



Comparing migratory connectivity across species: The importance of considering the pattern of sampling and the processes that lead to connectivity

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Measuring the degree of migratory connectivity – how much and where different populations of species mix as they migrate over their annual cycle – is important because it informs the understanding of the evolution of migration, how populations will be affected by both habitat and climate change, and which areas to prioritize for conservation. But existing measures of connectivity may be difficult to compare because they measure different things and are confounded by sampling bias. Here we use tagging data from all available published landbird tracks up to July 2019 (224 populations, 86 species and 1524 individuals tracked in the three main global flyways) to identify robust measures to compare migratory connectivity across species. We consider two widely used descriptive measures: (1) degree of breeding population overlap on the non-breeding grounds and (2) Mantel correlation, which tests the degree of spatial autocorrelation between the breeding and non-breeding individuals; as well as one causative measure of the main process that leads to connectivity patterns: migratory spread of individuals from the same breeding population across the non-breeding area. We investigated the sensitivity of these three measures to the distance between breeding locations of sampled populations (breeding distance) and their sample size. We also considered the confounding effects of migration distance because longer migrations decreased overlap and increased Mantel correlations and migratory spread. We found that the degree of overlap between breeding populations on the non-breeding grounds decreased with increasing breeding distance and increased with increasing sample size. Mantel correlation coefficients also increased significantly with increasing breeding distance; sample size did not affect accuracy, but precision was greatly improved above a sample size of about 15 individuals. Migratory spread, however, was independent of breeding distance; sample size had only small effects on accuracy and precision, with no significant effects when more than four individuals per population were included. Furthermore, migratory spread was highly positively correlated with the maximum non-breeding range. Overlap and Mantel correlations were highly confounded by the spatial pattern and amount of sampling, whereas migratory spread was relatively unconfounded, even by migratory distance. Although any descriptive migratory connectivity measure can help set priorities by determining current areas for conservation on the non-breeding grounds, migratory spread, which leads to these patterns, needs fewer data, is comparable, and gives information on evolutionary flexibility and so ability to deal with changing habitat and climate.

Keywords: Mantel correlation, migration, migratory spread, non-breeding distribution.

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Migratory connectivity describes how, when and where different breeding populations of migrants stay separated or mix on their non-breeding grounds (Marra *et al.* 2019, Knight *et al.* 2021).

Low connectivity occurs where animals mix on the non-breeding grounds and is associated with large non-breeding ranges; high connectivity occurs where populations of breeding animals have largely separate, distinct non-breeding ranges and is associated with deterministic migration routes and smaller ranges (Webster *et al.* 2002, Newton 2008). Understanding the degree of migratory connectivity shown by any migrant animal species is a conservation priority because many long-distance migrant populations are declining (Robbins *et al.* 1989, Sanderson *et al.* 2006, Holmes 2007, Rosenberg *et al.* 2019, Burns *et al.* 2021) and because it determines how populations will be affected by both habitat and climate change (see Martin *et al.* 2007, Gilroy *et al.* 2016, Koleček *et al.* 2018, Patchett *et al.* 2018). Populations that show high connectivity as a result of selection to use specific, highly targeted non-breeding areas will be greatly affected by even relatively small losses of habitat in those localized areas, and also shifting habitat due to anthropogenic effects such as climate change (Cresswell 2014). In contrast, populations that have not undergone selection to use specific non-breeding areas and that show low connectivity, with large non-breeding areas, will only be partially affected by any local habitat losses or shifts, but most of the population will be affected by changes that occur anywhere on the non-breeding grounds (Cresswell 2014). High connectivity species then require a specific local network of reserves, whereas low connectivity species require land sharing solutions over a large area (Finch *et al.* 2017).

Connectivity measures either quantify the underlying evolutionary processes that drive connectivity (i.e. potential migratory connectivity) or describe the observed connectivity patterns that result (i.e. actual migratory connectivity). At its simplest, migratory connectivity arises because individuals from a breeding population vary in their directions of migration (routes) and the distances that they migrate (Finch *et al.* 2017). These can be measured either as the variation between the spread of, and distance migrated by, individuals in a brood, or at the population level by sampling random individuals. They can be considered measures of the underlying cause of connectivity because changes to them through selection lead to higher or lower connectivity. Where there is low variation within individuals from the same breeding location, the population will end up in the

same, discrete non-breeding areas, whereas a high degree of variation will end up with the population distributed over a wide area of the non-breeding grounds, inevitably mixing with other breeding populations. We can measure this as 'migratory spread': as individuals spread out – migrating in different directions from a source breeding population – so they end up further apart and therefore this spreading out can be characterized by the average spacing in the non-breeding area between any pair of individuals from the same breeding population (Finch *et al.* 2017). Migratory spread will then result in a pattern of distribution, such as a non-breeding range, characterized by the distance between the furthest apart individuals. These resultant patterns of non-breeding dispersal relative to breeding distribution can then be described further in terms of connectivity, by measuring the degree of overlap of two populations on the non-breeding grounds or the Mantel correlation coefficient (Ambrosini *et al.* 2009). Mantel correlation coefficients average the correlation between the distances from an individual to all other individuals of a sampled breeding population with distance between the individual and all other individuals in their non-breeding population, so providing a measure of the degree of spatial autocorrelation. Values typically lie between 0 and 1, where the relative spatial pattern on the breeding grounds is respectively random (no connectivity) or exactly the same (perfect connectivity). Methods to assess migratory connectivity using Mantel correlation coefficients can be improved in accuracy if breeding population tracking locations are naturally spatially clustered into regions, and estimates of abundance are available for these populations (see Cohen *et al.* 2018), but these criteria are not met for many migratory species. We therefore have three main measures associated with connectivity: a causative or evolutionary measure (migratory spread) and two descriptive measures (overlap and Mantel correlation; Fig. 1).

A causative or evolutionary-based measure of connectivity provides information about the adaptive potential for change in migratory routes and non-breeding ranges, whereas a descriptive measure provides a current snapshot of the distribution and linkage between breeding and non-breeding populations. But connectivity is often not put into this context of whether it is measuring the processes that give rise to potential connectivity or

