Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin *Erithacus rubecula*: a continent-wide analysis

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Summary

1. Many partially migratory species show phenotypically divergent populations in terms of migratory behaviour, with climate hypothesized to be a major driver of such variability through its differential effects on sedentary and migratory individuals.

2. Based on long-term (1947–2011) bird ringing data, we analysed phenotypic differentiation of migratory behaviour among populations of the European robin *Erithacus rubecula* across Europe.

3. We showed that clusters of populations sharing breeding and wintering ranges varied from partial (British Isles and Western Europe, NW cluster) to completely migratory (Scandinavia and north-eastern Europe, NE cluster).

4. Distance migrated by birds of the NE (but not of the NW) cluster decreased through time because of a north-eastwards shift in the wintering grounds. Moreover, when winter temperatures in the breeding areas were cold, individuals from the NE cluster also migrated longer distances, while those of the NW cluster moved over shorter distances.

5. Climatic conditions may therefore affect migratory behaviour of robins, although large geographical variation in response to climate seems to exist.

Key-words: climate change, *Erithacus rubecula*, European robin, mortality, partial migration, phenotypic differentiation

Introduction

Climate is changing rapidly with dramatic increases in temperature, in particular at high latitudes (IPCC 2013). Because the distribution of many species closely tracks isotherms during the coldest month (e.g. Root 1988), increasing temperatures have affected distribution, phenology and migration of birds and other organisms (Parmesan & Yohe 2003; Møller, Fiedler & Berthold 2010). Some of the most dramatic effects of climate change

include shifts in the timing of migration by birds and other migratory organisms (review in Lehikoinen & Sparks 2010). However, the analysis of such phenotypic variation has rarely been extended to the behaviour of individuals.

Amateur and professional ornithologists have ringed millions of birds for more than 100 years providing a unique data base of capture and recovery data. Surprisingly, these data have only been analysed to a small extent to investigate the effects and the consequences of climate change (but see Ambrosini *et al.* 2011, 2014). A few studies on Northern Hemisphere migrants have

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demonstrated reductions in migration distance over time, most notably in short-distance migratory birds (Fiedler, Bairlein & Köppen 2005; Maclean *et al.* 2008; Visser *et al.* 2009; Lehikoinen *et al.* 2013), but also in a long-distance migrant (Ambrosini *et al.* 2011), coherent with patterns of global warming. Moreover, Visser *et al.* (2009) provided a link between migration and climate change by showing that short-distance migrants wintered closer to their Dutch breeding grounds in years with milder winters. However, that study was limited to one breeding area only, while other studies lacked an explicit mechanistic link between migration and climate change.

Migration entails marked costs, mainly in terms of mortality, but so does residency during periods of severe winter weather (Newton 2008). However, several studies suggest that a climate warming scenario should result in fewer migrants (e.g. Pulido, Berthold & van Noordwijk 1996; Pulido & Berthold 2010), but also lower mortality of residents thanks to warmer winters (e.g. Sanz-Aguilar *et al.* 2012). Indeed, populations of birds can change from partially migratory to resident in a few generations, as shown by selection experiments (Pulido, Berthold & van Noordwijk 1996). Because polymorphic populations of migrants and residents are common in partial migrants (Chapman *et al.* 2011; Pulido 2011), rapid changes in current climatic conditions should result in rapid changes in migratory behaviour.

Here, we analysed an existing data base on migration of individuals in order to quantify the effects of climate change on the proportion of individuals that migrated ('migration propensity' hereafter) and on migration distance. To this end, we developed a novel framework for the statistical analyses of ring recoveries. We used a large data base of ring recoveries of the European robin *Erithacus rubecula* L (hereafter robin), which is a model species for studies of partial migration (Adriaensen & Dhondt 1990) for which genetic variation in migratory behaviour has been demonstrated (Biebach 1983).

Winter temperatures are likely to be the most important ultimate selection pressure affecting migration propensity and distance in birds (Visser *et al.* 2009). However, winter temperatures in the breeding areas are not actually experienced by individuals that migrated from the study area in autumn and are experienced by resident individuals only after they had decided not to migrate. We therefore aimed at assessing the potential mechanisms driving variation in migration propensity and distance according to the winter temperatures. For instance, robins may use summer or autumn temperatures (i.e. the temperature actually perceived by birds soon before autumn migration; robin migration peaks in September-October; Cramp *et al.* 2004) as proxies of winter temperatures and adjust their migration behaviour accordingly. Alternatively, variation in migratory behaviour according to the winter temperatures may be the consequence of differential mortality of resident and migratory birds. Indeed, migratory behaviour is under genetic control in many bird species (Berthold

1996; Newton 2008), and, therefore, winter temperatures may affect the genetic structure of a population. For example, resident individuals or those migrating shorter distances could increase in a population in the winter following a mild winter season, resulting in a population-level decline of migration propensity and distance. Such changes may translate to time-lagged effects of winter temperatures on mean migration propensity and distance of a population (Dhondt 1983).

Based on these hypotheses, we analysed migration propensity and distance according to the summer and autumn temperatures of year i at the breeding grounds, whose effect would suggest phenotypically plastic adjustment of migration behaviour. In addition, we analysed migration propensity and distance according to the winter temperature in the breeding grounds in year $i - 1$, whose effect would suggest that changes in migration behaviour are driven, at least partly, by differential mortality of resident and migratory individuals. Finally, to gain insight into the potential mechanisms driving a plastic adjustment of migratory behaviour according to the winter temperatures, we investigated temporal autocorrelation in temperatures between years or seasons. Temporal autocorrelation of temperatures may in fact allow birds to forecast winter environmental conditions and to adjust their migration behaviour accordingly. We therefore investigated whether summer and autumn temperatures of year i in the breeding areas predicted winter temperatures of year i in the same areas and whether winter temperatures in year $i - 1$ predicted winter temperatures in year i.

Overall, the objectives of this study were to: (i) identify clusters of migrants with similar migratory behaviour (i.e. similar breeding and wintering ranges); (ii) identify differences in migratory propensity and migration distance among clusters; and (iii) link migration propensity and distance to temperature in the breeding areas during the coldest winter month. Migration propensity and distance were expected to increase during severe winters compared with milder ones; (iv) assess long-term shifts in breeding or wintering grounds of populations; and (v) identify potential mechanisms that may explain variation in migration propensity and distance of individuals according to the winter temperatures in the breeding areas.

Materials and methods

DATA SET

For individually ringed birds, the EURING Data Bank (EDB) includes information on date and locality at ringing, as well as subsequent encounters ('ring recoveries') of birds ringed in Europe. Hence, ring recoveries include both ringing and finding information of any bird that has been re-encountered. In 2012, we obtained from the EDB all records for robins with at least one record in April–June and one record in November–February, that is in the focal months of reproduction and wintering for robins (Cramp *et al.* 2004). Before the analyses, we carefully checked for data consistency and excluded any dubious case (e.g.

individuals recovered at sea). In addition, in order to reduce heterogeneity, we selected all records from individuals shot or found dead in winter and discarded the rest (see Supporting Information for further details). The final data base used for the analyses consisted of two geographical locations (one for breeding and one for wintering) for 1111 robins in the period 1947–2011. Supporting Information provides additional details on the rationale behind this selection procedure as well as on the fields of EURING code used for data selection.

MIGRATION DISTANCE AND MIGRATORY CONNECTIVITY

To identify geographical populations of robins with similar migration tactics, we applied the method proposed by Ambrosini, Møller & Saino (2009) for the analysis of migratory connectivity. Migratory connectivity is the degree to which individuals from the same breeding site migrate to the same wintering site (Webster *et al*. 2002; Trierweiler *et al*. 2014), and its intensity can be assessed by a Mantel test. Since the analyses showed evidence for connectivity (see Results), we identified the main clusters in which the population could be divided which represent groups of robins that both breed and winter close together. We emphasize that this analysis is based only on the reciprocal position of individuals both at breeding and wintering grounds, and it does not take into account the actual distance migrated by each individual. Supporting Information and Figure S1 provide further details on these analyses.

Migration distance was calculated as the great circle (orthodrome) distance between breeding and wintering locations of each individual. The radius of the home range of robins was estimated to be 0·571 km, corresponding to the geometric mean natal dispersal distance in the UK (Paradis *et al*. 1998). Robins that were found in winter within this distance from the breeding location were considered residents, while those found at longer distances were considered migratory. Although the geometric mean is an unbiased estimator of dispersal distance (Paradis *et al*. 1998), the choice of threshold distance may be considered arbitrary, so we checked for consistency of our results by rerunning the analyses with different thresholds (namely 1, 2, 3, 5, 7, 10, 20, 30, 50, 70 and 100 km).

CLIMATIC DATA

We used the R package RNCEP (Kemp *et al*. 2012) to retrieve temperature data from the NCEP/NCAR Reanalysis 1 model (parameter 'air.sig995' at level 'surface', representing air temperature at the surface of the Earth) for November–February in Europe. This model provides temperature data with a global scale at a spatial resolution of 2·5 × 2·5° latitude × longitude ('cells' hereafter) for the period 1948–2011 (robin records during winter spanned 1949–2011, so no data had to be discarded). For each cell, we calculated mean monthly temperatures for November–February, and for each winter (i.e. from November of year i to February of year $i + 1$), we selected the coldest of these months as predictor in the analyses. Temperatures were centred within cells in order to obtain temperature anomalies. We then assigned to each robin the temperature anomaly of the coldest month of the winter (November–February) when it was recaptured, recorded in the cell where it was found during the breeding season. For example, if a bird was found breeding in cell A in 1986,

and wintering in 1987 in cell B, we determined for cell A the temperature anomaly of the coldest month of the winter 1987 (i.e. from November 1987 to February 1988). Hereafter, we refer to these temperature anomalies as 'winter temperatures'. The rationale behind this procedure is that individuals are expected to be faithful to their breeding grounds (at least at the coarse spatial scale of 2·5° × 2·5° latitude × longitude that we are considering), but would move longer distances from the breeding grounds according to the harshness of the climatic conditions of a given winter at the breeding grounds (Visser *et al*. 2009).

We also calculated monthly mean temperature anomalies at each cell for June–October and selected: (i) the warmest month in each summer (i.e. June–August of year i, 'summer temperatures') and (ii) the coldest month in each autumn (September–October of year i, 'autumn temperatures'). Finally, we also associated winter temperature anomalies of winter $i - 1$ with robin data in winter i to investigate the effect of harshness of the preceding winter on migration behaviour.

POPULATION INDICES

We obtained breeding population indices for robins from Austria, Czech Republic, Denmark, Finland, France, Germany, Hungary, Netherlands, Norway, Poland, Spain, Sweden (Cuervo & Møller 2013), and from United Kingdom (data kindly provided by the British Trust for Ornithology) (Fig. S2). We then associated with each individual the population index of the country where it was observed during the breeding season and for the year when it was found at the wintering grounds (winter i, see above). This information was available for 357 of 1111 individuals (32·1%). Population indices were in all cases expressed as the proportional variation in population consistency with respect to a reference year, which, however, differed among countries. We rescaled these indices so that the population index in the reference year always equalled zero. In this way, marginal means for the other variables estimated the effect under scrutiny at the population level in the reference year for that country.

