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# European Breeding Bird Declines Associated With Narrower Climatic Niches

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## ABSTRACT

**Aim:** Anthropogenic climate change has increasingly been identified as a major threat to global biodiversity. However, the extent of this threat is likely to be uneven across species, due to differences in life histories or exposure to environmental change. The range of climatic conditions a species experiences across its range extent, known as the realised climatic niche, may be an indicator of species resilience to climate change. Species with large range extents, occurring across diverse climatic conditions, are expected to be less affected by climate change due to lower physiological constraints and tolerance to a wider range of climates. However, this may not be the case if local populations are adapted to specific environmental conditions. In this study, we investigate whether the extent of the species' realised climatic niche, also known as the climatic niche breadth, is linked to their long-term population trends.

**Location:** Europe.

**Taxon:** Birds.

**Methods:** We extract climate data across the breeding-only and resident ranges of 159 European bird species and use an ordination method to produce a representation of the species climatic niches. We then relate the niche breadth of each species to their range area and incorporate this relationship, along with the species' diet, main habitat type, migratory status and average body mass, to investigate their relationship with the species long-term population trend.

**Results:** Species with small range areas showed larger variation in climatic niche breadth than species with larger ranges. For species with similar range areas, those with broader climatic tolerance were less likely to be declining than those with narrow climatic niches.

**Main Conclusions:** These findings can help us understand the threats associated with climate change and allow for rapid assessment of the importance of climatic factors on population trends, providing an invaluable tool for targeting habitat conservation.

## 1 | Introduction

In the face of the global biodiversity and climatic crises, understanding the drivers of species population trends is of key importance to revert or slow biodiversity declines (Poiani et al. 2011). Climate has been shown to be a major influence, impacting population dynamics and spatial distributions of many species (Parmesan and Yohe 2003; Spooner et al. 2018; Intergovernmental Panel

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On Climate Change [IPCC] 2023). Species responses to climate change, including phenological and behavioural changes, can vary with factors such as body mass, diet type, migratory strategy, or main type of habitat used, with some groups being more affected than others (Gordo et al. 2013; Rushing et al. 2020; Martay et al. 2023). For example, long-distance migratory species have suffered stronger population declines than either short-distance migrants or resident species (Lees et al. 2022), with climate-driven phenological changes resulting in mismatches between the peak of food abundance and migrant arrival identified as one of the causes for these declines (Both et al. 2006; Jones and Cresswell 2010; Lameris et al. 2018). Many species are experiencing changes in climatic suitability across their ranges as a result of climate change, particularly within breeding sites (Howard et al. 2020; Martay et al. 2023). Many areas currently occupied may become unsuitable in the near future, causing species distributions to shrink due to local extinctions, or shift towards new areas with suitable conditions (Huntley et al. 2008; Chen et al. 2011; McCaslin and Heath 2020). This is possible because populations can grow faster in areas with high climatic suitability and may be limited in areas with less suitable conditions, with consequences for population trends and long-term persistence (Ruegg et al. 2021). These lines of evidence suggest that species with narrower climatic niches, that is, the range of climatic conditions that species tolerate and in which populations are able to persist, may be more vulnerable to the impacts of environmental change, although this prediction has seldom been tested at large spatial scales.

Species' range area has been shown to be a good predictor of responses to climate change (Schwartz et al. 2006), as well as declines in abundance (Collen et al. 2011) and vulnerability to habitat loss (Staude et al. 2020). While species distributions are determined by the interplay of a range of factors, species occupying smaller areas are more likely to have more specific climatic requirements compared to widespread species (Pigot et al. 2010; Graham et al. 2010; Freeman et al. 2022). Furthermore, the scale at which a species' distributional or phenological shifts occur, triggering any potential mismatches with resources, may only affect a relatively smaller proportion of a large range compared to that of narrowly distributed species. Hence, based on climate conditions alone, species with larger range areas would be expected to tolerate and thrive in a wider range of conditions and be relatively more resilient to changes in climate (Schwartz et al. 2006; Ohlemüller et al. 2008). However, many widespread species have been facing population declines (Elliott et al. 2010; Burns et al. 2021) which, among other factors, have been attributed to climate change (Howard et al. 2020; Buchan et al. 2023).

