fewer but stronger links (26%) with six southern African countries (Finch et al., 2015). In turn, Ospreys (*Pandion haliaetus*) have contrasting patterns across populations, with Finish breeding birds dispersing broadly across 11 countries in Africa (Saurola, 2020), whereas birds from the UK appear to concentrate in just five western African countries (Mackrill, 2017), particularly in Senegal and Gambia (together hosting 62% of that population; Appendix S11). These syntheses provide key information to support species-focused international cooperation efforts, including through species' action plans. For example, the Flyway Action Plan for the European roller strongly recommends habitat protection (e.g., through agri-environment schemes) and additional research and monitoring in non-breeding areas (Tokody et al., 2017); our results indicate that focusing those efforts on Namibia, Angola and Botswana would benefit populations breeding across Europe (Appendix S11).

Our country-level syntheses (Appendix S10) reveal opportunities for governments and other stakeholders to prioritize bilateral or multilateral cooperation among countries sharing important migratory links. For example, tracking data for 11 species breeding in Germany reveals 56 migratory links with 27 African countries, with Mali standing out as particularly important for four of these populations (link strength ≥ 40%). For Angola, 11 species create 24 migratory links with 16 countries in Europe, including major links (strength ≥ 67%) with Hungary, Portugal and Denmark. Knowledge of migratory links between countries can foster strategic conservation action, including scientific and monitoring programs, capacity building, technical exchanges, and education and social empowerment initiatives. For example, the expertise of conservationists how to reduce electrocution and poisoning of Egyptian Vultures in the Balkans is now being applied to reduce these threats along the eastern flyway, after tracking identified where these threats were most prominent (Oppel et al., 2021). For some countries, these collaborations may be a cost-effective way to deliver on national conservation priorities, and could therefore be explicitly incorporated into national biodiversity plans and strategies.

At the flyway scale, the data we have synthesized (Appendices S8-S11; Fig. 4) can directly inform the two key policy instruments under the Convention on Migratory species already promoting the coordinated conservation of African-Eurasian migratory landbirds and raptors: the AEMLAP and the Raptors MOU. Even though these results are based on current knowledge (thus on incomplete and biased data), they indicate that cooperation between countries in Europe and in West Africa is strategic for the effective implementation of both agreements. Mauritania and Mali, in particular – two countries with poor protection measures for migratory birds (Runge et al., 2015) – are connected by important migratory links (≥33%) to 14 European countries, for 19 and 22 populations of landbirds and raptors respectively (Appendix S11). Given the generally poor knowledge of the conservation needs of, and threats faced by, migratory bird populations on their non-breeding grounds, prioritising countries like Mali and Mauritania for on-the-ground research can greatly

enhance understanding of threats across multiple populations and inform direct conservation action (Vickery et al., 2014). Conversely, countries like Spain and Sweden host relatively high numbers of species that spend their non-breeding season in African countries (Figure 4c,f; Appendices S10 & S11), thus holding a high responsibility for the conservation of this shared heritage.

Substantial knowledge gaps remain

Our results also highlight that the currently existing tracking data are incomplete (Appendix S12). Indeed, across all 2565 populations (1982 of landbirds, 583 of raptors) of long-distance migratory landbirds and raptors in Europe (i.e., 118 species across 43 countries), only 123 (4.8%) have been tracked (3.4% for landbirds, 9.6% for raptors). Across the populations analyzed (i.e., with at least three migration records), sample sizes were generally small (on average 11.1 individuals for landbirds; 8.6 for raptors), which means that for many of them the number of migratory links is likely to have been underestimated (Fig. 1c). Among the species tracked, only a fraction of the total European population was represented in our dataset (19.6% [range 0.012- 100] for landbirds; 48.8% [3.34 – 99.2] for raptors). Moreover, coverage of tracked populations is biased towards just a few countries in western and central Europe, with 50% of the migration records we collated (translating into 44% of the migratory links) coming from birds tagged in just five countries (Spain, Sweden, Czech Republic, Germany and Italy; Appendix 10). Eastern European countries tend to be less studied, as testified by fewer links (Fig. 4b,f; Appendix S10) and higher percentages of gap species (Fig. 5a,d) per country. The paucity of tracking data from central Asian countries led us to exclude this region altogether.

