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Migratory diversity predicts population declines in birds

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Abstract

Declines in migratory species are a pressing concern worldwide, but the mechanisms underpinning these declines are not fully understood. We hypothesised that species with greater within-population variability in migratory movements and destinations, here termed 'migratory diversity', might be more resilient to environmental change. To test this, we related map-based metrics of migratory diversity to recent population trends for 340 European breeding birds. Species that occupy larger non-breeding ranges relative to breeding, a characteristic we term 'migratory dispersion', were less likely to be declining than those with more restricted non-breeding ranges. Species with partial migration strategies (i.e. overlapping breeding and non-breeding ranges) were also less likely to be declining than full migrants or full residents, an effect that was independent of migration distance. Recent rates of advancement in Europe-wide spring arrival date were greater for partial migrants than full migrants, suggesting that migratory diversity may also help facilitate species responses to climate change.

Introduction

A wide range of migratory birds, mammals, fish and invertebrates have shown population declines in recent decades (Wilcove & Wikelski 2008), with causes linked to climate change (Both et al. 2006; Møller et al. 2008) and habitat loss (Robbins et al. 1989; Sanderson et al. 2006; Berger et al. 2008) among other factors. Migrants can experience 'multiple jeopardy' owing to their reliance on different sites across the annual cycle, potentially increasing their risk of exposure to spatially-heterogeneous threats (Wilcove & Wikelski 2008; Vickery et al. 2014). Importantly, declines have not been uniform across migratory species (Sanderson et al. 2006; Thaxter et al. 2010; Vickery et al. 2014), implying that some traits associated with migration might confer particular sensitivity to environmental change. Identifying these traits could help us determine which species are at greatest risk of continuing decline.

Some lines of evidence suggest that the magnitude of migratory movements made by species can influence their vulnerability to environmental change (Wilcove & Wikelski 2008). Among birds, for example, long-distance migrants have shown steeper declines than residents and short-distance migrants (Sanderson et al. 2006; Morrison et al. 2013). However, such simple classifications of migration distance obscure a complex spectrum of within-species variation in migratory movements. Often, for example, populations comprise a mixture of individuals that migrate longer and shorter distances, or vary significantly in migration direction (Chapman et al. 2011a; Vardanis et al. 2011). This diversity of migratory movement determines the spatial distribution of the population during the non-breeding season, which in turn has important implications for population dynamics (Sutherland & Dolman 1994, Runge et al. 2014).

By expressing a diverse range of migratory movements, some populations are able to spread widely across many sites during the non-breeding period (Fig. 1A). In others, migratory movements cause populations to converge within smaller non-breeding areas (Fig. 1B). We hypothesize that this characteristic, which we term ‘migratory dispersion’, could play an important role in determining the resilience of populations to environmental change. In a simple network model of a migratory population (Appendix S1), networks with low migratory dispersion show greater declines following non-breeding habitat loss than those with high dispersion (Fig 2A-D). Indeed, these models predict that migratory dispersion can have a greater influence on population resilience than the allied phenomenon of ‘migratory connectivity’ (Fig. S1), which relates to the intermixing of individuals from different breeding sites within non-breeding sites (Webster et al. 2002). Despite considerable interest in the implications of migratory connectivity (e.g. Taylor & Norris 2010; Betini et al. 2015), the importance of migratory dispersion has received little attention.

In some species, the expression of migratory behaviour itself varies between individuals, such that populations contain both residents and migrants (Lundberg 1988). Such ‘partial migration’ has been observed widely across both marine and terrestrial biomes, and in a wide range of taxonomic groups (including invertebrates, fish, birds and mammals; Chapman et al. 2011b). However, it is unclear whether this component of migratory diversity also influences of the resilience of populations to environmental change (Chapman et al. 2011b). Network models again suggest that partially migratory populations may be more resilient to changes such as habitat loss than fully migratory populations, if those changes occur in non-breeding sites (Fig. 2C).

Here, we examine the link between migratory diversity and population resilience using data on recent trends for 340 European breeding bird species. Despite rapid improvements in individual tracking technology, we still lack the capacity to quantify between-individual variation in migratory movements for the majority of these species. We can, however, draw inferences about their migratory diversity using map-based metrics of seasonal change in species distributions. We use these to test whether migratory dispersion (measured as the relative difference in size between breeding and non-breeding ranges) and partial migration strategies (measured as partial overlap between breeding and non-breeding ranges) influence the probability that species have declined over recent decades, controlling for other species traits and climatic niche characteristics.

We also hypothesize that migratory diversity might be linked to changes in mean spring arrival date of migratory species. Previous work has shown that advances in mean spring arrival date are closely correlated with recent population trends in some European migratory birds, with declines being more severe among species that have failed to advance their mean arrival dates (Møller et al. 2008). A link between arrival advancement and migratory diversity could arise if species with diverse migratory strategies also show greater variation in the timing of movement (López-López et al. 2014). To examine this, we assess the correlation between migratory diversity metrics with interspecific variation in the advancement of mean spring arrival, and assess whether arrival advancement and migratory diversity play complementary roles in explaining species population trends. These analyses help us pinpoint species traits associated with resilience to anthropogenic change, with potential utility in assessments of species vulnerability.

Methods

Population trend and distribution data

We used data compiled from country-specific monitoring programs for two periods: a 1990–2000 census compiled in *Birds in Europe* (BirdLife International 2004) and a 2001-2012 census compiled in the *European Red List of Birds* (BirdLife International 2015). For each census period, we used the trend estimates to class each species as either declining, stable, increasing or fluctuating in population size across Europe.

To quantify the breeding and non-breeding ranges of each species, we used current distribution maps (BirdLife International and NatureServe 2014) constrained to Eurasia west of 52°E for breeding and Africa and Eurasia west of 52°E for non-breeding (excluding areas occupied only during passage). In subsequent analyses, we excluded any species whose European breeding populations migrate primarily to areas outside the study area (e.g. in Asia), as well as those with non-breeding populations in Europe or Africa that originate from outside the study area (Table S1). We also excluded fully-pelagic species, and species that breed extensively within sub-Saharan Africa, leaving 340 species for analysis (Table S1).