REGRESSION MODELS OF MIGRATION PROPENSITY AND DISTANCE

We first analysed whether an individual stayed during winter within its breeding home range (i.e. moved < 0·571 km) or migrated (i.e. moved 0·571 km or more; 'migration propensity' hereafter). Migration propensity was modelled according to the year (the winter when an individual was recovered in the wintering grounds, see above), winter temperatures and position (latitude and longitude) of the breeding grounds by using generalized linear mixed models (GLMMs) assuming a binomial error distribution. Cell identity was entered as a random effect accounting for residual spatial variability in migration propensity not accounted for by the latitudinal and longitudinal gradients. This analysis was run only on the north-west cluster because almost all individuals in the north-east cluster migrated (see Results).

We analysed the distance travelled by individuals that migrated (i.e. moved more than 0·571 km; individuals that moved < 0·571 km were excluded) according to the same predictors listed above plus cluster identity and its interactions with the other predictors. For this analysis, we used a linear mixed model (LMM) assuming a Gaussian error distribution, whereby cell identity was entered as a random effect and variances were estimated

independently for each cluster to account for heterogeneity in variance among clusters (details not shown). The frequency distribution of migration distance had a large excess of very small values (Fig. S3). However, plots of model residuals did not show marked deviations from normality (Fig. S4), so no data transformation was applied.

Covariates included in all models were centred within cluster before analyses and were only weakly correlated ($|r| \leq 0.126$ in all cases). Hence, this linear model was able to disentangle the independent effects of long-term trend in temperatures (or of long-term shift in any other variable not included in the analyses), which was accounted for by the year covariate, from the year-to-year variation in temperatures, which was accounted for by the winter temperature covariate.

Finally, we estimated effect size of each predictor as Pearson's correlation coefficient calculated from model coefficients and associated SE according to the formulae provided in Nakagawa & Cuthill (2007) and coefficients of determination of models (pseudo-R^2) based on the likelihood-ratio test and calculated according to Negelkerke (1991) by considering (conditional) or not considering (marginal) variance explained by random effects.

POTENTIAL MECHANISMS DRIVING VARIATION IN MIGRATION PROPENSITY AND DISTANCE ACCORDING TO THE WINTER TEMPERATURES

In order to assess the potential mechanisms driving changes in migration propensity and distance according to the winter temperatures, we reran the analyses by including: (i) summer and autumn temperature of year i instead of winter temperatures in year i; and (ii) winter temperatures of year $i - 1$ instead of winter temperatures in year i. In addition, we investigated whether winter temperatures correlated with summer or autumn temperatures or with winter temperatures in the preceding year. To this end, we mapped values of the partial correlation coefficients (while removing the effect of year) between winter temperature on the one hand and summer and autumn temperatures and winter temperatures in the preceding year on the other hand.

Also in these analyses, temperatures included in all models as predictors were only weakly correlated with year ($|r| \leq 0.363$; all correlation coefficients calculated on data centred within cluster).

ACCOUNTING FOR OTHER EFFECTS POTENTIALLY INFLUENCING MIGRATION PROPENSITY AND DISTANCE

Population size may alter the proportion of migrants and the distance they travel by affecting intraspecific competition for resources during winter. In addition, population size may bias the estimates of the variation in migration propensity and in distance travelled because, for example, reduced competition during winter may prompt a larger proportion of individuals to spend winter in their breeding grounds. To check for robustness of our results against this potential source of bias, we reran models of migration propensity and distance with population indices as a covariate. Country was included as a further random grouping factor, besides cell identity, to account for repeated measures of the same population index for all individuals in a country. However, the random structure of each model was simplified by comparing AIC values of models including the two random terms or

only one of them (see Zuur *et al.* 2009 for the rationale behind this procedure).

Juveniles may show higher migration propensity than adults because they are usually socially subordinate and therefore less likely to acquire the best territories, which in turn offer the best chances to survive winter (Newton 2008). Individuals were therefore classified as adults or juveniles according to the estimated age when they were found dead in winter (see Supporting Information for details on how birds were classified as adults or juveniles).

Information on potentially confounding effects may be unavailable for all individuals, and, consequently, analyses accounting for them may fail in detecting statistically significant effects because of low statistical power due to reduced sample size. Hence, we tested the power of analyses by rerunning 499 times the same model fitted on the whole data set (i.e. without the potentially confounding effect) on a subset of data randomly chosen from the whole data set. At each run, we randomly selected: (i) a number of individuals equal to that used in the model accounting for the confounding effect; and (ii) a number of individuals *in each cluster* equal to that in the analysis accounting for confounding effects. Power was then calculated as the proportion of tests where an effect that was significant for the whole data set was statistically significant also for the subset of data (with $\alpha = 0.05$).

LONG-TERM TEMPORAL TRENDS IN MIGRATION DISTANCE AND PATTERNS OF MIGRATORY CONNECTIVITY

We investigated temporal shifts in breeding or wintering grounds of robins by multivariate regression models where latitude and longitude in the breeding or the wintering grounds were regressed on year. Multivariate regressions were also used to investigate patterns of individual migration within cluster by modelling position (latitude and longitude) in the wintering grounds according to the latitude and longitude in the breeding grounds. These models therefore indicated how a shift by 1° in latitude or longitude at the breeding grounds translates into the position of individuals at the wintering grounds.

In all these analyses, qq-plots indicated that model residuals deviated from normality (details not shown). Significance of multivariate models was therefore assessed by a randomization approach whereby we randomly shuffled values of the year covariate 999 times and then assessed significance of the model by comparing the rank of the Pillai's lambda coefficient of the model fitted on original data with the distribution of values obtained from the randomization. All analyses were run in R 3.0.1 (R Core Team 2013) using packages LME4 and NLME.

Results

PATTERNS OF MIGRATORY CONNECTIVITY AND CLUSTERING OF POPULATIONS

The Mantel test disclosed statistically significant migratory connectivity ($r_M = 0.479$, $P < 0.001$, 999 permutations), and cluster analysis indicated that robins could be assigned to two clusters (*oasw* = 0.497, indicating 'weak' cluster structure; Rousseeuw 1987; Fig. 1). The first clus-

ter included 515 birds, mainly from UK and Belgium (north-west cluster hereafter). This cluster consisted of 80·0% of birds breeding in the UK or Ireland, probably belonging to the *melophilus* subspecies, and of 20·0% of birds breeding on the continent, probably belonging to the *rubecula* subspecies. In addition, 43·7% of birds in this cluster were sedentary (when the migration distance threshold was set to 0·571 km; Table 1).

The second cluster included 596 birds, mainly from Germany, Czech Republic and Poland (north-east cluster hereafter), which were almost entirely migratory (99·3% moved more than 0·571 km; Table 1). Difference in migration propensity between clusters was statistically significant ($\chi^2_1 = 376.77$, $P < 0.001$). Records classified in either cluster spanned very similar ranges of time (Fig. S5).

VARIATION IN MIGRATION PROPENSITY

Migration propensity of birds in the NW cluster increased over time, but was unaffected by winter temperature anomalies (Table 2). The temporal increase in migratory propensity was confirmed in the analyses including population indices and age of birds (Supporting Information). However, the effect of year was no longer statistically significant when the threshold used to separate sedentary

Table 1. Summary results of migration behaviour of individuals from each cluster

Cluster	Sample size	Proportion of migrants (% of individuals that moved ≥ 0.571 m)	Mean migration distance (SE) (km)	Range of migration distances (min – max) (km)
NW	515	56·3	100·1 (12·1)	1·0–1070·6
NE	596	99·3	1787·6 (29·3)	3·0–3740·8

from migratory birds was set to values ≥ 3 km (Supporting Information). Migration propensity also increased with latitude and longitude within this cluster (Table 2). Significance of the latitude and longitude effects was confirmed with threshold values up to 100 km and in the analysis including age of birds, but not in that including population indices (Supporting Information). However, in the latter analysis the effect of latitude was similar to that recorded for the whole sample (see Tables 2 and S1), and power analysis suggested that lack of statistical significance of these effects may be due to low power (≤ 0.595) of the tests run on a sample of reduced size. The model including population indices also showed that the proportion of migratory robins decreased at increasing breeding population indices (Table S1). Finally, including age of birds into the model did not affect the results and showed
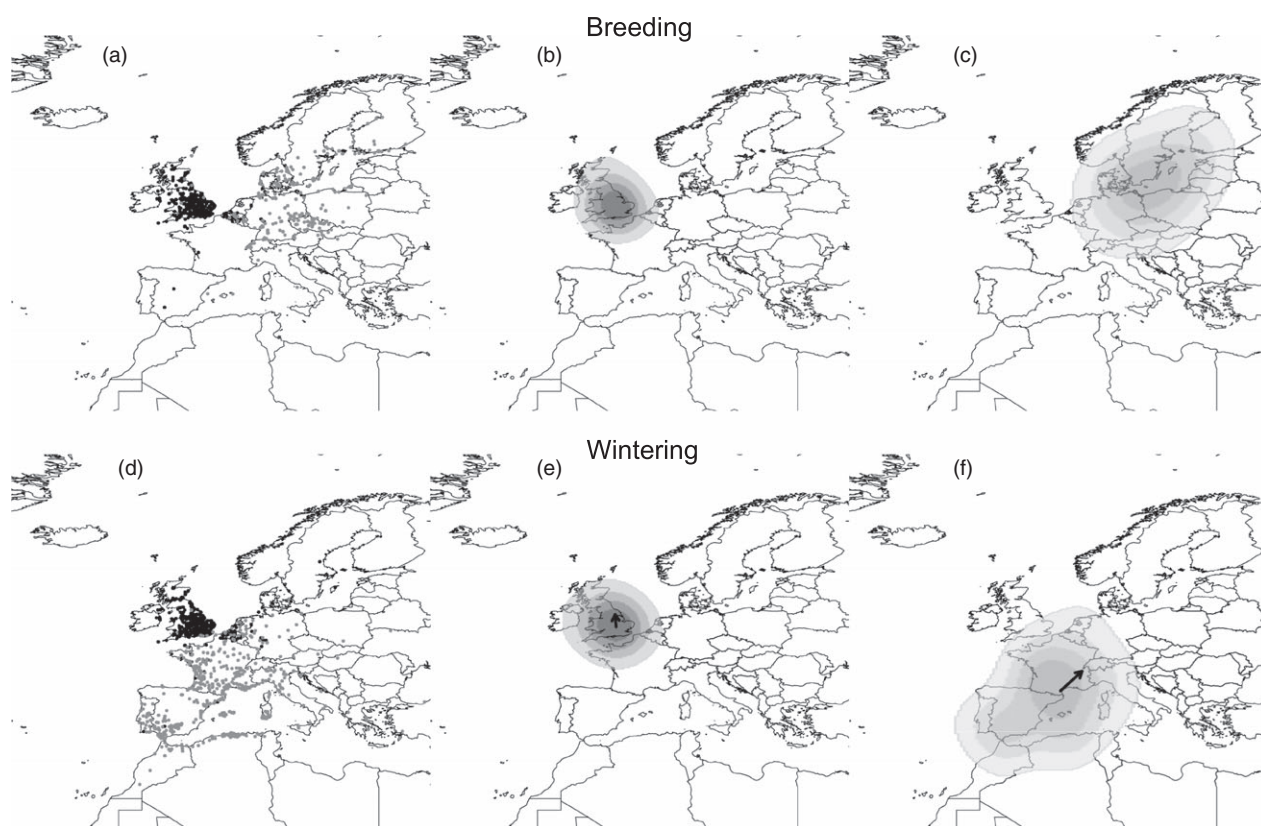
Breeding

Wintering

Fig. 1. Position of individual robins in (a) their breeding and (d) their wintering grounds. Black = NW cluster (*n* = 560), light gray = NE cluster (*n* = 702). Kernel density plots of the clusters identified by the migratory connectivity analysis during breeding (b-c) and wintering (e-f). Arrows indicate direction of the shifts in the wintering grounds.

that adult and juvenile robins of the NW cluster did not differ in migratory propensity (Supporting Information).