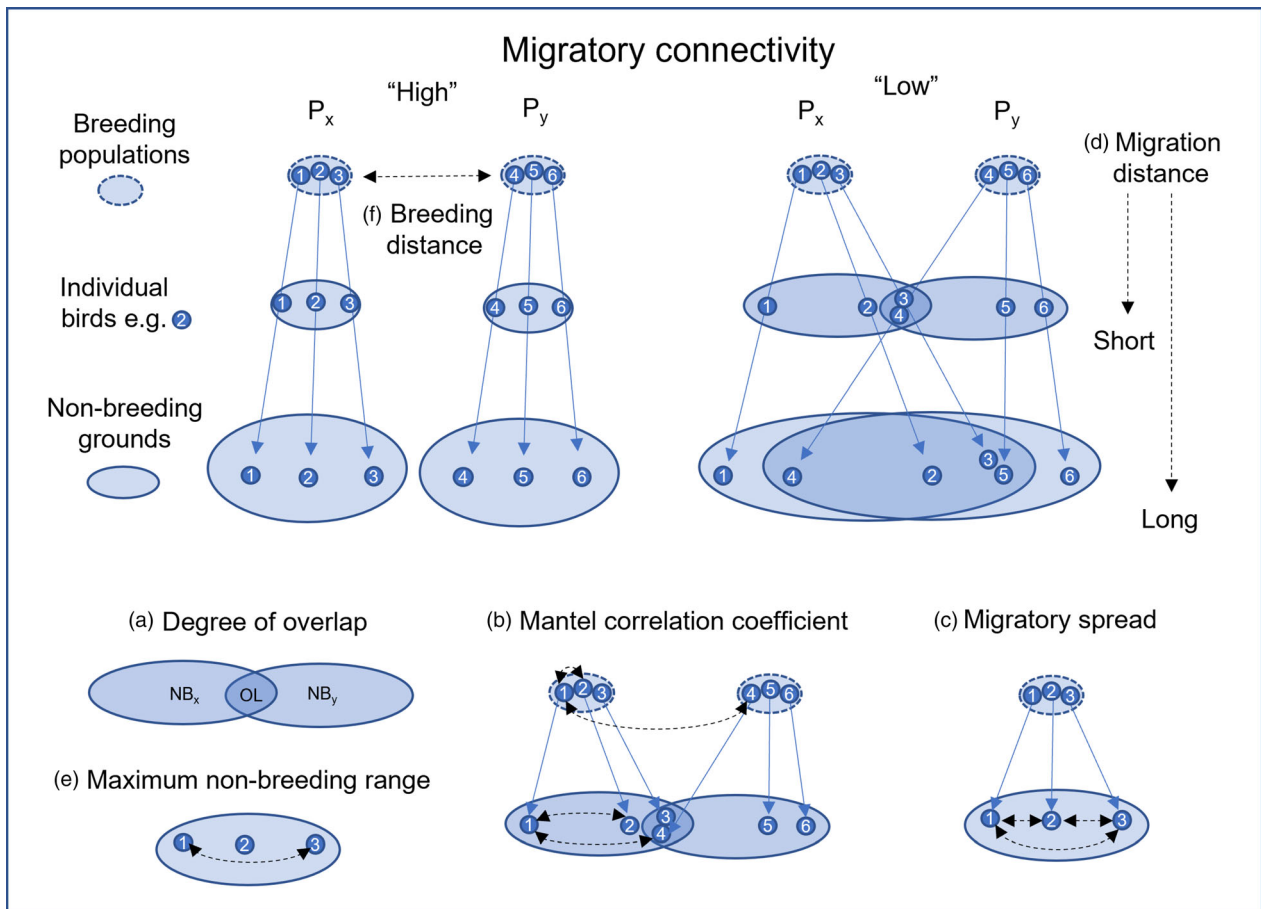


Figure 1. Two scenarios of connectivity: 'high', where three individuals within two different tracked populations (P_x and P_y) at a point on the breeding grounds end up together in the same areas of the non-breeding ground so that individuals from P_x and P_y stay segregated, and 'low' where the three individuals within the two tracked populations end up mixed on the non-breeding grounds. The difference between the two scenarios can be described by (a) degree of overlap of the sampled populations' (P_x and P_y) non-breeding ranges. For the high connectivity scenario, there is no range overlap; for the low connectivity scenario the degree of overlap is high, with an overlap of about 66%. The difference between the two scenarios can also be described by (b) Mantel correlation coefficient, where the distances of individual 1 to individuals 2–6 (and individual 2 to individuals 1, 3–6, and so on for all individuals) are correlated between the breeding and non-breeding grounds. For the high connectivity scenario the Mantel correlation would be very close to 1; for the low connectivity scenario the Mantel correlation would be closer to 0 because neighbours have changed, so the relative distances between specific individuals on the non-breeding grounds do not match the relative distances between the same individuals on the breeding grounds. These measures are descriptive because they just describe the observed degree of spatial difference between the breeding and the non-breeding population – how likely neighbours in a breeding population will end up as neighbours on the non-breeding grounds. These measures arise, however, by a process – the degree to which individuals within a tracked breeding population spread out in different migratory directions, and so their eventual migratory spread on the non-breeding grounds, and also their migration distance. (c) Migratory spread for each tracked population is measured as the average distance between, for example for population P_x , individual 1 and individuals 2–3 (and between individual 2 and individuals 1 and 3, and between individual 3 and individuals 1 and 2). In the high connectivity scenario, migratory spread is lower than in the low connectivity scenario because individuals tracked from locations P_x and P_y end up spread at greater distances apart on the non-breeding grounds. (d) Migration distance is measured as the average distance between the breeding and the non-breeding grounds for all individuals in a sample population. As migration distance increases, the degree of Mantel correlation will be lower, but overlap and average migratory spread will be higher; for example, in the low connectivity scenario, a short migration distance leads to high Mantel correlation coefficient, low migratory spread and low overlap, but a high migration distance leads to the reverse. As migration distance and/or migratory spread increases so the (e) maximum non-breeding range will increase. Note that individuals in a breeding population, e.g. P_x or P_y , are in the same place (i.e. no distance between individuals) to reflect the sampling pattern of almost all tracking studies where multiple individuals are tagged at effectively the same location. But distinct breeding populations, e.g. P_x and P_y , are separated by at least 100 km and (f) breeding distance is the distance separating them.

describing the observed connectivity patterns, yet this is important for the utility and comparability of the different measures of connectivity. For example, how distribution and population change arise due to habitat or climate change is best understood in terms of natural selection on individual variation in migratory spread or migration distance. In contrast, which migratory routes and areas on the non-breeding grounds should be protected to conserve particular breeding populations is best understood in terms of distinct or overlapping non-breeding ranges. The lack of distinction between whether connectivity is framed in terms of potential or actual connectivity also leads to a lack of comparability between degrees of connectivity (Taylor 2019). For example, well spatially separated breeding populations of Barn Swallows *Hirundo rustica* in Europe might show high actual connectivity because they apparently have largely non-overlapping non-breeding grounds (Ambrosini *et al.* 2009), yet populations share the same high degree of variation in migratory spread and migration distance (von Ronn *et al.* 2015).

A further issue when considering the utility and comparability of connectivity measures is that they are frequently confounded by spatial and sample size variation. The most frequent problem precluding an accurate measure of connectivity and the ability to compare different species is the lack of consideration of the initial spatial pattern of populations sampled (Vickers *et al.* 2021). For example, as in the Barn Swallow example above, two tracked breeding populations that are far apart from each other initially are much less likely to overlap on the non-breeding grounds regardless of any particular species-specific characteristics which might affect their degree of migratory connectivity. This bias should also affect Mantel correlation coefficients, which are frequently used to calculate an apparently standard measure of connectivity (Cohen *et al.* 2018). The distance of migration will also confound comparisons of connectivity because it fundamentally affects the degree of overlap, Mantel correlation and migratory spread (Fig. 1). As migration distance increases, we expect non-breeding locations of individuals from the same breeding population to spread further apart, and so overlap to increase and Mantel correlations to decrease (Finch *et al.* 2017). A further frequent problem in comparing different estimates of connectivity is variable sample size (Cohen *et al.* 2018, Vickers *et al.* 2021). The degree of

migratory spread, and so the non-breeding range of a population and its degree of overlap with other populations will increase with sample size, although eventually reaching an asymptote. And because most tracking studies have small sample sizes (McKinnon & Love 2018), most population range estimates are therefore particularly likely to be dependent on sample size, making connectivity comparisons unreliable.

Connectivity measures therefore differ in their potential accuracy, their ease of collection and their utility in terms of both conservation and understanding the evolution of migrant birds. Although this has been well established theoretically (e.g. Cohen *et al.* 2018, Vickers *et al.* 2021), the potential effects of these biases within the empirical measurements of migratory connectivity has not been explored in detail (Finch *et al.* 2017). Here we explore this using landbird migration tracks up to July 2019 from populations where at least two adult individuals (range 2–48) were tracked to a more southerly non-breeding area (1524 individuals from 224 breeding grounds populations and 86 species). First, we determine how the degree of overlap in distribution on the non-breeding grounds, Mantel correlation coefficients and migratory spread are affected by variable spatial sampling on the breeding grounds (i.e. how far apart breeding populations are), sample size and migratory distance. We then discuss how the different connectivity measures perform in terms of their ease of collection and utility. We conclude that migratory connectivity should always be defined in terms of its utility (whether it is a causative measure that gives rise to patterns of connectivity or a descriptive measure that simply describes the resultant pattern of connectivity).

