Low migratory connectivity is common in long-distance migrant birds

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Summary

1. Estimating how much long-distance migrant populations spread out and mix during the non-breeding season (migratory connectivity) is essential for understanding and predicting population dynamics in the face of global change.

2. We quantify variation in population spread and inter-population mixing in long-distance, terrestrial migrant land-bird populations (712 individuals from 98 populations of 45 species, from tagging studies in the Neotropic and Afro-Palearctic flyways). We evaluate the Mantel test as a metric of migratory connectivity, and explore the extent to which variance in population spread can be explained simply by geography.

3. The mean distance between two individuals from the same population during the non-breeding season was 743 km, covering 10–20% of the maximum width of Africa/South America. Individuals from different breeding populations tended to mix during the non-breeding season, although spatial segregation was maintained in species with relatively large non-breeding ranges (and, to a lesser extent, those with low population-level spread). A substantial amount of between-population variation in population spread was predicted simply by geography, with populations using non-breeding zones with limited land availability (e.g. Central America compared to South America) showing lower population spread.

4. The high levels of population spread suggest that deterministic migration tactics are not generally adaptive; this makes sense in the context of the recent evolution of the systems, and the spatial and temporal unpredictability of non-breeding habitat.

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

Key-words: climate change, migration, migratory connectivity, migratory dispersal, population declines

Introduction

Migratory animals are currently suffering global declines (Bolger *et al.* 2008; Brower *et al.* 2012; Gilroy *et al.* 2016), and their conservation requires an understanding of 'migratory connectivity', that is, how breeding and non-breeding sites are connected via the trajectories of individual migrants (Webster *et al.* 2002; Martin *et al.* 2007; Runge *et al.* 2014, 2015; Vickery *et al.* 2014; Bauer, Lisovski & Hahn 2016). Migratory connectivity is typically described along a continuum from low (weak, or diffuse) to high (strong). Under low connectivity, individual migrants from a particular breeding population spread over a large area during the non-breeding season, mixing with individuals from different breeding populations, while strong connectivity reflects the use of discrete, population-specific non-breeding areas (Webster *et al.* 2002; Newton 2008). For example, Great Reed Warblers,

Acrocephalus arundinaceus, from a single European breeding population can be found spread across most of West Africa during the non-breeding season (Lemke *et al.* 2013), whereas Common Nightingales, *Luscinia megarhynchos*, from spatially separate European breeding populations retain reasonable spatial separation on their West African non-breeding grounds (Hahn *et al.* 2013).

