

1 **Title: Low migratory connectivity is common in long-distance migrant**

2 **birds**

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9
10 **Running headline:** Low migratory connectivity

11 **Keywords:** climate change, migration, migratory connectivity, migratory dispersal,
12 population declines

15 **Abstract**

- 16 1. Estimating how much long-distance migrant populations spread out and mix during
17 the non-breeding season (migratory connectivity) is essential for understanding and
18 predicting population dynamics in the face of global change.
- 19 2. We quantify variation in population spread and inter-population mixing in long-
20 distance, terrestrial migrant land-bird populations (712 individuals from 98
21 populations of 45 species, from tagging studies in the Neotropic and Afro-Palearctic
22 flyways). We evaluate the Mantel test as a metric of migratory connectivity, and
23 explore the extent to which variance in population spread can be explained simply by
24 geography.
- 25 3. The mean distance between two individuals from the same population during the non-
26 breeding season was 743 km, covering 10–20% of the maximum width of Africa /
27 South America. Individuals from different breeding populations tended to mix during
28 the non-breeding season, though spatial segregation was maintained in species with
29 relatively large non-breeding ranges (and, to a lesser extent, those with low
30 population-level spread). A substantial amount of between-population variation in
31 population spread was predicted simply by geography, with populations using non-
32 breeding zones with limited land availability (e.g. Central America compared to South
33 America) showing lower population spread.
- 34 4. The high levels of population spread suggest that deterministic migration tactics are
35 not generally adaptive; this makes sense in the context of the recent evolution of the
36 systems, and the spatial and temporal unpredictability of non-breeding habitat.

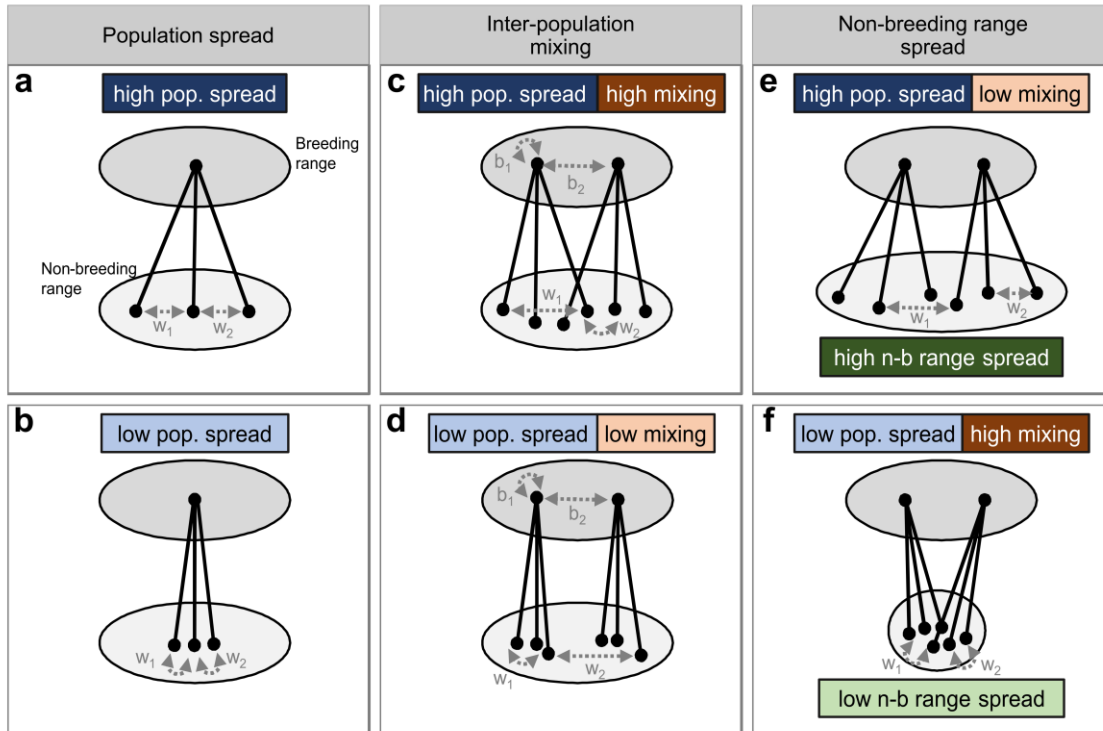
37 5. The conservation implications of generally low connectivity are that the loss (or
38 protection) of any non-breeding site will have a diffuse but widespread effect on
39 many breeding populations. Although low connectivity should engender population
40 resilience to shifts in habitat (e.g. due to climate change), we suggest it may increase
41 susceptibility to habitat loss. We hypothesise that because a migrant species cannot
42 adapt to both simultaneously, migrants generally may be more susceptible to
43 population declines in the face of concurrent anthropogenic habitat and climate
44 change.

45 **Introduction**

46 Migratory animals are currently suffering global declines (Bolger et al. 2008; Brower et al.
47 2012; Gilroy et al. 2016), and their conservation requires an understanding of ‘migratory
48 connectivity’, i.e. how breeding and non-breeding sites are connected via the trajectories of
49 individual migrants (Webster *et al.* 2002; Martin *et al.* 2007; Runge *et al.* 2014; Vickery *et*
50 *al.* 2014; Runge *et al.* 2015; Bauer, Lisovski & Hahn 2016). Migratory connectivity is
51 typically described along a continuum from low (weak, or diffuse) to high (strong). Under
52 low connectivity, individual migrants from a particular breeding population spread over a
53 large area during the non-breeding season, mixing with individuals from different breeding
54 populations, whilst strong connectivity reflects the use of discrete, population-specific non-
55 breeding areas (Webster *et al.* 2002; Newton 2008). For example, Great Reed Warblers
56 *Acrocephalus arundinaceus* from a single European breeding population can be found spread
57 across most of West Africa during the non-breeding season (Lemke *et al.* 2013), whereas
58 Common Nightingales *Luscinia megarhynchos* from spatially separate European breeding
59 populations retain reasonable spatial separation on their West African non-breeding grounds
60 (Hahn *et al.* 2013).

61 Migratory connectivity has two key spatial components, which are often conflated.
62 ‘Population spread’ (a population-level trait) describes the degree to which individuals from a
63 single breeding population spread out during the non-breeding season (**Fig. 1a & b**), whilst
64 inter-population mixing on the non-breeding grounds (a species- or multi-population-level
65 trait) describes the degree to which individuals from different breeding populations mix or
66 co-occur during the non-breeding season (**Fig. 1c & d**). Generally speaking, high population

67 spread will promote inter-population mixing on the non-breeding grounds (**Fig. 1c**; ‘weak’
68 connectivity *sensu* Webster *et al.* 2002) whilst low population spread will reduce it (**Fig. 1d**;
69 ‘strong’ connectivity). The relationship between population spread and inter-population
70 mixing should be mediated, however, by the relative size of the non-breeding range (‘non-
71 breeding range spread’, a species-level trait). Here, we define non-breeding range spread as
72 the net area covered by individuals from all focal populations of a species; this combines
73 information on migratory dispersion *sensu* Gilroy *et al.* (2016; i.e. the size of the species’
74 non-breeding range relative to its breeding range) as well as the spatial separation of focal
75 breeding populations. Thus, a relatively small non-breeding distribution (or a relatively short
76 distance between focal breeding populations) will promote inter-population mixing on the
77 non-breeding grounds even if population spread is low (**Fig. 1f**), whilst a larger non-breeding
78 range (or a greater distance between focal breeding populations) will reduce mixing even if
79 population spread is high (**Fig. 1e**).