The incompleteness of, and biases in our dataset result in important caveats to the interpretation of our results. Estimates of relative strength of migratory links per population (Appendix S11) need to be interpreted as approximations, particularly for populations with small numbers of tracked birds. For example, we estimated for the population of great spotted cuckoo *(Clamator glandarius)* breeding in Spain that 66% migrates to Mauritania and 33% to Senegal/Gambia, but this was based on just three individuals. Furthermore, for those populations tracked with archival tags (mainly GLS; where birds must be recaptured to recover the tracking data), spatial variation in mortality during the non-breeding season can affect the distribution and strength of migratory links.

In addition, insufficient and biased coverage of tracked populations across Eurasia can lead to strong underestimates of the importance of parts of the non-breeding range for many species. For example, all 25 migratory links we found for the lesser kestrel point to western African countries as major non-breeding grounds (Fig. 3). However, as only six populations were tracked, this does not indicate a lesser importance of other parts of the non-breeding range of this species. Indeed, lesser kestrels are known to also form important congregations in southern Africa, likely corresponding to populations breeding in eastern Europe and Asia (Rodríguez et al., 2011). More broadly, landbirds (Briedis et al., 2020) and raptors (e.g., Buechley et al., 2021) from western and central European countries tend to migrate along westerly routes and spend the non-breeding season in the western half of the sub-Saharan region, whereas birds from eastern breeding countries tend to migrate and spend the non-breeding season in the eastern half of the region. As a result, the tracking bias towards western European populations likely plays a substantial role in the spatial patterns we identified for sub-Saharan Africa, including the dominance of links (Fig 4b, e) and of species tracked

per country in western Africa (Fig. 4c,f), and the high numbers of gap species in eastern Africa (Fig. 5a,d). The flyway-level syntheses we present here (Fig. 4) thus need to be interpreted with caution: they reflect only those populations for which tracking data were available, and may not represent the broader European population, and even less so the overall flyway population.

Our dataset is also taxonomically biased, covering only 32% of the landbirds analyzed compared with 52% of raptors for which we could find tracking records. Besides the number of species, body size plays a major role in this bias, as devices for tracking smaller species have only been developed recently and, even today, larger devices have many advantages such as reliability, battery life and remote data transmission (Bridge et al., 2011). This explains why raptors were tracked earlier than landbirds (Fig. 1), and why raptors are better covered per country in terms of species tracked (on average, 7.5% landbirds, 14.6% raptors; Fig 4.c,g) and number of migratory links (Fig 4b,f), and accordingly why countries have lower percentages of gap species for raptors than for landbirds (Fig. 5a,c).

Towards a flyway-scale understanding of geopolitical connectivity

Obtaining a more complete understanding of the connectivity patterns created by migratory birds along the African-Eurasian flyway will necessarily involve collecting more tracking data. This needs a strategic approach involving all stakeholders – from scientists, to conservationists, policy makers and funders – because the associated costs and technical expertise are not trivial. Here, we propose a set of priorities for extending the coverage of tracking studies (Appendix S12) that can contribute substantially to a more representative understanding of the international connectivity patterns of migratory species along the African-Eurasian flyway. Despite corresponding to a small fraction (6.5%) of current knowledge gaps (Fig. 5a,c), these priorities are focused on those species most in need of conservation action (i.e., with decreasing European population) for which such understanding could make more of a difference.

