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Connectivity between countries established by landbirds and raptors migrating along the African-Eurasian flyway

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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.

25 Introduction

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

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

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

62 Despite these advances, tracking studies are still far from realizing their potential to inform flyway-
63 scale conservation of migratory birds, including in terrestrial environments (Katzner & Arlettaz,
64 2020). First, and despite the increasing recognition of the utility of global data repositories such as

65 MOVEBANK (Kays et al., 2021), much of the existing data are fragmented and confined to the
66 academic literature (Fraser et al., 2018), and remain difficult to find and access (Davidson et al.,
67 2020). Second, given that tracking studies are initiated with different underlying motivations (e.g.,
68 scientific, conservation) and their feasibility is constrained by a diversity of considerations (e.g.,
69 technology, species' ecology, access to funding), existing data tend to be biased towards particular
70 regions and species (Bernard et al., 2021). Even so, as the volume of data increases, it becomes
71 progressively more important to bring them together, synthesize them into formats that are
72 accessible to scientists and conservation practitioners, and translate their results into policy-relevant
73 scientific evidence (Dunn et al., 2019).

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

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

96 Methods

97 Study region

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

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

106 Species and populations

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

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

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

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

131 Definition of migratory link

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

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

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

150 **Compiling migration records from studies**

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

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

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

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

173 **Observed and inferred migratory links**

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

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

186 Estimating the strength of migratory links

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

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

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

200 Trends in knowledge

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

204 Tracking effort per population

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

207 Country-level connectivity

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

210 Species-level connectivity

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

217 Flyway-level connectivity

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

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

222 Knowledge gaps

223 Gaps per country

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

228 Priorities for tracking

229 We recommend that any flyway-wide strategy for tracking long-distance migratory birds to fill
230 knowledge gaps should: (i) prioritize species with decreasing populations (as per the European Red
231 List of Birds; 38 species, 31 landbirds, 7 raptors; Appendix S2); (ii) prioritize the countries across the
232 flyway holding the largest fractions of the population for which no migratory links are known; and
233 (iii) aim to spread tracking effort across species' ranges (i.e., across all sub-regions in both
234 continents), to ensure new tracking data captures the main ecological gradients and a range of
235 migratory strategies. Based on these premises, we identified for each species with decreasing
236 European population, in each sub-region (Appendix S1), a set of priority countries for future tracking,
237 defined as those needed to complement existing studies to ensure that there will be records
238 representative of at least 50% of the overall population of the sub-region (Appendix S2). For
239 example, the European turtle dove (*Streptopelia turtur*) breeds in Western Europe, with the sub-
240 regional population distributed across seven countries: Spain (73.8%), France (24.9%), Portugal
241 (0.9%), UK (0.2%), Belgium (0.2%), the Netherlands (<0.1%) and Luxemburg (<0.1%). Our dataset
242 includes migratory links for France and the UK (25.1% of the sub-regional population), so we
243 highlight the turtle dove in Spain as a priority for future tracking. Through this process, we obtained
244 a set of unique species-country combinations, each highlighting a particular species that we consider
245 a priority for tracking in a particular country, which we synthesized into a list to support future
246 tracking initiatives in each country.

247 Software

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

251 Results

252 Tracking studies, migration records and migratory links

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

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

262 Trends in knowledge

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

267 Tracking effort per population

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

271 Country-level connectivity

272 Mapping migratory links per country reveals their connections to other countries through the long-
273 distance migrations of bird populations – e.g., Spain (Fig. 2a). We found migratory links between 28
274 European countries and 43 sub-Saharan African countries, with substantial variation in the number
275 of links and species tracked per country. On average, each of the European countries analyzed had
276 19.4 (range 1 - 63) migratory links, established by 4.4 (1 – 14) species, linking them to 12.5 (1 - 27)
277 countries in sub-Saharan Africa. Conversely, each of the African countries had on average 14.7 (1 -
278 47) migratory links, established by 8.6 (1-21) species, linking them to 9.5 (1-17) European countries
279 (Table 1; Appendix S10).