METHODS

Migration data

Migration data came from all the tracking studies of landbird migrants that we could find in the published literature, either through systematic searches of bibliographic databases or cross-references from papers identified in this way. Our intention was to include all species of long-distance migrant landbirds, where any non-breeding locations obtained through tracking have been published. We used a database expanded from Patchett *et al.* (2018) to include all published

studies up to July 2019, and some additional studies that had been missed when constructing the original database. The final database, fulfilling data selection criteria below, contained breeding and non-breeding locations for 1524 individuals, from 224 populations of 86 species (Fig. 2; see Supporting Information Table S1 and [supplementary reference list](#) for all studies used in analysis). All data came from a comprehensive search of peer-reviewed tracking studies for all European and North American bird species classed as migratory land-birds (according to BirdLife; <http://www.birdlife.org/datazone/species/search>) by entering the terms [latin name] AND migra* AND (gps OR geolo* OR satellite) into the Web of Science online library or Google Scholar. From these studies, breeding and non-breeding locations of individual birds (i.e. the site where an individual spent most of the non-breeding period after migration) were extracted (or approximated from plotted map locations using Google Earth when precise coordinates were not given).

Our data were prone to two potential sources of error: imprecision in the translation of data from published figures to latitude–longitude coordinates via Google Earth ('translation error') and inaccuracy of solar geolocator-derived positions in the

original published data ('geolocator error'). Sensitivity analyses investigating whether these errors influence migratory connectivity measures and migratory spread were fully explored in Finch *et al.* (2017): translation and geolocator error were found to have a relatively small impact on these measures and were in all cases spatially unbiased and so were not considered further.

We restricted our study to the autumn (fall) migration of adult birds that were tagged on the breeding grounds in the northern hemisphere; we removed species with a sample size of one. Individuals of the same species tagged within 100 km of one another (which meant tagged at the same study site in almost all cases) were grouped into 'tracked populations', the principal unit of analysis (Fig. 1). Where there was more than one non-breeding site reported for an individual, we selected the non-breeding location where the individual spent the majority of the non-breeding period.

Analysis

Analysis was carried out using Generalized Linear Models using the libraries nlme, lmerTest and MuMIn in R (R Development Core Team 2014).

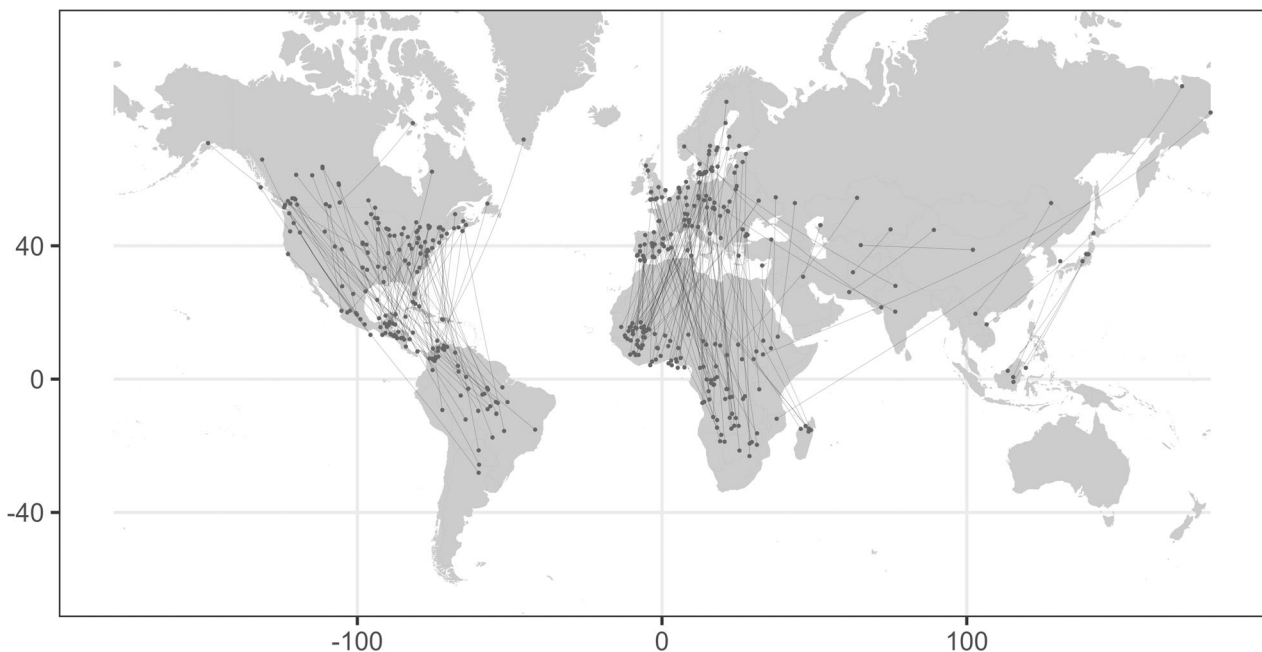


Figure 2. Plots of breeding sites connected to the central point of their non-breeding area for all birds tracked from each breeding population up to July 2019, i.e. the dataset analysed in this paper – 86 species, 224 populations, 1524 individuals. Each line represents an individual breeding population that has been tracked: the main sampling unit of this paper.

Model fit was assessed by visual inspection of residuals plotted against fitted values and quantile plots and were reasonable in all cases after log-transforming sample size. Predicted values were plotted using the `lme4`, `AICcmodavg` and `ggplot2` packages in R; variance was partitioned into main and random effects in mixed models using `MuMIn`. Models had overlap, Mantel correlation or migratory spread as the y -variable, and all had sample size, breeding distance and the quadratic of migratory distance as x -variables. Models where overlap was the y -variable included a random effect of species nested within family nested within order to control for taxonomic biases and uneven sampling across species. Models where Mantel correlation coefficients or migratory spread was the y -variable included a random effect of family nested within order to control for taxonomic biases (these analyses only had a single value per species).

Data were aggregated into means for every tracked population sampled per species (e.g. Supporting Information Fig. S1). The file aggregated by tracked population was then aggregated by flyway (Barn Swallow and Osprey *Pandion haliaetus* were sampled in more than one flyway) and then by species, to calculate species means. Mantel correlation coefficients and overlap required the tracking of individuals from different locations (tracked populations) and so were aggregated differently (see below).

The following metrics were calculated (Fig. 1):

Degree of overlap

We aggregated by flyway and species for all species that had two or more populations sampled (as above), but with at least four individuals in each population (to give reasonably credible minimum convex polygons of range). Then for each possible pair of population combinations within a species and flyway, a minimum convex spatial polygon defining the non-breeding range for the two populations was created using the `chull` function from the `alphahull` package in R. The area of each polygon was calculated using the function `gArea` and the area of overlap was calculated using the function `gIntersection` from the `rgeos` package in R. The overlap area as a proportion of each of the population's non-breeding range area was then calculated and the mean value of these was used as an index of overlap for analysis. The final aggregated file for the mean overlap analysis contained

a sample size of 29 species from 102 tracked populations, including an average of 24.8 individuals per tracked population pair.