Our proposed priorities are intended as an illustration of how the available data can underpin a strategic plan to guide research for filling knowledge gaps. Whilst we recommend the general principles proposed (i.e., prioritizing species most in need of conservation and tracking a demographically and ecologically representative sample of individuals in each case), stakeholders may well want or need to incorporate other factors into their decision-making process (e.g., economic costs, technical constraints, or expertise availability). We believe the data we have collated and synthesized here, integrated with initiatives using complementary ringing data such as the Eurasian African Bird Migration Atlas project (Spina et al., 2022), can support such strategic planning, namely through the AEMLAP and the Raptors MOU, as well as by the scientific community through initiatives like the Migratory Landbird Study Group (https://migrantlandbirds.org/).

Very few tracking studies have thus far been initiated in Africa (but see Meyburg et al., 2001; Blackburn et al., 2017) and we recommend that this imbalanced be redressed. Focusing tracking efforts in African countries will help complement the information obtained from birds tagged in their European breeding areas, giving us a better picture of the migratory links between the two continents and, thus, creating a fairer information base for all countries in the flyway to make decisions for the establishment of international collaborations. Moreover, some of the birds tracked

in Africa will migrate to eastern breeding grounds (e.g., Rodríguez et al., 2011; Sokolovskis et al., 2018), providing much needed information of the eastern part of the flyway.

For tracking data to contribute to conservation policy, they need to be findable and accessible. Here we have focused on just the breeding and the main non-breeding countries for each bird. However, much more detailed information could be obtained from re-analyses of full tracks, including distributions across the annual cycle (Carneiro et al., 2020), stopover sites along migration routes (Knight et al., 2021), identification of key sites for conservation (Beal et al., 2021b; Morrick et al., 2021) and mortality hotspots (Klaassen et al., 2014), and of threats faced along the flyway (Oppel et al., 2021) across species and populations. Repositories such as MOVEBANK or the Seabird Tracking Database (http://seabirdtracking.org/), already host billions of animal locations (Kays et al., 2021) from across the globe in standardized formats, facilitating scientific collaborations (e.g., Davidson et al., 2020; Beal et al., 2021a), and providing a crucial link between scientists, practitioners and policy-makers. We therefore encourage researchers in future to deposit all tracking data in appropriate repositories such as these.

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Table 1. Summary of the state of knowledge regarding country-level and species-level connectivity. Values are presented as means (with range in parentheses).

Country-level connectivity

		Landbirds	**Raptors**
European countries	No. of known migratory links	14.1 (1 – 42)	10.1 (1 – 31)
	No. of tracked species	3.0 (1 – 7)	2.4 (1 – 7)
African countries	No. of known migratory links	8.9 (1 – 22)	6.5 (1 – 25)
	No. of tracked species	5.8 (1 – 13)	3.2 (1 – 8)

Species-level connectivity

		Landbirds	Raptors
Species	No. of known migratory links	10.7 (1 – 52)	16.6 (2 – 44)
	No. European countries (i.e. populations) tracked	2.3 (1 – 6)	4.0 (1 – 7)
	No. of African countries tracked	6.97 (1 – 27)	8.3 (1 – 25)
Populations	No. of known migratory links	4.6 (1 – 12)	4.2 (1 – 11)