80

81 **Figure 1** Migratory connectivity arises through both the spreading and mixing of breeding populations. In all
 82 panels, the grey ellipse represents a hypothetical species' breeding range, and the white ellipse the non-breeding
 83 ('winter') range; black points illustrate the breeding and non-breeding sites of individual migrants, connected by
 84 lines which represent their migratory trajectory. Individuals from the same breeding site are grouped into
 85 populations (one population in **a–b**, two in **c–f**). Population spread (**a**, **b**) is measured as the mean pairwise
 86 distance between the non-breeding sites of all individuals (w_1, w_2, \dots) from a focal breeding population, with
 87 high values indicating high population spread (**a**). Inter-population mixing on the non-breeding grounds (**c**, **d**), a
 88 multi-population-level trait, is measured as the Mantel correlation coefficient between the pairwise distance-
 89 matrix of the breeding sites of all individuals (b_1, b_2, \dots) and the corresponding distance-matrix of their non-
 90 breeding sites (w_1, w_2, \dots), with high positive correlations indicating low mixing (**d**). The relationship between
 91 population spread and inter-population mixing should be mediated by the relative size of the species' non-
 92 breeding range (non-breeding range spread, measured as the mean pairwise distance between the non-breeding
 93 sites of all individuals (w_1, w_2, \dots) regardless of breeding population; **e**, **f**).

94 An understanding of migratory connectivity – in terms of both population spread and inter-
95 population mixing – is important for predicting the response of migrants to environmental
96 change (Taylor & Norris 2010). Inter-population mixing on the non-breeding grounds
97 determines the extent to which different breeding populations experience similar non-
98 breeding conditions – and so the extent to which they are subject to the same potential drivers
99 of population change – as well as their potential to interact, for example, through density-
100 dependent processes (Esler 2000). Population spread determines the spatial scale of
101 environmental change to which a breeding population will be affected during the non-
102 breeding season, as well as its potential to track environmental change (Cresswell 2014).
103 Thus, a population or species which relies on only a few non-breeding sites should be
104 vulnerable to any environmental change at those sites, whereas one which spreads out over a
105 wide non-breeding area should be affected only by broad-scale environmental change and, by
106 ‘spreading risk’, may be more resilient (Gilroy *et al.* 2016). Note that, whilst our focus is on
107 the spatial components of migratory connectivity, the degree of temporal synchrony within
108 and between breeding populations also has important consequences for population spread and
109 mixing (Bauer, Lisovski & Hahn 2016). For instance, low temporal synchrony between two
110 breeding populations will reduce their potential to interact during the non-breeding season if
111 they end up using the same sites but at different times.

112 Patterns of migratory connectivity ultimately arise through variation in the migratory
113 trajectories of individual migrants. Because many adult land-birds capitalise on prior
114 knowledge by returning to their first (necessarily survivable) non-breeding site (Newton
115 2008), migratory connectivity in many cases should reflect the trajectories of successful
116 juveniles (Cresswell 2014). For many long-distance migrant land-birds, juveniles travel

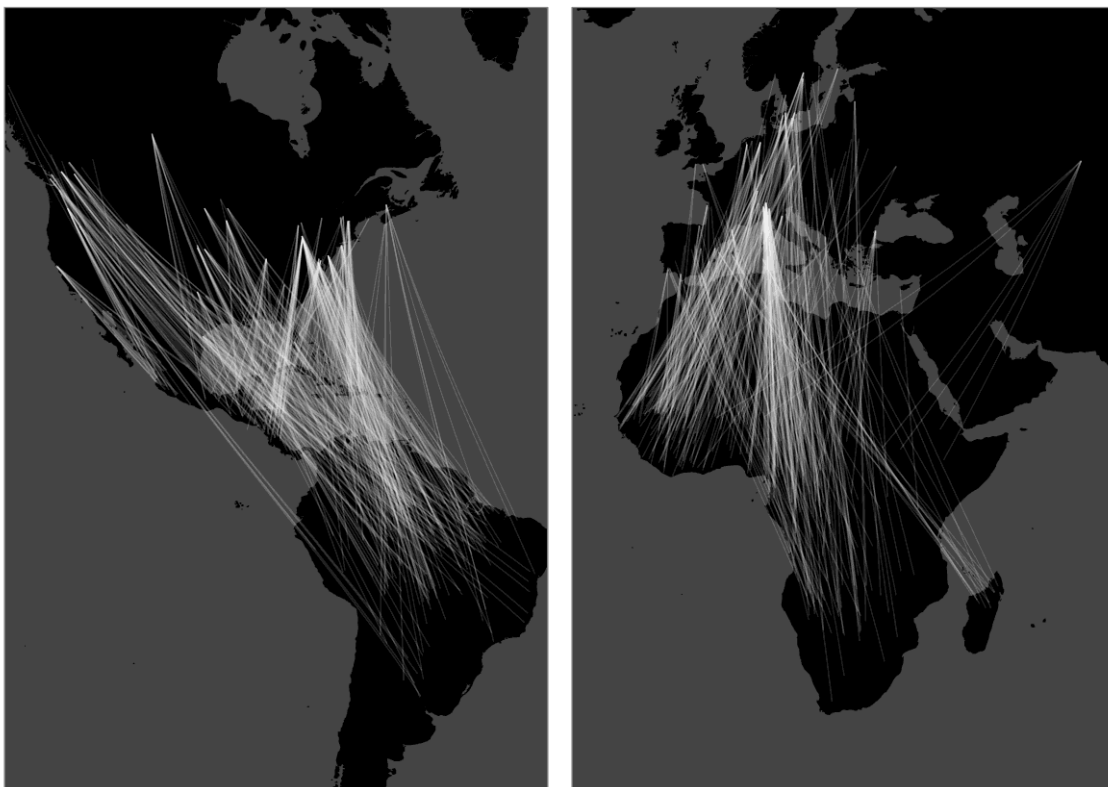
117 separately from (and often later than) adults, orienting in a particular direction at a particular
118 time of year to reach non-breeding grounds thousands of kilometers away (Newton 2008).
119 The specificity of these genetic instructions therefore plays an underlying role in defining
120 patterns of migratory connectivity. Deterministic genetic programs (promoting low spread
121 within a brood) are likely to be favoured when the spatial and temporal predictability of the
122 non-breeding environment is high, whilst less predictable environments might be expected to
123 erode selection for genetic determinism, resulting in a more variable, ‘bet-hedging’ strategy
124 (Botero *et al.* 2015).