Metrics of migratory diversity

We used two metrics to describe migratory diversity (Fig. 1). To measure migratory dispersion (i.e. the extent to which species inhabit larger or smaller areas in the non-breeding season, relative to breeding range size), we calculated the following index:

$$Dispersion = \frac{\log_{10}\left(A_{nonbreeding}\right) - log_{10}\left(A_{breeding}\right)}{\log_{10}(A_{breeding})}$$

where $A_{nonbreeding}$ and $A_{breeding}$ are the sizes of the two seasonal ranges, log-transformed to attain normality. The denominator controls for the expected positive relationship between breeding range size and diversity in migratory movements. To quantify partial migration, we classified each species according to migratory strategy ('full resident', 'partial migrant' or 'full migrant') using season-specific range maps. Although partial migration has been defined in many ways (see Chapman et al. 2011b), it usually refers the co-occurrence of migratory and non-migratory phenotypes within a population. Given the paucity of information on individual-level phenotypic variation across species, we classified migratory strategy simply according to the presence of overlap between breeding and non-breeding ranges: full migrants have zero overlap, residents have complete overlap, and partial migrants have overlap greater than zero and less than one. As such, both our partial migrant and resident classes could include some species with ‘stepping stone’ or ‘chain’ migration patterns that might result in seasonal range overlap despite a lack of fully resident phenotypes (Nilsson et al. 2008). Of the 340 species considered, we classified 49.7 % as partial migrants, 33.8% as full migrants and 16.5% as full residents.

Other predictors of population trends

We also hypothesized that species occupying a broader range of climatic conditions may be more resilient to environmental variability, and hence anthropogenic impacts. We modelled the breadth of species’ climatic niches during breeding and non-breeding periods, and measuring between-season niche conservatism, using methods adapted from Broennimann et al. (2012). First, we converted species range polygons into point grids using a 0.25° resolution. We then selected eight biologically-meaningful climate variables from the bioclim database (see Table S2; Hijmans et al. 2005) to develop multivariate PCA axes characterising climate variation across each species’ seasonal range (breeding=April-July, non-breeding=Nov-Feb) during the whole survey period (1990-2012). Axes were constrained within the seasonal maxima and minima of each variable, and calibrated on the full environmental space (Broennimann et al. 2012). We calculated an index of climate niche breadth by summing niche occupancy scores (z values) on the first two PCA axes across both seasons. We then used a PCA-env algorithm to evaluate the degree of overlap in occupied niches along the PCA axes between species’ breeding and non-breeding ranges, providing an index of climate niche similarity (conservatism) between seasons (Broennimann et al. 2012).

To account for other variables that might influence population trends, we also quantified habitat specialism and feeding guild for each species, as well as breeding and non-breeding range size and mean latitude (constrained to the study area), and body mass. For habitat specialism, we used ‘level 1’ habitat classes in the IUCN Habitats Classification Scheme (BirdLife International 2014). For simplicity, we used only classes listed as important in the breeding season, and pooled habitat subcategories into a 6-level factor: “forest”, “shrubland”, “farmland”, “rocky/tundra”, “wetland” and “general”, the latter including species with multiple level 1 associations. We classified feeding guilds from species accounts in Handbook of the Birds of the World Alive (www.**hbw**.com) using a 5-level factor (“omnivore”, “carnivore”, “insectivore”, “granivore”, “herbivore”). Body mass is included as it is a reliable proxy for a range of correlated life history characteristics (Blummerstein & Møller 2008; Gregory et al. 2009). We calculated mean migration distance for each species as the great circle distance between the centroids of breeding and non-breeding ranges. All mapping and analyses were carried out in R using packages ‘sp’, ‘raster’ and ‘FNN’ (R Development Core Team 2008).

Statistical analysis

We modelled between-species differences in population trends using Generalized Linear Mixed Models (GLMMs) with a family-level random effect to control for potential phylogenetic non-independence of trends. To examine how our predictor variables influence the probability of species decline across the whole survey period (1990-2012), we used a binomial response variable where ‘successes’ were the number of census periods in which a species was in decline, and ‘failures’ the number in which it was stable or increasing (excluding from consideration any periods where trends were unknown or fluctuating). We also repeated the analysis for each census period individually, again using a binomial response (1 = declining, 0 = stable or increasing), excluding species for which trends were unknown or fluctuating.

We centred and standardized all predictor variables to ensure commonality of scales (Schielzeth 2010). For variable pairs that were correlated after standardization (Pearson R>0.5 or < -0.5), we included whichever was deemed likely to have a more biologically meaningful link to the response variable (see Table S3; Burnham & Anderson 2002). Substituting these excluded variables had little influence on the results (Table S4). Because migratory strategy and migration distance are partially confounded (all residents have distance 0), we used a binary dummy variable to differentiate partial migrants from other species (i.e. 1=partial migrant, 0= fully migrant or resident). This allowed us to evaluate whether partial migration explains variation in population trends above that explained by migration distance alone.

We used an information-theoretic approach to account for model selection uncertainty and evaluate predictor effect sizes (Burnham and Anderson 2002). We compared all possible model combinations, ranking each model by its Akaike weight (AIC_w) and using summed weights (ΣAIC_w) as an index of relative importance for each term (Burnhan & Anderson 2002). To estimate the effect size of each parameter, we used model averaging across a confidence set containing all top-ranked models summing to 0.95 AIC_w. We used the ‘zeroes’ method for effect averaging (Grueber et al. 2011) which provides robust between-predictor comparisons. We inferred strong support for an effect whenever 95% confidence intervals for model-averaged effects excluded zero (Grueber et al. 2011). To assess overall model explanatory power, we calculated conditional and marginal R^2 values for the global model using methods described in Nakagawa & Schielzeth (2013).

For a subset of migratory species, we tested for relationships between the two migratory diversity metrics and advances in spring migration timing using univariate linear regressions. We obtained data on trends in mean Europe-wide spring arrival date from a published dataset for 89 European bird species (Møller et al. 2008, trends 1960-2006). We also repeated the full multi-model comparison for predictors of population trends within this 89 species subset, including the mean trend in arrival date as an additional predictor variable. This allowed us to compare the relative contributions of migratory diversity metrics and arrival date trend towards explaining variation in population trends.