One possible reason for the recent climate-related declines of widespread species is that the extent of and variation in climatic conditions are uneven across geographic space, with some conditions being more widespread than others (Huntley et al. 2016). Hence, while the two may generally be correlated (Dallas and Kramer 2022), a large area occupied is not necessarily synonymous with a large range of climatic conditions, indicating that the range area alone may not always be a sufficient predictor of the impacts of climate change on species (Ficetola et al. 2020). New hypotheses are, therefore, needed to help explain why some common wide-ranging species are currently facing sharp declines in abundance (Gaston and Fuller 2008; Gregory et al. 2019, 2023). In turn, biodiversity conservation planning needs to consider the level of exposure to climate change, and species' ability to tolerate and adapt to changing climatic conditions, and the extent to which these can be predicted from trait-related susceptibilities (Foden et al. 2013).

Species' climatic niche breadth can help predict responses to climate change (Herrera et al. 2018). Numerous studies have investigated the role of climate change as a driver of population declines (e.g. Jiguet et al. 2007; Jiguet, Gregory, et al. 2010; Tayleur et al. 2016), however, only temperature metrics have been used to define the climatic niche, which may lead to the omission of important across-species variability and produce an incomplete characterisation of the species' climatic niche (but see Ruegg et al. 2021; Hällfors et al. 2024). Furthermore, while the size of the species' range is usually considered in these studies, it is considered separately from the climatic niche. While range size is likely to be correlated with climatic niche breadth, this relationship is unlikely to be ubiquitous and species with similar range sizes may be exposed to different variability in climatic conditions. Disentangling the relationship between range size and climatic niche breadth could, therefore, provide important insights into species responses to climatic conditions and help explain the large variability in population trends. We aim to present a more complete view of the realised climatic niche while explicitly incorporating the effects of range size.

Birds are a well-studied taxon with high-quality population and distribution data available across broad spatial scales (e.g. Gregory et al. 2005; Ding et al. 2024). Due to this, they have been commonly used as indicator species in biodiversity assessments (Gregory et al. 2019; Fraixedas et al. 2020). The Pan-European Common Bird Monitoring Scheme (PECMBS) collates data from long-term population surveys carried out by regional schemes across Europe, allowing species population trends to be monitored over time (Gregory et al. 2005; Brlík et al. 2021). At the same time, wide-scale declines among bird species breeding in Europe have been observed (Burns et al. 2021). The wealth of data collected as well as the challenges faced by this taxonomic group make them an excellent taxon for testing hypotheses on climatic niche breadths.

Here, we aim to investigate whether the extent of the climatic niche breadth influences the long-term population trends of breeding birds in Europe. We account for range size, species traits such as migration strategy, main habitat type occupied, diet type and mass, as well as species' tolerance to human-modified environments. We predict that for two species with a similar breeding range size, the species with a narrower climatic niche breadth will be more likely to be declining.

## 2 | Methods

### 2.1 | Species Distributions and Population Trend Data

This study included distribution data for all bird species that have breeding or resident ranges in Europe and for which population trend data is available. The species' breeding and resident ranges were obtained from BirdLife International (2020). These have been collated and updated up to the year 2020. For each species,



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we obtained the slope of the population trend calculated over the years 1980–2019 from the PECBMS dataset which includes 170 species (Gregory et al. 2005; Brlík et al. 2021). Our final dataset included 159 species. The common pheasant (*Phasianus colchicus*) was removed due to it being a non-native species frequently released into the wild for hunting purposes. A further 10 species were removed as only a 10-year population trend was available for them (the minimum number of years over which a long-term trend was calculated was 22, median = 39; Supporting Information). The long-term European population trends of the species considered in our study varied between 0.91 and 1.07, with values of 1 suggesting that the population is stable, values above 1 indicating a population increase and values below 1—a decreasing population trend.

## 2.2 | Realised Climatic Niche Breadth

The study extent was limited to the geographic extent of Europe, bound at longitudes from −24.33° to 59.00° and latitudes between 34.92° and 75.00°. To represent the climatic conditions within the study extent, we used the 19 bioclim variables, averaged over the years 1970–2000 from WorldClim2 at 5-arcminute resolution (Supporting Information; Fick and Hijmans 2017). This 30-year climate norm period was considered the most appropriate to characterise the climate over the years in which the bird species population trends were calculated (Supporting Information).