125 Even under relatively deterministic genetic controls, variable weather and wind conditions
126 experienced *en route* (Elkins 1983), and the varying ability of migrants (and juveniles in
127 particular) to fully compensate for any major displacement from their genetically
128 predetermined migration trajectory (Perdeck 1958; Thorup *et al.* 2003; Thorup *et al.* 2011)
129 will result in deviations, which likely accrue with increasing migration distance. The extent to
130 which these deviations – on top of any phenotypic variance in initial departure direction –
131 affect population spread, will depend on various factors, including; the timing of migration,
132 with phenological synchrony exposing individuals to more similar weather and wind
133 conditions (Ouwehand *et al.* 2015; Bauer, Lisovski & Hahn 2016); geographical barriers *en*
134 *route* such as mountain ranges, deserts and oceans, which may create bottlenecks or force
135 detours (Delmore, Fox & Irwin 2012; Agostini, Panuccio & Pasquaretta 2015); the use of
136 social information *en route*, potentially acquired from experienced adults and facilitated by
137 congregations at bottlenecks (Williams & Kalmbach 1943; Thorup & Rabol 2001); and,
138 perhaps most fundamentally, continental configuration and the area of available land in the
139 species’ non-breeding range.

140 Recent advances in animal tagging technology provide a unique opportunity to explore
141 variation in migratory connectivity for a representative range of migratory species and
142 systems (Bridge *et al.* 2011). Having clarified the conceptual framework for understanding
143 migratory connectivity, we here quantify population spread and inter-population mixing
144 using data from 712 individual migrant land-birds tracked from 98 populations of 45 species
145 across two trans-continental flyways (the Neotropic and Afro-Palearctic; **Fig. 2, Table S1**),
146 evaluating the degree to which they show high or low migratory connectivity. We test the
147 influence of population spread and non-breeding range spread on inter-population mixing on
148 the non-breeding grounds (**Fig. 1d, e**), highlighting the importance of scale and addressing
149 the potential inadequacies of the Mantel test (Ambrosini, Moller & Saino 2009) as a stand-
150 alone metric of migratory connectivity.

151 We then construct a simple model to explain between-population variation in population
152 spread. We predict that populations using non-breeding ‘zones’ with more limited land
153 availability e.g. Ovenbirds *Seiurus aurocapilla* (Hallworth & Marra 2015) in Central
154 America or European Rollers *Coracias garrulus* in southern Africa (Finch *et al.* 2015) will
155 show lower population spread compared to those in zones with higher land availability, e.g.
156 Blackpoll Warblers *Setophaga striata* in South America (DeLuca *et al.* 2015) or Pied
157 Flycatchers *Ficedula hypoleuca* in western Africa (Ouwehand *et al.* 2016). This effect should
158 interact with relative breeding longitude because, for instance, populations breeding in
159 western North America and migrating to South America cannot spread out in a westerly
160 direction without ending up in the Pacific Ocean, or must migrate much longer distances than
161 eastern populations to utilize all available non-breeding habitat; the reverse should be true for
162 populations using the Central American non-breeding zone (e.g. Swainson's Thrush,

163 *Catharus ustulatus* Cormier *et al.* 2013). This simple ‘null model’ does not attempt to explain
164 all variation in population spread, but rather test the explanatory power of one potential
165 underlying mechanism; land availability. In this model we assume the simplest possible
166 situation – that migrants migrate in a southerly direction and spread out east to west over the
167 closest available land within the latitudinal zone of suitable non-breeding habitat, so that
168 breeding longitude will be a predictor of population spread. If land availability is a good
169 predictor of population spread, this lends support to a more stochastic migration tactic, with
170 generally high population spread prevented only by geographical constraints. We also include
171 species identity as a random effect, to test the extent to which populations belonging to the
172 same species (or family) share similar migration tactics (with high or low population spread),
173 irrespective of geography.



174

175 **Figure 2** Lines connect the breeding and non-breeding sites of 712 individual land-birds tracked from 98
176 northern hemisphere breeding populations of 45 species across two trans-continental flyways.

177 **Materials and methods**

178 *Data acquisition*

179 A comprehensive search of peer-reviewed tracking studies was conducted for all European
180 and North American species classed (according to BirdLife;
181 <http://www.birdlife.org/datazone/species/search>) as migratory land-birds by entering the
182 terms [*latin name*] AND *migra** AND (*gps* OR *geolo** OR *satellite*) into the Web of Science
183 online library. From these studies, breeding (i.e. tagging) and non-breeding (i.e. the site
184 where an individual spent the majority of the non-breeding period after migration) locations
185 of individual birds were extracted (or approximated from plotted map locations using Google
186 Earth when precise coordinates were not given). For individuals which moved between
187 several non-breeding sites, we recorded the location of the first only. We excluded species
188 with data from only one individual, and restricted our analyses to adult birds tagged during
189 the breeding season in the northern hemisphere. Individuals of the same species tagged
190 within 100 km of one another (which meant tagged at the same study site in almost all cases;
191 mean distance between two individuals assigned to the same breeding population = 8.8 km,
192 median = <1 km) were grouped into 'populations', the principle unit of analysis (**Table S1**).
193 We deliberately chose not to include ring-recovery data – which are extensive for some
194 migrant species, particularly in the Afro-Palearctic – due to the non-trivial issue of spatial
195 biases in re-encounter and reporting rates (Procházka *et al.* 2016). We defined the Afro-
196 Palearctic system of long-distance migrant birds as comprising all populations breeding in

197 Europe west of 65°E and with a non-breeding area in Africa south of 20°N. The Neotropic
198 system was defined as all populations breeding in North America and with a non-breeding
199 area south of 30°N.

200 *Metrics of population spread*

201 For the Afro-Palearctic system we collated data on 323 individuals from 50 populations of 29
202 species, with a mean of 6.5 (range = 2–48) individuals per population and 1.7 (1–6)
203 populations per species. In the Neotropic system, corresponding data were available for 389
204 individuals from 48 populations of 16 species, with a mean of 8.1 (range = 2–34) individuals
205 per population and 3.0 (1–8) populations per species.

206 As an initial metric of population spread we calculated, for each breeding population, the
207 maximum pairwise distance between individual non-breeding sites. ‘Maximum spread’
208 clearly increases with the number of individuals tracked per population (correlation between
209 maximum spread and number of individuals; $r = 0.62$, $d.f. = 96$, $p < 0.001$), though the
210 relationship must eventually reach an asymptote. To determine the approximate level of
211 maximum population spread at which this asymptote occurs, we modelled the effect of
212 sample size on maximum spread using linear mixed models with a random intercept of
213 species identity. Four alternative models were constructed using either sample size, the
214 natural logarithm of sample size, the quadratic of sample size, or the intercept only to
215 determine the best function to describe the relationship. The maximum distance between two
216 individuals from the same breeding population during the non-breeding season was best
217 explained by the logarithm of sample size (**Table S2**), with the fitted line levelling off at ~
218 3,000 km (**Fig. S1**).