Results

Effects of migratory diversity on bird declines

Of the 340 species considered, 42% had positive migratory dispersion scores, 41% had negative scores and 16% were fully resident (i.e. dispersion = 0). Model selection identified migratory dispersion as an important predictor of decline probability (Tables 1 & S5), with higher dispersion being associated with lower probability of decline (Fig. 3). This effect was consistent across both early and late census periods (Tables 1, S6 & S7). Partial migration was also identified as an important predictor of decline probability (Table 1 & S5), with partial migrants being less likely to decline on average than both full migrants and full residents over the whole study period, and in particular over the early census period (Fig. 4, Table S6). Both partial migration and migratory dispersion were consistently selected ahead of migration distance as predictors of declines (Tables 1, S5-7), indicating that they explain considerable variation in decline probabilities over and above that explained by between-species differences in migration distance. Although partial migrants tended to have shorter mean migration distances than full migrants (mean ~2,050 km ± 1,790 s.d. versus ~ 4,700 km ± 2,010), the partial migrant group contained many long-distance migrants (Fig. 5), with almost half of sub-Saharan migrants (45.7%) being classified as partial migrants.

For the subset of 86 species with available data on trends in mean spring arrival date, arrival trends were strongly associated with favourable population trends (Table 1), echoing previous findings (Møller et al. 2008). Partial migrants tended to show greater advancement in mean spring arrival date than full migrants (F = 13.96, P<0.001; Fig. S2). The effect of partial migration on decline probability became negligible when spring arrival trends were included in the model (Table 1), suggesting that the link between partial migration and population declines might be mediated by interspecific variation in spring arrival trends. Migratory dispersion, by contrast, was not correlated with trends in spring arrival (Fig. S3), and remained a strongly supported predictor of decline likelihood in this subset analysis (Table 1), suggesting that the effect of dispersion acts independently of trends in spring arrival timing.

Other predictors of population trends

Habitat specialism was an important predictor of population trends in all analyses, with all specialist classes showing higher probabilities of decline than habitat generalists (Table 1), with farmland specialists being particularly prone to decline (Table 1). Across the whole study period, and in particular 1990-2000, there was strong support for an effect of body mass on decline probability, with lighter species having higher decline probabilities (Table 1). Little support was found for effects of guild, breeding latitude, climate niche overlap or climate niche breadth in the full analyses (Table 1). Breeding latitude and niche breadth did, however, receive some support in the subset analysis including data on spring arrival trends, with decline probability tending to increase among species breeding at higher latitudes, and species with higher winter climate niche breadth (Table 1).

The global model for the whole survey period explained 23.2% of variation in probability of decline between species, of which 22.7% was attributable to fixed effects (Table S8). Levels of variance explained were somewhat higher for models fitted to 1990-2000 trend data alone (33.4%, Table S8) and somewhat lower for 2001-2012 trend data (18.8%, Table S8).

Discussion

Our results demonstrate that migratory diversity is an important predictor of recent population declines in migratory species. Species whose migratory movements allow them to occupy larger areas in the non-breeding season, relative to their breeding ranges, were less likely to decline than those whose populations are channelled into more restricted non-breeding ranges. Partially migratory populations were also less likely to decline than either full migrants or full residents. These patterns held true across both short and long-distance migrants, indicating that migratory distance *per se* does not necessarily confer heightened vulnerability to anthropogenic change. Rather, species with lower diversity in migratory movements and destinations may be more vulnerable than those with more diverse ranges and strategies. These interspecific differences help explain why some long-distance migrants have maintained favourable population trends while others have severely declined (Vickery et al. 2014).

Various mechanisms could drive the relationship between migratory diversity and the probability of population decline. One possibility, as implied by migratory network models (Fig. 2), is that diversity confers increased population-scale resilience to area-specific threats in the non-breeding range (e.g. habitat degradation and hunting pressure). Our findings are in broad accordance with model predictions that species with higher migratory dispersion may increase population resilience (Fig. 2A-D), and that partially migratory species may be more resilient than full migrants (Fig. 2E & F) if negative impacts primarily occur in the non-breeding range (Chapman et al. 2011b). Our results suggest that the dynamics of migratory populations are indeed sensitive to the number, size and distribution of occupied non-breeding sites, relative to the breeding range. While previous works have considered the consequences of spatial 'bottlenecks' arising as populations pass along migration corridors (e.g. Weber et al. 1999; Berger et al. 2008; Sawyer et al. 2009), little attention has been paid to the potential importance of equivalent 'bottlenecking' across non-breeding ranges. Our results suggest that this plays an important role in determining population vulnerability to environmental change.

Our findings also support the hypothesis that migratory diversity influences the capacity of species to respond to climate-driven shifts in resource phenology, as partial migrants showed greater rates of advancement in mean spring arrival date than full migrants (Fig. S2). In turn, these advances in arrival date are strongly linked to positive population trends (Møller et al. 2008). The relationship between partial migration and arrival advancement could arise if partial migrants, as well as expressing between-individual variation in migratory behaviour itself, also express greater variability in the timing of migratory movements than full migrants. Such variation could facilitate shifts in migration timing at the population scale, if early-arriving individuals are more likely to encounter successful breeding conditions, and the resulting offspring also migrate earlier (Gill et al. 2014). Moreover, resident individuals within partially migratory populations are predisposed to match the timing of breeding with shifting resource abundance peaks (Chapman et al. 2011b). The same is true for fully-resident species, although interestingly our models suggest that full residents have higher decline probabilities on average than partial migrants (Fig. 4). This result implies that migration does not necessarily increase the vulnerability of species to environmental change relative to full residence, if a flexible range of migratory strategies is expressed.

The mechanisms that underpin the expression of different migratory strategies across populations remain poorly understood. In birds, a large component of migratory behaviour is genetically determined (Biebach 1983; Pulido & Widmer 2005), implying that diversity might be tightly linked to the presence of heterogeneity in migratory gene expression across a population (Biebach 1983; Kaitala 1993; Piersma 2011), which in turn may be influenced by environmental or social cues. Within-individual plasticity in migratory behaviour can be considerable, particularly in partial migrants where migratory behaviour may change within an individual's lifetime (Nilsson et al. 2006; Olsson et al. 2006; Brodersen et al. 2008). It is notable that partial migration is an extremely widespread strategy in European birds (Chapman et al. 2011b), being found in 80% of the 55 avian families included in our study (compared with full migration, found in 42% of families). In most cases, the degree of population-scale migratory diversity expressed by a species is likely to depend on a complex interplay between genetic heterogeneity and individual responses to social cues and local environmental conditions. The relative strength of genetic versus social/environmental determination may have important consequences for population resilience to environmental change, as plasticity in response to external cues may facilitate more rapid population-scale change (Marra et al. 2005).