280 Species-level connectivity

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

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

297 Flyway-level connectivity

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

305 In Africa, the western sub-region stands out in terms of the number of migratory links for both
306 landbirds and raptors, in particular Mali (47 links; 21 species) but also Mauritania (33; 16), Nigeria
307 (29; 16), and Burkina Faso (27; 15). Countries in central and southern Africa also stand out for links
308 for landbirds (but not for raptors), in particular the Democratic Republic of Congo (26 links; 14
309 species), Angola (24; 11), Botswana (19; 8) and Namibia (17; 8). We found few links and few tracked
310 species for countries in Eastern Africa (e.g., Somalia, Kenya).

311 Knowledge gaps

312 The vast majority of long-distance migratory bird species in each country have not been tracked (Fig.
313 5a,c; Appendix S12). Within Europe, the average percentage of gap species per country was 96.7%
314 for landbirds (minimum 83.7% in Denmark; maximum 100% in 21 countries) and 90.4% for raptors
315 (minimum 58.3% in Germany; maximum 100% in 19 countries). In Africa, there were on average
316 87.8% gap species per country for landbirds (minimum 76.6% in the Democratic Republic of the
317 Congo; maximum 100% in three countries) and 79.7% for raptors (minimum 50% in Mauritania;
318 maximum 100% in Eritrea and Lesotho).

319 Priorities for future tracking

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

327 Discussion

328 A wealth of data on the African-Eurasian flyway

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

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

336 For example, existing data reveal how the Danish population of willow warblers (*Phylloscopus*
337 *trochilus*) disperses across nine countries in western and central Africa (Lerche-Jørgensen et al.,
338 2017), establishing migratory links of relatively low strength (average 11.1%), whereas European
339 rollers (*Coracias garrulus*) tagged in six European countries establish fewer but stronger links (26%)
340 with six southern African countries (Finch et al., 2015). In turn, Ospreys (*Pandion haliaetus*) have
341 contrasting patterns across populations, with Finish breeding birds dispersing broadly across 11
342 countries in Africa (Saurola, 2020), whereas birds from the UK appear to concentrate in just five
343 western African countries (Mackrill, 2017), particularly in Senegal and Gambia (together hosting 62%
344 of that population; Appendix S11). These syntheses provide key information to support species-
345 focused international cooperation efforts, including through species' action plans. For example, the
346 Flyway Action Plan for the European roller strongly recommends habitat protection (e.g., through
347 agri-environment schemes) and additional research and monitoring in non-breeding areas (Tokody
348 et al., 2017); our results indicate that focusing those efforts on Namibia, Angola and Botswana would
349 benefit populations breeding across Europe (Appendix S11).

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

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

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

379 Substantial knowledge gaps remain

380 Our results also highlight that the currently existing tracking data are incomplete (Appendix S12).
381 Indeed, across all 2565 populations (1982 of landbirds, 583 of raptors) of long-distance migratory
382 landbirds and raptors in Europe (i.e., 118 species across 43 countries), only 123 (4.8%) have been
383 tracked (3.4% for landbirds, 9.6% for raptors). Across the populations analyzed (i.e., with at least
384 three migration records), sample sizes were generally small (on average 11.1 individuals for
385 landbirds; 8.6 for raptors), which means that for many of them the number of migratory links is likely
386 to have been underestimated (Fig. 1c). Among the species tracked, only a fraction of the total
387 European population was represented in our dataset (19.6% [range 0.012- 100] for landbirds; 48.8%
388 [3.34 – 99.2] for raptors). Moreover, coverage of tracked populations is biased towards just a few
389 countries in western and central Europe, with 50% of the migration records we collated (translating
390 into 44% of the migratory links) coming from birds tagged in just five countries (Spain, Sweden,
391 Czech Republic, Germany and Italy; Appendix 10). Eastern European countries tend to be less
392 studied, as testified by fewer links (Fig. 4b,f; Appendix S10) and higher percentages of gap species
393 (Fig. 5a,d) per country. The paucity of tracking data from central Asian countries led us to exclude
394 this region altogether.

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

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

416 per country in western Africa (Fig. 4c,f), and the high numbers of gap species in eastern Africa (Fig.
417 5a,d). The flyway-level syntheses we present here (Fig. 4) thus need to be interpreted with caution:
418 they reflect only those populations for which tracking data were available, and may not represent
419 the broader European population, and even less so the overall flyway population.