219 As our principle metric of population spread we calculated the mean (rather than maximum)
220 pairwise distance between individual non-breeding sites for each population, which was only
221 weakly contingent on the number of individuals tracked per population ($r = 0.27$, $d.f. = 96$, p
222 $= 0.006$).

223 *Metric of inter-population mixing on the non-breeding grounds*

224 Metrics of inter-population mixing require the tracking of individuals from multiple
225 populations. For the Afro-Palearctic system 16 species were tracked from more than one
226 population, with a mean of 3.7 populations per species (range = 2–11) and 5.0 (1.5–31.7)
227 individuals per population. In the Neotropics, multi-population data were available for 12
228 species, with a mean of 4.1 populations per species (2–13) and 6.7 (1.5–17.0) individuals per
229 population.

230 For each of these species we quantified inter-population mixing as the Mantel correlation
231 coefficient (ranging from -1 to $+1$) between pairwise distance matrices of individual breeding
232 and non-breeding sites (Ambrosini, Moller & Saino 2009). This quantifies whether distances
233 between individual breeding sites are maintained during the non-breeding season. Strong
234 positive Mantel coefficients indicate that individuals which breed close together also spend
235 the non-breeding season relatively close together, and vice versa (i.e. low inter-population
236 mixing).

237 *Does inter-population mixing increase with population spread?*

238 To explore the conditions under which low inter-population mixing ('strong' connectivity)
239 occurs, we constructed a linear model with Mantel correlation coefficient as the dependent

240 variable (**Table 1**). As illustrated in **Fig. 1**, we expect high population spread to promote
241 inter-population mixing on the non-breeding grounds (i.e. reduce the strength of the Mantel
242 correlation), and high non-breeding range spread to reduce mixing (i.e. increase the Mantel
243 coefficient). For each species, we therefore calculated the mean population spread of all
244 constituent populations ('mean population spread'), as well as the mean pairwise distance
245 between all non-breeding sites, regardless of breeding population ('non-breeding range
246 spread'). We included both as fixed effects, in addition to the quadratic effect of non-
247 breeding range spread (because an initial plot of Mantel coefficient against species spread
248 illustrated a non-linear effect) and the mean pairwise distance between all breeding sites
249 (because increasing the spatial separation of focal breeding populations should reduce
250 migratory mixing).

251 *Does population spread depend on land availability or species identity?*

252 We then tested the explanatory power of (a proxy for) land availability using a linear mixed
253 model with population spread as the dependent variable (**Table 2**). We first assigned each
254 population, based on the mean latitude of individual non-breeding sites, into northern and
255 southern non-breeding 'zones', reflecting the profound differences in the land-to-sea ratio
256 above and below 12°N in the Neotropics (the approximate border of Central and South
257 America) and 4°N in the Afro-Palearctic (the latitude at which Africa narrows at the Gulf of
258 Guinea). The breeding longitude of a population (the mean longitude of individual breeding
259 sites for each population) represents its position with respect to land to the south of it, and so
260 the potential geographical constraints presented *en route*. For example, western European
261 populations which spend the non-breeding season in southern Africa are due north of the

262 Atlantic Ocean, so their population spread may be more constrained than populations from
263 eastern Europe.

264 Fixed effects were thus the three-way interaction between migration system (Afro-Palearctic
265 or Neotropic), non-breeding zone (north or south) and breeding longitude (centered
266 separately for Afro-Palearctic and Neotropical systems). This interaction represents the
267 location of breeding and non-breeding sites with respect to land configuration and
268 availability, and was used to explore the extent to which population spread depends on land
269 availability. We also included the interactions between non-breeding zone and either (i) mean
270 migration distance (great circle distance between mean breeding and non-breeding site) or (ii)
271 breeding latitude, because individuals departing with slight variation in bearing from a
272 starting point will inevitably spread over a wider area with increasing migration distance
273 (dependent on the number of stop-overs during migration). To account for the non-
274 independence of populations of the same species, we fitted a random intercept of species,
275 allowing us to compare the relative explanatory power of species identity versus the fixed
276 effects using marginal and conditional R^2 s (Nakagawa & Schielzeth 2013). To test for higher-
277 level taxonomic effects, we fitted additional models with hierarchical random intercepts of (i)
278 species nested within family and (ii) species nested within family nested within order.

279 All linear (mixed) models were fitted using maximum likelihood in the R package *nlme*.

280 Candidate models containing all possible combinations of fixed effects were evaluated
281 according to AICc using the package *MuMIn*. We use the ‘best’ model (with lowest AICc; >
282 2 AICc units below the second best model in all cases) for all predictions, with standard
283 errors estimated using the package *AICcmodavg* and marginal and conditional R^2 s in *MuMIn*.

284 Model fit was assessed by visual inspection of residuals plotted against fitted values and
285 quantile plots. We tested the influence of extreme values by re-running the best models with
286 and without data points with large Cook's distance values ('large' = in the upper 95th
287 percentile for each model). Exclusion of these apparently influential data points did not
288 qualitatively alter our model results and therefore our results do not appear to be driven by
289 outliers in any case.

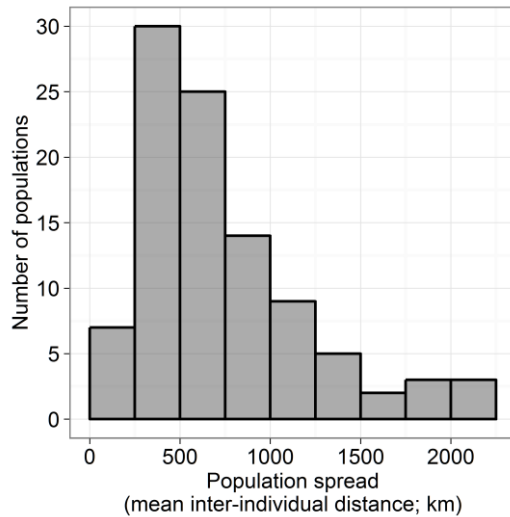
290 *Sensitivity to error*

291 Our data are potentially prone to two sources of error; imprecision in the translation of data
292 from published figures to latitude-longitude coordinates via Google Earth ('translation
293 error'), and inaccuracy of solar geolocator-derived positions in the original published data
294 ('geolocator error'). The sensitivity of our results to these sources of error was explored (see
295 **Appendix S1** in Supporting Information and **Figs S1 & S2**), but results were little affected,
296 suggesting that errors were unbiased and effects were relatively small.