Mantel correlation coefficients

For Mantel tests we aggregated as above by flyway and species, for all species that were sampled from more than one location in a flyway (i.e. tracked populations sampled at least 100 km apart) and then calculated the Mantel correlation for each species using the `mantelCor` function in R. This quantifies inter-population mixing as a value from -1 to $+1$ between pairwise distance matrices of individual breeding and non-breeding sites (Ambrosini *et al.* 2009), i.e. whether distances between individuals at the different breeding sites (and so their clustering) 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 (i.e. low inter-population mixing), and vice versa. The final aggregated file for the mean Mantel correlation analysis contained a sample size of 49 species from 1279 individual tracks, with an average of 26.1 individuals tracked per species, from a mean of 4.6 tracked populations per species.

Migratory spread

The mean of the distances between all possible pairs of individuals in the non-breeding area, from the same breeding population. All distances (in kilometres) here and elsewhere were calculated as great circle distances using the `distHaversine` function from the `geosphere` package in R. Models of migratory spread that contained breeding distance also required the tracking of individuals from separate locations (i.e. different tracked populations), so the same final aggregated data file for the Mantel correlation analysis was used (as above). Models of migratory spread that did not contain breeding distance used a larger dataset, however, because data from species that were sampled from only one tracked population could then also be used, as long as at least two individuals were tracked. The final aggregated file for the mean migratory spread analysis, excluding breeding distance, contained a sample size of 86 species from 224 tracked populations, including an average of 6.8 individuals per species. Models with and without breeding distance as a predictive variable were compared with Akaike's information criterion (AIC) and considered to be

identical in their predictive power if they differed in AIC by less than 2. 'Standardized' migratory spread was calculated using the predicted values for the final model without breeding distance using mean values for migration distance of 4864 km and sample size 4.9.

Migration distance

The mean of the distances between the breeding and non-breeding location for all individuals in the same breeding population. We included the quadratic of migration distance in all models because migration distance is eventually constrained by the geography of the flyways with land availability decreasing further south from the equator in all flyways (Finch *et al.* 2017).

Maximum non-breeding range

The maximum value of distance between all possible pairs of individuals in the non-breeding area, from the same breeding population. A model to determine how well migratory spread predicted maximum non-breeding range was tested, which included a random effect of species nested within family nested within order, and only one value per population where more than four individuals were sampled was included in the analysis.

Breeding distance

The mean of the distances between all possible pairs of breeding populations tracked or, in the case of two populations tracked, the distance between the two populations.

Sample size

Either the total number of individuals providing a non-breeding location from a tracked population or the total number of individuals tracked across all the populations sampled for each species. The log of sample size was used in all models because we expect there to be an asymptote in the effect of increasing sample size on the range of a population. Where an effect of sample size was found in a model, the model was re-run, removing studies with a small sample size (i.e. only including studies with sample size of more than 2 or 3 or 4 and so on) until no further significant effect of sample size was found, in order to determine the sample size above which any further change would make no difference to the estimate of overlap, Mantel correlation or migratory spread.

RESULTS

The degree of overlap between tracked breeding populations on the non-breeding grounds decreased significantly with increasing breeding distance (Table 1A, Fig. 3a), and increased significantly with the log of sample size (Table 1A, Fig. 3b) and the quadratic of migration distance (Table 1A, Fig. 3c).

Mantel correlation coefficient increased significantly (i.e. implying higher connectivity) with increasing breeding distance (Table 1B, Fig. 4a) and with the quadratic of migration distance (Table 1B, Fig. 4b). The mean value of the Mantel correlation coefficient did not change with the log of sample size (Table 1B, Fig. 4c), although its precision was greatly improved if more than 15 individuals were sampled (Fig. 4d inset in Fig. 4c). After controlling for breeding distance and average migration distance only eight species (16%) had Mantel correlation coefficients exceeding what might simply be predicted from these two parameters, indicating high connectivity (Fig. 4a).

Migratory spread did not change with breeding distance (Table 1C) and increased significantly with sample size (Table 1C, Fig. 5a) and the quadratic of migration distance (Table 1C, Fig. 5b). Inclusion of breeding distance in the model did not improve it (delta AIC + 2) and so it was removed, allowing a much larger sample size analysis (because single tracked breeding populations from a species could be included). In this larger analysis, migratory spread also increased significantly with sample size (Table 1D) and the quadratic of migration distance (Table 1D). But restricting the larger analysis to a sample size of more than four individuals removed any significant effects of log sample size on mean migratory spread (77.0 ± 74.6 km, $t_{47} = 1.03$, $P = 0.31$; 55 species, 105 tracked populations, 1189 individuals tracked, mean 11.3 individuals per population); precision remained similar with increasing sample size (Fig. 5a). Maximum non-breeding range and mean migratory spread were highly positively correlated (2.41 (migratory spread) $\pm 0.12 + (-97.9 \pm 125.6$ km; $t_{49} = 10.0$, $P < 0.0001$; marginal $R^2 = 0.79$; one value per tracked population where at least five individuals were sampled, sample size as in Model 1D above; Fig. 6).

Comparing the different measures in terms of their percentage change with respect to variation

Table 1. How (A) average percentage overlap between non-breeding ranges from two breeding populations of a species or (B) the Mantel correlation coefficient between breeding and non-breeding locations or (C & D) the migratory spread (the average spacing in the non-breeding area between any pair of individuals from the same breeding population) varies with sample size and distance between sampled breeding populations. Models where overlap was they-variable included a random effect of species nested within family nested within order; models where Mantel correlation coefficients or migratory spread where the y-variable included a random effect of family nested within order only had a single mean value per species.

	Value	se	df	t-value	P-value
A. Overlap					
(Intercept)	-0.810	0.305	69	-2.65	0.0099
Breeding distance	-8.57E-05	2.10E-05	69	-4.08	0.0001
Log sample size	0.208	0.0464	69	4.49	<0.0001
Migration distance	0.000319	0.000104	69	3.07	0.0031
Migration distance ²	-2.92E-08	1.10E-08	69	-3.50	0.0008
Marginal $R^2 = 0.32$	Random effect $R^2 = 0.47$				
102 pairs of overlapping populations from 29 species with a mean of 24.8 individuals per pair					
B. Mantel					
(Intercept)	-0.441	0.331	24	-1.33	0.20
Breeding distance	0.000458	0.0000945	24	4.85	0.0001
Log sample size	-0.0448	0.0537	24	-0.83	0.41
Migration distance	0.000282	0.000151	24	1.87	0.074
Migration distance ²	-3.21E-08	1.30E-08	24	-2.17	0.0399
Marginal $R^2 = 0.42$	Random effect $R^2 = 0$				
1279 tracked individuals from 49 species with a mean of 26.1 individuals per species					
C. Migratory spread					
(Intercept)	-318	306	24	-1.04	0.31
Breeding distance	-0.0219	0.08911	24	-0.25	0.81
Log sample size	133	46.9	24	2.83	0.0093
Migration distance	0.263	0.140	24	1.87	0.073
Migration distance ²	-2.12E-05	1.10E-05	24	-1.55	0.135
Marginal $R^2 = 0.32$	Random effect $R^2 = 0.09$				
1279 tracked individuals from 49 species with a mean of 26.1 individuals per species					
D. Migratory spread using larger sample size not requiring breeding distance					
(Intercept)	-88.7	185	135	-0.48	0.63
Log sample size	105	42.82	135	2.45	0.0157
Migration distance	0.240	0.0606	135	3.95	0.0001
Migration distance ²	-2.39E-05	1.10E-05	135	-3.30	0.0012
Marginal $R^2 = 0.11$	Random effect $R^2 = 0.20$				
1524 tracked individuals from 86 species with a mean of 6.8 individuals per species					

(from models in Table 1) in breeding distance (over a representative range of 100–1100 km), migration distance (over a representative range of 4000–8000 km) or sample size (over a representative range of 5–30) showed that Mantel was most sensitive to changes to breeding and migration distance, and overlap to sample size; migratory spread showed the least change (Fig. 7).