Migratory connectivity has two key spatial components, which are often conflated. 'Population spread' (a population-level trait) describes the degree to which individuals from a single breeding population spread out during the non-breeding season (Fig. 1a and b), while inter-population mixing on the non-breeding grounds (a species- or multi–population-level trait) describes the degree to which individuals from different breeding populations mix or co-occur during the non-breeding season (Fig. 1c and d). Generally speaking, high population spread will promote inter-population mixing on non-breeding grounds (Fig. 1c; 'weak' connectivity *sensu* Webster *et al.* 2002) while low population spread will reduce it (Fig. 1d; 'strong' connectivity). The relationship between population spread and inter-population mixing should be mediated, however, by the relative size of the non-breeding range ('non-breeding range spread', a species-level trait). Here, we define the non-breeding range spread as the net area covered by individuals from all focal populations of a species; this combines information on migratory dispersion *sensu* Gilroy *et al.* (2016) (i.e. the size of the species' non-breeding range relative to its breeding range) as well as the spatial separation of focal breeding populations. Thus, a relatively small non-breeding distribution (or a relatively short distance between focal breeding populations) will promote inter-population mixing on the non-breeding grounds even if population spread is low (Fig. 1f), while a larger non-breeding range (or a greater distance between focal breeding populations) will reduce mixing even if population spread is high (Fig. 1e).
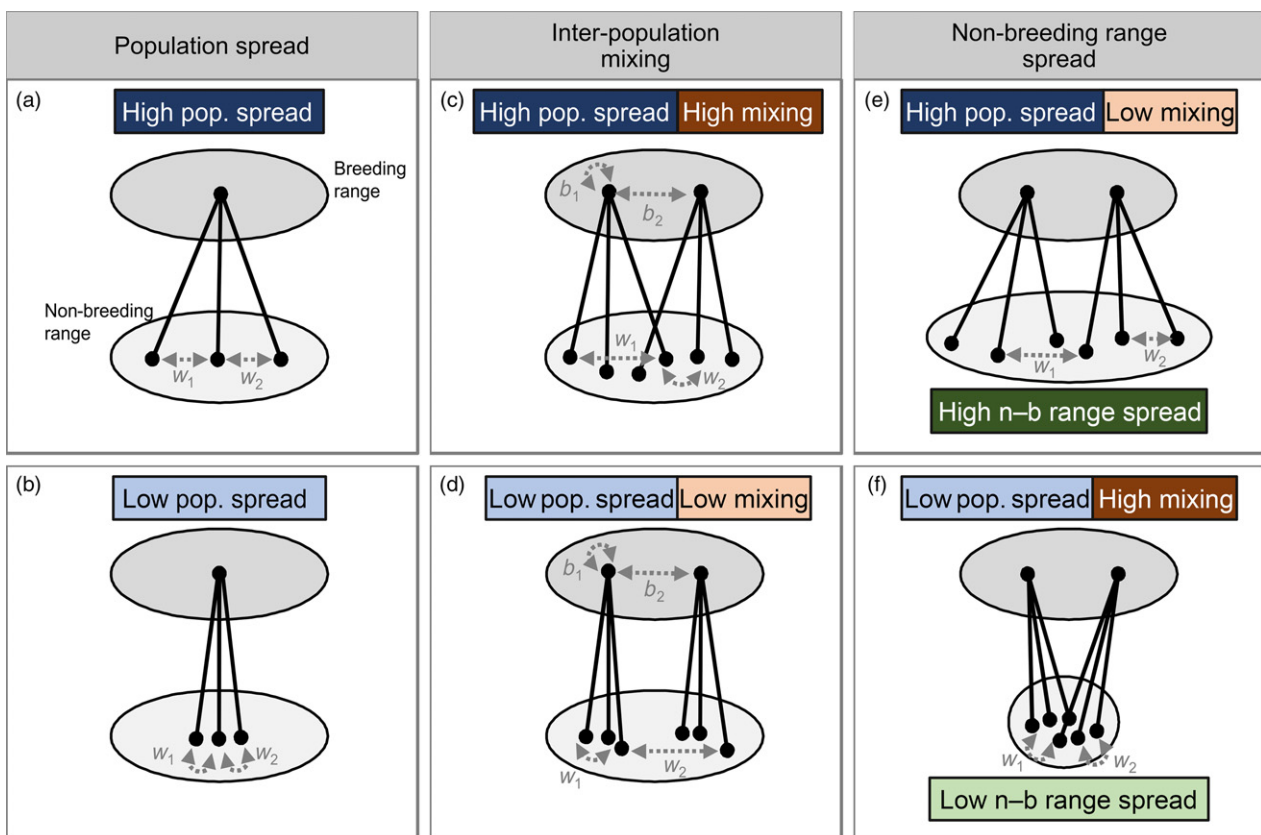
Fig. 1. Migratory connectivity arises through both the spreading and mixing of breeding populations. In all panels, the grey ellipse represents a hypothetical species' breeding range, and the white ellipse the non-breeding ('winter') range; black points illustrate the breeding and non-breeding sites of individual migrants, connected by lines which represent their migratory trajectory. Individuals from the same breeding site are grouped into populations (one population in a and b, two in c to f). Population spread (a, b) is measured as the mean pairwise distance between the non-breeding sites of all individuals (w_1, w_2, …) from a focal breeding population, with high values indicating high population spread (a). Inter-population mixing on the non-breeding grounds (c and d), a multi–population-level trait, is measured as the Mantel correlation coefficient between the pairwise distance-matrix of the breeding sites of all individuals (b_1, b_2, …) and the corresponding distance-matrix of their non-breeding sites (w_1, w_2, …), with high positive correlations indicating low mixing (d). The relationship between population spread and inter-population mixing should be mediated by the relative size of the species' non-breeding range (non-breeding range spread, measured as the mean pairwise distance between the non-breeding sites of all individuals (w_1, w_2, …) regardless of breeding population; e and f). [Colour figure can be viewed at wileyonlinelibrary.com]

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

Patterns of migratory connectivity ultimately arise through variation in the migratory trajectories of individual migrants. Because many adult land-birds capitalize on prior knowledge by returning to their first (necessarily survivable) non-breeding site (Newton 2008), migratory connectivity in many cases should reflect the trajectories of successful juveniles (Cresswell 2014). For many long-distance migrant land-birds, juveniles travel separately from (and often later than) adults, orienting in a particular direction at a particular time of year to reach non-breeding grounds thousands of kilometres away (Newton 2008). The specificity of these genetic instructions therefore plays an underlying role in defining patterns of migratory connectivity. Deterministic genetic programmes (promoting low spread within a brood) are likely to be favoured when the spatial and temporal predictability of the non-breeding environment is high, while less predictable environments might be expected to erode selection for genetic determinism, resulting in a more variable, 'bet-hedging' strategy (Botero *et al.* 2015).

Even under relatively deterministic genetic controls, variable weather and wind conditions experienced *en route* (Elkins 1983), and the varying ability of migrants (and juveniles in particular) to fully compensate for any major displacement from their genetically predetermined migration trajectory (Perdeck 1958; Thorup *et al.* 2003, 2011) will result in deviations, which likely accrue with increasing migration distance. The extent to which these deviations – on top of any phenotypic variance in initial

departure direction – affect population spread, will depend on various factors, including: the timing of migration, with phenological synchrony exposing individuals to more similar weather and wind conditions (Bauer, Lisovski & Hahn 2016; Ouwehand *et al.* 2016); geographical barriers *en route* such as mountain ranges, deserts and oceans, which may create bottlenecks or force detours (Delmore, Fox & Irwin 2012; Agostini, Panuccio & Pasquaretta 2015); the use of social information *en route*, potentially acquired from experienced adults and facilitated by congregations at bottlenecks (Williams & Kalmbach 1943; Thorup & Rabol 2001); and, perhaps most fundamentally, continental configuration and the area of available land in the species' non-breeding range.