297 **Results**

298 *Population spread*

299 The mean distance between two individuals from the same population during the non-
300 breeding season (i.e. population spread) was 743 km, spanning 10–20% of the maximum
301 width of Africa / South America. 62% of populations had mean inter-individual distances
302 greater than 500 km (**Fig. 3**).



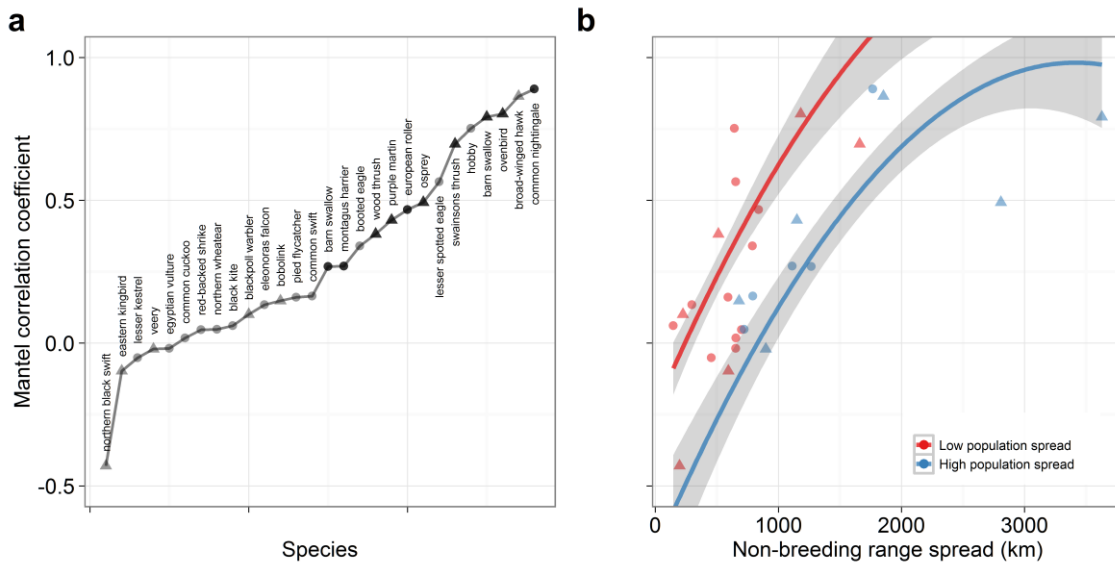
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304 **Figure 3** Distribution of mean inter-individual distance on non-breeding sites among 98 populations of migrant
 305 land-birds.

306 *Inter-population mixing*

307 Inter-population mixing on the non-breeding grounds was also high; the distance between
 308 two individuals during the breeding season generally corresponded poorly with the distance
 309 between the same individuals during the non-breeding season. Mantel correlation coefficients
 310 between pairwise distance matrices of individual breeding and non-breeding sites were
 311 statistically significant for only 10 out of 28 species and above 0.5 for just 7 (**Fig. 4a**),

312 indicating that most species appear to show weak, diffuse, connectivity.



313

314 **Figure 4** Mixing between individuals from different breeding populations of the same species during the non-
 315 breeding season is generally high. (a) The Mantel correlation between pairwise distance matrices of individual
 316 breeding and non-breeding sites is weak (below 0.5, indicating high inter-population mixing) for most of 28
 317 species of long distance migrant land bird. (b) The strength of the Mantel correlation coefficient increases with
 318 non-breeding range spread (x -axis) but decreases with population spread (red and blue colours), so that low
 319 inter-population mixing only occur in species with either high non-breeding range spread or low population
 320 spread. Each point represents a species; triangles are those from the Neotropic system and circles are those from
 321 the Afro-Palearctic. In (a) solid black points denote a significant ($p < 0.05$) Mantel correlation; grey points are
 322 not statistically significant. In (b) blue and red points represent species with above- or below-average population
 323 spread, respectively; blue and red lines are predictions for population spread values of 1059 km (90th percentile)
 324 and 292 km (10th percentile), respectively. Shaded regions are \pm S.E.

325 *Does inter-population mixing increase with population spread?*

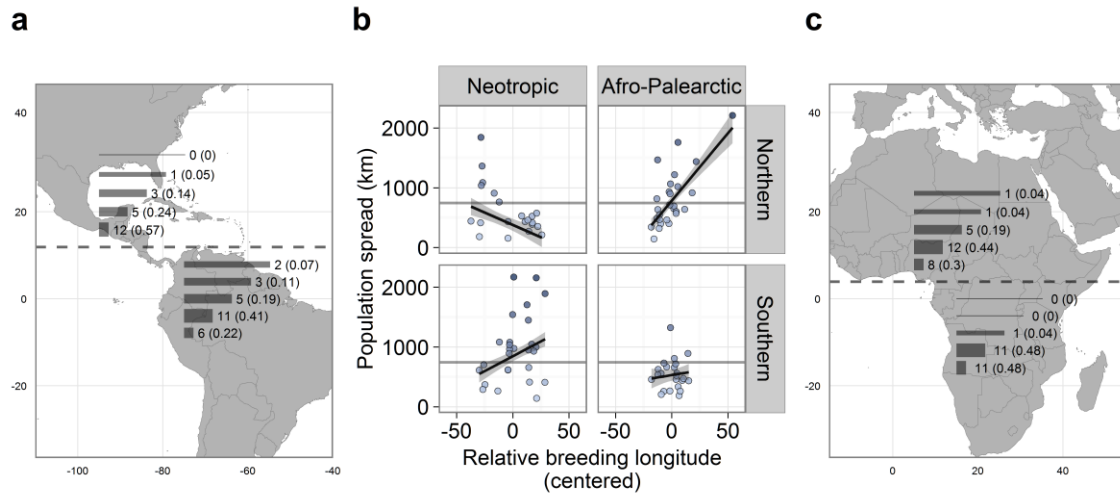
326 As expected, between-species variation in inter-population mixing on the non-breeding
 327 grounds was well predicted ($R^2 = 0.58$) by both total non-breeding range spread and mean

328 population spread (**Fig. 4b**), with no support for the effect of spread of breeding sites (**Table**
329 **1**). Inter-population mixing was low (high Mantel coefficient) only for species with high non-
330 breeding range spread and, to a lesser extent, species whose constituent populations had low
331 population spread (**Fig. 4b**).