Migratory diversity, whether arising through within-individual plasticity or between-individual heterogeneity, might also increase the likelihood that new non-breeding areas are colonized via the establishment of new migratory routes. Such colonisations are likely to be important in determining the long-term persistence of migratory populations under changing climates (La Sorte & Thompson 2007). Moreover, the colonization of new non-breeding sites could drive dynamic changes in migratory dispersion over time, with consequent implications for population dynamics. Species with greater capacity to spread to new non-breeding sites may therefore be more resilient to a range of environmental stressors, including both climate change and habitat loss. Dynamic shifts in the non-breeding ranges of migratory species have been demonstrated in a variety of taxa (see Robinson et al. 2009 for a review), but the behavioural mechanisms by which these shifts occur remain poorly understood.

Caveats

The effect of partial migration on decline probability was predominantly evident in the early census period, and partial migration was a weak predictor of declines in the late census period (Table 1). It is unclear why the positive effect of partial migration might have declined over time, but it appears to be associated with improving trends among full migrants in the second survey period, rather than an increase in the number of partial migrants declining. Over half of fully migratory species were in decline in 1990-2000 (50.4%), but this fell to 35.7% in 2000-2012, whereas the proportion of declining partial migrants remained fairly stable (33.1% in 1990-2000 versus 30.8% in 2000-2012). The factors driving this improvement in fortunes for fully migratory species are unclear, although this pattern could reflect the success of recent conservation interventions (Sanderson et al. 2015), given that migratory species are emphasized under Annex 1 of the EU Birds Directive (European Union 2009).

An important caveat associated with our results is that we use coarse species distribution maps that, although reflective of best current knowledge of range extents, do not capture fine-scale occupancy or abundance patterns within species' breeding, passage and non-breeding ranges (Rondinini et al. 2006). Our analyses do not account for the precise routes and staging areas used by populations during passage, as these are incompletely mapped for most species (Runge et al. 2014). As noted above, migratory populations can be highly vulnerable to threats occurring within migratory corridors or stop-over sites, if a high proportion of individuals pass through the same key areas (Weber et al. 1999; Berger et al. 2008). Such passage bottlenecks are perhaps most likely among species with low migratory dispersion, as well as those that migrate in large groups (e.g. waterbirds, many large mammals). Detailed mapping of the migration routes of declining migratory populations therefore remains an important conservation priority (Runge et al. 2014).

By taking a single trend value for each species, our analyses assume that trends within a given time window are constant across the whole European range. In fact, evidence suggests that population trends of migratory species can be highly heterogeneous in space (Villard & Maurer 1996; Morrison et al. 2013). Future analyses accounting for this heterogeneity, perhaps by using country-level rather than region-wide trend data, may offer more nuanced insights into relationships between migratory behaviour and population vulnerability. In particular, it may be possible to examine whether within-range population trend heterogeneity correlates with spatial heterogeneity in migratory behaviour (e.g. by comparing resident and migratory populations in partial migrant species). For the purposes of this study, we assume that mean Europe-wide trend estimates provide a robust, if coarse, index of interspecific variation in vulnerability to recent environmental change.

Conclusions

The power of map-based metrics of migratory diversity to explain population trends suggests that they could be useful in evaluating species vulnerability to future anthropogenic threats. Because our metrics use only coarse distributional data, they can be easily generated using current estimates of species' seasonal distributions. Such metrics may be particularly useful in regions where estimates of population trends are lacking, such that more detailed assessments of species vulnerability are precluded. Migratory diversity metrics can provide conservation-relevant information for almost any species where reasonably accurate distributional data are available, even if those data are of low resolution.

Understanding how migratory diversity contributes to species vulnerability might also help in the design and implementation of species-specific conservation management plans. Species with low migratory dispersion, for example, might be expected to benefit from a focus on conservation actions within the non-breeding distribution, such as the increased protection or restoration of habitats in key areas (Runge et al. 2015). The potential efficacy of such actions for species with low migratory dispersion is exemplified by the positive population trends of a handful of species (e.g. the pink-footed goose *Anser brachyrhynchus* and barnacle goose *Branta leucopsis*) that have highly restricted non-breeding ranges, and yet have maintained favourable population trends thanks to pro-active conservation measures (MacMillan et al. 2004). It is important to note, however, that management should always be informed by detailed examinations of the likely demographic drivers of population declines, and where in the annual cycle these drivers are likely to operate. By incorporating migratory diversity into future network-based analyses of migratory populations, it may be possible to come to an improved understanding of these complex seasonal drivers.

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Supplementary material

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Table 1 Performance of candidate variables in explaining the probability of population decline. Effect sizes reflect model-averaged parameter estimates $\hat{\beta}$ and bootstrap 95% confidence intervals. Results are shown for model selection applied to the full dataset (340 species) across the whole study period (1990-2012), plus each census period individually. We also re-ran the analysis for a subset of 89 species with data on trends in mean Europe-wide spring arrival date. Model averaged parameter estimates with confidence intervals that do not overlap zero are shown in bold.