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

We then construct a simple model to explain the between-population variation in population spread. We predict that populations using non-breeding 'zones' with more limited land availability, for example, Ovenbirds *Seiurus aurocapilla* (Hallworth & Marra 2015) in Central America or European Rollers, *Coracias garrulus*, in southern Africa (Finch *et al.* 2015) will show lower population spread compared to those in zones with higher land availability, for example, Blackpoll Warblers, *Setophaga striata*, in South America (DeLuca *et al.* 2015) or Pied Flycatchers, *Ficedula hypoleuca*, in western Africa (Ouwehand *et al.* 2016). This effect should interact with relative breeding longitude because, for instance, populations breeding in western North America and migrating to South America cannot spread out in a westerly direction without ending up in the Pacific Ocean, or must migrate much longer distances than eastern populations to utilize all available non-breeding habitats; the reverse should be true for populations using the Central American non-breeding zone (e.g. Swainson's Thrush, *Catharus ustulatus* Cormier *et al.* 2013). This simple 'null model' does not attempt to explain all variation in a population spread, but rather tests the explanatory power of one potential underlying mechanism: land availability. In this model, we assume the simplest possible situation – that migrants
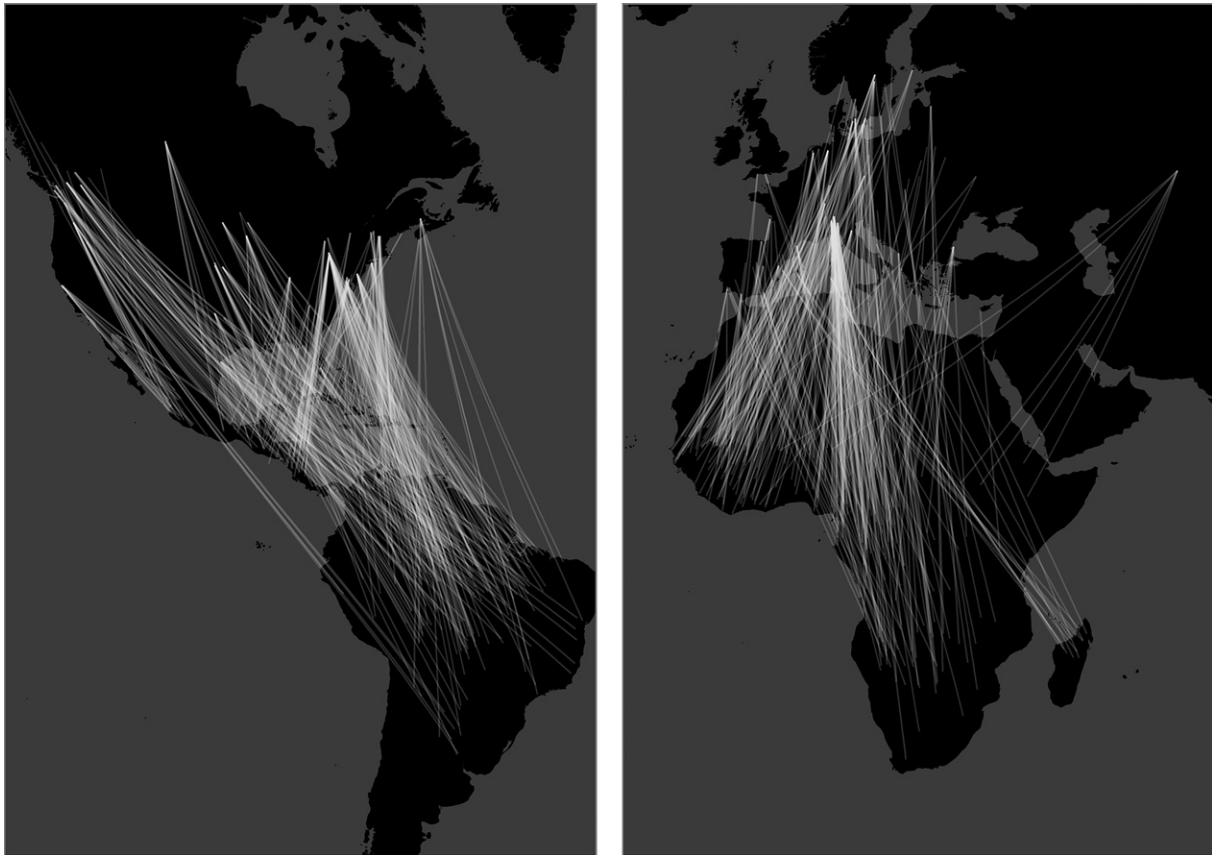
Fig. 2. Lines connecting the breeding and non-breeding sites of 712 individual land-birds tracked from 98 northern hemisphere breeding populations of 45 species across two trans-continental flyways.

migrate in a southerly direction and spread out east to west over the closest available land within the latitudinal zone of suitable non-breeding habitat, so that breeding longitude will be a predictor of population spread. If land availability is a good predictor of population spread, this lends support to a more stochastic migration tactic, with generally high population spread prevented only by geographical constraints. We also include species identity as a random effect, to test the extent to which populations belonging to the same species (or family) share similar migration tactics (with high or low population spread), irrespective of geography.