To obtain the climatic data within each species' European breeding distribution, the WorldClim2 rasters, containing the 19 bioclim variables, were cropped to match the species distribution polygons (obtained from BirdLife International 2020), then the points and associated values of each of the variables were extracted. This approach assumes the current bird distributions have, on average, remained constant over the 30 years covered by the climate information used in this study.

To construct the species' climatic niches, we followed the framework outlined by Broennimann et al. (2012). The scaled and centred 19 bioclim variables were transformed through principal component analysis (PCA-env) using the *ade4* package (Dray and Dufour 2007). The PCA was carried out with climatic data for the entire study extent; therefore, constraining the climatic niche within the range of climatic conditions available across the geographic extent of Europe (Broennimann et al. 2012). The number of principal components (axes) was set to two, as these cumulatively explained over 70% (73.47%) of the variance in the data (Supporting Information). These new orthogonal axes represent the climatic niche of each species using dimensions created as a combination of climatic variables (Broennimann et al. 2012).

The principal component scores corresponding to data points within each species' breeding and resident distribution were used to produce a hypervolume representing the species climatic niche (Blonder et al. 2014). This was repeated separately for each of the species. The hypervolume was constructed using the support vector machine algorithm with default parameters from the package *hypervolume* (Blonder et al. 2018, 2023; Supporting Information). The volume of the shape obtained was then taken as a measure of the breadth of the realised climatic niche. As we only use two dimensions, the metric representing the realised climatic niche is the area of the resulting shape; however, for clarity, we refer to this as the volume.

## 2.3 | Niche Breadth and Population Trend Relationship

The range of climatic conditions experienced by species, and thus the breadth of their climatic niche, has been shown to be correlated with the area of the species' range (Ficetola et al. 2020). The larger the area occupied, the more likely it is to encompass a broader variety of climatic conditions. We produced an index of climatic niche breadth to range area by dividing the species' realised niche breadth (i.e. the climate niche volume) by the species' breeding-only and resident area (within the study extent). An increasing value of this index indicates a broad climatic niche breadth relative to the range area, while a low value suggests that the climate niche of that species is relatively narrow for the area of its range. This niche breadth/range area index was then related to the species long-term population trends in Europe (PECBMS). An alternative approach would be to obtain the residuals of the relationship between the niche breadth and species range size. However, due to the non-linear relationship between the niche breadth and range area, as well as unequal residual variances across the range of fitted values (heteroscedasticity), this approach was considered unsuitable (Supporting Information).

Across the 159 breeding bird species, the long-term population trend was available for a different number of years, ranging between 40 and 22 years. For each species, we calculated the proportion of the maximum number of years for which the trend was produced. Hence, records for species for which the population trend was calculated over the full 40 years received a value of 1, while others were assigned a proportionally lower number. This enabled us to give more weight to the species that had a population trend estimated over a longer period, which may capture responses to climate change across broader temporal scales.

Furthermore, depending on species life histories (e.g. habitat associations, migratory strategy), the breeding climatic niche obtained may represent a different proportion of the species' entire niche. For example, the overall realised climatic niches of migratory species with large wintering areas outside of Europe, and, therefore, the climatic variability these species encounter, may be underrepresented in this study. This is also linked with population trends, as factors outside of the extent of this study may have a strong impact on migratory species (Howard et al. 2020). Thus, to account for these differences across species, we included a weight in our model, calculated as an average of two proportions: (1) the proportion of the total species distribution area falling within the study extent and (2) the proportion of years over which the species population trend was calculated.

We classified each species' diet type as feeding mainly on invertebrates ('Invertebrate'), plants and/or their seeds ('Plant/Seed'), vertebrates or through scavenging ('VertScav'), or omnivorous ('Omnivore') following the EltonTraits 1.0 dataset (Wilman et al. 2016). Moreover, migration strategy may also influence



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vulnerability to environmental change (Samplonius et al. 2018), and this study includes both migrant and resident species. Thus, we categorised the migration strategy of each bird species as resident, partial or full migrant, following Gilroy et al. (2016). We also included natural logarithm-transformed body mass of each species, obtained from the EltonTraits 1.0 dataset (Wilman et al. 2016). Body mass is also a good proxy for species longevity, as the rate of any change will be different for species with a slower generational turnover (which also tend to be larger overall). While our species list includes multiple avian groupings, we have not accounted for phylogenetic relationships as similar studies looking at population trends, as well as climatic niches and range areas, have not identified a significant association with these (Koleček et al. 2014; Kambach et al. 2019). Finally, while evidence of the importance of niche position and the latitudinal gradient in climate has been previously demonstrated (e.g. Jiguet, Devictor, et al. 2010; Dallas and Kramer 2022), we have not included this in our analysis because any summary metric of the species' range is unlikely to be adequate for species with disjunct distributions.