Dataset:	**Whole period 1990-2012**		**Early period 1990-2000**		**Late period 2001-2012**		**Spring arrival dataset (n = 89) 1990-2012**	
Variable:	**$\hat{\beta}$ (LCI, UCI)**	**ΣAICc**	**$\hat{\beta}$ (LCI, UCI)**	**ΣAICc**	**$\hat{\beta}$ (LCI, UCI)**	**ΣAICc**	**$\hat{\beta}$ (LCI, UCI)**	**ΣAICc**
Partial migration	**-0.53 (-0.96, -0.11)**	0.98	**-1.11 (-1.74, -0.47)**	1.00	0.04 (-0.45, 0.46)	0.21	-0.01 (-1.27, 1.26)	0.22
Migratory dispersion	**-0.27 (-0.49, -0.05)**	0.95	**-0.27 (-0.67, -0.04)**	0.90	**-0.20 (-0.45, -0.03)**	0.83	**-0.65 (-1.26, -0.05)**	0.84
Migration distance	0.22 (-0.04, 0.48)	0.61	**0.22 (0.02, 0.76)**	0.81	0.07 (-0.21, 0.34)	0.24	0.24 (-0.65, 0.58)	0.22
Climate niche overlap	0.10 (-0.13, 0.33)	0.32	0.10 (-0.16, 0.51)	0.36	0.04 (-0.19, 0.26)	0.22	-0.03 (-0.66, 0.59)	0.20
Climate niche breadth	0.21 (-0.01, 0.42)	0.72	0.21 (-0.02, 0.60)	0.68	0.14 (-0.10, 0.37)	0.31	**0.66 (0.12, 1.19)**	0.87
Mean breeding latitude	-0.11 (-0.35, 0.12)	0.33	-0.11 (-0.67, 0.03)	0.66	0.20 (-0.03, 0.45)	0.47	**0.66 (0.04, 1.27)**	0.65
Body mass	**-0.33 (-0.61, -0.06)**	0.96	**-0.33 (-1.03, -0.02)**	0.95	-0.21 (-0.49, 0.07)	0.45	-0.98 (-2.82, 0.86)	0.63
Habitat *:		1.00		0.97		1.00		1.00
Farmland	**2.17 (1.28, 3.07)**	-	**2.17 (0.73, 3.26)**	-	**2.35 (1.30, 3.41)**	-	**6.13 (3.03, 9.23)**	-
Forest	0.59 (-0.30, 0.48)	-	0.59 (-0.99, 1.50)	-	0.84 (-0.21, 1.89)	-	2.09 (-0.46, 4.65)	-
Shrubland	**1.20 (0.25, 2.16)**	-	1.20 (-0.68, 2.10)	-	**1.55 (0.44, 2.67)**	-	1.62 (-1.07, 4.31)	-
Rocky	**1.03 (0.04, 2.02)**	-	1.03 (-0.93, 1.84)	-	**1.62 (0.46, 2.78)**	-	2.60 (-0.26, 5.40)	-
Wetland	**1.24 (0.37, 2.13)**	-	1.24 (-0.22, 2.25)	-	**1.65 (0.60, 2.69)**	-	**2.93 (0.49, 5.37)**	-
Guild *:		0.06		0.01		0.34		0.02
Omnivore	0.56 (-0.12, 1.25)	-	0.03 (-0.81, 1.09)	-	0.93 (-0.17, 1.69)	-	-1.34 (-3.77, 1.10)	-
Insectivore	0.07 (-0.62, 0.75)	-	0.05 (-1.19, 0.71)	-	0.36 (-0.35, 1.07)	-	-0.21 (-2.50, 2.07)	-
Granivore	0.48 (-0.38, 1.34)	-	0.01 (-1.24, 1.16)	-	1.05 (-0.16, 1.94)	-	0.04 (-2.73, 2.80)	-
Herbivore	0.15 (-0.90, 1.20)	-	0.05 (-1.18, 1.86)	-	-0.16 (-1.29, 0.98)	-	1.45 (-1.50, 4.40)	-
Spring arrival trend	n/a	n/a	n/a	n/a	n/a	n/a	**0.78 (0.14, 1.43)**	0.86

*For categorical variables, parameter estimates are given relative to a reference category (‘general’ for habitat, ‘carnivore’ for guild

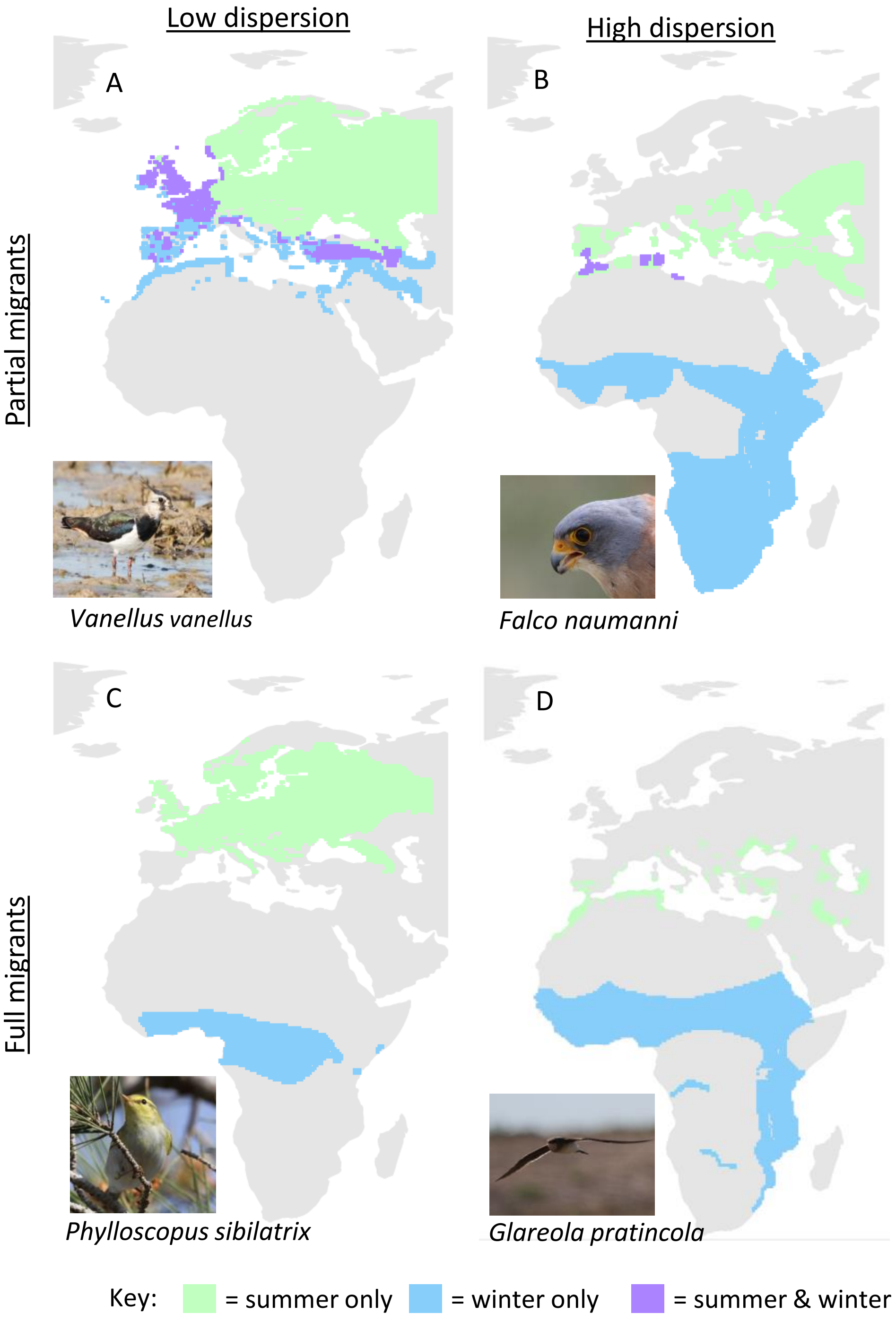
Figure 1 Examples of within-species migratory diversity. Partial migrants (A & B) are migratory species that occur in some parts of their range all year; full migrants (C & D), by contrast, vacate their breeding ranges entirely during the non-breeding period. Migratory dispersion reflects the extent to which species occupy larger or smaller non-breeding ranges relative to the breeding period. Examples show species with relatively low (A & C) and high (B & D) levels of dispersion.