VARIATION IN MIGRATION DISTANCE

Migration distance differed between clusters, being longer in the NE than in the NW cluster (Tables 1 and 3). Winter temperature differentially affected migration distance depending on cluster (Table 3; Fig. 2a,b). Indeed, milder winter temperatures determined a statistically significant decrease in migration distance of individuals from the NW cluster, but a statistically significant increase in those from the NE one (Table 3). The effect size of temperature on migration distance of individuals from the NE cluster was, however, smaller than that for individuals from the NW cluster (Table 3).

The statistical significance of the cluster by winter temperature interaction was not confirmed in the analysis including population indices (Table S2). However, this could be due to restriction of the data set to recent (mainly post-eighties) years for most countries (Fig. S2), as suggested by the fact that the same effect was not statistically significant in an analysis not including population index but restricted to the same data set, and by the low power of the test run on a smaller sample (Supporting Information). Similarly, the cluster by winter temperature interaction became not statistically significant when the threshold was set to ≥ 30 km, probably due to a large reduction in sample size in the NW cluster which reduced the power of the test to 0·503 (see Supporting Information for details). In contrast, significance of the cluster by winter temperature interaction was confirmed by the analyses including age (Supporting Information).

Migration distance decreased through time in the NE, but not in the NW cluster (Table 2, Fig. 2c,d). The effect of year on migration distance of individuals from the NE

Table 2. Fixed effects of the binomial GLMM model of migration propensity (proportion of individuals that moved more than 0·571 km; see Methods) of robins in the NW cluster. All variables were centred to their mean values within the cluster before the analysis. Sample size is 515 individuals

Effect	χ^2	d.f.	P	Coef.	SE	Effect size
Intercept	4·70	1	0·030	0·421	0·152**	
Year	23·66	1	<0·001	0·034	0·007***	0·208
Winter temperature	1·58	1	0·209	0·077	0·061	0·055
Latitude	4·58	1	0·032	0·124	0·057*	0·093
Longitude	5·45	1	0·020	0·102	0·043*	0·101

AIC = 672·4, Marginal Pseudo-R^2 = 0·098, Conditional Pseudo-R^2 = 0·113.
Significance of each term was assessed by likelihood-ratio tests. χ^2 values, associated d.f. and P). Pseudo-R^2 values were calculated according to Negelkerke (1991), while effect sizes according to Nakagawa & Cuthill (2007). Asterisks denote coefficients that differ significantly (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) from zero. The random effect (grid identity) variance is 0·121.

cluster was about 2·5 times larger than that of temperature. Conversely, the effect of temperature was about twice as large as that of year on individuals from the NW cluster. A reduction in migration distance was also confirmed in all analyses run on different data subsets (Supporting Information).

Migration distance increased with latitude in both clusters, but more so for the NE cluster than for the NW cluster (Table 2, Fig. 2e,f). Finally, individuals of both clusters breeding more eastwards also migrated over longer distances (Table 2, Fig. 2g,h).

ANALYSES WITH SUMMER AND AUTUMN TEMPERATURES AND WITH WINTER TEMPERATURES IN THE PRECEDING YEAR

Summer or autumn temperatures or winter temperatures in the preceding year had no detectable effect on migration propensity of robins of the NW cluster ($\chi^2_1 \leq 2.22$, $P \geq 0.136$, |effect size| ≤ 0.066; other details not shown). Similarly, interaction effects between cluster and summer, autumn or winter temperatures in the preceding year had no statistically significant effect on migration distance ($\chi^2_1 \leq 2.27$, $P \geq 0.132$, |effect size| ≤ 0.043; effect sizes were here calculated based on slopes for either cluster; other details not shown). After removal of the cluster by temperature interaction, migration distance decreased at higher summer temperatures, (coef. $\pm$ SE: -16.019 ± 8.292; $\chi^2_1 = 4.22$, $P = 0.040$, effect size = -0.054; other details not shown), with an effect size comparable to that of winter temperature in cluster NW (Table 3). This effect was not confirmed in the analysis including population indices and age of birds ($\chi^2_1 \leq 0.26$, $P \geq 0.612$), and its statistical significance varied from significant to marginally not significant (P-values between 0·013 and 0·069) at varying threshold levels, while effect size ranged between -0.053 and -0.085. Conversely, autumn or winter temperatures in the preceding year had no detectable effect even after removal of non-significant interactions ($\chi^2_1 \leq 0.16$, $P \geq 0.692$, |effect size| ≤ 0.010; other details not shown).

SHIFTS IN BREEDING AND WINTERING GROUNDS AND PATTERNS OF INDIVIDUAL MOVEMENTS WITHIN CLUSTERS

We observed no shift in breeding grounds of NW or NE cluster (Pillai's $\lambda \leq 0.013$, $P_{random} \geq 0.163$). In contrast, wintering grounds of both clusters shifted. In particular, those of the NW cluster shifted northwards (azimuth 355·6°) by 0·04° per year (Pillai's $\lambda = 0.046$, $P_{random} = 0.001$), while those of the NE cluster shifted towards north-east (azimuth 47·7°) by 0·08° per year (Pillai's $\lambda = 0.035$, $P_{random} < 0.001$) (Fig. 1).

Wintering location of individuals of both clusters changed significantly with both latitude and longitude of the breeding grounds (Pillai's $\lambda \geq 0.021$, $P_{random} < 0.001$). Coefficients of the model indicated that, for individuals of

Table 3. Linear mixed effect model of migration distance of robins (excluding birds that moved < 0·571 km, see Methods). Sample size is 882 individuals (NW: n = 290, NE: n = 592). Covariates (year, winter temperature, latitude and longitude) were centred to their mean values before analyses

Effect	χ^2	d.f.	P	Cluster	Coef.	SE	Effect size
Cluster	1342·03	1	<0·001	NW	179·588	31·203*** a	
				NE	1800·708	44·252***b	
Year	1·22	1	0·269				
Winter temperature	5·14	1	0·023				
Latitude	10·78	1	0·001				
Longitude	12·54	1	<0·001				
Cluster × Year	14·89	1	0·001	NW	−0·748	0·676 c	−0·029
				NE	−7·928	1·741*** d	−0·094
Cluster × Winter temp.	8·66	1	0·003	NW	−13·642	6·017* e	−0·059
				NE	19·305	9·444*f	0·039
Cluster × Latitude	34·30	1	<0·001	NW	22·714	6·917***g	0·086
				NE	81·516	7·664***h	0·269
Cluster × Longitude	2·33	1	0·127	NW	16·391	4·628***	0·093
				NE	27·684	5·519***	0·131

AIC = 12902·4, Marginal Pseudo-R^2 = 0·484, Conditional Pseudo-R^2 = 0·861.
Significance of each term was assessed by likelihood-ratio tests (χ^2 values, associated d.f. and P). Asterisks denote coefficients that differ significantly (*P < 0·05, ***P < 0·001) from zero, and different letters denote effects that differ significantly (P < 0·05) in *post hoc* tests. Coefficients (marginal means and SEs) are reported for each cluster. Pseudo-R^2 values were calculated according to Negelkerke (1991), while effect sizes according to Nakagawa & Cuthill (2007). The random effect (grid identity) variance is 43318·0, and residual variance is 23072·0.

the NW cluster, a 1° increase in breeding latitude was associated with a 0·85° increase in wintering latitude (azimuth of the direction of shift 353·3°). In addition, an eastwards shift of 1° in breeding longitude translated into a 0·77° eastwards shift in wintering longitude (azimuth 91·5°). Hence, a unit increase in both breeding latitude and longitude was associated with a net shift by 1·20° towards north-east (azimuth 46·4°) of the wintering grounds of individuals of the NW cluster.

For individuals of the NE cluster, a 1° increase in breeding latitude translated into only a 0·42° shift towards west–north-west (azimuth 293·1°) and an eastward shift by 1° in breeding longitude was associated with an eastward shift of 0·47° (azimuth 94·7°) in wintering location. Hence, a unit increase in both breeding latitude and longitude determined a net shift of 0·15° towards north-east (azimuth 32·9°) in the wintering grounds of individuals of the NE cluster.

Hence, position in the wintering grounds of individuals from both clusters tends to mirror their position in the breeding grounds, but individuals breeding further northeast tend to migrate longer distance, and more so for individuals of the NE cluster than for those of the NW one.

SPATIAL VARIATION OF TEMPERATURE ANOMALIES

Winter temperatures showed generally increasing trends in Europe (Fig. S6a). Detrended correlations between summer and winter temperatures indicated generally positive correlations in Northern Europe, and negative correlations in north-western Italy, Switzerland, southern France, Iberian Peninsula and the Mediterranean coast of Africa, from Morocco to Tunisia (Fig. S6b). In contrast, detrended correlations between autumn and winter temperatures were generally negative across Europe (Fig. S6c). The spatial pattern of variation in detrended correlations between winter temperature of consecutive years was correlated positively in northern Europe and negatively in the Iberian Peninsula and the western Mediterranean basin (Fig. S6d).

Discussion

SPATIAL PATTERNS OF MIGRATORY CONNECTIVITY AND MIGRATORY BEHAVIOUR

Many partially migratory species show phenotypic divergence in migratory behaviour among populations, with climate hypothesized to drive such divergence through effects on mortality (Newton 2008). Here, we first found that European robins show migratory connectivity (see Ambrosini, Møller & Saino 2009 and Supporting Information), with two clusters of populations at a continental scale, which show phenotypic differentiation in migration tactic ranging from partly to completely migratory. This result is consistent with previous knowledge of the movements of this species (Cramp *et al.* 2004) and with the results of Korner-Nievergelt, Liechti & Thorup (2014).