332 *Does population spread depend on land availability or species identity?*

333 Between-population variation in population spread was remarkably well predicted by our
334 land availability model. On average, population spread was highest for populations spending
335 the non-breeding season in South America (mean \pm S.D. = 960.5 ± 555.2 km) and the
336 northern African zone (807.1 ± 474.3 km) compared to Central America (608.2 ± 424.0 km)
337 and the southern Africa zone (536.8 ± 257.7 km; **Fig. 5**), as expected if reduced relative land
338 availability limits population spread. There was also strong support for the interaction
339 between non-breeding zone and breeding longitude (**Table 2**). Thus, North American
340 populations spending the non-breeding season within the northern zone spread out more if
341 they came from western breeding sites, whereas those migrating to the southern zone spread
342 out more if they come from eastern breeding sites (**Fig. 5b**). In the Afro-Palearctic system,
343 populations spending the non-breeding season in the northern zone spread out more if they
344 come from eastern breeding sites (**Fig. 5b**), and those in the southern zone generally had low
345 spread regardless of breeding longitude (though there was limited variance in breeding
346 longitude for these populations). Together, the interaction between system, non-breeding
347 season zone and breeding longitude explained 38% of between-population variation in
348 population spread, with species identity contributing an additional 25%, ($R^2_m = 0.38$; $R^2_c =$

349 0.63). There was no support for higher-level phylogenetic effects, or the additional fixed
 350 effects of migration distance or breeding latitude (**Table 2**).



351

352 **Figure 5** Between-population variation in population spread is predicted largely geography. (a) and (c) show the
353 frequency distribution of population spread in the Neotropic (a) and Afro-Palearctic (c) migration systems. The
354 length of each horizontal bar represents population spread (250, 750, 1250, 1750 and 2250 km), and the weight
355 of each bar represents the number of populations falling into each 500 km bin. Numbers to the right of each bar
356 give the number (and proportion) of populations in each zone falling into each 500 km bin. Horizontal dashed
357 lines show the divide between northern and southern zones in each system, above and below which the availability
358 of land on a continental scale changes profoundly. (b) shows model predictions for the interaction between
359 breeding longitude (*x*-axis), system (columns) and non-breeding zone (rows; shaded regions are \pm S.E). Each
360 point represents a breeding population. The horizontal line intercepts the *y*-axis at the mean overall value of
361 population spread (average distance on the non-breeding ground between any two individuals from the same
362 breeding population = 743 km).

363 **Discussion**

364 Long-distance migrant land-bird populations, on average, spread out and mix over a
365 continent-wide scale non-breeding area. Population spread was often on the scale of
366 thousands of kilometers, particularly for populations with apparently high non-breeding land
367 availability. Inter-population mixing on the non-breeding grounds was low, with only a few
368 species having strong, positive Mantel correlations; these tended to be species with high total
369 non-breeding range spread or whose constituent breeding populations had low population
370 spread.

371 *The Mantel test and inter-population mixing*

372 Few species had strong Mantel correlation coefficients, suggesting that for most species,
373 individuals from different breeding populations occupy overlapping, rather than discrete,
374 non-breeding quarters. Our results indicate that when low inter-population mixing does

375 occur, this is due to high total non-breeding range spread (**Fig. 4b**, blue points in top right) as
376 often as to low population spread (**Fig. 4b**, red points in top left). Non-breeding range spread
377 was a stronger predictor of Mantel correlation coefficient than population spread, and species
378 with large total non-breeding ranges (e.g. Common Nightingale *Luscinia megarhynchos*, with
379 non-breeding individuals in our dataset spanning 40° longitude) remained spatially
380 segregated even if population spread was high. Correspondingly, species with small non-
381 breeding ranges (e.g. Eleonora's Falcon *Falco eleonora*, with non-breeding individuals
382 restricted to 6° longitude) mixed extensively, even if population spread was low. This
383 highlights a limitation in the migratory connectivity nomenclature, in which 'strong
384 connectivity' is used to refer simultaneously to low inter-population mixing and low
385 population spread (Webster *et al.* 2002; Taylor & Norris 2010); our results suggest that the
386 former does not necessarily depend on the latter.

387 In isolation, the Mantel test is therefore of limited value because it does not distinguish
388 between spatial segregation due to low population spread (**Fig. 1d**, the 'textbook' example of
389 strong migratory connectivity) and segregation due to high total non-breeding range spread
390 (**Fig. 1e**). Clearly, this distinction is important for understanding migrant population
391 dynamics in the face of environmental change. We suggest that future studies report
392 population spread (mean inter-individual distance) in conjunction with Mantel test results, to
393 better disentangle the properties of migratory connectivity (**Fig 4b**).

394 *Population spread*

395 Although population spread was, on average, relatively high (mean = 743 km), it ranged from
396 140 km (Blackpoll Warbler *Setophaga striata* from north-eastern USA) up to 2210 km

397 (Pallid Harrier *Circus macrourus* from north-central Kazakhstan). A substantial portion of
398 this between-population variation was explained simply by geography; population spread was
399 lower for populations using non-breeding zones with lower land availability (southern Africa
400 and Central America). This effect interacted with breeding longitude; North American
401 populations spending the non-breeding season in the Central America spread out less if they
402 come from eastern breeding sites, possibly because land is more limited in the Caribbean
403 islands than in continental Central America. On the other hand, those migrating to South
404 America spread out more if they come from eastern breeding sites, perhaps due to the
405 migration routes of western populations being constrained by the Pacific Ocean. Similarly, in
406 the Afro-Palearctic system, populations migrating to the northern zone spread out more if
407 they come from eastern breeding sites, possibly because western breeders are constrained by
408 the Atlantic Ocean.

409 Clearly, other factors co-vary or are confounded with our indirect measure of land
410 availability, so the exact mechanism underlying the observed relationship is uncertain, and
411 much variance in population spread is still to be accounted for. In particular, it is difficult to
412 distinguish between non-breeding land availability and constraints presented *en route*.
413 Barriers such as mountain ranges and deserts, and land bottlenecks such as the Central
414 American isthmus or the Straits of Gibraltar may cause routes to funnel (e.g. Lopez-Lopez,
415 Garcia-Ripolles & Urios 2014) independently of land availability in the non-breeding area.
416 The presence of such geographical features *en route* may well co-vary with breeding
417 longitude (e.g. central and eastern European populations may have more opportunities to
418 cross the Mediterranean than western ones) and could contribute to the observed relationship
419 between ‘land availability’ and migratory spread. Although the effect of these barriers and

420 bottlenecks likely interact with species-specific traits (e.g. flight mode; Alerstam 2001), they
421 should affect all species to some extent. Equally, however, these barriers may cause migrants
422 to converge on a common route, diluting any predictive signal of breeding longitude.

423 Dominant weather patterns may also vary between these zones, and may influence the degree
424 of variation in population spread, though we are not aware of any mechanism by which
425 weather would result in the systematic directional differences observed here.

426 Breeding longitude may also affect population spread through its influence on migration
427 direction. Populations without suitable non-breeding habitat to the south of their breeding site
428 must take a more oblique ‘angle of attack’, so may spread out further across an east-west
429 oriented non-breeding range. However, the observed effect is opposite to that expected under
430 this hypothesis; that is, population without suitable non-breeding habitat to the south of their
431 breeding site spread out *less*, not more.