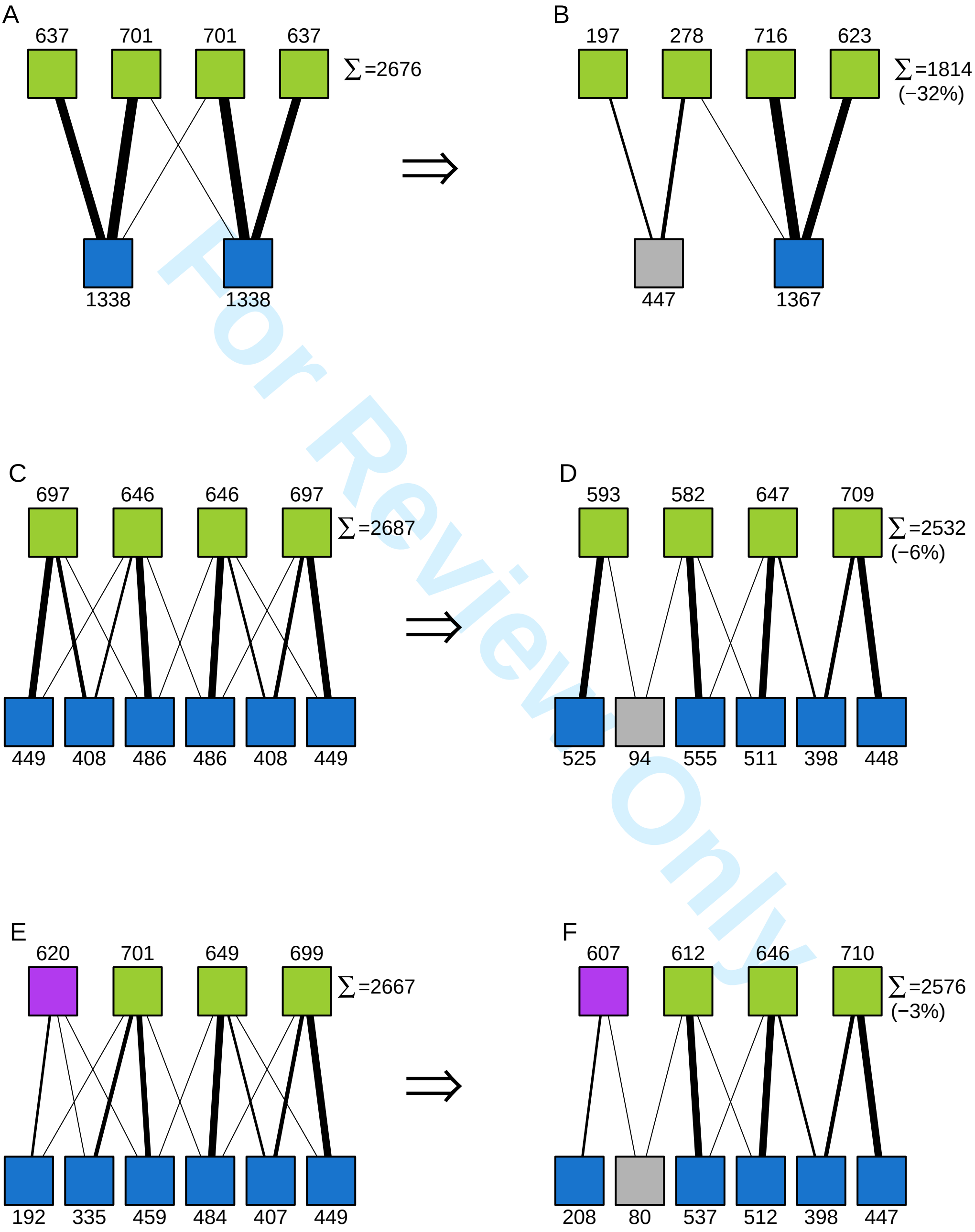
Figure 2 Hypothetical population networks with varying migratory diversity. Networks consist of ‘nodes’ (squares) representing equally-sized areas occupied in the breeding (green) or non-breeding season (blue), connected by ‘edges’ reflecting migration routes (lines, width indicates number of individuals using each route). Numbers show the model-derived equilibrium population sizes at each node in each scenario (details given in Appendix S1). Populations with low migratory dispersion (A) show marked declines following an 80% loss of habitat at one non-breeding node (B, grey=impacted node). For an equivalent population with higher migratory dispersion (C), the same level of habitat loss has a markedly lower impact (D). For a partially migratory population, where a proportion of individuals at one breeding node are resident (E, purple = partially migratory node), the impact is further reduced (F).

