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Climate-driven shifts in migratory strategy and ecological niche in a partially migratory songbird

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Abstract

Background

Anthropogenic environmental alteration is particularly challenging for migratory species, as they have to adapt to changing conditions both in breeding and non-breeding areas. One way in which migratory animals might respond to changes in conditions is by varying their migratory propensity. The European robin (*Erithacus rubecula*) exhibits partially migratory behaviour across much of its distribution range, which presumably enables it to respond flexibly to a rapidly changing environment.

Methods

To characterise spatiotemporal changes in the migration strategy of robins at the European scale, we analysed EURING ring recovery data (1960–2020). Additionally, we conducted randomisation analyses of ERA5 climate data to establish a statistical relationship between changes in migratory strategy and climate variables.

Results

Our results show that the annual recovery rate of migratory robins ringed during the breeding season decreased by 77% over the study period, despite a simultaneous increase in ringing effort. Both the ringing data and the randomisation analyses of climate data indicate a northward shift in breeding and wintering distribution of migratory robins ('climate niche tracking'). Low January temperatures and deeper snow cover at breeding sites appear to be positively correlated with frequency of migrants, whereas no such correlation was found for precipitation. We have found no evidence for a between-year change in individual migration strategy, which would be indicative for a plastic response by individual robins to environmental conditions.

Conclusions

Over the course of a few decades, the European robin has altered its migration strategy in response to climatic changes across much of Europe. Thus, the species' flexible partially migratory behaviour may enable robins to keep pace with rapid anthropogenic environmental changes. Further research is needed to determine whether individuals can alter their migratory behaviour in response to environmental conditions, and to what extent the behavioural changes observed at the population level are attributable to selective processes.

Background

The growing human population and the resulting anthropogenic changes to climate, land use and biodiversity have a dramatic influence on global ecosystems [1–5]. Seasonal animal migration is particularly threatened worldwide by the decoupling of ecological systems [6, 7], as adaptations are necessary both in winter and summer habitats and en route [8]. It has been shown that migratory bird species that cannot respond to changing environmental conditions decline [9, 10], especially drastic for long-distance migratory species [9, 11]. Thus, a deeper understanding of the effects of changing environmental conditions on migratory behaviour of wild species is essential for efficient nature conservation efforts.

An adaptive response of seasonal migration to rapidly advancing climate change has been described for numerous bird species, particularly regarding migration phenology [12–18]. A decrease of migration distances was observed in some species [19–21], changes in migratory direction and non-breeding grounds [22, e.g. 23] as well as a northward shift of breeding and/or non-breeding areas [19, 21, 24–26], a phenomenon also referred to as "climate niche tracking" [27–29]. For partially migratory populations - i.e. geographically confined populations comprising both resident and migratory individuals-, Berthold [30, 31] predicted a decrease in the propensity to migrate with globally increasing temperatures. In line with this prediction, a growing number of European migratory species have adapted an increasingly resident phenotype and are now increasingly successfully overwintering in Central Europe [19, 32, 33]. The relationship between the observed changes in migratory strategies and climate change is usually assessed on the population level and mostly correlative, while the proof of direct causality remains challenging, and other factors of global changes, such as altered land use, increasing light pollution, hunting pressure or anthropogenic food supply could also be causally involved [reviewed by 19, 32, 33, 34]. It is also often not known to what extent individuals can adapt their migratory behaviour and strategy to changing environmental conditions through phenotypic plasticity, or whether the changes observed at the population level can be explained by natural selection, i.e., microevolutionary processes. Phenotypic plasticity is usually assumed to be the primary underlying mechanism for observed rapid migratory changes [13, 15, 35, but see 36]. However, it has been shown for the blackcap (*Sylvia atricapilla*) that microevolutionary change in migratory strategy is possible within a few generations under appropriate selection pressure [23, 31, 34, 37, 38].

The European robin (*Erithacus rubecula*) is a common breeding bird throughout Europe and is characterized by variable migratory strategies. Apart from Eastern Europe (from where almost no ringing data is reported), the European robin population is predominantly partially migratory, with the exception of resident populations at the southern and western ends of the species' distribution range and obligate migratory populations at the northern edge (Fig. 1a) [39, 40]. Due to the high amount of additive genetic variance (Biebach 1983), the robin's migratory behaviour is thought to be highly susceptible for microevolutionary processes, analogous to that of the blackcap with its even wider repertoire of migratory strategies exhibited across its distribution range [31, 41]. So far, however, it is unclear to what extent individual migration strategy of robins is controlled by genetic [42] and demographic factors such as sex and age [43, 44] and what role environmental factors [43] play in shaping individual migratory phenotype. It is also not known whether individuals can change their strategy annually [43].

Here we analyse EURING (European Union for Bird Ringing) ring recovery data from 1960 to 2020 combined with ERA5 modelled climate data to assess robin migration patterns and their changes over time on a European scale. Ring recovery data are geographically and temporally irregularly distributed and additionally biased due to varying legislation across Europe [45], as well as differing ringing practices [46] and documentation requirements [46, 47], but despite these limitations have proven to be suitable for detecting long-term changes in population patterns due to climate change [19, 35, 48]. For the robin, a shift in wintering areas to the north and east in connection with rising winter temperatures has been reported based on ringing data analyses [24].