We observed that both migration propensity of individuals from the NW cluster and distance migrated by individuals of both clusters changed according to the geographical position within the cluster, suggesting that individuals breeding to the north and the east were more likely to migrate (NW cluster) and moved longer distance (both clusters) than those breeding to the south and the west. This is expected based on the general pattern of
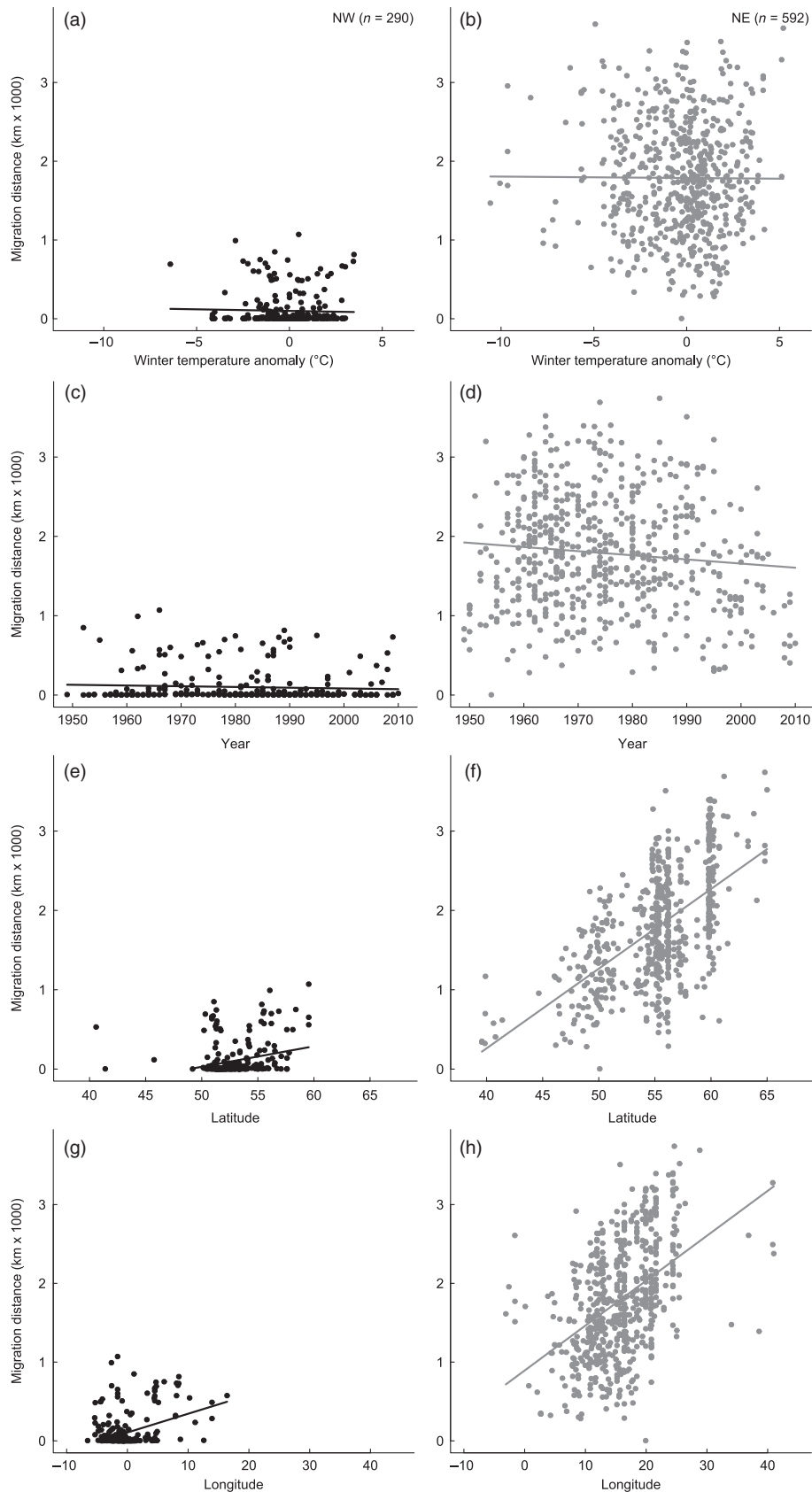
Fig. 2. Migration distance (km, excluding birds that moved < 0·571 km, see Methods) as a function of winter temperature in the breeding areas (a, b), winter of recovery (c, d), breeding latitude (e, f) and breeding longitude (g, h). Regression lines are shown for ease of interpretation.

variation in climatic conditions in Europe, with winter temperatures generally decreasing northwards and eastwards (Newton & Dale 1996). Interestingly, these patterns could be observed *within* the two clusters of individuals we identified, suggesting that geographical variation exists in migration behaviour of robins throughout Europe and occurs at different spatial scales.

While the increase in migration distance with longitude was similar in both clusters, an increase in latitude determined an increase in migration distance that was approximately eight times larger for individuals of the NE than for the NW cluster. This larger effect of latitude in the NE cluster is probably because robins breeding in eastern Scandinavia tended to winter further east than those from the west (Cramp *et al*. 2004). Moreover, the presence of the Mediterranean basin prevents individuals from the north-eastern part of this cluster to winter further northeast.

TEMPORAL VARIATION IN MIGRATORY BEHAVIOUR AND THE EFFECTS OF POPULATION TRENDS

We observed an increase in the proportion of migratory individuals in the NW cluster through time. This effect was confirmed in analyses including potentially confounding effects like population indices and age of birds, but disappeared when the threshold used to differentiate between sedentary and migratory robins was set to 3 km or more. This effect seems sensitive to the value of the threshold used to differentiate migratory and resident individuals, which, however, was chosen based on an estimate of home range of this species in the UK, that is in the area where the majority of individuals from the NW cluster breed. Therefore, caution is needed when considering this result.

We found a decrease in migration propensity in years when breeding population index was larger. This observation contrasts with the hypothesis that migratory individuals are mainly socially subordinates that could not find a suitable territory for spending the winter at their breeding grounds (Newton 2008). We can speculate that in years when general ecological conditions are better, not only populations increase, but also a larger fraction of birds may find suitable conditions for wintering at their breeding grounds.

Our continent-wide analysis also suggested that robins of the NE cluster tended to migrate over shorter distances in recent years and that this long-term effect may be due to an eastward shift in wintering grounds of this cluster during the last 60 years (Fig. 1f). A northward shift of the wintering grounds of the NW cluster could also be detected (Fig. 1e). However, this shift was much smaller and probably did not determine a detectable reduction in the distance migrated by individuals of this cluster. The long-term reduction in migration distance observed in the NE cluster is consistent with the documented shift of the wintering ranges of migratory birds towards their breeding grounds due to climate change (Visser *et al*. 2009; Ambrosini *et al*. 2011). However, our analyses differentiated between long-term effects, potentially due to long-term variation in *any* of the ecologically relevant factors, including the generally increasing temperatures, and year-to-year variation in winter temperatures around the general trend, and identified a long-term effect determining a temporal reduction in migration distance for individuals of the NE cluster, and divergent short-term effects on individuals of either cluster.

EFFECTS OF CLIMATIC VARIABILITY ON MIGRATORY BEHAVIOUR

We detected no effect of winter temperature on migration propensity of robins of the NW cluster, the only cluster for which this analysis could be run since the NE cluster included almost only migratory individuals. In addition, we observed differential effects of winter temperature on distance migrated by robins of different clusters (Table 3 and Fig. 2a,b), since robins of the NW cluster migrated over longer distances in cold winters, while those of the NE cluster migrated over shorter distances. It is usually assumed that migratory birds should respond to favourable winter conditions by reducing migration distance or even by wintering at their breeding grounds in order to reduce the cost of long migrations (Newton 2008). However, for robins, the decision on whether to migrate or not may depend more on social interactions or resource availability in the local breeding territory than on general climatic conditions (Adriaensen & Dhondt 1990). Admittedly, this hypothesis is speculative because local resource availability during winter should depend, among other factors, also on winter temperature. In addition, this hypothesis implies that socially dominant individuals should more likely become residents. However, we found no detectable effect of age on migration propensity, with adult robins migrating over longer, rather than shorter, distances than juveniles (see Supporting Information). Similarly, females should migrate more than males because they are socially subordinates (Adriaensen & Dhondt 1990). Unfortunately, we could not test this latter hypothesis because the sex of individuals was unknown in our study. However, the fact that we could not distinguish male and female robins may have caused the unexpected age effect on migration distance. Indeed, since the analysis of migration distance is based only on individuals that migrated (i.e. moved $\geq$ 0·571 m), the adults may include a larger proportion of females than the juveniles, because most adult males are expected to show a lower migratory propensity and are therefore excluded from the analysis. Hence, the (unknown) sex ratio of adults included in the analysis of migration distance may be more female biased than that of juveniles, causing the unexpected result that, on average, old individuals migrate longer distances than young ones.

We observed a differential effect of winter temperature on migration distance in the two clusters, a discrepancy

that is difficult to explain. On the one hand, the decrease in migration distance at increasing winter temperature observed for individuals from the NW cluster fits with the hypothesis of plastic migration behaviour of individuals, which should stay closer to their breeding grounds in favourable winters. On the other hand, individuals of the NE cluster showed an opposite behaviour. It may be speculated that individuals of the NW cluster, which are partial migrants and stay much closer to their breeding grounds than individuals of the NE cluster, show a greater plasticity in the response to variation in winter conditions than individuals from the NE cluster, which are almost entirely obligate migrants moving over long distances.

WHY DO POPULATIONS DIFFERING IN MIGRATORY BEHAVIOUR RESPOND DIFFERENTLY TO ENVIRONMENTAL CUES?

Theoretical models of migration behaviour predict that the expression of migration or sedentariness should vary among populations living under markedly different environmental conditions and according to the environmental variables (Pulido, Berthold & van Noordwijk 1996; Pulido 2011). The temperature of the coldest winter month in the breeding areas is a good proxy for the harshness of winter ecological conditions. However, our analyses seem to indicate that temperature influenced the distance travelled by individuals of different geographical populations in opposite ways, but did not influence their migration propensity. This may suggest that environmental conditions affect different aspects of migratory behaviour of individuals and that different populations of robins showed different reaction norms to winter temperatures.