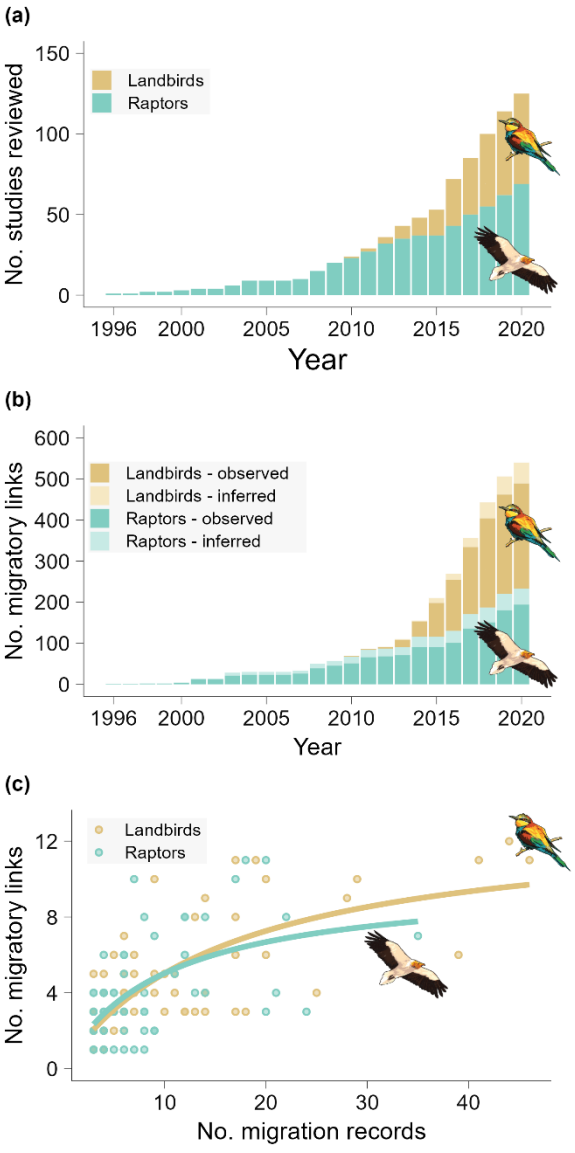

Figure 1. (a) Cumulative number of studies tracking migratory landbirds and raptors across the African-Eurasian flyway over time. (b) Corresponding cumulative number of migratory links (connecting a breeding European country to a non-breeding sub-Saharan African country, for a given species) over time. Only data up to 2020 are shown in panels (a) and (b) (120 studies, 532 links; hence excluding two studies, 12 links) in order to present only years with complete data. (c) Relationship between the number of migration records per population and the number of migratory links derived from them (solid lines obtained through nonlinear regressions).