Our objectives are, to - on the level of the European population - selectively characterise migratory strategy for robins ringed at their breeding sites, to assess a statistical relationship between changes in migratory strategy and changing climatic factor. We hypothesise

that (1) the proportion of migratory individuals would decrease over time in response to globally increasing temperatures and that (2) breeding and non-breeding grounds of migrants should shift northwards consistent to climate niche tracking. In addition to our population level approaches we utilise the individual level information of the ringing data to check if we can identify individual robins that change their migration strategy between years. We hypothesised, that (3) if plasticity contributes to behavioural changes in robin populations, the dataset might include records of individuals, that had changed their migration strategy between years. If no change in individual strategies can be identified, this either means that our method does not allow us to detect them, or indicates that they are indeed very rare, which suggests that changes in migratory propensity at the population level are at least partly driven by natural selection.

Methods

Ringing, ring-recovery and climate data

Ringing and ring-recovery data for the European robin across its distribution range were derived from the EURING [49]. For our analyses we requested two datasets: one dataset containing 100,000 ringing records selected at random from the entire EURING dataset to estimate breeding phenology across Europe [following 50], and one dataset containing all ring-recovery data of robins ringed during the breeding season (April to August) and recovered during the winter months (November to January), in order to infer changes in migration patterns over time. Our overall ring-recovery dataset comprises 46,696 records spanning from 1909 to 2022 and included ringing reports of 17,258 robins ringed in Europe and 29,438 reports of recoveries in Europe and Africa. Additionally, we used publicly available information on the robin ringing totals of various European ringing centres to estimate ringing effort across the distribution range [51].

The Falsterbo Bird Observatory in Sweden has been recording spring and autumn migration of Scandinavian migratory birds in a standardised form since 1980. These daily ringing totals are publicly

available [52]. Here, we used the robin ringing totals for the spring and autumn migration to compare these with the EURING ringing data for Swedish robins ringed during the breeding season. To assess changes in the winter survival of migrants over time, we also calculated the percentage of spring ringing totals with reference to those of the previous autumn (i.e. calculated as percentage of returnees).

To evaluate our ringing data in an environmental context and test for the influence of climate variables on migration patterns, we used ERA5 modelled environmental data provided by the Copernicus Climate Change Service, which are available as GRIB files in the Copernicus Climate Data Store [53]. As estimates for the winter climatic conditions, we used the mean January midnight temperatures, precipitation amounts, and snow depths of the ringing and recovery sites from 1960 to 2020.

The ringing and climate data were analysed using R Statistical software (v 4.3.2., R Core Team 2023). For data management, analysis and modelling we used the packages *tidyverse* [54], *lme4* [55], *car* [56], *geosphere* [57], *raster* [58] and *lubridate* [59], for visualization *ggplot2* [60], *berryFunctions* [61], *rworldmap* [62] and *ggpubr* [63].

Selection of a migratory robin subset and correction for ringing effort

For subsequent analyses we curated a subset of migratory robins. To accurately select migratory individuals that are ringed in their breeding area and not during transit, differences in breeding phenology across Europe have to be considered. To characterise breeding phenology [according to 50] we combined both EURING datasets. We classified a subset of 2,469 robins as “breeding” based on information on brood patch, status 'N' (= breeding) or nestling age. We defined 11,167 robins as “migrating” based on information about fat score > 2 [64] and calculated fuel load according to Kelsey et al. [65] (the annual distribution of “migrating” and “breeding” robins is shown in Fig. S1 a). For each robin, the nearest 250 breeding robins and the nearest 250 migrating robins were determined using the “great circle distance” (distHaversine from *Geosphere 1.5–18*) [57]. Density curves of the ringing day of year of the closest migrating and the closest breeding robins were plotted for each robin (for an example see in Fig. S1 b). The start of the breeding season was defined as the day on which the probability of breeding exceeds the probability of migration, and vice versa for the end of the breeding season (Fig. S1 b, dotted vertical lines). To describe breeding phenology, we employed linear regression models (LM). To avoid pseudoreplication, we calculated the mean of the breeding start and end days in 1° grid cells. The start and end of the breeding season (day of year) was modelled as a function of latitude and longitude, both as main effects and as an interactive term (latitude * longitude) (Figs. S1 e and f, Suppl. 1.2).

The type of data contributed to the EURING database by European ringing schemes is not uniform. In particular, the documentation of local recaptures is handled very differently by ringing schemes and has also changed considerably and inconsistently over the time of the study period [47]. This makes it impossible to infer the exact number of resident birds or the proportion of migratory birds in Europe; we thus exclusively focus our analyses on migratory robins. We restricted subsequent analyses to the

period from 1960 onwards, as data of sufficient quality and consistency have been available from most ringing centres since then, and this period aligns with documented climate change trends relevant to our research questions.