Short-distance migratory bird species are known to have advanced timing of spring migration more than long-distance ones in recent years, suggesting that they are better able to adjust their migration schedule to changing climatic conditions (Rubolini *et al.* 2007; Lehikoinen & Sparks 2010; Saino *et al.* 2011; Morganti 2015). Our findings suggest that similar patterns may occur at the within-species level. For instance, robin populations migrating over shorter distances (NW cluster) did not show long-term shifts in the geographical location of their wintering grounds, but reduced migration distance in cold winters. Conversely, populations that migrated longer distances and were almost completely migratory (NE cluster) showed a clear temporal shift in the location of their wintering grounds, and adjusted their migration behaviour to climate conditions in an opposite way comparted to that of partially migratory populations. However, the relative size of these effects indicated that, in the partially migratory NW cluster, the effect of winter temperature on migration distance was twice as strong as the effect of the long-term shift in wintering grounds, while in the entirely migratory NE cluster the effect of the long-term shift in wintering grounds was more than twice as strong as the effect of winter temperature. Hence, the adjustment of migration behaviour according to the contingent climatic conditions may occur differentially also among different geographical populations of the same species and may depend on their relative degree of migratoriness.

WHICH ENVIRONMENTAL CUES AFFECT MIGRATION BEHAVIOUR?

The effect of winter temperature on migration behaviour of individuals may arise from phenotypically plastic responses or from differential selection in resident and migratory birds coupled with temporal autocorrelation of winter temperatures in consecutive years (see Introduction). In addition, winter temperatures at the breeding grounds are only experienced by residents, so that a phenotypic plastic response of robins may arise from their ability to anticipate overall winter harshness while they are still at the breeding grounds, that is in autumn or even earlier. Alternatively, some individuals may leave the breeding grounds during winter in direct response to harsh temperatures, as found in the European blackbird *Turdus merula* (Fudickar *et al.* 2013). To assess the mechanisms driving robin responses to winter climate, we reran the analyses by including summer and autumn temperatures, as well as winter temperature in the preceding year, and found that migration distance decreased at increasing summer temperature in both clusters. However, the summer temperature effect was not confirmed in analyses controlling for population index or age, and at different values of the threshold used to differentiate sedentary and migratory robins. Hence, the evidence that summer temperatures affect migration behaviour is weak. However, it may suggest that birds use summer temperatures they experience at their breeding grounds to forecast future winter conditions and adjust their migration behaviour accordingly. Such long-term weather forecast may be based on correlations between summer and winter temperatures, which, albeit weak, are generally negative in Europe (Fig. S6c). However, the analyses indicate that birds tend to migrate less after warm summers and that warm summers are also associated with cold winters in most of Europe (Fig. 6c). As a result, birds should migrate shorter distances in cold winters, as seems to occur for the NE but not for the NW cluster. Alternatively, we can speculate that winter temperatures show spatial autocorrelation throughout Europe and that robins may decide to migrate farther if they experience harsh winter conditions in the place where they are. Hence, variation in migration distance may be the result of a direct response to contingent winter conditions, as has been recently demonstrated in a blackbird population (Fudickar *et al.* 2013). Unfortunately, the available data do not allow testing this hypothesis on robins because multiple recaptures of the same individuals within the same winter are very rare.

METHODOLOGICAL ASPECTS

Analyses based on ring recoveries may be affected by several sources of bias, which ultimately derive from the large spatial and temporal heterogeneity in sampling effort (Fiedler 2003; Fiedler, Bairlein & Köppen 2005; Visser *et al.* 2009). Indeed, variation in ringing and recovery effort across Europe may blur the analyses because robin populations breeding in different parts of Europe segregate in the wintering quarters. Our analyses should, however, be robust with respect to this potential source of bias because: (i) we restricted our analyses only to birds shot or recovered dead, because they were always reported to the EDB by all national ringing schemes, and further selected the data to remove as much heterogeneity as possible (see Supporting Information); (ii) clusters identified geographical populations with a connection between breeding and wintering ranges, and we incorporated this information in all analyses (see also Ambrosini *et al.* 2011 for a similar approach); (iii) we accounted for possible spatial variation within clusters by including latitude and longitude as covariates and cell identity as a random factor in all analyses; and (iv) temperature anomalies and dates were centred within cluster, so that analyses were unaffected by the differences in the time span covered by ring recoveries in different clusters (Fig. S3).

From a methodological point of view, the power analyses we applied to the tests run on different subsets of data demonstrated that a reduction in sample size dramatically lowered the power of the tests to detect effects. Hence, the analyses of ring recoveries should be based on the largest possible data set, so that the attempt to remove as much heterogeneity as possible from the data should be carefully balanced with the necessity to use very large samples in order to detect true biological effects. In addition, the attempt to control for potentially confounding effects (e.g. population indices or age of bird) in the analysis should be carefully considered whenever inclusion of these effects determines a marked reduction in sample size because this information is not available for all individuals.

CONCLUDING REMARKS

In conclusion, robin populations, which are only partially migratory and migrate short distances, only slightly shifted their wintering grounds, but seemed to respond to variation in winter temperature by year-to-year modification of migration distance. Conversely, individuals from the NE cluster, which almost entirely migrate long distances, have largely shifted their wintering grounds, and respond less tightly to variation in winter temperature than those of the NW cluster, although their response is opposite to what was expected. The novel analytic framework we developed allows extending previous findings by Visser *et al.* (2009) from a local to a continental scale and may prove suitable for retrospectively investigating the consequences of climate change across a broad range of migratory species, providing much needed information on the effects of climate change at the individual level.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.5fn37 (Ambrosini *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details on the migratory connectivity analysis and on cluster identification.

Appendix S2. Additional details on methods.

Appendix S3. Analyses of migration propensity run on different datasets and including potentially confounding effects.

Appendix S4. Analyses of migration distance run on different datasets and including potentially confounding effects.

Figure S1. Schematic representation of positions of hypothetical individuals (dots of different colours) in the breeding and in the wintering quarters.

Figure S2. Demographic indices in each country included in the study.

Figure S3. Frequency distribution of migration distance, defined as the great-circle distance between the ringing and the recovery sites.

Figure S4. (a) Qq-plot and (b) histogram of normalized residuals from the LMM model of migration distance shown in Table 3.

Figure S5. Boxplot of the years in which robins were recovered at their wintering grounds per cluster.

Table S1. Binomial GLMM of migration propensity (proportion of individuals that moved more than 0·571 km) including population index as a covariate and cell identity as a random grouping factor.

Table S2. Mixed model of migration distance (distance travelled by robins that moved more than 0·571 km, see Methods) including population index as a covariate and country as a random grouping factor.

Supporting Information

Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin *Erithacus rubecula*: a continent-wide analysis

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Details on the migratory connectivity analysis and on cluster identification

The analysis of migratory connectivity and the following subdivision of European robins *Erithacus rubecula* into clusters of individuals showing similar migration behaviour was based on the framework of analysis proposed by Ambrosini, Møller & Saino (2009). We will not discuss the technical details of the analyses here, since we refer to the above mentioned paper, but will only highlight some aspects of this method that are relevant for the analyses presented in this paper.

Basically, the analyses can be divided in two steps. The first aims at assessing the intensity of migratory connectivity, which can be defined as a measure of "how closely individuals of migratory species spatially cluster throughout the annual cycle" (Veen 2013). According to this definition, strong connectivity implies that individuals share similar breeding and wintering locations, while weak connectivity implies that individuals from different breeding populations mix at their wintering grounds and vice versa. The degree of migratory connectivity can be evaluated by observing the reciprocal position of individuals at the breeding and at the wintering grounds. Ambrosini, Møller & Saino (2009) proposed a quantitative measure of migratory connectivity based on the correlation between the matrix describing the distance between all pairs of individuals when they are at their breeding grounds and that describing the distance between the same individuals when they are at their wintering grounds. In particular, the degree of migratory connectivity can be assessed by a Mantel test on great circle (orthodromic) distance matrices between individuals calculated separately for the breeding and the wintering grounds (Ambrosini, Møller & Saino 2009). A strong correlation indicates that individuals maintain the same reciprocal positions, and therefore there is strong migratory connectivity. Conversely, if individuals mix, correlation between distance matrices will be low. It is important to notice that the only information included in this analysis is the distance between

individuals at the breeding and the wintering grounds (i.e. information represented by the red arrows in Figure S1).

The second step of the analysis aims at identifying the clusters of individuals sharing breeding and wintering grounds, and it is based on a cluster analysis run on a combination of the matrices indicating the distance between individuals at the breeding and the wintering grounds. This analysis can be performed with the *pam* procedure in the *cluster* library in R 3.0.2 (R Core Team 2013). The *pam* procedure is a clustering algorithm that partitions observations in a number of clusters identified a priori. As a measure of the goodness of the classification of data into a given number of clusters, the procedure returns the overall average silhouette width (*oasw*), a dimensionless coefficient ranging from -1 to 1. Increasing *oasw* values indicate better classification of data (Rousseeuw 1987), and the best number of clusters in which data can be partitioned can be chosen as the number that maximizes the *oasw*. We stress that the only information included in the analysis also in this case is the one represented by the red arrows in Figure S1.

In summary, the only information included in the analysis of the intensity of migratory connectivity and in that run to divide robins into clusters is the reciprocal position of individuals at the breeding and the wintering grounds (red arrows in Figure S1), *not* the distance travelled by individuals during migration (black arrows in Figure S1). Indeed, these analyses will give the same results when applied to hypothetical individuals that migrated different distances (black arrows), but are in the same reciprocal positions (red arrows) as depicted in parts A and B of Figure S1. Hence, migration distance is not taken into account during cluster identification.

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Figure S1. Schematic representation of positions of hypothetical individuals (dots of different colours) in the breeding and in the wintering quarters. Red arrows represent distances between individuals, black arrows distances travelled by individuals during migration. Migratory connectivity analyses are independent form migration distance (black arrows) and will return the same result when applied to individuals that migrate different distance (part a and b of the figure), but maintain the same reciprocal positions.
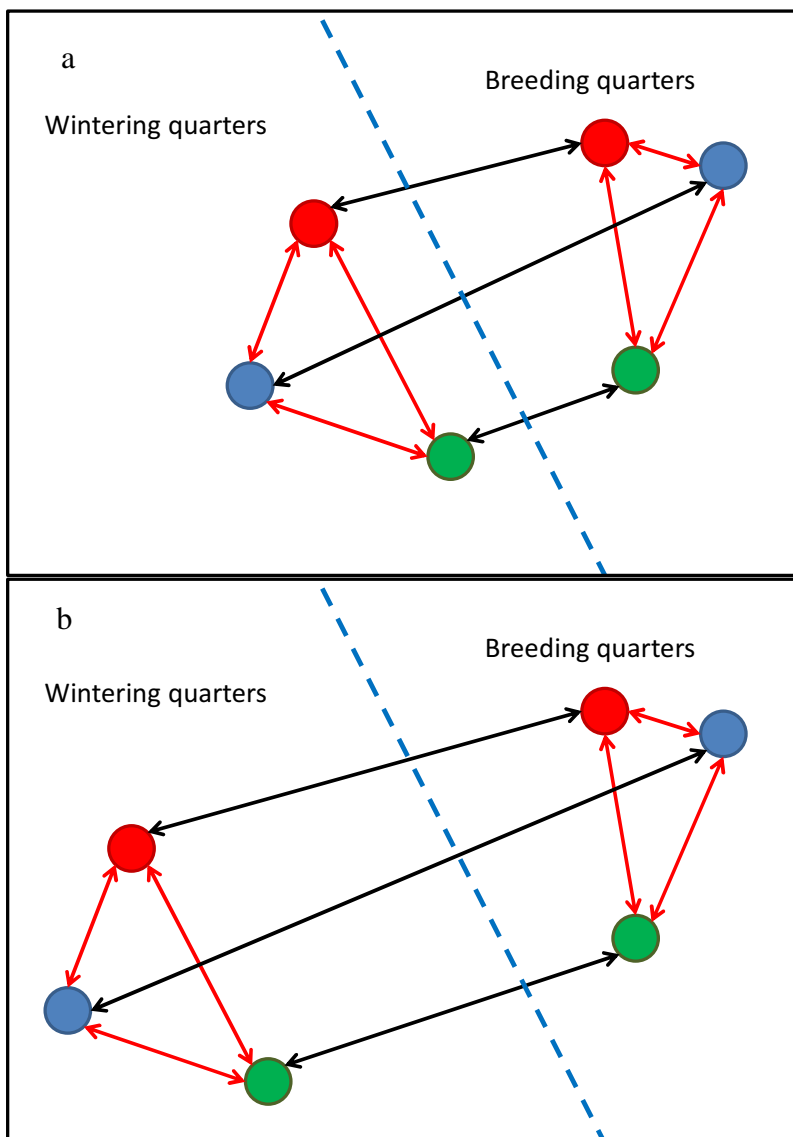
Additional details on methods