Habitat disturbance and loss were also identified as a key threat to bird populations, and different habitat types are likely to be affected to varying extents (Gregory et al. 2019). Hence, we included the main habitat type utilised by each species (farmland, forest, wetland, shrub and other) as a variable in the full model. This data was obtained from the PECBMS dataset, which included three habitat categories: forest, farmland and other. For all species that had their main habitat type classified as other, we used the dataset *Life-history characteristics of European birds* (Storchová and Hořák 2018) and Birds of the Western Palearctic (Cramp 1977–1994) to further subdivide this category into shrub, wetland and other.

We have also accounted for the anthropogenic transformations of the landscape which are a key factor affecting population dynamics and trends (Buchan et al. 2022), and, therefore, produced a variable representing the tolerance of a given species to human-modified habitats. This was done by first determining whether each species can be found in farmland, urban areas, plantation forests, or grazed areas during its breeding season. This data was obtained from Buchan et al. (2022) and completed for the missing species following Birds of the Western Palearctic (Cramp 1977–1994). The tolerance to human-modified habitats was then calculated as a sum of how many of these habitats the species is found in during the breeding season. This produced a category ranging between 1 and 4, where four means that the species is found in all these habitats, while one indicates that the species will be found in only one of these modified habitats in the breeding season.

To investigate the relationship between the species niche breadth/area index and their long-term population trends within our study area, we fitted a linear model with the weighted long-term slope of the population trend (from PECBMS) as the response variable and, as explanatory variables, the niche breadth/area index (natural logarithm-transformed), the level of tolerance to human-modified environments (factor 0 = low tolerance to 4 = high tolerance) and the following species traits: main diet type (factor with four levels: Invertebrate, Plant/Seed, Vert/Scav, Ominvore), migration strategy (factor with three levels: resident, partial migrant, full migrant), average species body mass (natural-log transformed) and main habitat type (factor with five levels: farmland, forest, wetland, shrub and other).

All possible subsets model selection and model averaging was then carried out using the 'dredge' function from the *MuMIn* package (Bartoń 2023). Selection was done based on model AICc and models were considered equally parsimonious when within $\Delta AICc < 2$ (Burnham and Anderson 2002). The adjusted criterion (AICc) was used due to a relatively low sample size ($N = 159$) resulting in a data to estimated model parameter ratio being $> 40$ (Burnham and Anderson 2002). Marginal means were calculated and post hoc covariate level comparisons were carried out based on the full model average and with average values of remaining covariates using the package *emmeans* (Lenth 2024). All data preparation and analyses were carried out in R v4.2.1 (R Core Team 2022).

## 3 | Results

### 3.1 | European Climatic Niche

The distribution of the 159 species included in this study was plotted in geographic space, showing that a maximum of 121 species co-occur in central Europe (Figure 1a). Within the species included in this study, 58 species had a decreasing population trend (slope $< 0.99$), populations of 68 species were stable ($0.99 \leq$ slope $\leq 1.01$) and 33 species were increasing (slope $> 1.01$). Among species with smaller distribution areas ($< 2{,}500{,}000\,km^2$), 7 species are declining, 12 are stable and 12 have increasing population trends. Out of the 31 species with medium-sized distributions ($2{,}500{,}000 \leq$ distribution area $\leq 5{,}000{,}000\,km^2$), 14 are declining, 12 are stable and only 5 are increasing. Similarly, for the 97 species with large distributions ($> 5{,}000{,}000\,km^2$), 37 species are declining, 44 have stable trends and 16 are increasing.

The realised climatic niche breath given by the first two principal components cumulatively explained 73.47% of the variance within the dataset, with the individual principal components one (PC1) and two (PC2) explaining 42.06% and 31.41% of the variance, respectively. Both temperature- and precipitation-related variables contributed to the principal components (Supporting Information). PC1 was composed of mainly precipitation variables, as well as variables relating to temperature seasonality, while PC2 included temperature averages, extremes and temperature variability (Supporting Information). The resulting representation of the realised climatic niches of the 159 species was nested, with a maximum niche overlap of 152 species (Figure 1b). We found a strong positive relationship between the realised climatic niche and the range size (Figure 1c); however, species with small range areas showed larger variation in climatic niche breadth than species with larger range areas.