Materials and methods

DATA ACQUISITION

A comprehensive search of peer-reviewed tracking studies was conducted for all European and North American species classed (according to BirdLife; http://www.birdlife.org/datazone/species/search) as migratory land-birds by entering the terms [*latin name*] AND *migra** AND (*gps* OR *geolo** OR *satellite*) into the Web of Science online library. From these studies, breeding (i.e. tagging) and non-breeding (i.e. the site where an individual spent the majority of the non-breeding period after migration) locations of individual birds were extracted (or approximated from plotted map locations using Google Earth when precise

coordinates were not given). For individuals who moved between several non-breeding sites, we recorded the location of the first non-breeding site only. We excluded species with data from only one individual, and restricted our analyses to adult birds tagged during the breeding season in the northern hemisphere. Individuals of the same species tagged within 100 km of one another (which meant being tagged at the same study site in almost all cases; mean distance between two individuals assigned to the same breeding population = 8·8 km, median = <1 km) were grouped into 'populations', the principle unit of analysis (Table S1 in Appendix S1). We deliberately chose not to include ring-recovery data – which are extensive for some migrant species, particularly in the Afro-Palearctic system– due to the non-trivial issue of spatial biases in re-encounter and reporting rates (Procházka *et al.* 2016). We defined the Afro-Palearctic system of long-distance migrant birds as comprising all populations breeding in Europe west of 65°E and with a non-breeding area in Africa south of 20°N. The Neotropic system was defined as all populations breeding in North America and with a non-breeding area south of 30°N.

METRICS OF POPULATION SPREAD

For the Afro-Palearctic system, we collated data on 323 individuals from 50 populations of 29 species, with a mean of 6·5 (range = 2–48) individuals per population and 1·7 (1–6) populations per species. In the Neotropic system, corresponding data were available for 389 individuals from 48 populations of 16

species, with a mean of 8·1 (range = 2–34) individuals per population and 3·0 (1–8) populations per species.

As an initial metric of population spread we calculated, for each breeding population, the maximum pairwise distance between individual non-breeding sites. 'Maximum spread' clearly increases with the number of individuals tracked per population (correlation between maximum spread and number of individuals; $r = 0.62$, d.f. = 96, $P < 0.001$), although the relationship must eventually reach an asymptote. To determine the approximate level of maximum population spread at which this asymptote occurs, we modelled the effect of sample size on maximum spread using linear mixed models with a random intercept of species identity. Four alternative models were constructed using either sample size, the natural logarithm of sample size, the quadratic of sample size or the intercept only to determine the best function to describe the relationship. The maximum distance between two individuals from the same breeding population during the non-breeding season was best explained by the logarithm of sample size (Table S2 in Appendix S1), with the fitted line levelling off at c. 3000 km (Fig. S1 in Appendix S1).

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

METRIC OF INTER-POPULATION MIXING ON THE NON-BREEDING GROUNDS

Metrics of inter-population mixing require the tracking of individuals from multiple populations. For the Afro-Palearctic system, 16 species were tracked from more than one population, with a mean of 3·7 populations per species (range = 2–11) and 5·0 (1·5–31·7) individuals per population. In the Neotropics, multi-population data were available for 12 species, with a mean of 4·1 populations per species (2–13) and 6·7 (1·5–17·0) individuals per population.

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

DOES INTER-POPULATION MIXING INCREASE WITH POPULATION SPREAD?

To explore the conditions under which low inter-population mixing ('strong' connectivity) occurs, we constructed a linear model with Mantel correlation coefficient as the dependent variable (Table 1). As illustrated in Fig. 1, we expect high population spread to promote inter-population mixing on the non-breeding grounds (i.e. reduce the strength of the Mantel correlation), and high non-breeding range spread to reduce mixing (i.e. increase the Mantel coefficient). For each species, we therefore calculated the mean population spread of all constituent populations ('mean population spread'), as well as the mean pairwise distance between all non-breeding sites, regardless of breeding population ('non-breeding range spread'). We included both as fixed effects, in addition to the quadratic effect of non-breeding range spread (because an initial plot of Mantel coefficient against species spread illustrated a nonlinear effect) and the mean pairwise distance between all breeding sites (because increasing the spatial separation of focal breeding populations should reduce migratory mixing).

DOES POPULATION SPREAD DEPEND ON LAND AVAILABILITY OR SPECIES IDENTITY?

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

Fixed effects were thus the three-way interaction between migration system (Afro-Palearctic or Neotropic), non-breeding zone (north or south) and breeding longitude (centred separately for Afro-Palearctic and Neotropical systems). This interaction represents the location of breeding and non-breeding sites with respect to land configuration and availability, and was used to explore the extent to which population spread depends on land

Table 1. Model summaries for the top (95% confidence) set of linear models for species-level Mantel coefficient

| Model | Parameter estimate | | | | | k | AICc | Δ_i | w_i | R^2_{adj} |
	intercept	*b.dist*	*pop.spread*	*nb.spread*	*nb.spread*^{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

b.dist = mean distance between all breeding sites; *pop.spread* = mean population spread; *nb.spread* = non-breeding range spread, mean distance between all non-breeding sites; k = number of parameters in model; Δ_i = difference in AICc between ith model and 'best' model; w_i = Akaike model weight (calculated across all possible models); R^2_{adj} is adjusted r-squared; / = variable absent.