RATIONALE FOR DATA SELECTION CRITERIA

In Europe, ringing schemes provide data on birds ringed and recovered to the EURING Data Bank (EDB; see http://www.euring.com/). However, ringing schemes have historically adopted different procedures for processing and storing reports of birds that have been ringed and subsequently re-encountered (see http://www.euring.org/data_and_codes/obtaining_data/recovery_definitions.htm for full details on these different procedures). Differences in reporting procedures may largely affect the proportion of migrant birds if, for example, birds re-encountered close to the ringing site are not reported. However, all ringing schemes have always reported birds found dead. For this reason, we selected all records from individuals found dead in winter (EURING code 'condition' in 1-2; see du Feu *et al.* 2010 for details on EURING code). In addition, we discarded the following data from the analyses in order to reduce heterogeneity as far as possible (Paradis *et al.* 1998): birds that were in poor condition or had an accident when ringed (EURING code 'condition' in 4-5); birds that were kept for more than 13 h during ringing or birds that have been moved or held extensively during ringing (EURING code 'manipulated' equal to C, F, T, M); birds that were intentionally killed by man other than shot (EURING code 'circumstances' equal to 0 or 2); birds that were not found freshly dead (EURING code 'condition' equal to 3); birds for which the dates and places of ringing and/or recovery were not recorded accurately to the nearest 1 week for both the ringing and the finding date (EURING code 'date accuracy' in 4-8) or to the nearest 100 km for the ringing or finding places (EURING code 'coordinates accuracy' equal to 6 or 9).

After this selection, only four individuals had more than one record in either the breeding or the wintering period. In these cases, we selected respectively the northernmost and the southernmost one because these positions should reflect final destination of birds (see Ambrosini, Møller & Saino 2009 and Ambrosini *et al.* 2011 for a similar approach). The final database thus consisted of two

geographical locations (one for breeding and one for wintering) for 1111 robins in the period 1947-2011.

CRITERIA USED FOR ASSESSING AGE TO ROBINS

For assigning age, we used the reported age code (EURING code 'Age scheme', du Feu et al. 2010) at ringing. Specifically, birds that were ringed in spring with age code ≥ 4 were classified as adults when found dead in winter, whereas birds that were ringed in spring with age code 1 or 3 and found dead in or before February of the subsequent year were classified as juveniles (214 individuals = 19.3%). In addition, all birds that were found dead in winter at least 12 months after ringing were classified as adults, irrespective of reported age at ringing (including birds whose age at ringing was not known, i.e. age code 0 or 2; overall 391 individuals = 35.2% were considered adults).

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Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1998) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, 67, 518-536.

Figure S2. Demographic indices in each country included in the study.
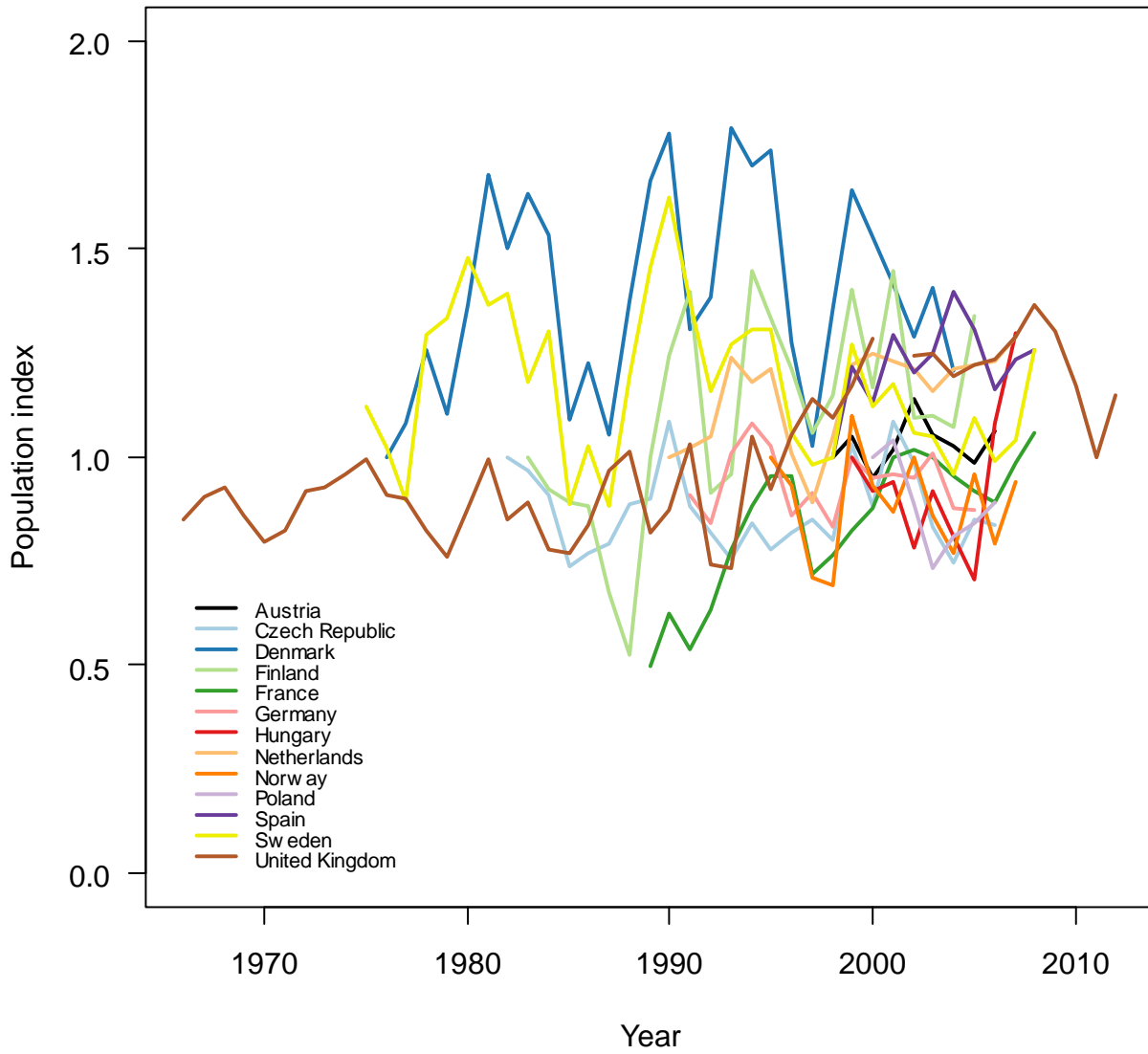
Figure S3. Frequency distribution of migration distance, defined as the great-circle distance between the ringing and the recovery sites. Only the 882 individuals that moved more than 0.571 km (see Methods) are shown.
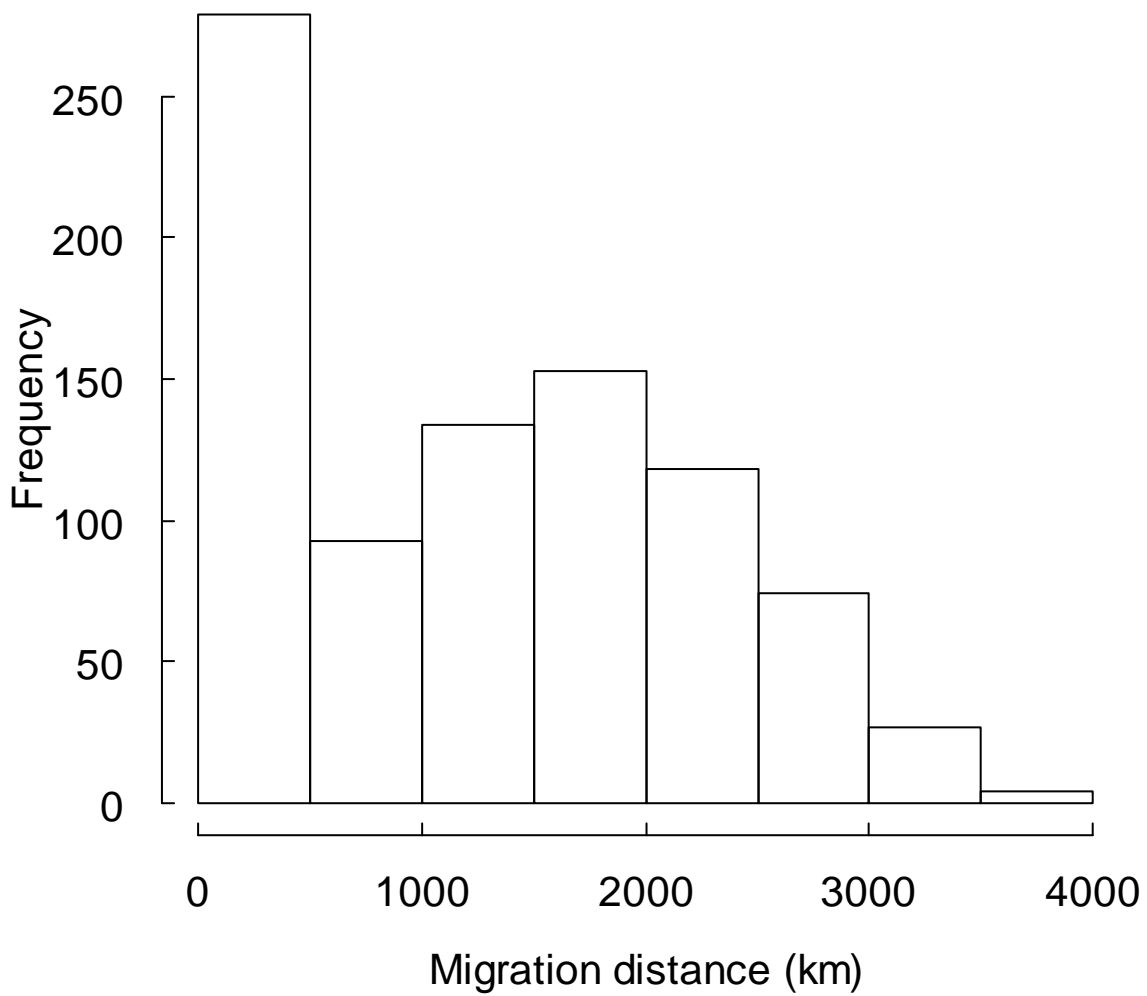
Figure S4. a) Qq-plot and b) histogram of normalized residuals from the LMM model of migration