The transition from dispersal behaviour to “true” migration cannot be clearly recognized from the calculated migratory distances (Fig. S2). To be sure that we are focussing our analyses on migratory robins, we decided to classify distances between breeding and wintering sites of ≥ 100 km as migratory behaviour (see distribution of migratory distances in Fig. S2). We also ran our analyses for a less stringent dataset, also including robins that exhibit shorter distance movement (at least 35 km, according to the standard deviation (SD) of breeding dispersal described by Paradis for robins in 1998 [66]) as well as for birds migrating longer distances (more than 285 km according Biebach [42]).

As recaptures due to shooting, hunting, and trapping, including recaptures by ringers, are temporally and spatially biased, e.g. due to the entry into force of the Birds Directive [45] or changes in ringing efforts (Fig. S3), we restricted our further analyses to unintentional recoveries, i.e. neither shot, hunted or trapped (notSHT). We also excluded recoveries where any information on the circumstances of recovery was missing to exclude illegally hunted recaptures as reliably as possible.

To account for changes in ringing effort over time, we corrected the number of recovered migrants for each scheme using the ringing totals published on the EURING website [51] (Table S4). For each ringing scheme, we defined the mean of the 2010–2014 ringing totals as 1 and used the average relative ringing effort to adjust the annual totals of recovered migrants in Europe. We modelled the number of recovered migratory birds as a function of ringing year using generalized linear models (GLM) for Poisson (P) distributed data. In case of overdispersion, GLM of the quasi-Poisson (qP) family were used.

Analyses of climate variables for the selected robin subset

To assess how environmental variables in winter drive the propensity to migrate in robins, we assigned monthly averaged January climate variables for midnight temperature, snow depth and precipitation to each breeding site (BS) and wintering (non-breeding) site (WS) of our subset of 377 recovered migratory robins (notSHT) for the ringing years 1960–2019.

We used linear models to characterise temporal climatic trends in climate values averaged across all 377 BS and WS for each year of the study period, reflecting climate change at BS and WS. In addition, we modelled the climate variables exclusively for the sites and years where birds were ringed at their BS or recovered at their WS, capturing the climatic conditions actually experienced by the birds throughout the study period; hereafter referred to as "observed BS" and "observed WS".

We used a randomization approach to test whether the climatic trends at observed BS and WS differed significantly from the overall trend across all sites and years. We considered this randomization approach particularly appropriate because the observed BS and WS represent a systematically selected, and thus non-random subset of all available site-year combinations: they reflect only those locations and

years in which birds were actually recorded, and the temporal distribution of recorded migratory individuals was uneven across the study period, introducing a systematic bias. We therefore randomly drew 10,000 samples from the full dataset of all BS and WS (n = 22,600 site-year combinations), each matching the size of the migratory subset (n = 377), weighted by the annual number of recorded migrants to reflect the observed temporal structure of the data. For each random sample, a linear regression of the climate variable explained by year was calculated (the distribution of the slope coefficients is shown in Fig. 3b-d). We calculated the p-value as the probability that the slope coefficient of the linear model of the observed BS or WS lies within the 95% confidence interval of the randomisation slope coefficient distribution (two-sided test).

Results

Changing migratory strategy over time

We could identify records of 2,586 robins that were recovered in at least two different winters (dominated by resident robins from the United Kingdom), of which only three individuals were migrants. None of these 2,586 robins changed their individual migration strategy between years.

According to our estimates of breeding phenology, 7,738 robins from the EURING database of ring recoveries were ringed during the local breeding season in the analysed period from 1960 to 2019 and recovered in winter (Fig. S1, Table S1), 714 of which were migrants. Our method does not ensure the complete removal of migrating birds from the dataset as we cannot exclude that for some locations birds might still be passing through while the local population is already breeding. This likely influences our results, as in spring, migrants originating from colder, more northerly breeding regions were included. However, as a plausible gradient with respect to the onset of the breeding season could be identified across Europe on a large scale (Suppl. 1), we refer to the above-mentioned 714 migratory robins hereinafter as ‘ringed at breeding site (BS)’.

In the analysed subset of 377 migratory robins that were unintentionally recovered (notSHT), the annual number of recoveries in Europe declined significantly between 1960 and 2020 (Fig. 1c), despite a significant increase in ringing effort over that time span (Fig. 1b). The generalised linear models (GLM) show a decrease in the number of migrating robins by about 77% from 12 migratory recoveries in 1960 to less than three individuals in 2020 (GLM(P), $p < 0.001$). When ringing effort is taken into account, the GLM predicts a decrease of 92.5% from around 31 migratory recoveries in 1960 to just over two individuals in 2020.

These findings suggest that the frequency of migratory robins has declined across Europe since the 1960s. We also compared changes in migration patterns across the various ringing centres in order to identify spatial patterns in Europe. Of the 14 ringing schemes that contributed to our analysed robin subset with at least five migratory recoveries between 1960 and 2020 (see Table S5), ringing totals are

available for ten of them (Table S4, Fig. 1d, Fig. S5). For these 10 ringing schemes, the corrected number of migratory robin recoveries decreased significantly in all cases (Table S5, Fig. S5, Fig. 1d).