### 3.2 | Climatic Niche Breadth and Long-Term Population Trends

The climatic niche breadth to range area index was a good predictor of bird population declines across Europe, together with



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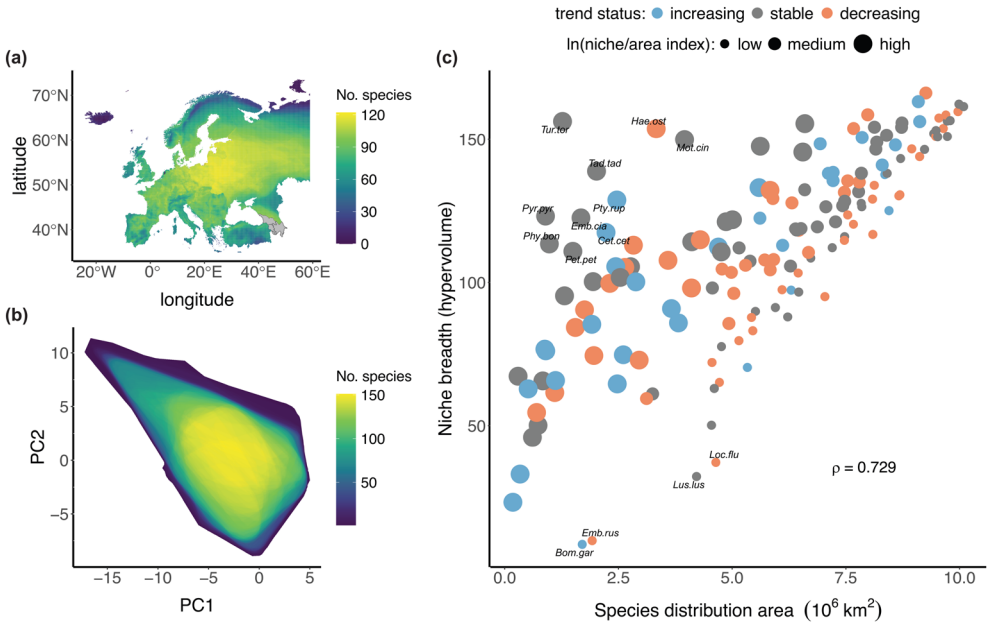


**FIGURE 1** | Distribution and overlap of species ranges within the study extent (a); the overlap of estimated hypervolumes representing the realised climatic niche of the focal species across the breeding and resident parts of their ranges within Europe (b); and the relationship between the realised climatic niche breadth (area of the hypervolume) and the range area (c), with the Spearman's correlation coefficient ($\rho$) and the colours indicating the species status according to the PECBMS long-term population trend: Increasing (blue; slope $<1.01$), stable (grey, $0.99 \leq \text{slope} \geq 1.01$) and decreasing (red, slope $<0.99$), and size showing the value of the natural logarithm of the niche to area index for each species, grouped based on quantiles, where values below −11.01 are classified as 'low' (33rd quantile), between −11.01 and −10.72 as 'medium' and above −10.72 as 'high' (67th quantile); Abbreviated species names are given for those species with a particularly broad niche for their range area (i.e. those with niche breadth of over 100 and area below $2.5 \times 10^6\,km^2$ or niche breadth over 145 and area below $5.0 \times 10^6\,km^2$) or those with a very narrow niche breadth for their range area ($1.0 \times 10^6 < \text{area} < 5.0 \times 10^6\,km^2$ and niche breadth $< 50$). Species range maps from BirdLife International (2020).