Table 2. Model summaries for the top (95% confidence) set of linear mixed models predicting population spread

Model	Parameter estimate										k	AICc	Δ_i	w_i	R^2_m	R^2_c
	intercept	b.lon	mig.dist	system	zone	b.lon × system	b.lon × zone	mig.dist × zone	system × zone	b.lon × system × zone						
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	−9·4	/	−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	/	/	−0·3	/	/	9	1445·1	7·31	0·013	0·27	0·54
9	−169·7	5·8	0·2	111·0	1304·1	/	/	−0·3	/	/	8	1445·1	7·36	0·012	0·26	0·53

b.lon = mean breeding longitude; mig.dist = mean migration distance; k = number of parameters in model; Δ_i = difference in AICc between *i*th model and 'best' model; 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. Results for the global model in which migration distance was replaced with breeding latitude are not shown, but the top model was the same, albeit with even higher Akaike weight (w_i = 0·725).

availability. We also included the interactions between the non-breeding zone and either (i) the mean migration distance (great circle distance between mean breeding and non-breeding site) or (ii) breeding latitude, because individuals departing with slight variation in bearing from a starting point will inevitably spread over a wider area with increasing migration distance (dependent on the number of stopovers during migration). To account for the non-independence of populations of the same species, we fitted a random intercept of species, allowing us to compare the relative explanatory power of species identity versus the fixed effects using marginal and conditional R^2s (Nakagawa & Schielzeth 2013). To test for higher level taxonomic effects, we fitted additional models with hierarchical random intercepts of (i) species nested within family and (ii) species nested within family nested within order.

All linear (mixed) models were fitted using maximum likelihood in the R package *nlme*. Candidate models containing all possible combinations of fixed effects were evaluated according to AICc using the package *MuMIn*. We use the 'best' model (with lowest AICc; >2 AICc units below the second best model in all cases) for all predictions, with standard errors estimated using the package *AICcmodavg* and marginal and conditional R^2s in *MuMIn*.

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

SENSITIVITY TO ERROR

Our data are potentially prone to two sources of error; imprecision in the translation of data from published figures to latitude–longitude coordinates via Google Earth ('translation error'), and
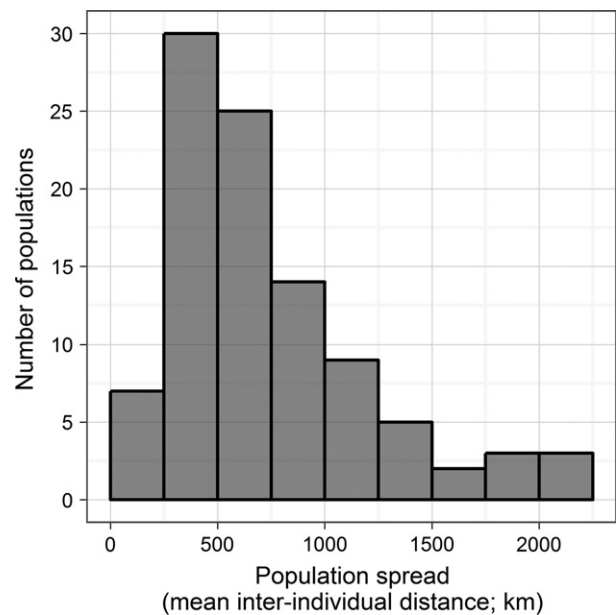
Fig. 3. Distribution of mean inter-individual distance on non-breeding sites among 98 populations of migrant land-birds.

inaccuracy of solar geolocator-derived positions in the original published data ('geolocator error'). The sensitivity of our results to these sources of error was explored (see Figs. S1 and S2 in Appendix S1), but results were little affected, suggesting that errors were unbiased and effects were relatively small.

Results

POPULATION SPREAD

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

INTER-POPULATION MIXING

Inter-population mixing on the non-breeding grounds was also high; the distance between two individuals during the breeding season generally corresponded poorly with the distance between the same individuals during the non-breeding season. Mantel correlation coefficients between pairwise distance matrices of individual breeding and non-

breeding sites were statistically significant for only 10 out of 28 species and above 0·5 for just 7 (Fig. 4a), indicating that most species appear to show weak, diffuse connectivity.

### DOES INTER-POPULATION MIXING INCREASE WITH POPULATION SPREAD?

As expected, between-species variation in inter-population mixing on the non-breeding grounds was well predicted ($R^2 = 0.58$) by both total non-breeding range spread and mean population spread (Fig. 4b), with no support for the effect of spread of breeding sites (Table 1). Inter-population mixing was low (high Mantel coefficient) only for species with high non-breeding range spread and, to a lesser extent, species whose constituent populations had low population spread (Fig. 4b).

DOES POPULATION SPREAD DEPEND ON LAND AVAILABILITY OR SPECIES IDENTITY?