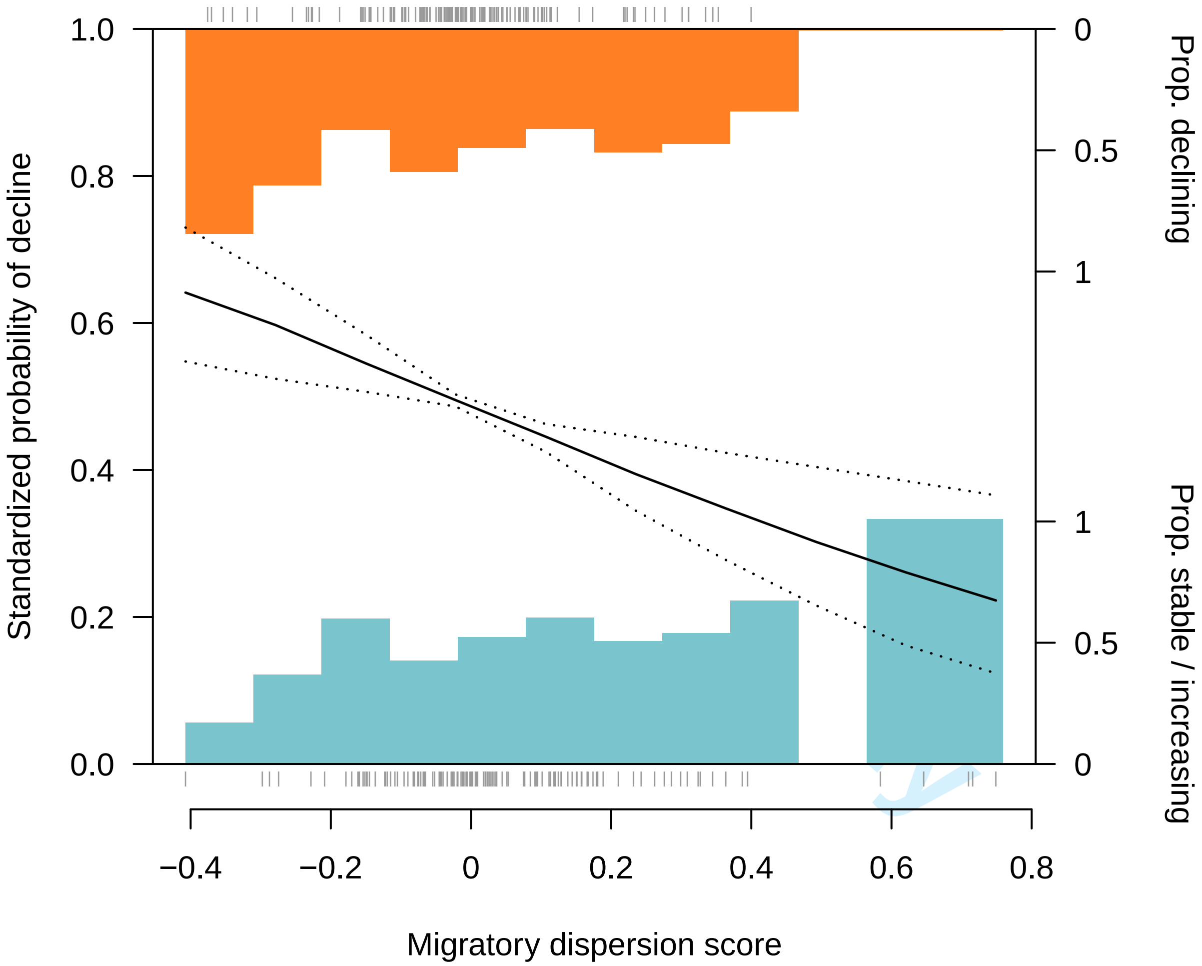
Figure 3 Population trends in relation to migratory dispersion. Lines show the model-averaged slope and bootstrap 95% confidence intervals from a model set predicting the declines over the whole study period (1990-2012). Bars show the proportion of species that were stable or increasing (blue lower bars) or declining (orange, inverted upper bars) in relation to migratory dispersion (binned data). Tick marks above and below bars show the locations of individual data points on the x axis (lower = stable or increasing species, upper = declining species).

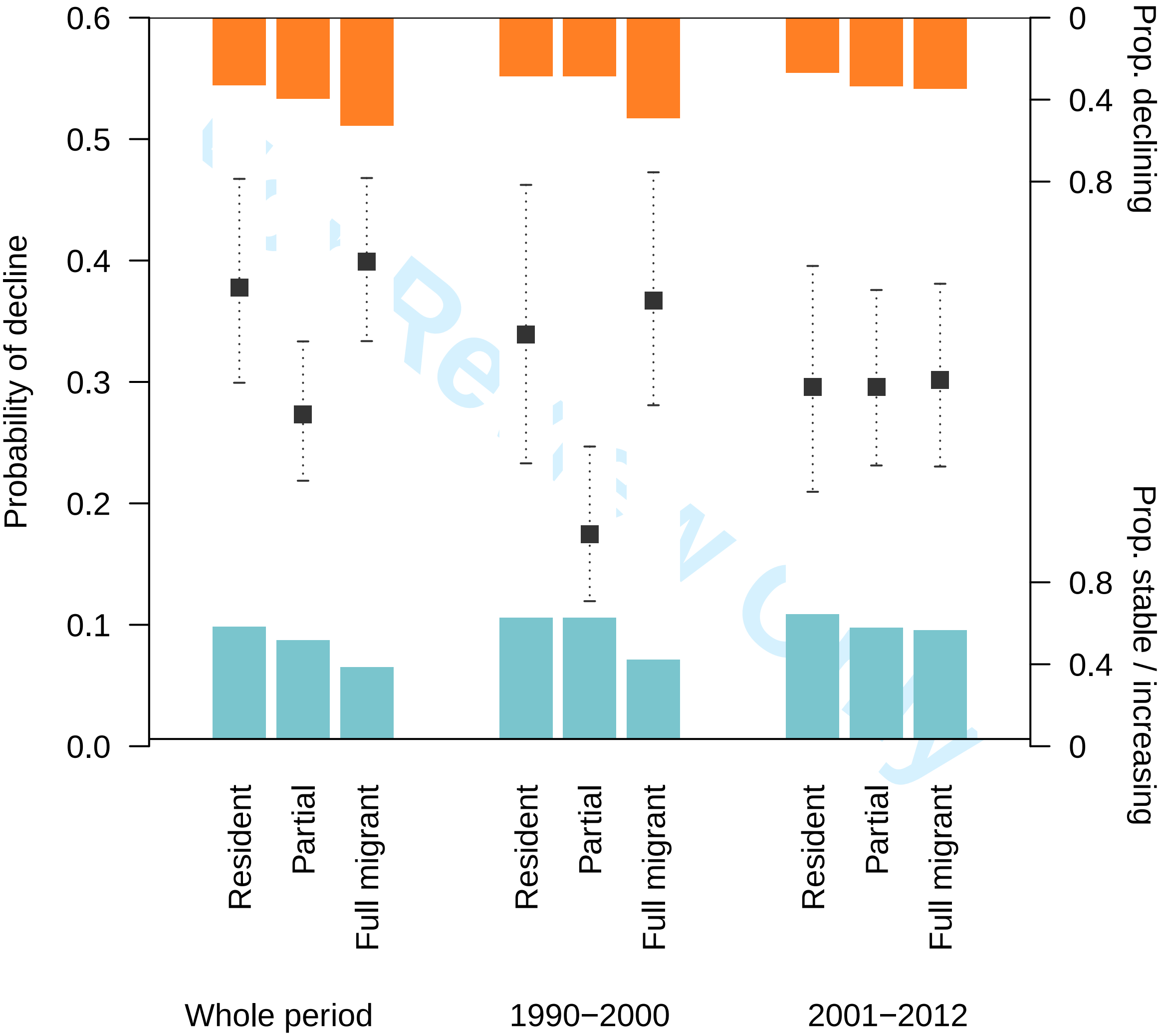
Figure 4 Population trends in relation to migratory strategy. Points and error bars show mean model-averaged predictions and bootstrap 95% confidence intervals for each strategy, from models explaining the probability of decline across the whole survey period, and to census period individually. Bars show the proportion of species in each class that were stable or increasing (blue, lower bars) or declining (orange, inverted upper bars) in any given survey period.