420 Our dataset is also taxonomically biased, covering only 32% of the landbirds analyzed compared with
421 52% of raptors for which we could find tracking records. Besides the number of species, body size
422 plays a major role in this bias, as devices for tracking smaller species have only been developed
423 recently and, even today, larger devices have many advantages such as reliability, battery life and
424 remote data transmission (Bridge et al., 2011). This explains why raptors were tracked earlier than
425 landbirds (Fig. 1), and why raptors are better covered per country in terms of species tracked (on
426 average, 7.5% landbirds, 14.6% raptors; Fig 4.c,g) and number of migratory links (Fig 4b,f), and
427 accordingly why countries have lower percentages of gap species for raptors than for landbirds (Fig.
428 5a,c).

429 Towards a flyway-scale understanding of geopolitical connectivity

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

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

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

456 in Africa will migrate to eastern breeding grounds (e.g., Rodríguez et al., 2011; Sokolovskis et al.,
457 2018), providing much needed information of the eastern part of the flyway.

458 For tracking data to contribute to conservation policy, they need to be findable and accessible. Here
459 we have focused on just the breeding and the main non-breeding countries for each bird. However,
460 much more detailed information could be obtained from re-analyses of full tracks, including
461 distributions across the annual cycle (Carneiro et al., 2020), stopover sites along migration routes
462 (Knight et al., 2021), identification of key sites for conservation (Beal et al., 2021b; Morricks et al.,
463 2021) and mortality hotspots (Klaassen et al., 2014), and of threats faced along the flyway (Opell et
464 al., 2021) across species and populations. Repositories such as MOVEBANK or the Seabird Tracking
465 Database (<http://seabirdtracking.org/>), already host billions of animal locations (Kays et al., 2021)
466 from across the globe in standardized formats, facilitating scientific collaborations (e.g., Davidson et
467 al., 2020; Beal et al., 2021a), and providing a crucial link between scientists, practitioners and policy-
468 makers. We therefore encourage researchers in future to deposit all tracking data in appropriate
469 repositories such as these.

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

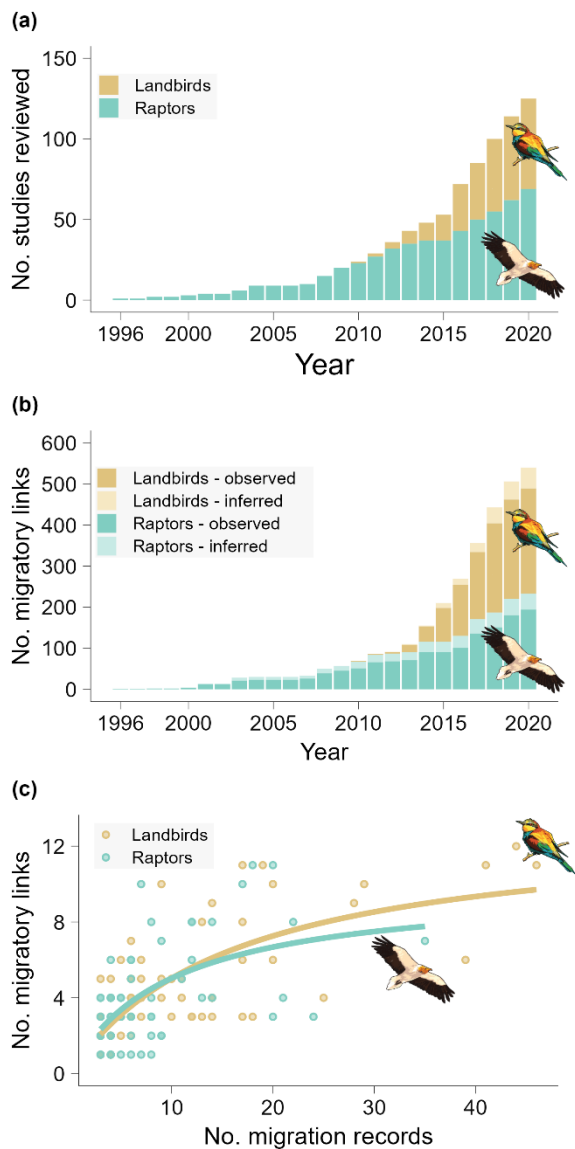
Country-level connectivity

		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)