432 *A null model of connectivity*

433 We deliberately chose a simple null model of population spread, essentially representing one
434 end of the connectivity spectrum (i.e. individuals from a breeding population spread out into
435 all available land to the south of them, rather than using a discrete, population specific non-
436 breeding area) and neglected other mechanisms which may explain variation in population
437 spread. We show a very clear result: the breeding longitude of a population, and whether it
438 spends the non-breeding season in either Central or South America or northern or southern
439 Africa explains more variation in population spread (38%) than does species identity (25%).
440 Whether driven by non-breeding land availability, geographical features *en route*, or some
441 other mechanism, much variation in population spread can be explained by geography alone

442 and, when our measure of land availability is high, populations often spread over the scale of
443 thousands of kilometers.

444 This provides a starting point for understanding the mechanisms of connectivity in migrant
445 land-birds, but does not mean, of course, that any specific population's spread can be
446 predicted from our model. Clearly some populations have high connectivity, even when land
447 availability is apparently high. But put simply, for many migrant land-birds, there is little
448 need to invoke any mechanism more complicated than a null model of individuals flying
449 towards all available land at a suitable latitude that provides habitat for the non-breeding
450 season. Selection may have occurred for higher connectivity in some species, but in many
451 cases it seems that high population spread – perhaps because of a *lack* of selection for use of
452 population specific non-breeding areas – is the norm.

453 *Evolutionary context*

454 The implication of our results is that, for many species, selection has not resulted in a
455 deterministic strategy for non-breeding site selection. This is consistent with non-breeding
456 conditions being generally variable and unpredictable, leading to a system whose emergent
457 properties resemble bet-hedging (Reilly & Reilly 2009; Botero *et al.* 2015). We suggest that
458 the general low connectivity shown here is likely to be adaptive, because long-distance
459 migration systems almost certainly represent recently evolved adaptive responses to dynamic
460 global climatic conditions (Cresswell, Satterthwaite & Sword 2011; Fryxell & Holt 2013).
461 Climatic variability and its consequent effects on the location of suitable habitat has been
462 (Wanner *et al.* 2008; Svenning *et al.* 2015) and remains (Nicholson 2001) characteristic of
463 most long distance migration systems. An individual strategy of producing offspring with

464 high phenotypic variance in departure direction (i.e. diversified bet-hedging; Botero *et al.*
465 2015) will likely result in some individuals encountering suitable conditions even as habitat
466 zones shift in response to climate change (**Fig. 6**); such a response has probably been
467 observed in rapid shifts in non-breeding grounds for Blackcaps *Sylvia atricapilla* (Berthold *et*
468 *al.* 1992).

469 Clearly, low connectivity is not an absolute rule, and there are several mechanisms through
470 which connectivity may be strengthened (see **Table S3** for specific examples). Not least,
471 there is good evidence for a genetic basis for many migratory traits including departure
472 direction (Berthold *et al.* 1992), although these innate controls vary between individuals
473 (Thorup, Rabøl & Erni 2007; Reilly & Reilly 2009) and in their sensitivity to environmental
474 perturbations such as crosswinds during migration. This is particularly true for naïve juvenile
475 migrant birds, which may not compensate for natural or experimental displacement (Thorup
476 *et al.* 2011; Horton *et al.* 2016), and whose routes tend to be repeated as adults in subsequent
477 years (Cresswell 2014). Further variation in migratory spread will arise because of variation
478 in current and historic land and sea barriers (Alerstam 2001), migratory bottlenecks (Newton
479 2008), timing of migration (Bauer, Lisovski & Hahn 2016), weather (Elkins 1983), use of
480 social information (Nemeth & Moore 2014), habitat shifts during the non-breeding season
481 (Moreau 1972) and age and sex dependent differences in migratory capability (Stewart,
482 Francis & Massey 2002) or habitat use (Marra, Sherry & Holmes 1993) (**Table S3**).

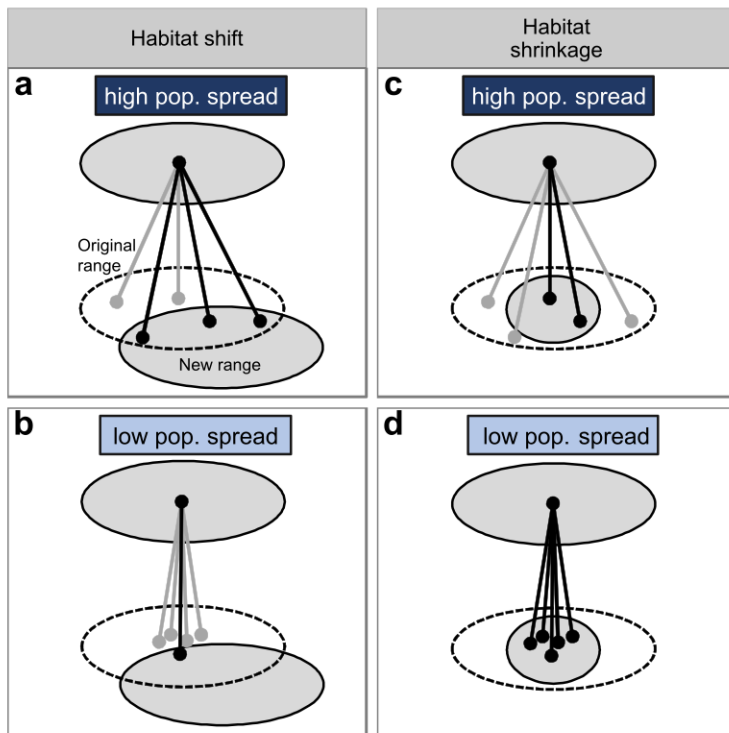
483 We would encourage the testing of hypotheses regarding the importance of these mechanisms
484 for explaining residual variation in migratory spread. For example, we expect species using
485 non-breeding habitats which are spatially and temporally predictable over many generations

486 to have lower population spread (Botero *et al.* 2015). Population spread may also be lower in
487 soaring migrants, which are generally reliant on thermals and incapable of long sea crossings,
488 so are often forced through bottlenecks (Alerstam 2001).

489 *Conservation implications*

490 Although low connectivity may facilitate rapid range shifts in response to climate change, it
491 may not be a good strategy when habitat availability is reduced overall. A greater proportion
492 of a population with high spread will still reach suitable habitat if its location shifts (**Fig. 6**),
493 for example, due to climate change, compared to a population with low spread, leading to
494 greater resilience of high-spread populations (Gilroy *et al.* 2016). However, if suitable habitat
495 becomes less available overall (due to habitat loss) then a greater proportion of a population
496 with high spread will miss the shrinking habitat, whereas a population with low spread may
497 still reach the target (**Fig. 6**). Consequently, climate-induced shifts in non-breeding habitat –
498 or any temporal unpredictably in the location of suitable non-breeding habitat – might select
499 for high spread and lower connectivity, whilst suitable habitat becoming restricted to specific
500 localized areas should favour the reverse. There is therefore no optimum level of connectivity
501 if climate change and habitat destruction act simultaneously and with opposing directions of
502 selection. However, species whose migration route includes a substantial longitudinal shift
503 could encounter a wide range of non-breeding habitat with even a small range of migration
504 starting angles, so may be less affected. Linking population-specific levels of connectivity to
505 flexibility in non-breeding range under climate and habitat change has not yet been explicitly
506 investigated because data on accurate connectivity and how it varies from year to year have
507 not been available.