Between-population variation in population spread was remarkably well predicted by our land availability model. On average, population spread was highest for populations spending the non-breeding season in South America (mean ± SD = 960·5 ± 555·2 km) and the northern
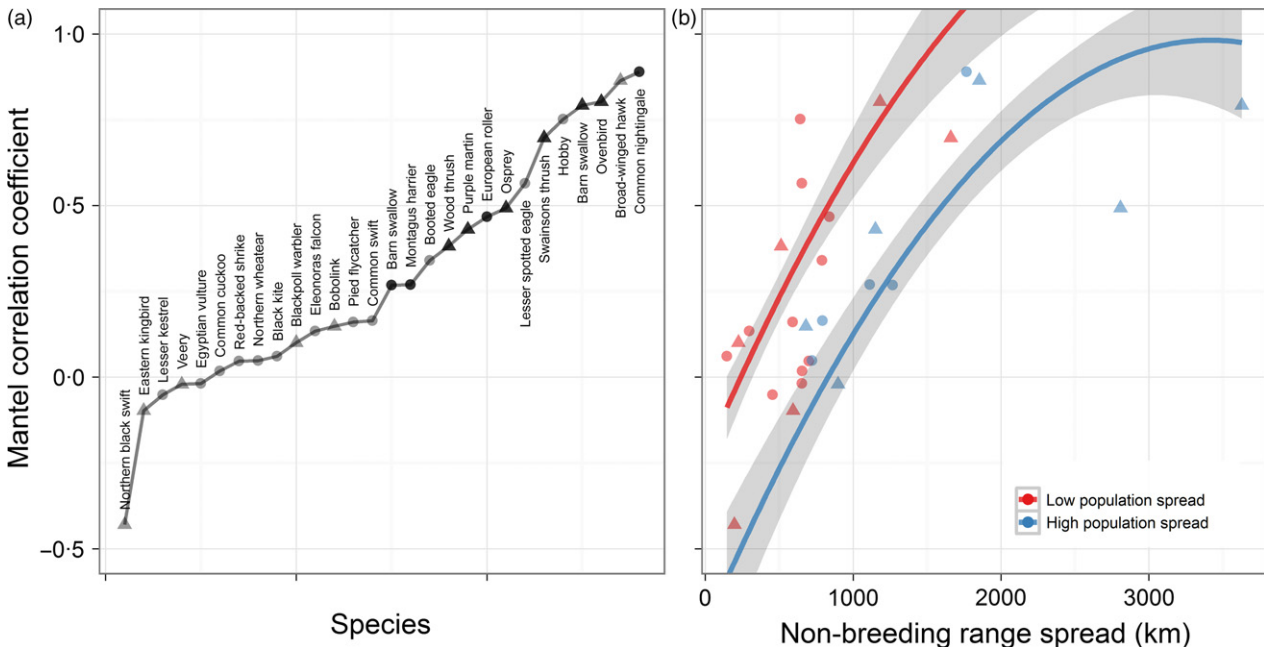
Fig. 4. Mixing between individuals from different breeding populations of the same species during the non-breeding season is generally high. (a) The Mantel correlation between pairwise distance matrices of individual breeding and non-breeding sites is weak (below 0·5, indicating high inter-population mixing) for most of 28 species of long-distance migrant land-birds. (b) The strength of the Mantel correlation coefficient increases with non-breeding range spread (*x*-axis) but decreases with population spread (red and blue colours), so that low inter-population mixing only occur in species with either high non-breeding range spread or low population spread. Each point represents a species; triangles are those from the Neotropic system and circles are those from the Afro-Palearctic. In (a), solid black points denote a significant (*P* < 0·05) Mantel correlation; grey points are not statistically significant. In (b), blue and red points represent species with above- or below-average population spread respectively; blue (upper) and red (upper) lines are predictions for population spread values of 1059 km (90th percentile) and 292 km (10th percentile) respectively. Shaded regions are ±SE. [Colour figure can be viewed at wileyonlinelibrary.com]
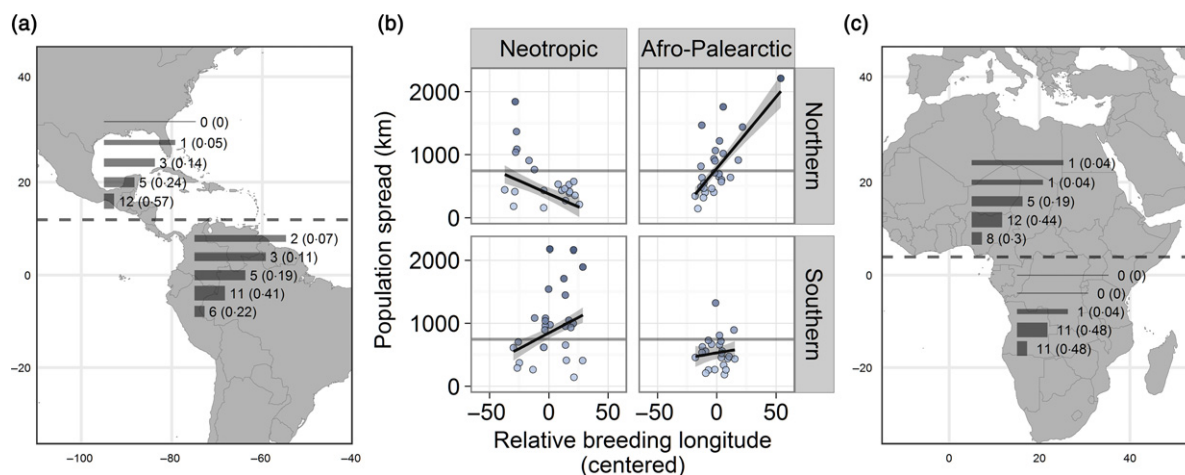
Fig. 5. Between-population variation in population spread is predicted largely geography. (a and c) Show the frequency distribution of population spread in the Neotropic (a) and Afro-Palearctic (c) migration systems. The length of each horizontal bar represents population spread (250, 750, 1250, 1750 and 2250 km), and the weight of each bar represents the number of populations falling into each 500 km bin. Numbers to the right of each bar give the number (and proportion) of populations in each zone falling into each 500 km bin. Horizontal dashed lines show the divide between northern and southern zones in each system, above and below which the availability of land on a continental scale changes profoundly. (b) Shows model predictions for the interaction between breeding longitude (*x*-axis), system (columns) and non-breeding zone (rows; shaded regions are ±SE). Each point represents a breeding population. The horizontal line intercepts the *y*-axis at the mean overall value of population spread (average distance on the non-breeding ground between any two individuals from the same breeding population = 743 km). [Colour figure can be viewed at wileyonlinelibrary.com]