Swedish case supports northward distribution shift and changes of migration strategy

In our subset of the migrants ringed during breeding season (n = 744), robins from Sweden (n = 128) are the most numerous compared to other European countries of origin, which is why we have complemented our study with Swedish migration data to validate our overall results. In contrast to the declining recovery numbers of Swedish robins in our subset ringed exclusively during the breeding season, the ringing totals of migrating robins in southern Sweden [52] have remained constant since the start of standardised migratory bird surveys in 1980, both during autumn and spring migration (linear regression for spring ringing totals: $p = 0.460$, $R^2 = -0.01$, for autumn ringing totals: $p = 0.880$, $R^2 = -0.02$) (Fig. 2a). The rate of returning individuals to their breeding grounds (the percentage of spring ringing totals in relation to the previous year's autumn ringing totals), as an estimate of winter survival, has also remained constant since 1980 at approximately 50% ($p = 0.690$, $R^2 = -0.01$) (Fig. 2a, dotted line). Our EURING dataset reveals a significant northward shift in latitude of migrants ringed in Sweden ($p < 0.001$, $R^2 = 0.1$, in the subset notSHT: $p = 0.009$, $R^2 = 0.08$).

Since around 2000, only a few Swedish migratory robins have been ringed south of the 58th parallel (Fig. 2c).

In contrast to ringing sites, the recovery latitudes of Swedish migrants did not change significantly (in the subset notSHT: $p = 0.077$, $R^2 = 0.03$). Instead, the recovery latitudes of the entire European subset of migratory robins (notSHT, n = 377) shifted northwards ($p = 0.023$, $R^2 = 0.01$). The migratory distance has not been shortened significantly ($p = 0.162$, $R^2 = 0.01$), confirming a northward shift of the entire migratory robin population distribution (for linear regression results see Table S3).

Climate change as a driver of changing migratory behaviour

Linear regression models of the climate variables over time (annual mean climate values across all 377 ringing and recovery locations in the study period, representing climate change) show a significant increase of 3.14°C of the mean January midnight temperature for the BS (Fig. 3b, dashed red lines). In the WS, the mean January midnight temperature

rose significantly by 2.53°C (Fig. 3b, dashed blue lines). The mean snow depth in January decreased significantly by 0.97 cm at the BS, but only marginally by 0.21 cm at the WS (Fig. 3c, dashed red and blue lines, respectively). No significant change over time was detected for January precipitation at either BS or WS (Fig. 3d, dashed lines) (for linear regression results see Table 1).

Linear regression models based exclusively on climate data from the respective ringing and recovery years (observed BS and WS) reveal no significant change in neither January temperature, snow depth,

nor precipitation over the entire study period 1960–2019 (Fig. 3b-d, solid lines, for linear regression results see Table 1). The largely constant climatic conditions at the observed BS and WS suggest that the migratory part of the robin population tracks its climatic niche. Our randomisation analyses with 10,000 randomly selected samples (using data from all years and sites) reveals a significantly lower increase in temperature for observed BS ($p = 0.0184$, Fig. 3b) and WS ($p = 0.006$, Fig. 3b) than would be expected by chance. The increase in snow depth in the observed BS also differs significantly ($p < 0.001$, Fig. 3c) from the significant decrease that would have been expected based on the randomisation. In contrast, the observed decrease in snow depth at the WS (Fig. 3c), and the changes in precipitation at BS and WS (Fig. 3d) did not differ from changes expected under randomisation. Overall, the results of the randomisation analyses support a northward shift

in breeding and wintering areas in response to increasing winter temperatures and decreased snow depth in BS, in the sense of climate niche tracking, but not in response to precipitation.

Table 1

Results of linear regression models of annually means of climate variables for breeding sites (BS) and wintering sites (WS) over the ringing and recovery years (1960–2020). Regression models including annual means for all BS or WS (dashed lines in Fig. 3b-d) represent climate change and are compared to regression models including exclusively the climate data in the ringing and recovery year (observed BS and WS, respectively, solid lines in Fig. 3, b-d).

BS	**Ø 1960**	**Ø 2020**	**(DF) F**	**β ± SD**		**p-value**	**R^2**
Temperatur (C°)							
all BS	-1.87	1.27	(1, 58) 9.257	0.0523	± 0.017	**0.0035****	0.1228
observed BS	-1.1	0.25	(1, 58) 0.912	0.0236	± 0.024	0.3437	-0.0015
Snow depth (cm H2O equiv.)							
all BS	2.11	1.14	(1, 58) 10.01	-0.016	± 0.0051	**0.0025****	0.1325
observed BS	0.955	2.58	(1, 58) 1.682	0.0272	± 0.0209	0.1998	0.0114
Precipitation (cm)							
all BS	0.2	0.24	(1, 58) 2.496	0.0008	± 0.0005	0.1196	0.0247
observed BS	0.2	0.23	(1, 58) 0.560	0.0006	± 0.0007	0.4575	-0.0075
WS							
Temperatur (C°)							
all WS	4.22	6.75	(1, 58) 14.5	0.0422	± 0.0111	**< 0.001*****	0.1863
observed WS	4.92	6.11	(1, 58) 1.28	0.0199	± 0.0176	0.2625	0.0047
Snow depth (cm H2O equiv.)							
all WS	0.38	0.17	(1, 58) 5.935	-0.004	± 0.0015	**0.0179***	0.0772
observed WS	0.36	0.13	(1, 58) 1.649	-0.004	± 0.003	0.2042	0.0109
Precipitation (cm)							