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Species-level connectivity

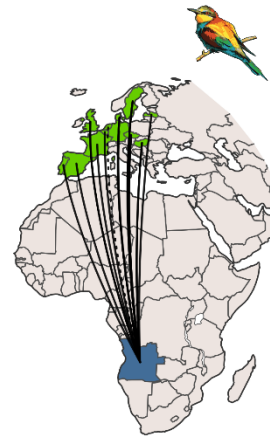
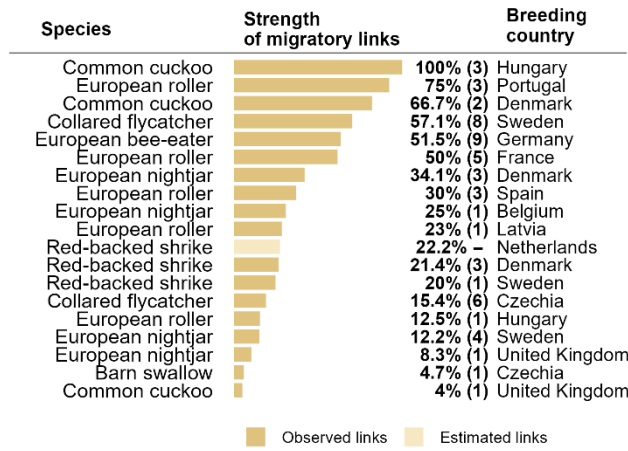
		Landbirds	Raptors
Species	No. of known migratory links	10.7 (1 – 52)	16.6 (2 – 44)
	No. European countries (i.e. populations) tracked	2.3 (1 – 6)	4.0 (1 – 7)
	No. of African countries tracked	6.97 (1 – 27)	8.3 (1 – 25)
Populations	No. of known migratory links	4.6 (1 – 12)	4.2 (1 – 11)



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

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(a) Angola - landbirds (56)



(b) Spain - raptors (80)