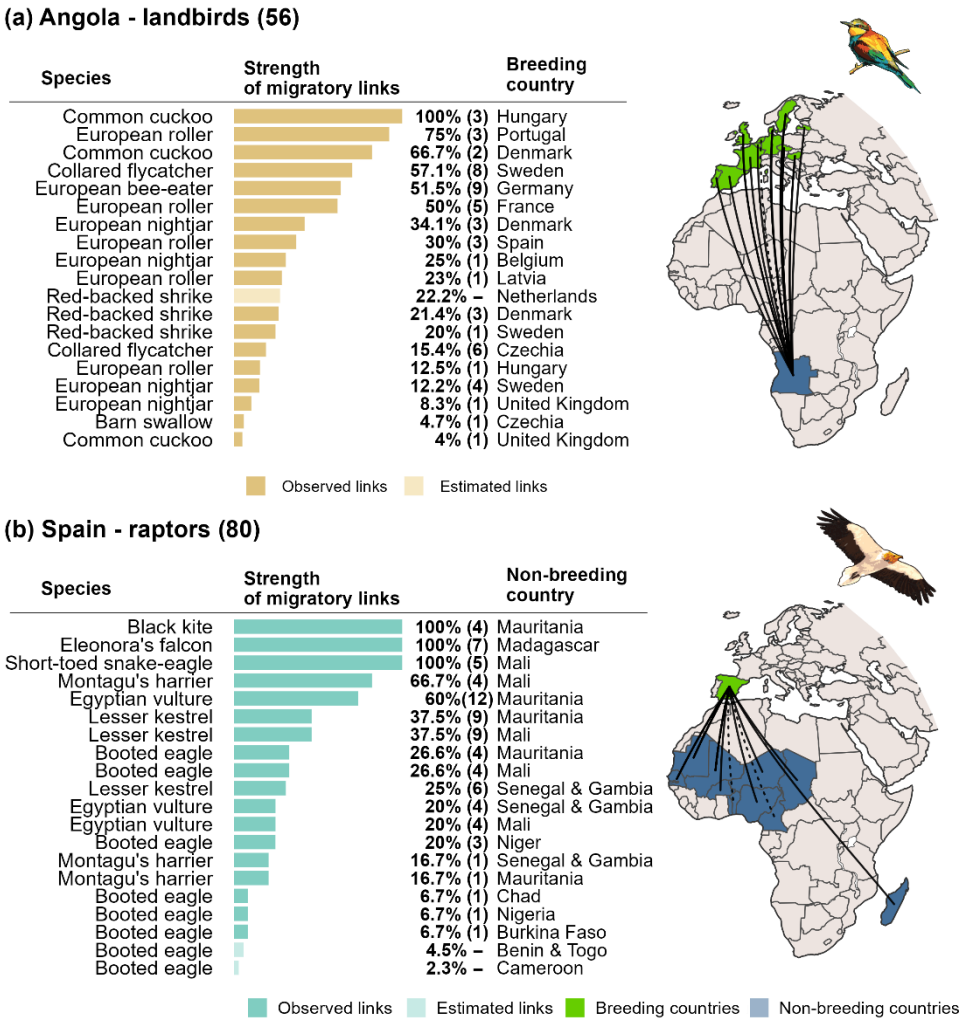

Figure 2. Mapping country-level connectivity, illustrated for (a) landbirds in Angola and (b) raptors in Spain. For each country, we present the list of all migratory links by decreasing order of strength, indicating in each case the species creating the link and the country it connects to. Sample size of tracked individuals are in parentheses. The maps represent how the migratory links (observed: solid lines; inferred: dotted lines) connect the countries in Europe (in green) to countries in sub-Saharan Africa (in blue). Detailed results for all countries in Appendix S10.