508 Explicitly modelling the relationship between population declines and migratory connectivity
 509 requires a larger dataset than is currently available. We predict that, if non-breeding
 510 conditions are driving inter-annual variation in population trend, high inter-population mixing
 511 on the non-breeding grounds should promote synchrony in population trends. Additionally,
 512 populations with low spread may be expected to have more negative population trends (e.g.
 513 Jones *et al.* 2008).



514

515 **Figure 6** Population spread determines the response of populations to non-breeding habitat change. The number
 516 of individuals successfully reaching suitable non-breeding sites (black lines) following either a shift (**a, b**) or a
 517 reduction (**c, d**) in the area of suitable non-breeding habitat depends on the degree of migratory spread. A
 518 greater proportion of a population with high spread will still reach suitable habitat if its location shifts (e.g. due
 519 to climate change) compared to a low spread population (**a** and **b**), but if suitable habitat becomes less available
 520 overall (due to habitat loss) then a greater proportion of a population with high spread will miss the shrinking
 521 habitat, whereas a population with low spread may still reach the target (**c** and **d**). Note that we consider the

522 simple situation where migration is in a southerly direction and nonbreeding habitat availability is spread out
523 east-west perpendicular to migration direction. We also assume that individual migrants cannot make large-scale
524 movements in response to habitat loss.

525 The management implications of high migratory spread and low connectivity in the Afro-
526 Palearctic and Nearctic flyways are that changes in the availability or quality of any non-
527 breeding site will have a diffuse but widespread effect on breeding populations of a species
528 (Sutherland & Dolman 1994; Taylor & Norris 2010). Additionally, tracking studies aimed at
529 identifying population-specific non-breeding areas amenable to targeted conservation
530 strategies may often fail, given the general pattern of high population spread. Instead, a more
531 process-driven approach to better understanding the mechanisms by which land-birds
532 navigate the globe in time and space – and how these processes might change through the
533 Anthropocene – may be a more informative and cost-effective use of tracking technologies.
534 On a positive note, conservation of any site in the Africa or Central/South America should
535 benefit (diffusely) many different breeding populations of European and North American
536 migratory land birds. Conversely, continued habitat loss and degradation in non-breeding
537 areas will detrimentally affect very many populations form across a wide breeding area in the
538 northern hemisphere. This may help explain why – despite species-specific proximate causes
539 of population decline (Vickery *et al.* 2014) and a wide range of ecological traits – migrant
540 species are, on the whole, declining relative to residents (Sanderson *et al.* 2006; Bolger *et al.*
541 2008; Brower *et al.* 2012; Gilroy *et al.* 2016).

542

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550 **Data accessibility:** Data and R scripts have been prepared for archiving in the Dryad data
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552

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- 684

685 **Table 1.** Model summaries for the top (95% confidence) set of linear models for species-
686 level Mantel coefficient. *b.dist* = mean distance between all breeding sites, *pop.spread* =
687 mean population spread, *nb.spread* = non-breeding range spread, mean distance between all
688 non-breeding sites. *k* = number of parameters in model; Δ_i = difference in AICc between *i*th
689 model and ‘best’ model; w_i = Akaike model weight (calculated across all possible models);
690 R^2_{adj} is adjusted r-squared. / = variable absent.

Model	Parameter estimate					<i>k</i>	AICc	Δ_i	w_i	R^2_{adj}
	<i>intercept</i>	<i>b.dist</i>	<i>pop.spread</i>	<i>nb.spread</i>	<i>nb.spread</i> ²					
1	-0.04	/	-7E-3	0.001	-1E-6	5	2.8	0	0.69	0.58
2	-0.06	3E-5	-6E-3	0.001	-2E-6	6	5.9	3.1	0.15	0.57
3	-0.21	/	/	0.001	-1E-6	4	7.4	4.6	0.07	0.47
4	0.2	/	-6E-3	0.0005	/	4	8.3	5.4	0.05	0.46

691

692 **Table 2.** Model summaries for the top (95% confidence) set of linear mixed models predicting population spread *b.lon* = mean breeding
693 longitude; *mig.dist* = mean migration distance. *k* = number of parameters in model; Δ_i = difference in AICc between *i*th model and ‘best’ model;
694 w_i = Akaike model weight (calculated across all models); R^2_m and R^2_c are conditional and marginal r-squared, respectively. / = variable absent.
695 Results for the global model in which migration distance was replaced with breeding latitude are not shown, but the top model was the same,
696 albeit with even higher Akaike weight ($w_i = 0.725$).

Model	Parameter estimate										<i>k</i>	AICc	Δ_i	w_i	R^2_m	R^2_c
	<i>intercept</i>	<i>b.lon</i>	<i>mig.dist</i>	<i>system</i>	<i>zone</i>	<i>b.lon</i> × <i>system</i>	<i>b.lon</i> × <i>zone</i>	<i>mig.dist</i> × <i>zone</i>	<i>system</i> × <i>zone</i>	<i>b.lon</i> × <i>system</i> × <i>zone</i>						
1	782.9	22.6	/	-403.5	-252.4	-30.9	-19.4	/	719.5	37.6	10	1437.8	0.00	0.487	0.38	0.63
2	512.2	19.7	0.1	-302.5	406.6	-26.1	-15.6	-0.1	588.0	28.9	12	1439.9	2.13	0.167	0.40	0.64
3	853.5	23.4	-0.02	-423.5	-209.0	-32.3	-20.0	/	727.5	37.9	11	1440.1	2.30	0.154	0.38	0.63
4	225.2	13.4	0.1	-137.5	931.5	-12.3	/	-0.2	392.6	/	10	1442.1	4.29	0.057	0.33	0.58
5	242.2	12.3	0.1	-165.2	852.1	-13.1	3.6	-0.2	434.6	/	11	1443.9	6.09	0.023	0.34	0.59
6	-72.5	5.7	0.2	/	1293.8	/	/	-0.3	/	/	7	1443.9	6.17	0.022	0.24	0.53
7	-43.2	5.4	0.2	-42.5	1022.6	/	/	-0.3	302.3	/	9	1444.1	6.31	0.021	0.29	0.56
8	6.7	11.9	0.2	73.3	1302.9	-9.4	/	-0.3	/	/	9	1445.1	7.31	0.013	0.27	0.54

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9	-169.7	5.8	0.2	111.0	1304.1	/	/	-0.3	/	/	8	1445.1	7.36	0.012	0.26	0.53
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