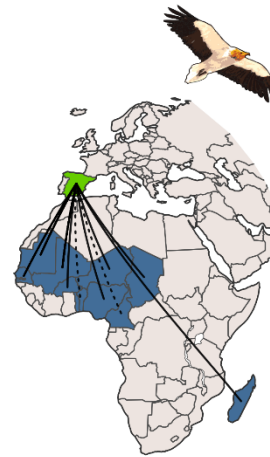
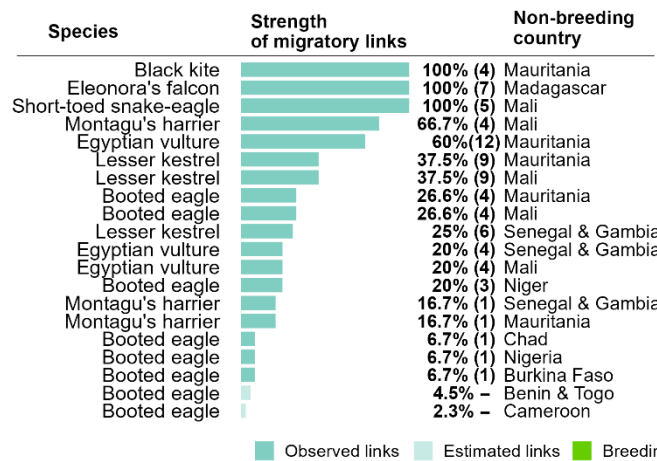
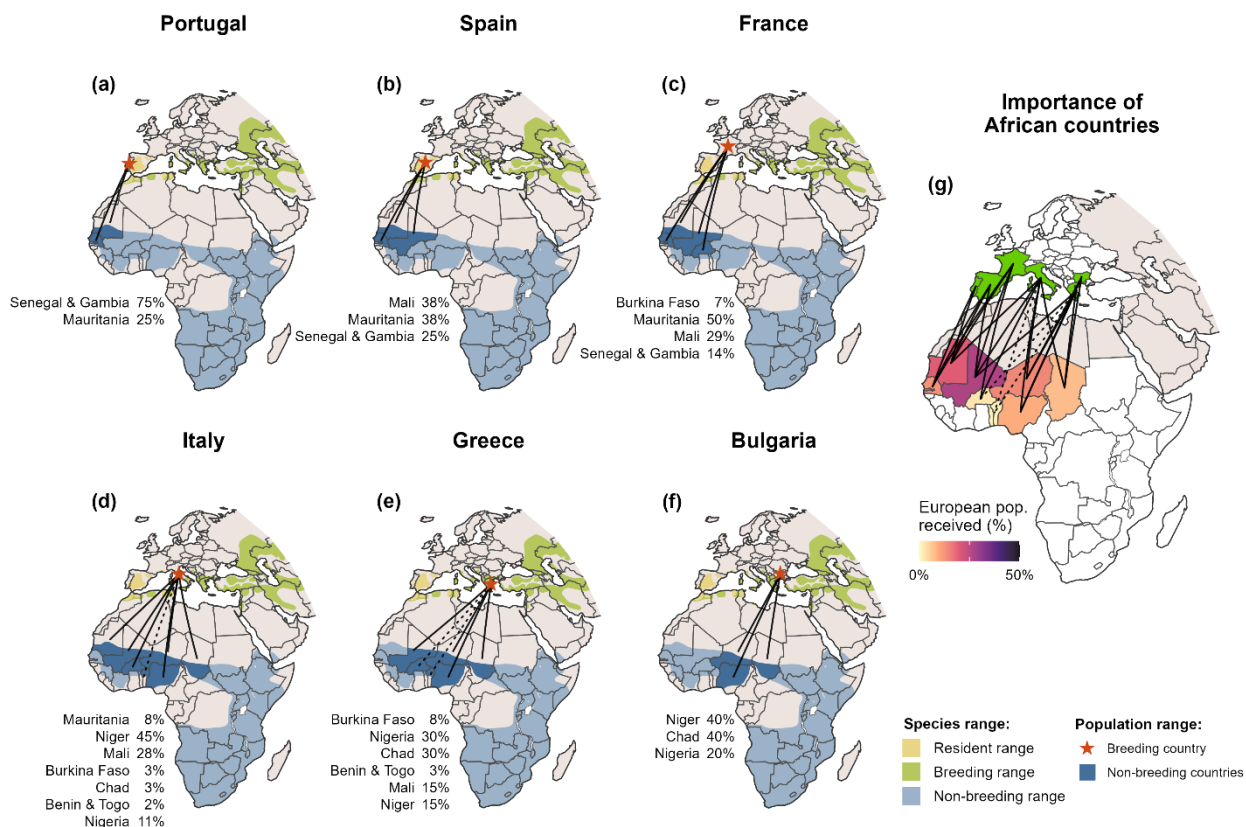
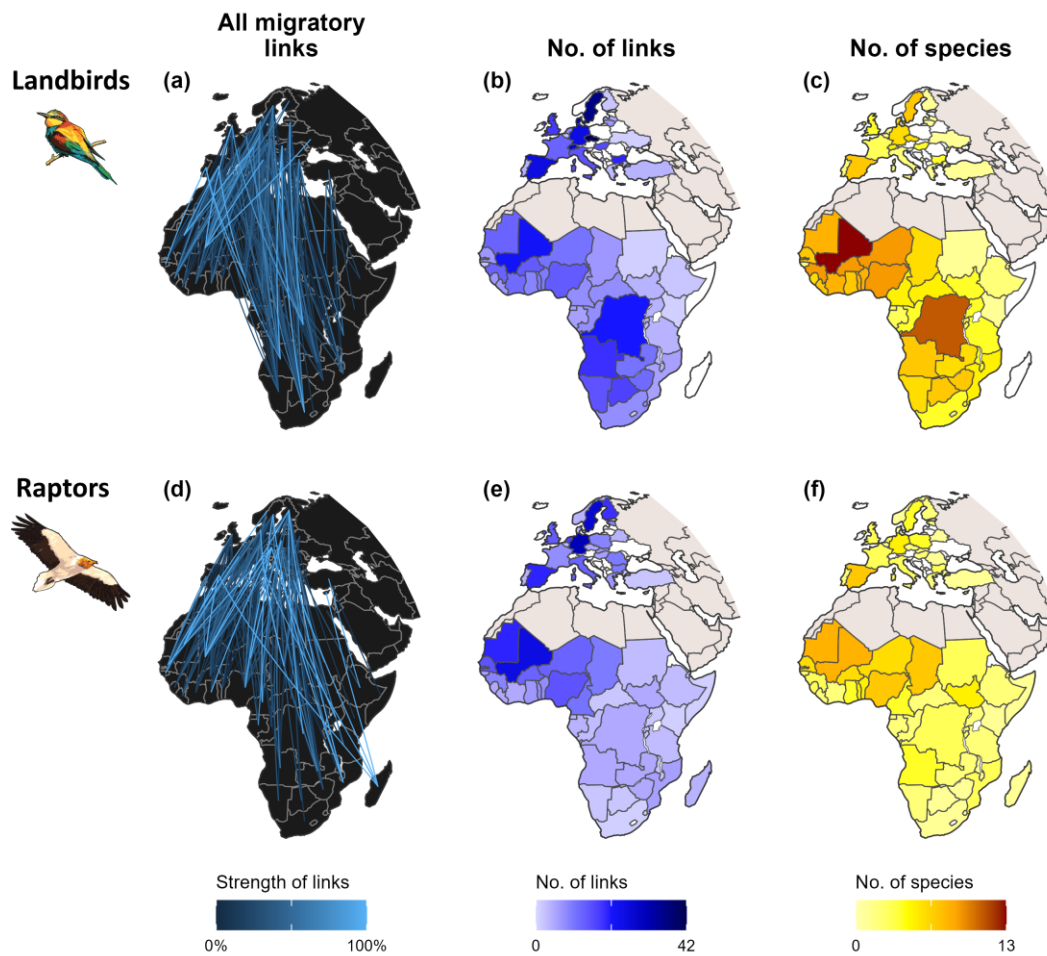