BS	Ø 1960	Ø 2020	(DF) F	β ± SD		p-value	R^2
all WS	0.26	0.26	(1, 58) 0.001	-0.0002	± 0.0006	0.985	-0.0172
observed WS	0.24	0.28	(1, 58) 0.863	0.0006	± 0.0006	0.3569	-0.0023

Discussion

Quantitative analyses of European robins ringed at their breeding sites between 1960 and 2019 reveal a significant decline in the number of migratory recoveries across Europe of approximately 77%, despite a threefold increase in ringing effort over the same period. Our randomisation analysis of climate data indicate that the contemporary breeding and wintering areas of migratory robins have shifted north/northeast, which is consistent with previous observations on robins [21, 24, 25, 68] and has also been described for other migratory bird species [19, 21, 25, 26]. Hence, our results suggest that the European robin is responding to climate change both by reducing migratory propensity across most of Europe, as predicted by Berthold for partially migratory species [30, 31], and by a northward shift in the distribution of the migratory phenotype, consistent with climate niche tracking [27–29, 69].

In contrast to our findings that recoveries of migratory robins ringed during their breeding season are declining, the ringing totals of robins in southern Sweden during migration have remained constant since 1980 [52]. However, the autumn ringing totals in Falsterbo are constant despite significant robin population growth in Sweden over the study period, which can be attributed to an expansion of the breeding range to the north [67, 70]. The Swedish bird survey also reported a significant growth in the winter (but not summer) population in the southern parts of the country since 1975 [67] (Fig. S7), indicating an increasingly successful wintering of robins in southern Sweden. In our analysed EURING subset, the migratory Swedish robins originate from increasingly higher latitudes, whereas very few have been recovered originating from the southern parts of Sweden (south of N58°) since the late 1990s (Fig. 2c). This indicates a trend towards increasing residency in southern Sweden and a northward shift in the distribution of migratory individuals within Sweden, which is consistent with our observations at the European level. Bird ringing in Scandinavia is unevenly distributed geographically, with the majority of bird ringing activities happening in the southern parts of the countries, while less frequently carried out in the north (Fig. 2b, Fig. S8). The breeding population of migratory robins, which is increasingly shifting northwards, is therefore likely to become progressively underrepresented in breeding-season ringing activities. In contrast, bird recording during migration through the southern parts of the country is likely not affected by the northward shift. This may partly explain why the number of recovered Swedish migrants in the EURING data has decreased significantly, while the Falsterbo ringing totals during autumn migration in southern Sweden have remained unchanged (whereby robins might originate from higher latitudes) (Fig. 2a). Additionally, it should be taken into account that Norwegian and Finnish robins

also migrate partly via Falsterbo [71]. The robin population in southern Finland has almost doubled since 1975 [72], which may contribute to the Falsterbo ringing totals remaining constant.

Apart from a northward shift in the migratory bird population to latitudes not reliably covered within the usual bird ringing range as well as an overall change in the robin's migratory strategy towards increased residency as an adaptation to warmer climate, additional factors may account for the decline in migratory recovery reports. For instance, ringing data may not reliably reflect true spatiotemporal population dynamics, possibly due to a reduced likelihood of citizens reporting a ring find. This assumption seems to be supported by the fact that the number of migrants recaptured by verified ringers has risen slightly, albeit not significantly, during the study period (Fig. S6). However, when recapture numbers by ringers are adjusted for the simultaneously increased ringing effort, a similar pattern of decline emerges as observed for the analysed subset of unintentionally (not-SHT) recovered migrants (Fig. S6). Apparently, the decline in the number of migratory individuals has been overcompensated by an increase in ringing effort, thereby masking the actual decrease.

Since ringing data limit reliable conclusions about the size of the resident part of the robin population, a general decline in the total population[73] cannot be ruled out as a possible cause of the decline in migratory robin recoveries. As migratory propensity in a partially migratory population is assumed to be density dependent [74–76], even a slight population decline, or just poorer breeding success [76], may have a disproportionately negative effect on the number of migrants. According to the European Bird Census Council, however, the robin breeding population in Europe is stable (EBBA2, 2022) and the general population trend has even increased significantly since 1980 (PECBMS, 2024). Although local, small scale population declines have been observed in northern breeding countries of migratory robins in recent years [67, 77, 78], we found no evidence that an overall decline in robin populations could be the main driver of the observed decline in migratory robin recoveries in Europe, particularly in the 1980s and 1990s.