distance shown in Table 3. In b) a Gaussian curve has been superimposed on the histogram.
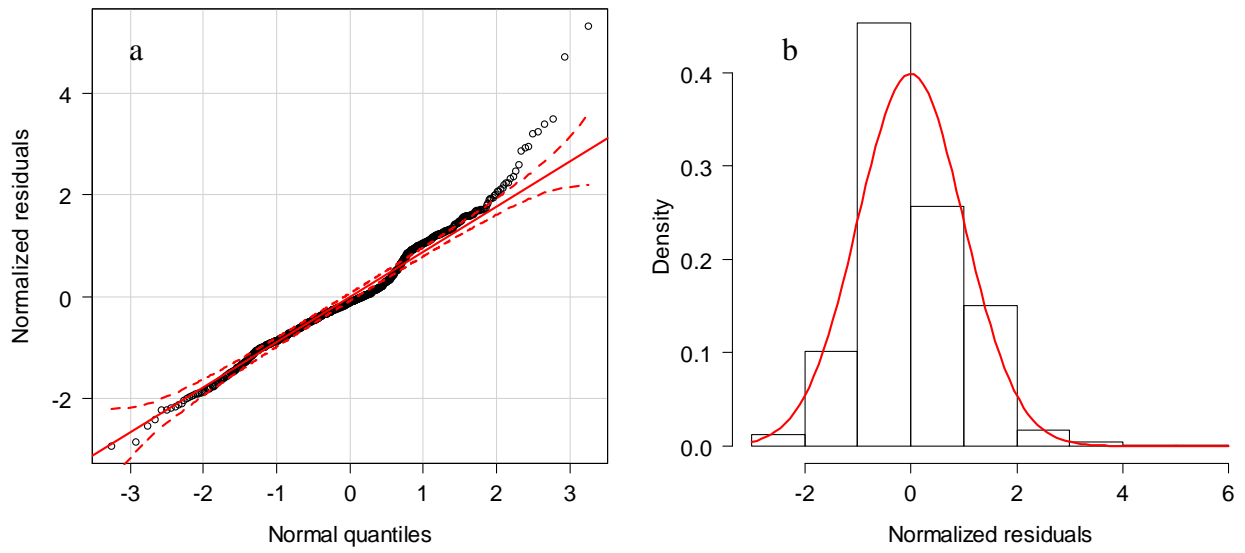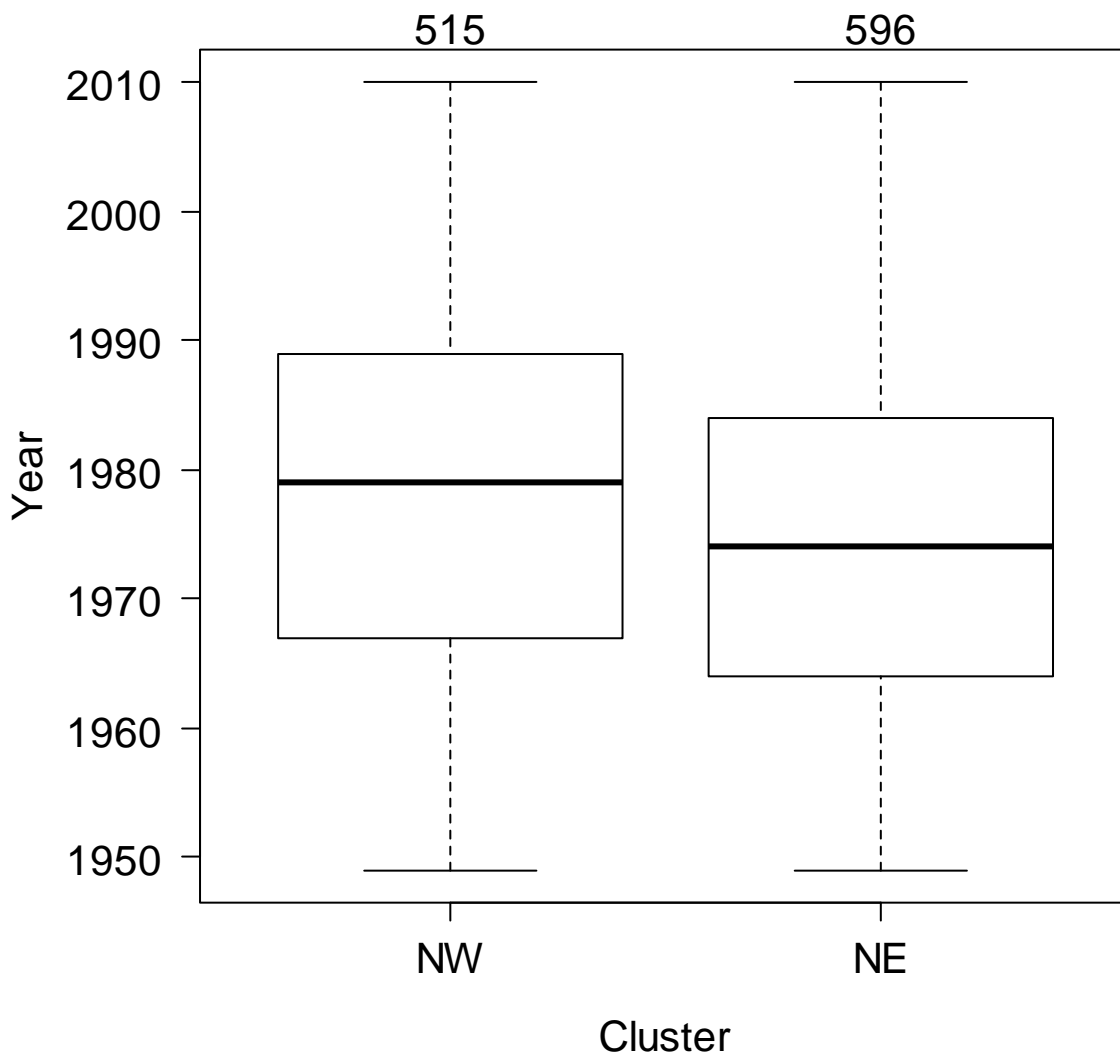
Figure S5. Boxplot of the years in which robins were recovered at their wintering grounds per cluster. The solid lines represent the median values, the top and the bottom of the boxes represent the first and the third quartiles, whiskers include 95% of data. Numbers above the graph denote sample sizes.

Analyses of migration propensity run on different datasets and including potentially confounding effects

Analysis of migration propensity including population indices indicated a significant decrease of migration propensity at increasing values of population indices (Table S1). This analysis also confirmed the increase in migration propensity with year, but not the variation in migration propensity with latitude and longitude (Table S1). However, size of the latitude effect was similar to that reported on the whole model (see Tables 2 and S1). Conversely, longitude seemed not to explain variation in migration propensity once that population index was accounted for. Non-significance of these effects may be due to the reduction in sample size, since both latitude and longitude were not significant ($\chi^2_1 \leq 3.19$, $P \geq 0.074$) in a model not including population indices, but restricted to the same dataset used for the analysis including population indices. In addition, power analysis indicated that power of the test to detect a significant latitude or longitude effect decreased to 0.434 and 0.595, respectively, when sample size was equal to that of the analysis including population index.

When we re-ran the analysis of migration propensity using different distance thresholds to differentiate between sedentary and migrant robins, we found that the effect of year was no longer significant when the threshold value was set to ≥ 3 km. In contrast, significance of both the latitude and longitude effects was confirmed when this threshold was set up to 100 km (other details not shown).

Finally, when we analysed migration propensity in a model including age and its interactions with winter temperature (sample size for the NW cluster was only 171 juveniles and 211 adults), beside all the predictors listed in Table 2, we found no significant effect of age or its interaction ($\chi^2_1 \leq 0.43$, $P \geq 0.512$, |effect size| ≤ 0.034 in all cases). Removal of the non-significant interaction from the model did not result in a significant effect of age (details not shown). Significance of all the other effects

listed in Table 2 did not change qualitatively with the exception of latitude that turned not significant ($\chi^2{}_1 = 0.90$, $P = 0.343$, effect size = 0.049; other details not shown).

By comparing the results of these additional analyses with those run on all individuals, it appeared that the increase in migration propensity of robins of the NW cluster through time was confirmed in all the analyses, but disappeared when a slightly larger distance threshold was used to differentiate sedentary from migratory birds. Geographical variation in migration propensity was not confirmed in the analysis including population indices, though latitude still had an effect of similar size than that observed on the whole sample, and only a longitudinal variation appeared in the analysis including bird age.

The fact that the proportion of migratory robins decreased in years when summer population index was larger contrasts with the hypothesis that individuals that could not find a suitable territory for wintering should be more prone to migrate, because this would determine an increase, rather than a decrease, in migration propensity in years with increased population. We can speculate that larger population indices are achieved in years with better general conditions, which in turn may prompt more birds to winter in their breeding grounds.

Table S1. Binomial GLMM of migration propensity (proportion of individuals that moved more than 0.571 km) including population index as a covariate and cell identity as a random grouping factor. The NE cluster was excluded from the analysis because almost all individuals of this cluster migrated. Sample size is 327 robins. Covariates (year, winter temperature, latitude and longitude) were centred to their mean values before the analysis. Significance of each term was assessed by likelihood ratio tests (χ^2 values and associated *df* and *P*). Coefficients are reported with the relative SE. Asterisks denote coefficients that differ significantly (** $P < 0.01$, *** $P < 0.001$) from zero. Pseudo-R^2 values were calculated according to Negelkerke (1991) while effect sizes according to Nakagawa and Cuthill (2007). The random effect (cell identity) variance is 0.204. Effects whose significance differs from that in the model in Table 2 are bolded.