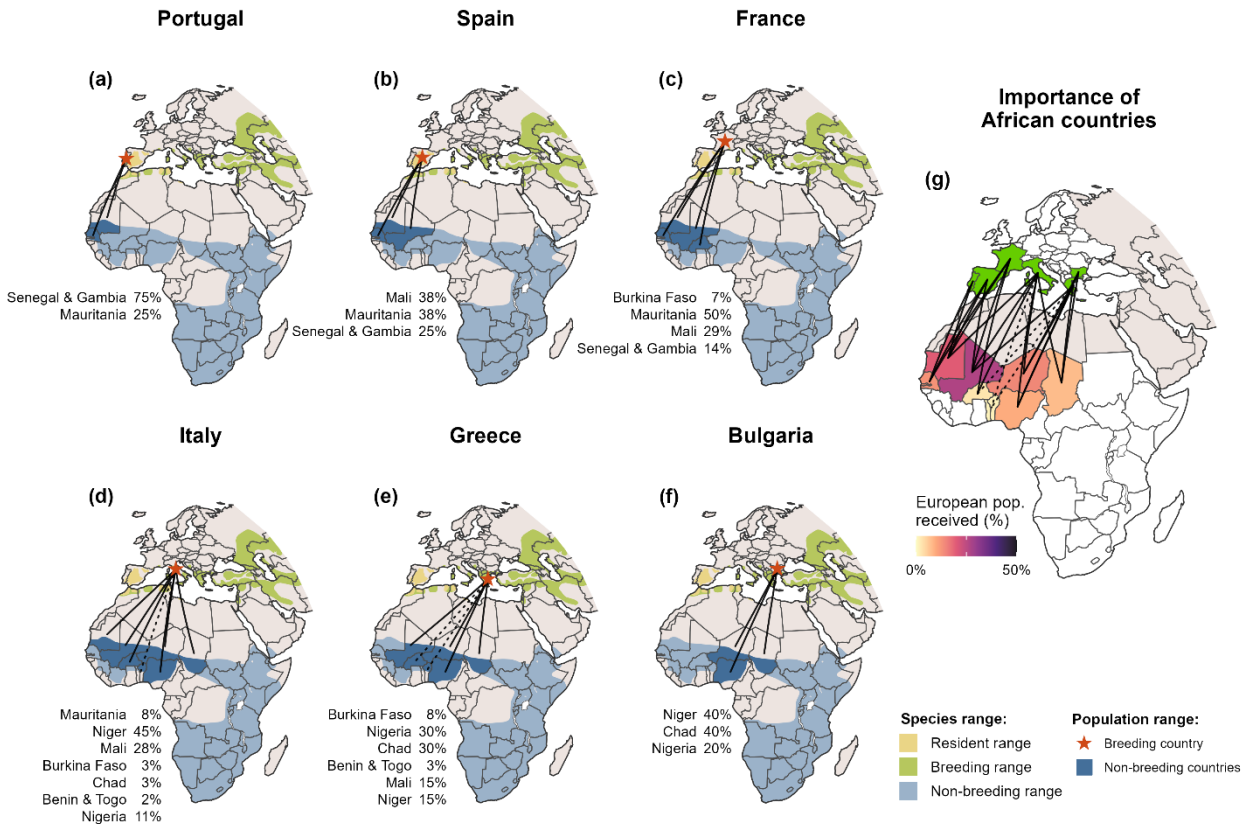

Figure 3. Mapping species-level connectivity, illustrated for the lesser kestrel (*Falco naumanni*). (a - f) Connectivity between countries for each of the six populations of lesser kestrel in our dataset, each map corresponding to the set of birds that breed in a given European country (Portugal, Spain, France, Italy, Greece and Bulgaria) with sample size of tracked individuals between parentheses. Lines represent the migratory links (full lines: observed; dotted lines: inferred), with their respective strength indicated alongside the map. (g) Importance of each country in sub-Saharan Africa as non-breeding grounds for the European population of lesser kestrel, as revealed by the migration links (lines coded as in the other panels). Countries in sub-Saharan Africa are colored according to the percentage of the total European population they host during the non-breeding season. Detailed results for all species in Appendix S11.