Possible mechanisms explaining the reduced migratory propensity to migrate

If the observed decline in the frequency of migratory robins across Europe could be explained to a relevant extent by a switch of the migratory phenotype towards residency, the underlying mechanisms may include (1) disadvantages of the migratory strategy in terms of survival and/or fitness, or (2) advantages of the resident strategy, or (3) a combination of both. Migration is generally associated with high energy costs [79, 80, but see 81], and increased mortality [82–87]. Furthermore, it is assumed that the survival of migrants is increasingly compromised by human impacts, such as the destruction of breeding, non-breeding and stopover habitat, illegal hunting, climate change and light pollution [6, 11, 88]. For the European robin, though, the Falsterbo ringing data do not indicate that winter survival, at least of Scandinavian migrants, has deteriorated significantly since 1980, rather the opposite. However, Adriaensen et al. (1990) found that, in a Belgian partially migratory robin population, local survival rates of resident robins were two to three times higher than those of migrants and that mating success and

breeding probability of migrants only approached those of resident robins after severe winters with high losses among residents. If mild winters would lead to selection against migrants in this way [87, 89] the observed decline in the frequency of migratory robins in Europe might be primarily explained by improved survival of resident robins as an effect of milder winters due to global warming. According to ERA5 climate data, the mean January midnight temperature in southern Sweden has increased by up to 4.36°C (e.g. near Jönköping, at N58°, E14°) between 1960 and 2020 [53], which might explain a significant improvement in winter survival of resident robins in southern Sweden as has been suggested by the Swedish bird survey data [67].

It is conceivable that other anthropogenic factors of global change might act synergistically and further improve the survival and the fitness of resident robins. The ongoing urbanisation is assumed to be associated with a reduction in migratory propensity [90–93], whereby residents may benefit from even warmer temperatures in the city [91, 94, 95], from artificial light at night (Byrkjedal et al., 2012), and anthropogenic food supply [34, 96], which could additionally lead to carry over effects improving reproductive success of residents in the subsequent breeding season [97]. Which of the factors are decisive for the observed strategy changes in European robin migratory behaviour is difficult to quantify so far, and their significance is likely to vary in different environments.

It also remains unclear whether the observed migratory strategy changes are best to be explained by phenotypic plasticity or whether they reflect natural selection processes. So far, a change in migration strategy of one individual robin between different years – which would indicate a plastic response to environmental conditions – has not been demonstrated with certainty [43]. In line with this, our EURING ring-recovery data set did not reveal any evidence of a change in individual migration strategy between years. However, the probability of multiple recoveries, especially live recaptures among migrating individuals, is too low to rule out a change in strategy with absolute certainty. Nevertheless, a change in migration strategy may not be as common as has been demonstrated in other partial migrants, such as in shags [98–100] or skylarks [101]. It is therefore conceivable that the observed changes in robin behaviour reported here at the population level, could at least partly be driven by natural selection.

Conclusion

Our findings indicate that the European robin population is adapting to rapidly changing environmental conditions by altering its migratory strategy towards predominantly resident behaviour and by shifting the distribution of migratory individuals northwards, a phenomenon known as climate niche tracking. Our observations are in line with the findings of numerous previous studies conducted worldwide on various migratory species, underscoring the ongoing and advanced transformation in migratory behaviour patterns, which could have unpredictable consequences for global ecosystems. In contrast to many other, especially long-distance migratory species, the behavioural and likely genomic variability of the European robin enables a flexible shift in the migration landscape to keep up with rapid environmental change. Careful characterisation of individual behaviour and recording of individual migration strategy over several consecutive years, for example through tracking, would be required in order to conclusively

clarify to what extent the changes in migration patterns observed at the population level are due to the ability of individuals to adapt their migration strategy to environmental conditions or rather to the natural selection of behaviourally fixed individuals.

Abbreviations

BS – Breeding sites/ ringing locations

WS – Wintering sites/ recovery locations

notSHT – not shot, hunted or trapped

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

All authors have approved the manuscript for submission.

Availability of data and materials

The ring recovery data used in this study were obtained from the EURING Data Bank and are not publicly available due to data sharing restrictions. Requests for access may be directed to EURING (www.euring.org). ERA5 climate reanalysis data are freely available from the Copernicus Climate Change Service (https://cds.climate.copernicus.eu).

Competing interests

All authors declare that they have no competing interests.

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Authors' contributions

M.L., G.L., J.W., and C.L. contributed to the conceptualisation and methodological design of the study. All statistical analyses were carried out by A.G. with input from G.L., J.W. and P.S.. All authors contributed to

the interpretation of the results. A.G. wrote the final manuscript with input from all authors. All authors approved the final manuscript.