DISCUSSION

This study evaluated how different connectivity measures perform in terms of their accuracy, sample size and utility. The two descriptive measures of connectivity, degree of overlap and Mantel

correlation coefficient, were both strongly determined by sampling characteristics, particularly the initial spatial distribution of tracked populations. Put simply – tracked breeding populations that were far apart initially were more likely to end up far apart on the non-breeding grounds. Sample size significantly affected accuracy and precision of all the measures, but much less so for migratory spread where only more than four individuals tracked was sufficient to give a precise value. The measure of the process that gives rise to connectivity patterns, migratory spread, was found to be more reliable, unaffected by the spatial pattern of sampling on the breeding grounds, relatively little affected by migration distance, and could easily be

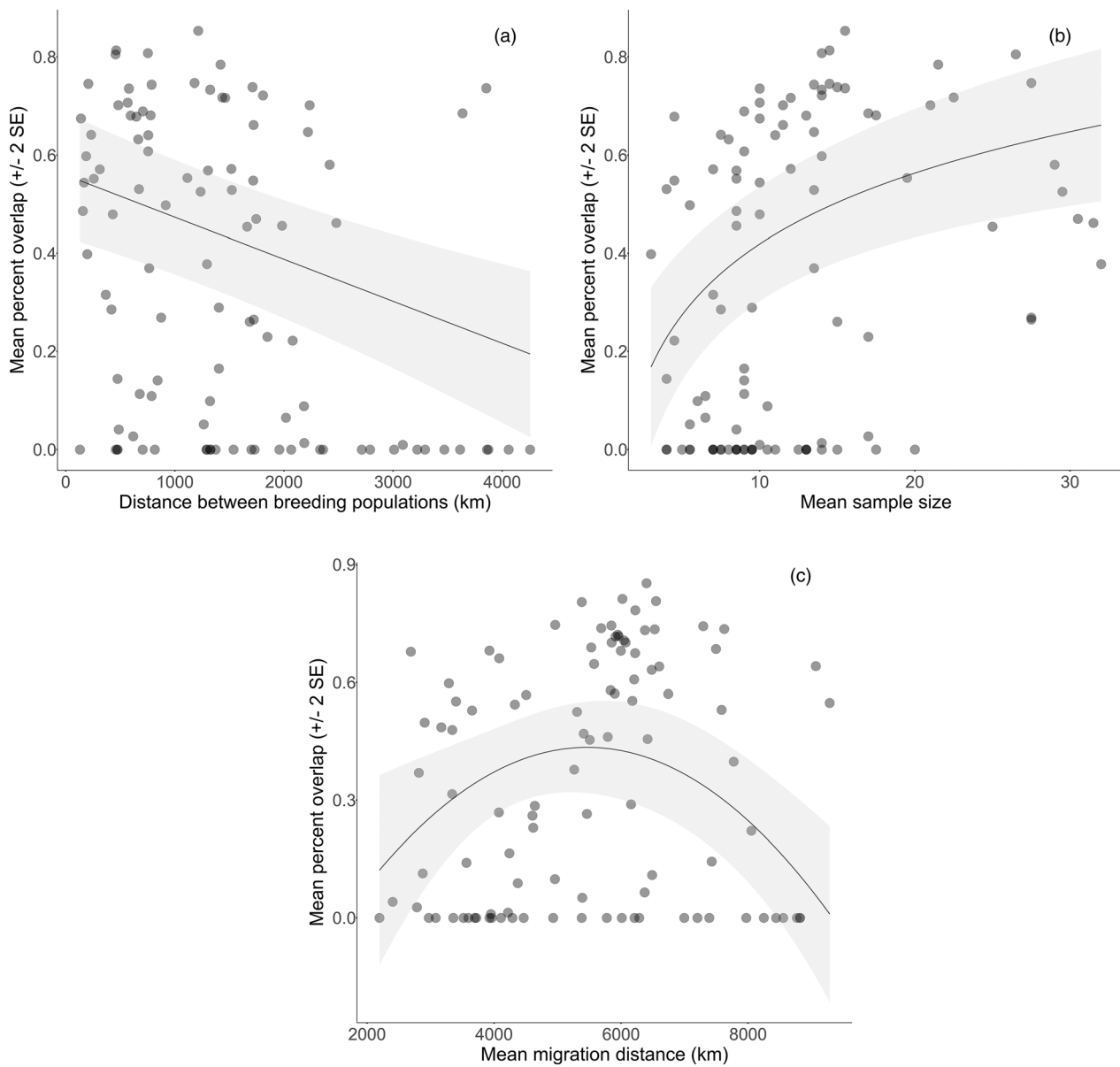


Figure 3. Predicted values for mean per cent overlap for distance between breeding populations (a), mean sample size (b) and migration distance (c), from the overlap model in Table 1A. For each predicted line, the other variables in the model have been set to mean values.

measured with a small sample size from a single tracked breeding population. We conclude that migratory connectivity is only a useful comparative measure across populations or species when it controls for variation in degree of and spatial pattern of sampling. We also highlight that the appropriate measure to describe migratory connectivity depends on whether a study aims to describe an

observed pattern of connectivity, or whether it aims to measure something that causes the observed pattern of migratory connectivity, and so that would be subject to natural selection.

The importance of considering the spatial pattern of sampling of breeding populations and sample size has been shown theoretically (Cohen *et al.* 2018, Vickers *et al.* 2021) and empirically