Effect	χ^2	df	P		Coef.	SE		Effect size
Intercept	**0.01**	**1**	**0.930**		**-0.020**	**0.230**		
Year	24.94	1	< 0.001		0.077	0.015	***	0.262
Winter Temperature	3.10	1	0.078		0.163	0.092		0.095
Latitude	**3.19**	**1**	**0.074**		**0.157**	**0.087**		**0.097**
Longitude	**0.24**	**1**	**0.632**		**-0.047**	**0.096**		**-0.026**
Population Index	7.17	1	0.007		-3.418	1.271	**	-0.144

AIC = 422.1, Marginal Pseudo-R^2 = 0.135, Conditional Pseudo R^2 = 0.151

Analyses of migration distance run on different datasets and including potentially confounding effects

The analysis of migration distance including population indices did not confirm the significance of the interactions between cluster and year, winter temperature, latitude and longitude (Table S3). A model excluding these non-significant interactions disclosed a significant effect of year (coef. = -1.711 $\pm$ 0.760 SE km year^{-1}, $\chi^2_1 = 5.06$, $P = 0.024$, effect size = -0.099) and latitude *per se* (coef. =: 25.813 $\pm$ 4.280 SE km degree^{-1}, $\chi^2_1 = 36.38$, $P < 0.001$, effect size = -0.257), but indicated no variation in migration distance with winter temperature or longitude ($\chi^2_1 \leq 0.45$, $P \geq 0.503$, |effect size| ≤ 0.098; other details not shown).

Also in this case, the lack of any winter temperature effect may be due to the fact that analyses including population indices restricted the dataset, particularly for the NE Cluster (from 592 to 29 individuals, see Tables 3 and S2). Indeed, winter temperature, *per se* or in interaction with cluster, was not significant either in a model without population index among its predictors but restricted to the same dataset used for the analysis including it ($\chi^2_1 \leq 0.32$, $P \geq 0.568$, effect size ≤ 0.032, other details not shown). In addition, power analysis indicated that power of the test to detect any significant effects of cluster by year or cluster by temperature interactions decreased to 0.419 and 0.289, respectively, when overall sample size was equal to that of the analysis including population index, and to, respectively, 0.140 and 0.120 when sample size *at each cluster* was set equal to that of the analysis including population index. Conversely, the power of detecting a significant cluster by latitude interaction was still 0.807 when sample size was reduced to 215 individuals randomly chosen from the whole sample, but was only 0.383 when sample size was 186 individuals from the NW and 29 from the NE cluster.

When we re-ran the analysis using different values of the migration distance threshold, we observed that the cluster by winter temperature interaction turned non-significant when the threshold was set

to $\geq$ 30 km, while the significance of all the other effects was unchanged (details not shown). However, when the distance threshold was set to $\geq$ 30 km sample size in the NW cluster was reduced from 290 to 87 individuals or less, and the power of the test to detect a significant cluster by year or cluster by winter temperature interaction decreased to 0.579 or less. Winter temperature *per se* was also non-significant when we re-ran the model excluding the cluster by winter temperature interaction while changing the threshold value (details not shown).

The cluster by year interaction also turned not significant when the threshold was set to $\geq$ 70 km, when the power of the test to detect a significant interaction was still 0.908 (sample size was 68 individuals in the NW cluster and 591 in the NE one). However, when we removed the non-significant interaction, year effect was significant for any distance threshold (details not shown). Finally, the cluster by latitude interaction was always significant for all threshold values (details not shown).

The model including age and its interactions with cluster and winter temperature, beside all the other predictors, indicated no significant effect of the age by cluster and of the age by winter temperature interactions ($\chi^2_1 \leq 2.37$, $P \geq 0.12$, |effect size| ≤ 0.059 in all cases). In contrast, after removal of the non-significant interactions, age was highly significant, and indicated that adult robins migrated significantly longer distances than juveniles (coef. $= 55.269 \pm 18.973$ SE km, $\chi^2_1 = 9.76$, $P = 0.002$, effect size $= 0.116$). Significance of all the other predictors listed in Table 3 did not vary (details not shown).

Hence, the significance of the cluster by winter temperature interaction was not confirmed in the analysis including population indices. However, the lack of significance in the analysis including population indices could be due to restriction of the dataset to recent (mainly post-eighties) years for most countries, as suggested by the fact that winter temperature was not significant in an analysis not including population index, but restricted to the same dataset, and to a lower power of the statistical test due to reduced sample size. Conversely, significance of the cluster by winter temperature

interaction was confirmed by the analysis including bird age and by those run by setting migration
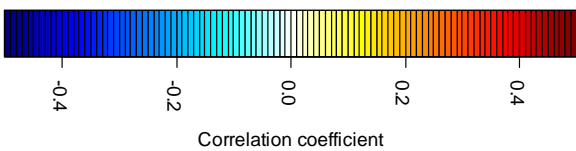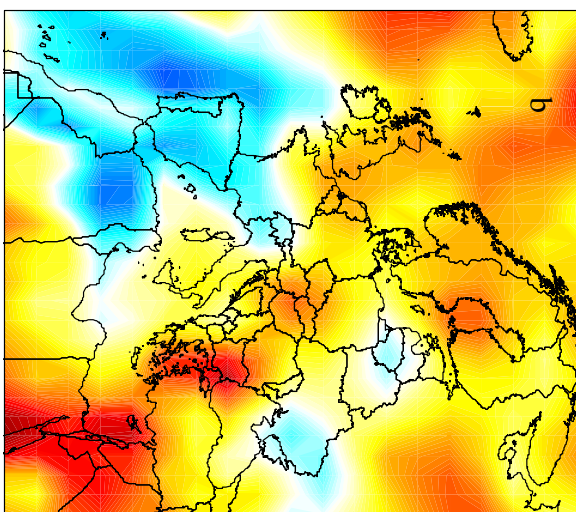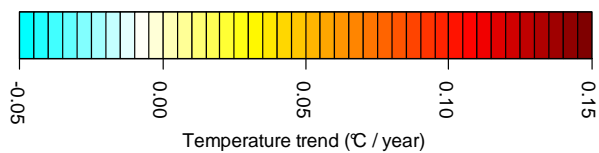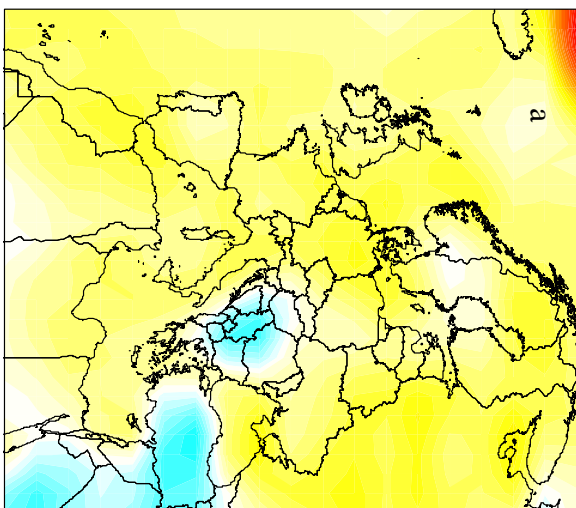
distance to up to 30 km.

Table S2. Mixed model of migration distance (distance travelled by robins that moved more than 0.571 km, see Methods) including population index as a covariate and country as a random grouping factor. Sample size is 215 robins (NW: n = 186, NE: n = 29). Covariates (year, winter temperature, latitude and longitude) were centred to their mean values before the analyses. Significance of each term was assessed by likelihood ratio tests (χ^2 values and associated *df* and *P*). Coefficients (marginal means) are reported for each cluster with the relative SE. Asterisks denote coefficients that differ significantly (* $P < 0.05$, *** $P < 0.001$) from zero, and different letters denote effects that differ significantly ($P < 0.05$) in post-hoc tests. Pseudo-R^2 values were calculated according to Negelkerke (1991) while effect sizes according to Nakagawa and Cuthill (2007). The random effect (country) variance is 301044.8 and residual variance is 193675.4. Effects whose significance differs from that in the model in Table 3 are bolded.

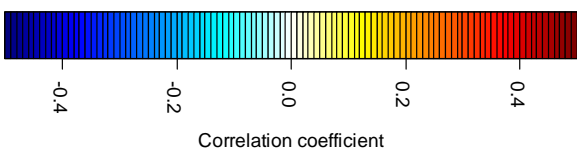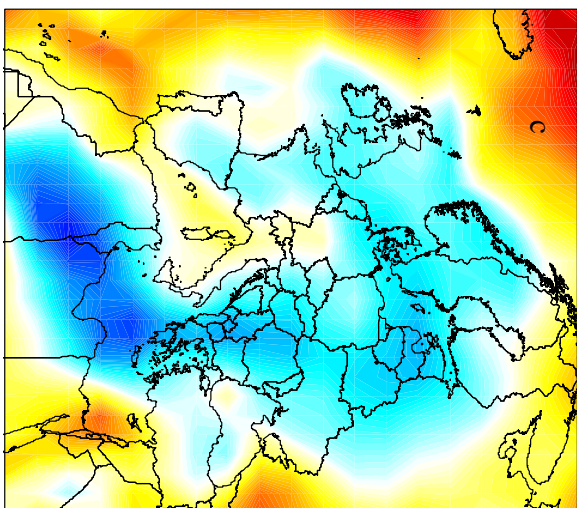| Effect	χ^2	df	P	Cluster	Coef.	SE		Effect size
Cluster	19.85	1	< 0.001	NW	606.530	197.253	*** a	
				NE	1530.407	163.707	*** b	
Year	4.75	1	0.129					
Winter temperature	0.06	1	0.808					
Latitude	34.53	1	< 0.001					
Longitude	0.21	1	0.647					
Cluster x Year	**1.89**	**1**	**0.169**	NW	-1.661	0.762	*	-0.122
				NE	-21.226	14.197		-0.084
Cluster x Winter temp.	**0.25**	**1**	**0.619**	NW	1.078	4.432		0.014
				NE	24.980	47.972		0.029
Cluster x Latitude	**1.39**	**1**	**0.238**	NW	25.135	4.278	***	0.315
				NE	69.376	37.400		0.104
Cluster x Longitude	**0.86**	**1**	**0.353**	NW	-2.362	5.155		-0.026
				NE	24.313	28.219		0.049
Population Index	0.46	1	0.496		37.880	55.703		0.038

AIC = 2560.2, Marginal Pseudo-R^2 = 0.308, Conditional Pseudo-R^2 = 0.966.

1   Figure S6. Maps of a) trends in winter temperatures in Europe, calculated as the slope of the minimum monthly mean temperature in each winter for

2   the period 1948-2011; b) partial correlation coefficients between mean temperature in the warmest month in June-August (summer temperature) and

3   mean temperature of the coldest month in December-February (winter temperature), after removing the effect of year (detrended correlations); c)

4   detrendend correlations between mean temperature in the coldest month in September-October (autumn temperature) and winter temperature; d)

5   detrended correlations between winter temperature in year i and in year i-1.