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Figures

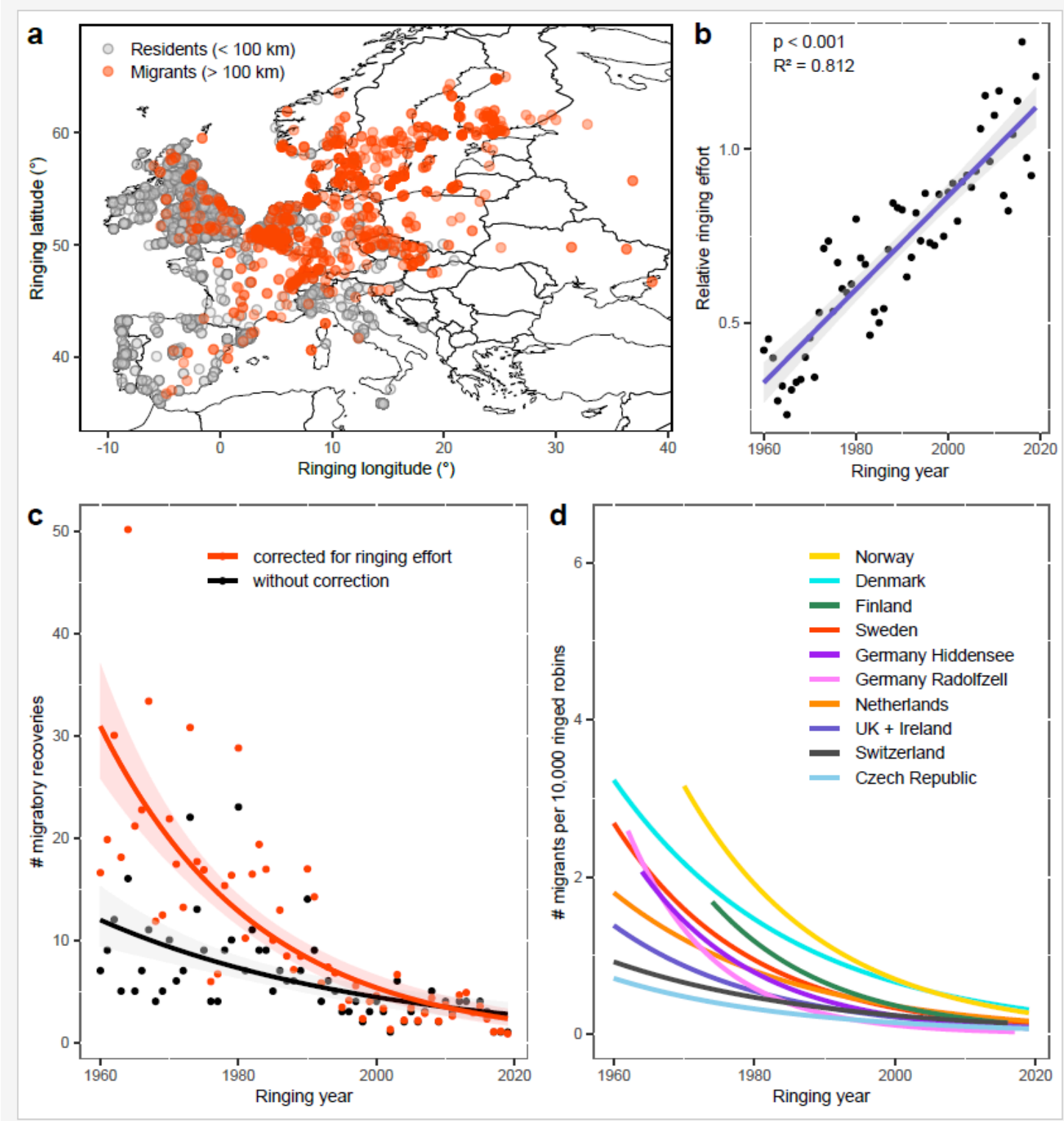


Figure 1

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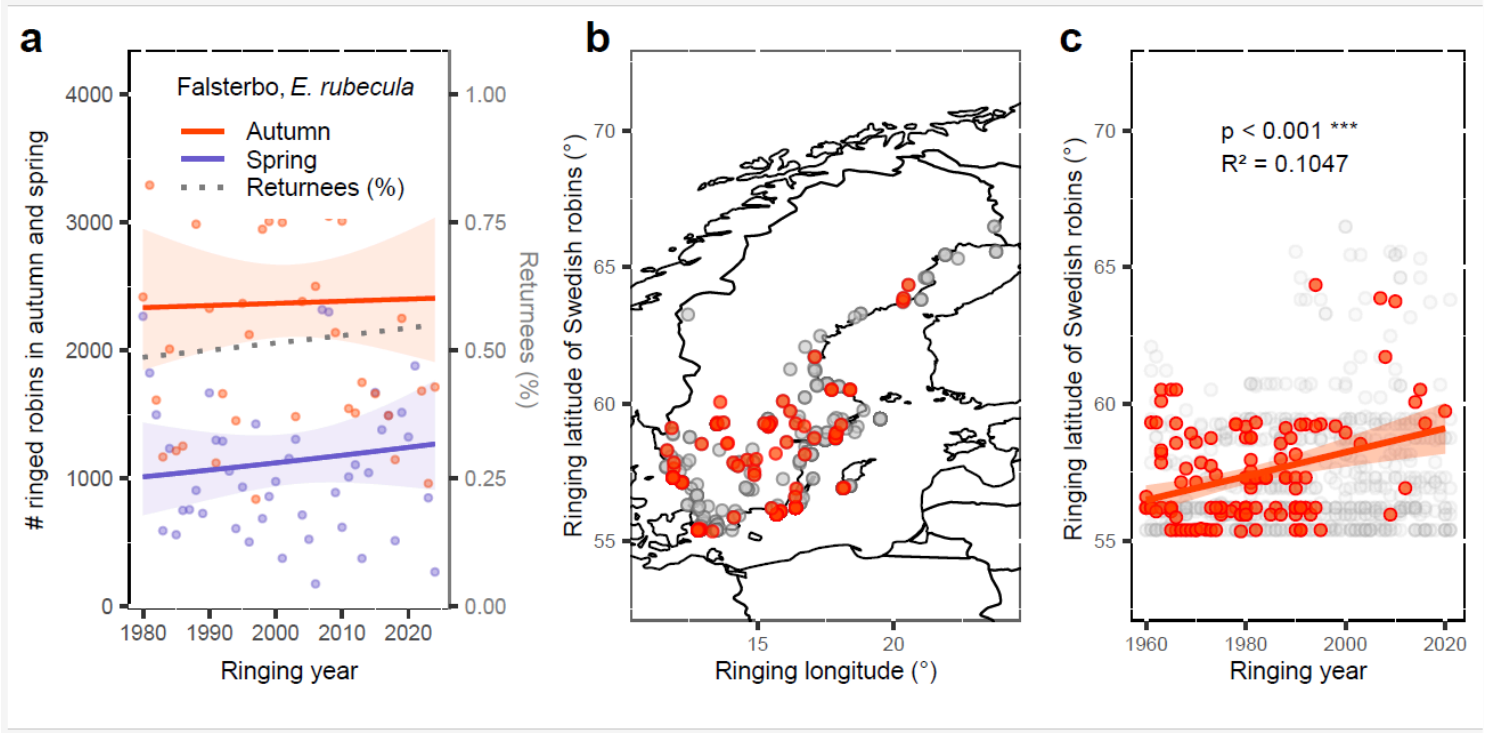