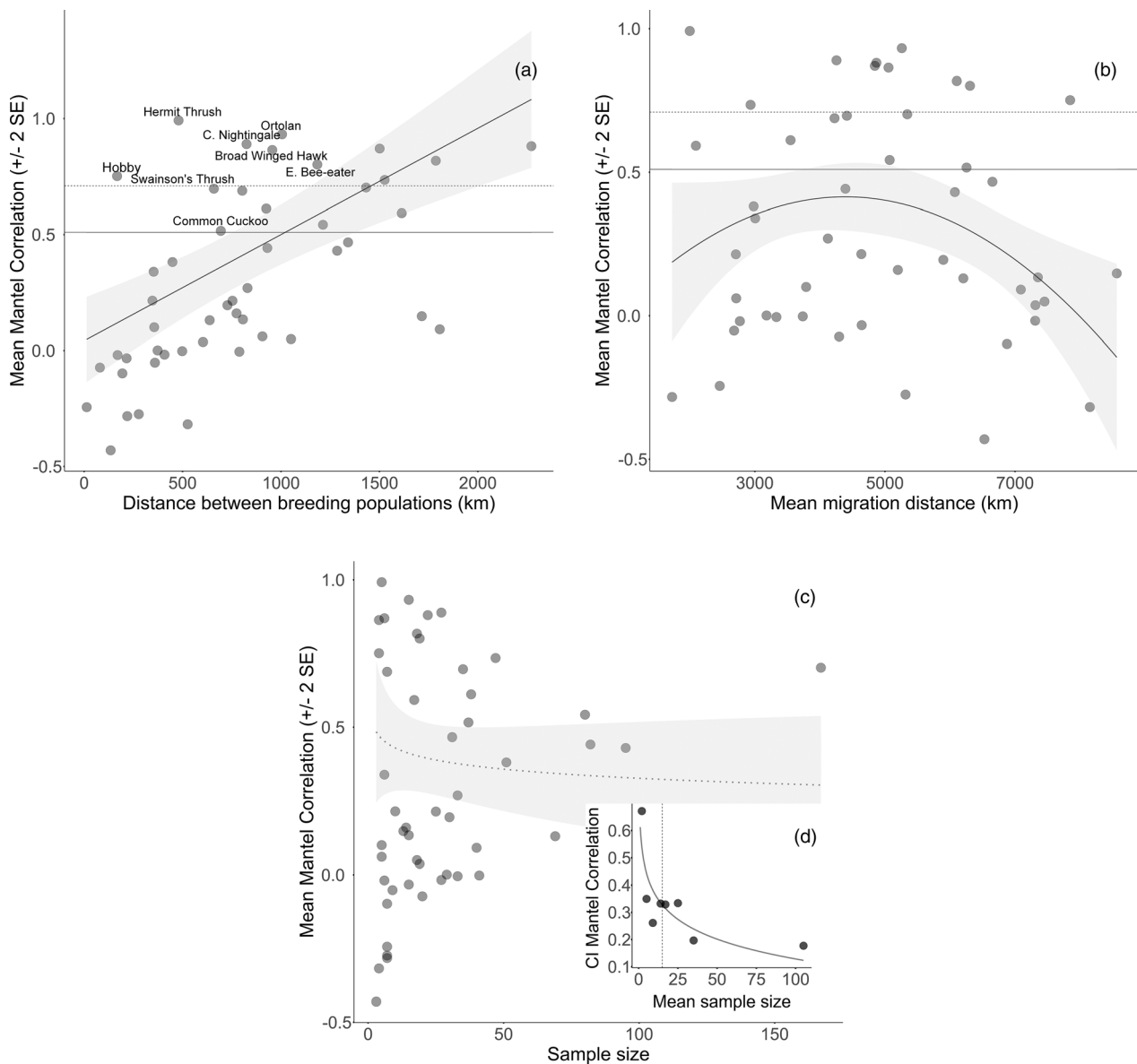


Figure 4. Predicted values for Mantel correlation coefficient for distance between breeding populations (a), migration distance (b) and sample size (c) from the Mantel model in Table 1B. For each predicted line, the other variables in the model have been set to mean values. Note that there were no significant effects of sample size on the mean value of the Mantel correlation but the precision of the correlation coefficient did vary significantly (d, inset graph in c; the relationship between the confidence interval CI of the coefficient and the sample size pooled into eight classes to equalize approximately the sample size of species across them: $CI = (-0.105 \pm 0.03 * \log(\text{sample size}) + 0.613 \pm 0.082)$, $\text{adj } R^2 = 0.65$, $P < 0.01$). The solid horizontal line is plotted at Mantel correlation = 0.51 where a 'reasonable' structure is inferred and the dashed horizontal line is plotted at Mantel correlation = 0.71 where a 'strong' structure is inferred (see Rousseeuw 1987).

for Mantel correlation coefficients (Finch *et al.* 2017). This study provides further, more comprehensive evidence and provides the first empirical measure of its reliability and sampling effort required for accuracy. Very few connectivity

studies consider the initial spatial pattern of sampling of the breeding populations. This does not matter if the purpose of the study is simply to describe observed migratory connectivity, i.e. the current non-breeding distribution patterns of

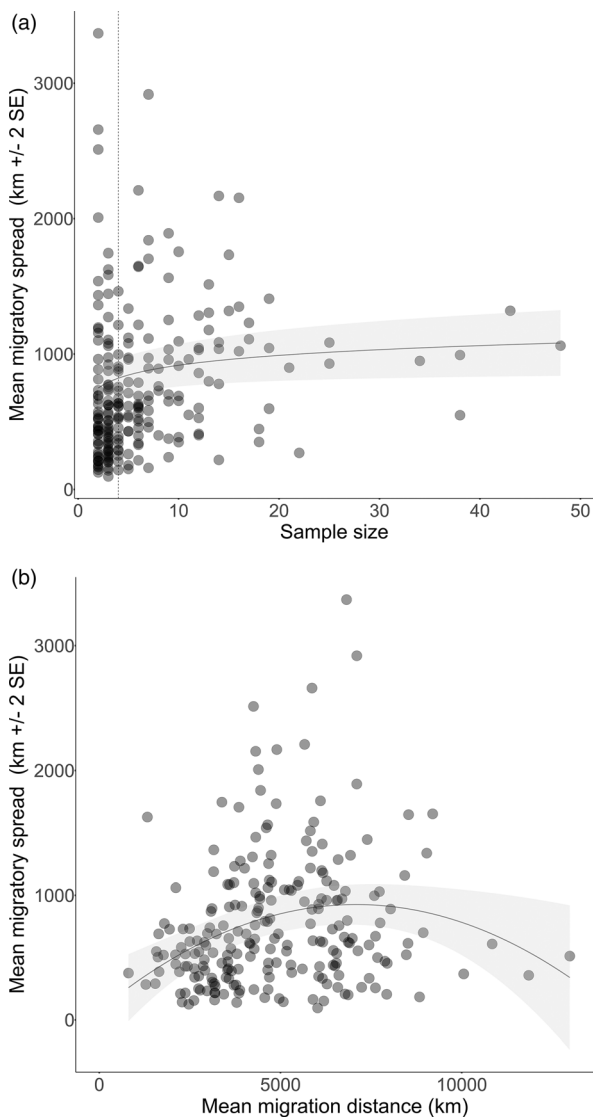


Figure 5. Predicted values for mean migratory spread for sample size (a) and migration distance (b), from the migratory spread model in Table 1D. For each predicted line, the other variables in the model have been set to mean values. Note that there were no significant effects of breeding distance so this graph is not plotted; the term was removed from Model 1C, so that the larger dataset allowing the use of single populations (i.e. without any variation in breeding distance) could be used (Model 1D). The dotted line in (a) indicates a sample size of 4, above which there is no further significant variation in migratory spread with increasing sample size.

specific breeding populations. Any measure of the overlap or segregation of tracked breeding populations on the non-breeding grounds can successfully describe the current distribution of these populations, for example to provide a map of potential protected areas to prioritize on the non-breeding

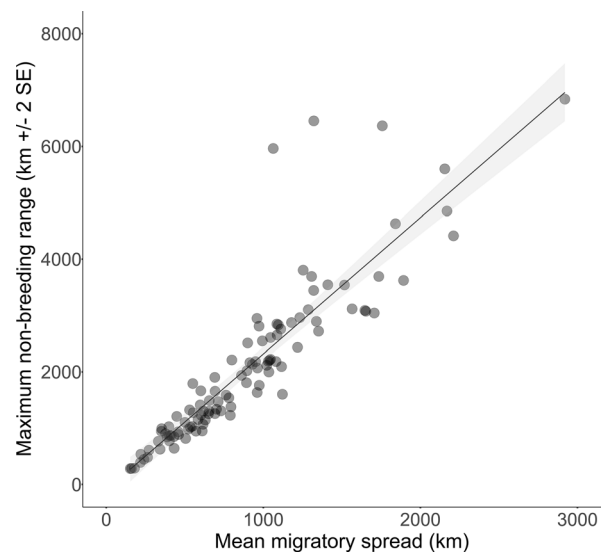


Figure 6. The relationship between maximum non-breeding range and migratory spread (predicted values from a model of maximum mean population spread \sim migratory spread, random = ~ 1 |order/family/species).

grounds for any specific breeding population, and many of the studies included here specifically aimed to identify non-breeding areas in this way. But if the intention is to understand evolutionary connectivity – the degree to which any breeding population has undergone natural selection on genes that control migration direction and distance, and thus range, mixing and overlap of populations (i.e. the deterministic control of migration) – then measures such as migratory spread that operate at the level of the individuals are needed (Winger *et al.* 2019). If the measure is also reliable, then comparisons across species can also be made to understand further the evolution of migration.