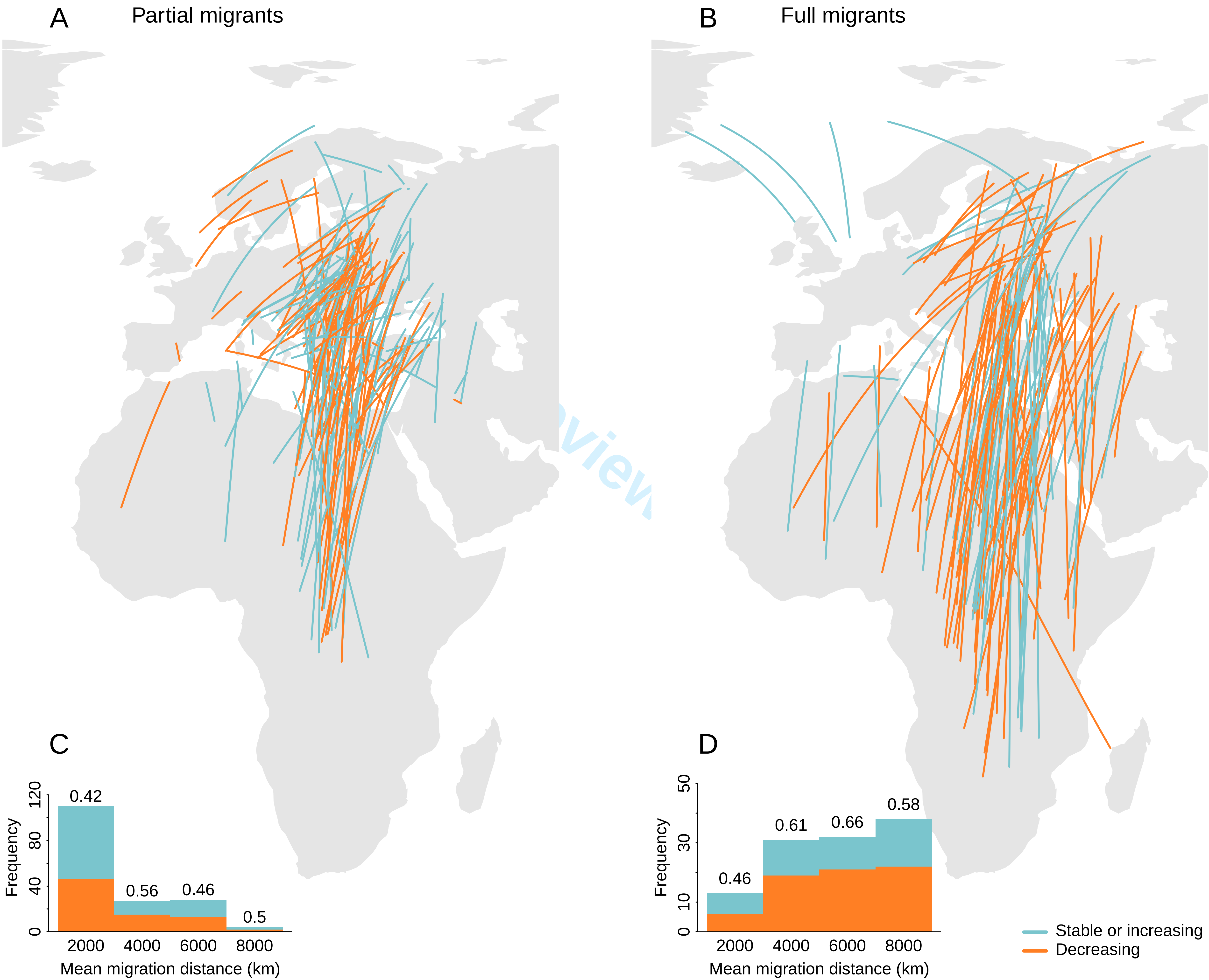
Figure 5 European bird declines in relation to migration strategies. Lines show great circle routes linking breeding and non-breeding range centroids for all non-pelagic migratory species, color-coded according to population trend (orange = decreasing in one or more survey period, blue = stable or increasing in both survey periods). Species are classed as either partial migrants (A) or full migrants (B) from the presence or absence of seasonal range overlap. Histograms show the frequency distribution of mean migration distance for partial (C) and full migrants (D); numbers above bars show the proportion of species in decline within each distance bin.


Low dispersion
High dispersion
Partial migrants
Full migrants
A
B
C
D
Vanellus vanellus
Falco naumanni
Phylloscopus sibilatrix
Glareola pratincola
Key: 🟩 = summer only 🟦 = winter only 🟪 = summer & winter


A
637
701
701
637
∑=2676
1338
1338
⇒
B
197
278
716
623
∑=1814
(−32%)
447
1367
C
697
646
646
697
∑=2687
449
408
486
486
408
449
⇒
D
593
582
647
709
∑=2532
(−6%)
525
94
555
511
398
448
E
620
701
649
699
∑=2667
192
335
459
484
407
449
⇒
F
607
612
646
710
∑=2576
(−3%)
208
80
537
512
398
447


1.0
0.8
0.6
0.4
0.2
0.0
Standardized probability of decline
0
0.5
1
Prop. declining
1
0.5
0
Prop. stable / increasing
−0.4
−0.2
0
0.2
0.4
0.6
0.8
Migratory dispersion score


0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability of decline
0
0.4
0.8
Prop. declining
0.8
0.4
0
Prop. stable / increasing
Resident
Partial
Full migrant
Resident
Partial
Full migrant
Resident
Partial
Full migrant
Whole period
1990−2000
2001−2012


A
Partial migrants
B
Full migrants
C
Frequency
0
40
80
120
0.42
0.56
0.46
0.5
2000
4000
6000
8000
Mean migration distance (km)
D
Frequency
0
10
30
50
0.46
0.61
0.66
0.58
2000
4000
6000
8000
Mean migration distance (km)
Stable or increasing
Decreasing