African zone (807·1 ± 474·3 km) compared to Central America (608·2 ± 424·0 km) and the southern Africa zone (536·8 ± 257·7 km; Fig. 5), as expected if reduced relative land availability limits population spread. There was also strong support for the interaction between non-breeding zone and breeding longitude (Table 2). Thus, North American populations spending the non-breeding season within the northern zone spread out more if they came from western breeding sites, whereas those migrating to the southern zone spread out more if they come from eastern breeding sites (Fig. 5b). In the Afro-Palearctic system, populations spending the non-breeding season in the northern zone spread out more if they come from eastern breeding sites (Fig. 5b), and those in the southern zone generally had low spread regardless of breeding longitude (although there was limited variance in breeding longitude for these populations). Together, the interaction between system, non-breeding season zone and breeding longitude explained 38% of between-population variation in population spread, with species identity contributing an additional 25% ($R^2_{m} = 0.38$; $R^2_{c} = 0.63$). There was no support for higher level phylogenetic effects, or the additional fixed effects of migration distance or breeding latitude (Table 2).

Discussion

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

THE MANTEL TEST AND INTER-POPULATION MIXING

Few species had strong Mantel correlation coefficients, suggesting that for most species, individuals from different breeding populations occupy overlapping, rather than discrete, non-breeding quarters. Our results indicate that when low inter-population mixing does occur, this is due to high total non-breeding range spread (Fig. 4b, blue points in top right) as often as to low population spread (Fig. 4b, red points in top left). Non-breeding range spread was a stronger predictor of Mantel correlation coefficient than population spread, and species with large total non-breeding ranges (e.g. Common Nightingale *L. megarhynchos*, with non-breeding individuals in our dataset spanning 40° longitude) remained spatially segregated even if population spread was high. Correspondingly, species with small non-breeding ranges (e.g. Eleonora's Falcon, *Falco eleonorae*, with non-breeding individuals restricted to 6° longitude) mixed extensively, even if population spread was low. This highlights a limitation in the migratory connectivity nomenclature, in which 'strong connectivity' is used to refer simultaneously to low inter-population mixing and low population spread (Webster *et al.* 2002; Taylor & Norris 2010); our results suggest that the former does not necessarily depend on the latter.

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

POPULATION SPREAD

Although population spread was, on average, relatively high (mean = 743 km), it ranged from 140 km (Blackpoll Warbler *S. striata* from north-eastern USA) up to 2210 km (Pallid Harrier *Circus macrourus* from north-central Kazakhstan). A substantial portion of this between-population variation was explained simply by geography; population spread was lower for populations using non-breeding zones with lower land availability (southern Africa and Central America). This effect interacted with breeding longitude; North American populations spending the non-breeding season in Central America spread out less if they come from eastern breeding sites, possibly because land is more limited in the Caribbean islands than in continental Central America. On the other hand, those migrating to South America spread out more if they come from eastern breeding sites, perhaps due to the migration routes of western populations being constrained by the Pacific Ocean. Similarly, in the Afro-Palearctic system, populations migrating to the northern zone spread out more if they come from eastern breeding sites, possibly because western breeders are constrained by the Atlantic Ocean.

Clearly, other factors covary or are confounded with our indirect measure of land availability, so the exact mechanism underlying the observed relationship is uncertain, and much variance in population spread is still to be accounted for. In particular, it is difficult to distinguish between non-breeding land availability and constraints presented *en route*. Barriers such as mountain ranges and deserts, and land bottlenecks such as the Central American isthmus or the Straits of Gibraltar may cause routes to funnel (e.g. Lopez-Lopez, Garcia-Ripolles & Urios 2014) independently of land availability in the non-breeding area. The presence of such geographical features *en route* may well covary with breeding longitude (e.g. central and eastern European populations may have more opportunities to cross the Mediterranean than western ones) and could contribute to the observed relationship between 'land availability' and migratory spread. Although the effect of these barriers and bottlenecks likely interact with species-specific traits (e.g. flight mode; Alerstam 2001), they should affect all species to some extent. Equally, however, these barriers may cause migrants to converge on a common route, diluting any predictive signal of breeding longitude. Dominant weather patterns may also vary between these zones, and may influence the degree of variation in population spread, although we are not aware of any mechanism by which weather would result in the systematic directional differences observed here.