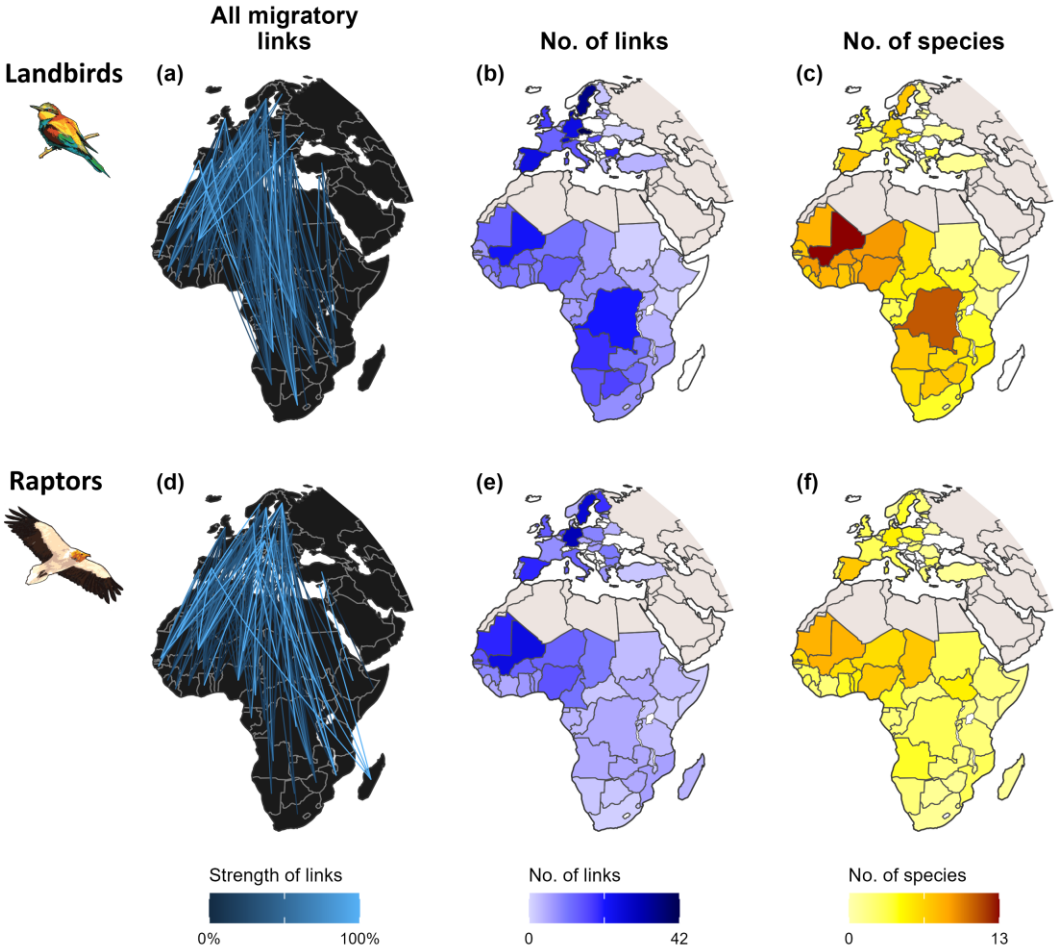

Figure 4. State of knowledge on the connectivity established between countries by landbirds and raptors migrating along the African-Eurasian flyway. (a, d) All migratory links (observed and inferred) obtained from the tracking studies reviewed. (b, e) Number of migratory links per country. (c, f) Number of species tracked per country.

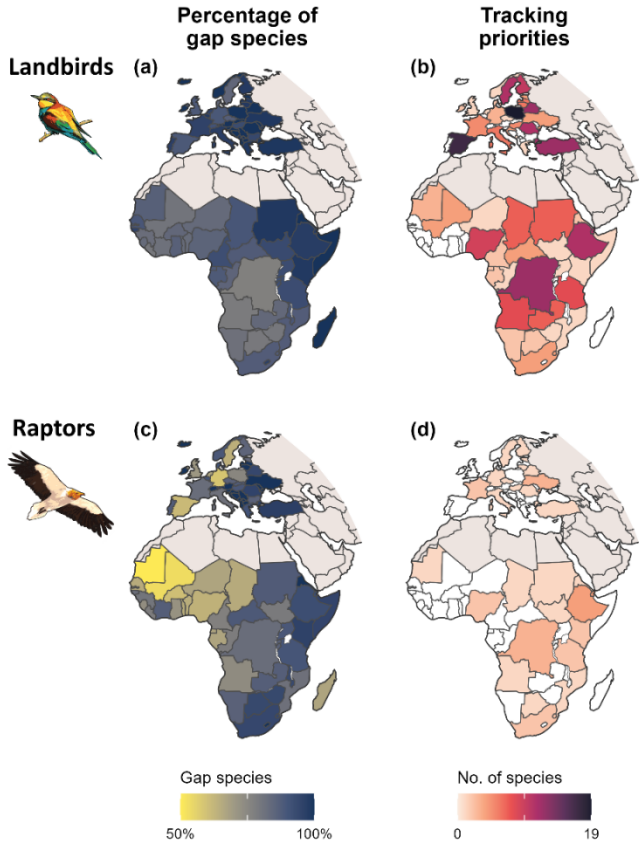

Figure 5. Gaps in knowledge, and tracking priorities for filling those gaps, of migratory connectivity between countries in the African-Eurasian flyway, synthesized per country separately for landbirds and raptors. (a, c) Percentage of migratory species that are gaps (i.e., no migratory links in our dataset). (b, d) Priority countries for future tracking studies, based on the number of species with decreasing European populations for which the country is a priority towards covering at least 50% of the species' population in each sub-region in Europe or in Africa (see Appendix S1 for map of sub-regions). Detailed results for all priority species-country combinations identified in Appendix S12.