Overall, migratory spread may provide the most useful measure of connectivity across species because it is unconfounded by spatial variation in breeding population sampling, accurate even with a relatively small sample size and because it measures individual variation generally, rather than describing a specific population distribution. Comparisons between the migratory spread of species can then tell us how much selection has acted on a species with respect to migratory connectivity. For example, we can predict a standardized mean migratory spread for each species in this study, controlling for migratory distance and sample size (Fig. 8, using the model in Table 1C with

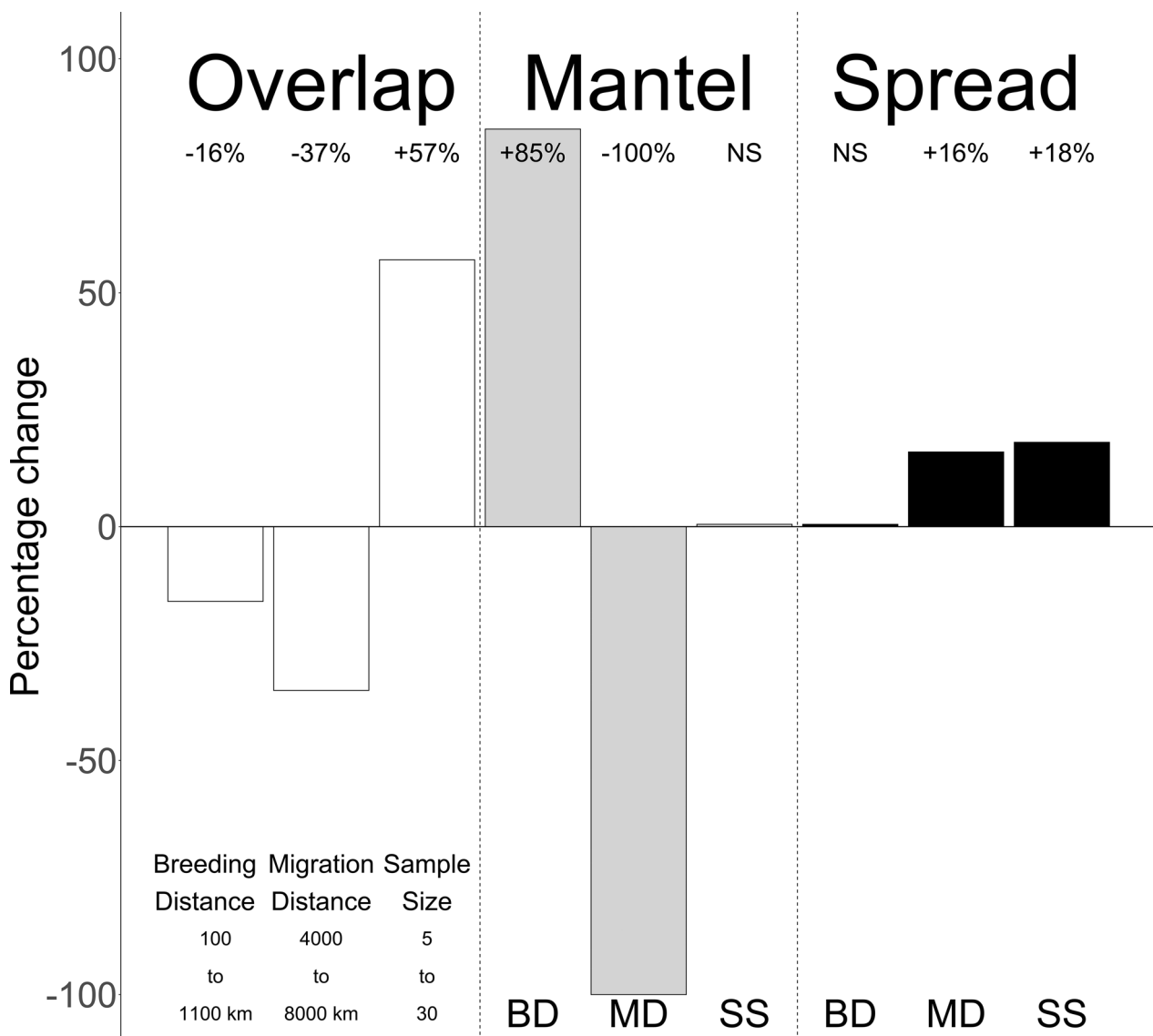


Figure 7. Summary of how the confounding variables influence overlap, Mantel correlation and migratory spread. Models A–C in Table 1 were run using a representative range of breeding distance (BD), migration distance (MD) and sample size (SS) from the observed dataset, and the change in values, expressed as a percentage of the higher value, was plotted. Where no bars are plotted (labelled NS) a relationship was not significant.

migratory distance and sample size set to mean values). Although there will be other sources of variation accounting for migratory spread, such as the availability of land at different non-breeding longitudes and latitudes (see Finch *et al.* 2017), such standardized migratory spread estimates begin to show the deterministic component of an individual species' migratory connectivity – their potential connectivity. Such comparisons can then show the similarity in migratory spread and so the evolutionary component of migratory connectivity

across many of the species in this study. For example, the interquartile range of migratory spread is only 165 km, or 21% of the median value of 736 km (Fig. 8), providing further support for the hypothesis that selection for high connectivity in a migratory species is actually unusual, rather than the norm (Finch *et al.* 2017). Overall, many even very ecologically different migrant species can therefore be shown to share similar connectivity processes (the highlighted blue area in Fig. 8) and so also may share the same mechanism of

establishing non-breeding ranges – a relatively untargeted dispersal of juveniles over a wide area – leading to similar patterns of population dynamics in the face of habitat and climate change (Cresswell 2014). These standardized comparisons can then also identify those species that have undergone selection for decreased migratory spread (Fig. 8): for example, the Ortolan Bunting *Emberiza hortulana* (Jiguet *et al.* 2019) and Swainson's Thrush *Catharus ustulatus* (Cormier *et al.* 2013), and species that have undergone less selection: for example, the Osprey (e.g. Elliott *et al.* 2007) and Barn Swallow (e.g. Burman *et al.* 2018).

The distinction between whether species are being compared in terms of evolutionary potential rather than observed connectivity is important to identify species that are likely to be resilient in the face of climate change (Taylor & Norris 2010, Cresswell 2014, Patchett *et al.* 2018). To illustrate this point, consider the distribution of the Lesser Kestrel *Falco naumanni* in Europe and Africa. All European breeding populations have now been tracked and their non-breeding areas mapped (Sarà *et al.* 2019). There is observed high connectivity because Iberian populations spend the non-breeding season in West Africa and Greek populations in Central Africa (see fig. 1 in Sarà *et al.* 2019). But from an evolutionary perspective, Lesser Kestrels tend towards low potential connectivity with a fairly average standardized migratory spread on the non-breeding grounds (see Fig. 8). The current observed distribution is largely a consequence of the breeding distribution, and Lesser Kestrels simply disperse approximately south. Clearly, from a current conservation point of view, Iberian populations are best served by policies targeted towards West Africa, and Greek populations by policies targeted towards Central Africa. Yet from a long-term conservation point of view, Lesser Kestrels are a typical generalist, bet-hedging migrant which is likely to use any suitable habitat available, and as the distribution of this shifts, then so probably will its non-breeding distribution. At the present time, there is habitat more or less directly to the south of all populations, so there has been no selection for targeted dispersal, and flexibility probably remains in the population to adapt to shifting locations of habitat.