Figure 2

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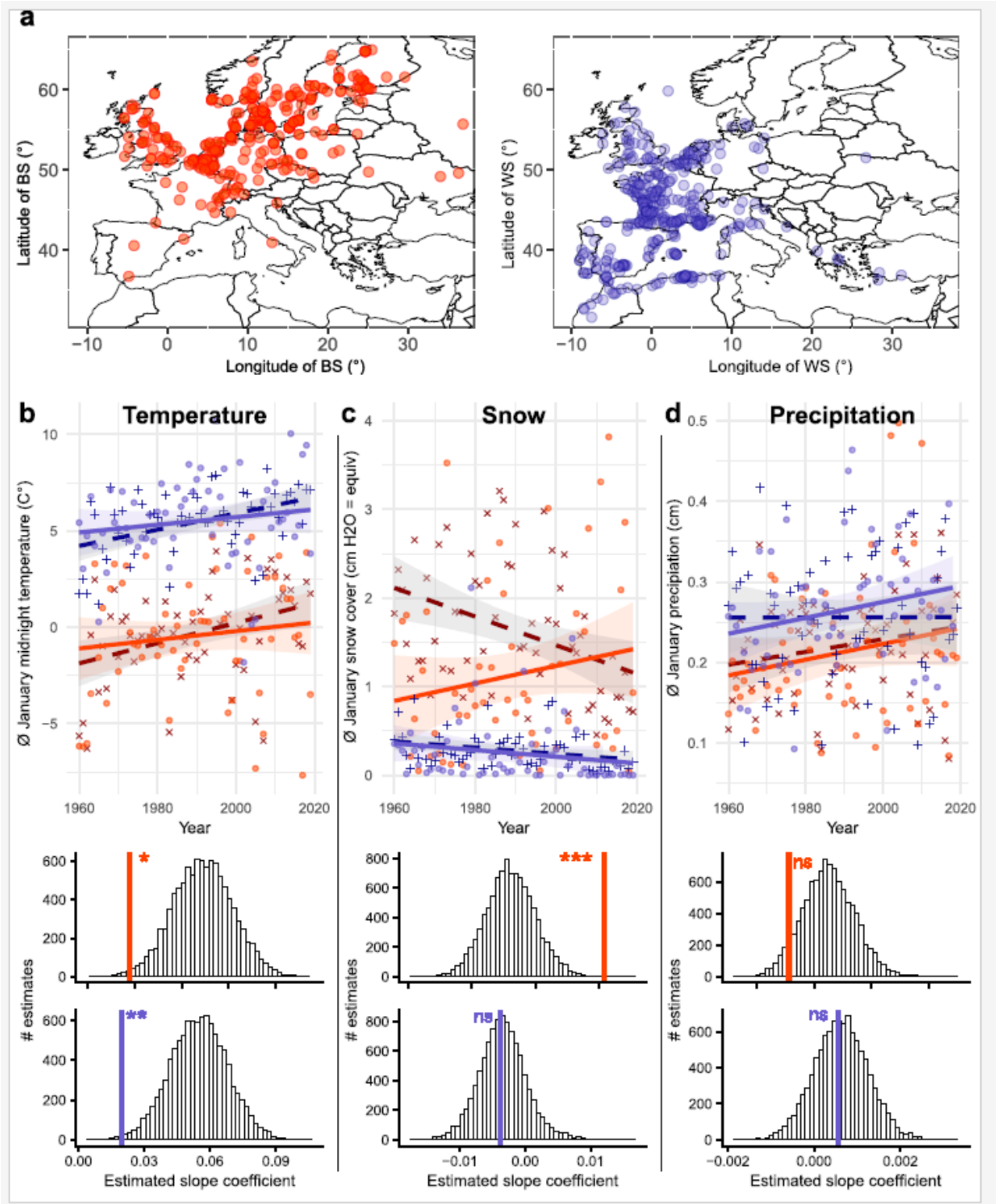


Figure 3

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