Figure 2. Mapping country-level connectivity, illustrated for (a) landbirds in Angola and (b) raptors in Spain. For each country, we present the list of all migratory links by decreasing order of strength, indicating in each case the species creating the link and the country it connects to. Sample size 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.



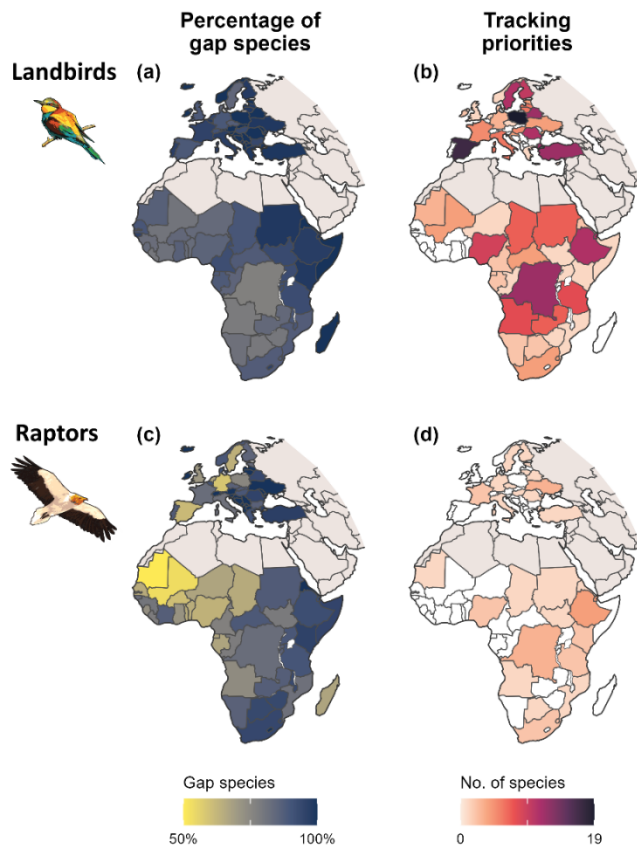
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685 Figure 3. Mapping species-level connectivity, illustrated for the lesser kestrel (*Falco naumanni*). (a - f)
 686 Connectivity between countries for each of the six populations of lesser kestrel in our dataset, each
 687 map corresponding to the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



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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.



700
 701 Figure 5. Gaps in knowledge, and tracking priorities for filling those gaps, of migratory connectivity
 702 between countries in the African-Eurasian flyway, synthesized per country separately for landbirds
 703 and raptors. (a, c) Percentage of migratory species that are gaps (i.e., no migratory links in our
 704 dataset). (b, d) Priority countries for future tracking studies, based on the number of species with
 705 decreasing European populations for which the country is a priority towards covering at least 50% of
 706 the species' population in each sub-region in Europe or in Africa (see Appendix S1 for map of sub-
 707 regions). Detailed results for all priority species-country combinations identified in Appendix S12.