Our results show that defining levels of connectivity for a species as high or low can be fundamentally flawed without terms and conditions to clarify whether it is simply a snapshot based on limited sampling. Of course, any pattern of connectivity

that is described – observed connectivity – may be useful for describing the range of a particular population of interest and so for framing a specific population-based, site-based conservation programme at a particular moment in time. For example, a Mantel correlation coefficient is useful to describe the connectivity in a particular species at a particular place, at a particular time, but it does not necessarily give much information about the relative degree of migratory connectivity compared with other species. Modifications to Mantel correlations that take into account the spatial clustering of the populations that are tracked, the relative or absolute abundance of these populations and various types of uncertainty in the tracking data could potentially give relatively unbiased and so comparable estimates of migratory connectivity (Cohen *et al.* 2018), but these require large amounts of additional data, or in the absence of this, assumptions. Only causative, potential migratory connectivity measures allow efficient and realistic comparisons across species, and inform, for example, how species might react differently to global patterns of habitat and climate change. This then begs the question of the utility any simple statement of migratory connectivity such as the value of a Mantel correlation coefficient without its context (Vickers *et al.* 2021). A far more useful, and comparative measure is the spread of a species during migration – ideally variation in departure directions during the first migration of juveniles from a breeding population – along with the influence of migration distance, and the geography across the breeding range, stopover locations on route and on the potential non-breeding grounds, and how these might lead to mixing of populations and impact on final non-breeding ranges. Ideally, we would measure migratory spread through tracking of juveniles and with tags that indicate where juveniles die as well as where they go during their first migration (e.g. Strandberg *et al.* 2010, 2012), although non-archival tags are still too large and heavy for most passerine species.

CONCLUSION

Connectivity in migratory species is frequently described in imprecise and subjective terms such as 'weak' or 'strong'. Even when measured quantitatively using degree of overlap or Mantel correlation coefficients, these are frequently highly confounded by sampling issues and so cannot be used in comparisons with other populations and

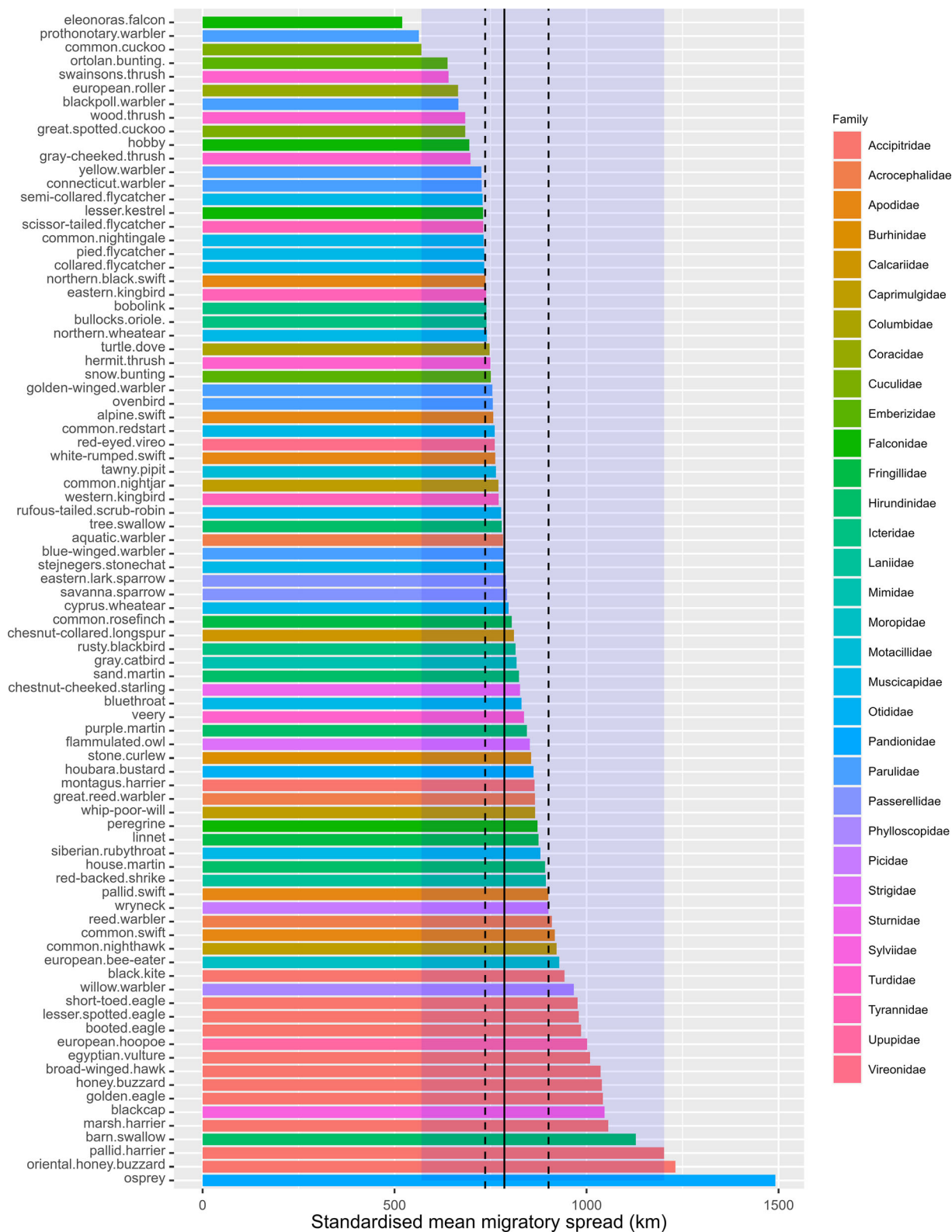


Figure 8. Standardized migratory spread for the 86 species considered in the study. Predicted values of migratory spread are plotted from the model in Table 1D using mean values for migration distance and sample size. Species are arranged in increasing order of migratory spread (i.e. high to low potential connectivity) and colour-coded according to Family. The blue-shaded bar encompasses 90% of species; the solid black vertical line is the median spread, and the dashed lines the lower and upper quartiles.

species unless there is good sampling design and clarity about the spatial pattern of sampling (Vickers *et al.* 2021). Migratory spread – the average spacing in the non-breeding area between any pair of individuals from the same tracked breeding population – is, however, a straightforward, robust quantitative measure and so one that can be compared meaningfully between populations and species. *All things being equal*, a species such as an Ortolan Bunting that has low migratory spread will inevitably have higher connectivity; a species such as a Barn Swallow that has high migratory spread will inevitably have lower connectivity. And because migratory spread is not a scale-dependent measure of connectivity (see Vickers *et al.* 2021), and is measured at the level of the individual and is relatively robust to sample size, migratory spread is perhaps the closest thing to a single ‘true’ connectivity value that we have.

We thank Tom Finch for partly constructing the database of migrant bird locations up to 2015. We thank the many diligent, inspiring and ground-breaking researchers who tagged the birds and published the maps used in this paper. We thank three anonymous referees for their comments, which have greatly improved the paper.

AUTHOR CONTRIBUTIONS

Will Cresswell: Conceptualization; methodology; software; data curation; supervision; resources; project administration; formal analysis; validation; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization.
Robert Patchett: Conceptualization; methodology; data curation; writing – review and editing; investigation; validation; formal analysis.

ETHICAL NOTE

None.

FUNDING

None.

CONFLICT OF INTEREST

We declare that there are no conflicts of interest with this paper.

Data Availability Statement

Data and R code used in analysis are available from the University of St Andrews Research Repository <https://research-repository.st-andrews.ac.uk/>.

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Received 17 November 2022;
Revision 26 June 2023;
revision accepted 19 July 2023.
Associate Editor: Inês Catry

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Species, populations and systems included in this study and the published studies from which location data were obtained

Figure S1. Raw data for migratory spread calculations showing the mean migratory spread averaged across individuals in a study and then these mean values averaged across studies for a species, with the number of studies (left hand number on each column) and overall number of individuals (right hand figure beside each column) measured.