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

A NULL MODEL OF CONNECTIVITY

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

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

EVOLUTIONARY CONTEXT

The implication of our results is that, for many species, selection has not resulted in a deterministic strategy for non-breeding site selection. This is consistent with non-breeding conditions being generally variable and unpredictable, leading to a system whose emergent properties
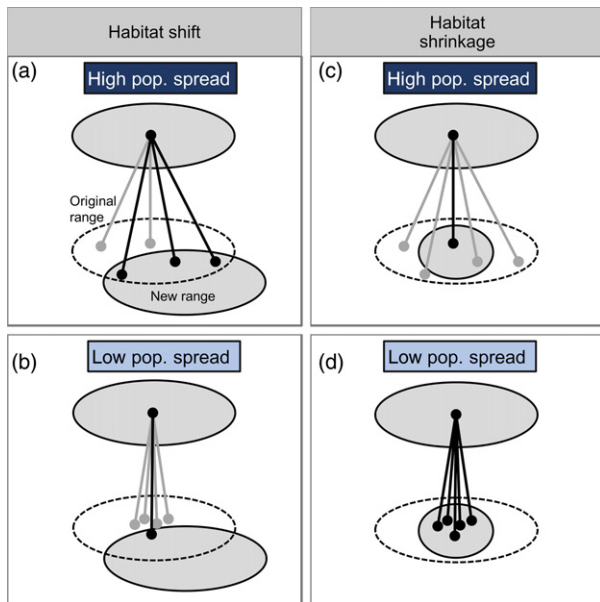
Fig. 6. Population spread determines the response of populations to non-breeding habitat change. The number of individuals successfully reaching suitable non-breeding sites (black lines) following either a shift (a and b) or a reduction (c and d) in the area of suitable non-breeding habitat depends on the degree of migratory spread. A greater proportion of a population with high spread will still reach a suitable habitat if its location shifts (e.g. due to climate change) compared to a low spread population (a and b), but if suitable habitat becomes less available overall (due to habitat loss) then a greater proportion of a population with high spread will miss the shrinking habitat, whereas a population with low spread may still reach the target (c and d). Note that we consider the simple situation where migration is in a southerly direction and nonbreeding habitat availability is spread out east–west perpendicular to migration direction. We also assume that individual migrants cannot make large-scale movements in response to habitat loss. [Colour figure can be viewed at wileyonlinelibrary.com]

resemble bet-hedging (Reilly & Reilly 2009; Botero *et al.* 2015). We suggest that the general low connectivity shown here is likely to be adaptive, because long-distance migration systems almost certainly represent recently evolved adaptive responses to dynamic global climatic conditions (Cresswell, Satterthwaite & Sword 2011; Fryxell & Holt 2013). Climatic variability and its consequent effects on the location of suitable habitat has been (Wanner *et al.* 2008; Svenning *et al.* 2015) and remains (Nicholson 2001) characteristic of most long-distance migration systems. An individual strategy of producing an offspring with high phenotypic variance in departure direction (i.e. diversified bet-hedging; Botero *et al.* 2015) will likely result in some individuals encountering suitable conditions even as habitat zones shift in response to climate change (Fig. 6); such a response has probably been observed in rapid shifts in non-breeding grounds for Blackcaps, *Sylvia atricapilla* (Berthold *et al.* 1992).

Clearly, low connectivity is not an absolute rule, and there are several mechanisms through which connectivity may be strengthened (see Table S3 in Appendix S1 for specific examples). Not least, there is good evidence for a genetic basis for many migratory traits including departure direction (Berthold *et al.* 1992), although these innate controls vary between individuals (Thorup, Rabol & Erni 2007; Reilly & Reilly 2009) and in their sensitivity to environmental perturbations such as crosswinds during migration. This is particularly true for naïve juvenile migrant birds, which may not compensate for natural or experimental displacement (Thorup *et al.* 2011; Horton *et al.* 2016), and whose routes tend to be repeated as adults in subsequent years (Cresswell 2014). Further variation in migratory spread will arise because of variation in current and historic land and sea barriers (Alerstam 2001), migratory bottlenecks (Newton 2008), timing of migration (Bauer, Lisovski & Hahn 2016), weather (Elkins 1983), use of social information (Nemeth & Moore 2014), habitat shifts during the non-breeding season (Moreau 1972) and age- and sex-dependent differences in migratory capability (Stewart, Francis & Massey 2002) or habitat use (Marra, Sherry & Holmes 1993) (Table S3 in Appendix S1).

We would encourage the testing of hypotheses regarding the importance of these mechanisms for explaining residual variation in migratory spread. For example, we expect species using non-breeding habitats which are spatially and temporally predictable over many generations to have lower population spread (Botero *et al.* 2015). Population spread may also be lower in soaring migrants, which are generally reliant on thermals and incapable of long sea crossings, so are often forced through bottlenecks (Alerstam 2001).

CONSERVATION IMPLICATIONS

Although low connectivity may facilitate rapid range shifts in response to climate change, it may not be a good strategy when habitat availability is reduced overall. A greater proportion of a population with high spread will still reach a suitable habitat if its location shifts (Fig. 6), for example, due to climate change, compared to a population with low spread, leading to greater resilience of high-spread populations (Gilroy *et al.* 2016). However, if suitable habitat becomes less available overall (due to habitat loss) then a greater proportion of a population with high spread will miss the shrinking habitat, whereas a population with low spread may still reach the target (Fig. 6). Consequently, climate-induced shifts in non-breeding habitat – or any temporal unpredictably in the location of suitable non-breeding habitat – might select for high spread and lower connectivity, while suitable habitat becoming restricted to specific localized areas should favour the reverse. There is therefore no optimum level of connectivity if climate change and habitat destruction act simultaneously and with opposing directions of selection. However, species whose migration route includes a substantial longitudinal shift could encounter a wide range of non-breeding habitats with even a small

range of migration starting angles, so may be less affected by simultaneous climate and habitat change. Linking population-specific levels of connectivity to flexibility in non-breeding range under climate and habitat change has not yet been explicitly investigated because data on accurate connectivity and how it varies from year to year have not been available.

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

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

Authors' contributions

T.F. and W.C. conceived the study, collected and analysed the data and wrote the paper equally; S.J.B. and A.M.A.F. provided theoretical discussion and wrote parts of the paper.

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Data accessibility

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Analysis of the sensitivity of the results to measurement error.

Appendix S2. Supplementary bibliography.