**TABLE 1** | Results of model selection for models explaining the long-term population trends. 1 = ln(index), 2 = habitat type, 3 = tolerance to human-modified environments, 4 = diet, 5 = ln(mass), 6 = migratory strategy.

| Variables | df | logLik | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|
| 1234 | 11 | 413.29 | −802.78 | 0.00 | 0.27 |
| 123 | 8 | 409.61 | −802.26 | 0.52 | 0.21 |
| 1236 | 10 | 411.46 | −801.43 | 1.35 | 0.14 |
| 12346 | 13 | 414.96 | −801.41 | 1.37 | 0.14 |
| 1235 | 9 | 410.23 | −801.26 | 1.52 | 0.13 |
| 12345 | 12 | 413.53 | −800.92 | 1.86 | 0.11 |

species traits and tolerance to human-modified environments. The model selection procedure indicated six equally parsimonious models (Table 1). The niche breadth to range area index, tolerance to human-modified environments and habitat type were included in all six top models. Diet was retained in three models, migration strategy in two and body mass in one of the six models (Table 1).

From the outcome of the full model average, species with a narrower realised climatic niche for a given area (low index values) were more likely to be declining compared to those with a relatively broader niche, which were more likely to be increasing (high index values; Table 2, Figure 2). Farmland species are experiencing greater population declines compared to species associated with other habitat types (Figure 2, Supporting Information) and species able to tolerate a greater number of human-modified environments were less likely to be declining (Table 2, Figure 2).

We found similar population trends across the five diet type groups considered here (Table 2, Figure 2, Supporting Information). Moreover, full and partial migrants, and resident species did not differ in their respective rates or directions of population change (Table 2, Figure 2, Supporting Information). Finally, populations were equally likely to decline or increase irrespective of body size (Table 2).

## 4 | Discussion

Faced with the challenges of the global biodiversity crisis and climate change, the rapid assessment of species' vulnerability to environmental change has become of paramount importance to address the challenges associated with species conservation. While previous research has focused on population trends and the size of species' ranges to prioritise conservation action (Myers et al. 2000), this study shows that variation in climatic conditions (i.e. realised niche breadth) within a species range can provide greater nuance in understanding species' resilience to factors that affect their population trends. In particular, we show that the climatic niche breadth to range area index can help predict which species may be more vulnerable to population declines. We find that for species occupying a similar area



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**TABLE 2** | Full average model parameter estimates based on six linear models identified as equally parsimonious in all possible subsets model selection procedure, explaining the variation in the species long-term population trend as a function of index of realised climatic niche breadth to range area (ln transformed), main habitat (reference = wetland), level of tolerance to human-modified environments (Tol; 0–4), diet type (reference = VertScav), body mass (ln transformed) and migration strategy (reference = resident). The adjusted $R^2$ of the global model was 0.250.

| Parameter | Estimate | SE | Adj. SE | *z*-value | *p* |
|---|---|---|---|---|---|
| **Intercept** | **1.105** | **0.031** | **0.031** | **35.945** | **<0.001** |
| **Ln(niche breadth/area)** | **0.010** | **0.003** | **0.003** | **3.744** | **<0.001** |
| **Habitat(Wetland: Farm)** | **−0.020** | **0.005** | **0.005** | **3.956** | **<0.001** |
| Habitat(Wetland: Forest) | 0.001 | 0.005 | 0.005 | 0.137 | 0.891 |
| Habitat(Wetland: Other) | 0.000 | 0.005 | 0.005 | 0.062 | 0.950 |
| Habitat(Wetland: Shrub) | −0.004 | 0.006 | 0.006 | 0.549 | 0.583 |
| **Tol. to human env.** | **0.004** | **0.002** | **0.002** | **2.704** | **0.007** |
| Diet(VertScav:Invert) | −0.005 | 0.007 | 0.007 | 0.749 | 0.454 |
| Diet(VertScav:Omniv) | −0.003 | 0.006 | 0.006 | 0.556 | 0.578 |
| Diet(VertScav:Plant) | −0.008 | 0.009 | 0.009 | 0.875 | 0.381 |
| Ln(body mass) | 0.000 | 0.001 | 0.001 | 0.336 | 0.737 |
| Mig(Resident: Long) | 0.000 | 0.003 | 0.003 | 0.121 | 0.904 |
| Mig(Resident: Partial) | 0.002 | 0.004 | 0.004 | 0.485 | 0.628 |

*Note:* Lines in bold indicate statistically significant effects at alpha level 0.05.

of geographic space, those with broader climatic niches, and, therefore possibly higher climatic tolerances, are more likely to be increasing compared to species with relatively narrower climatic niches.

Our study highlights the considerable variability across species in the relationship between niche breadth and range area. This is particularly true for species with relatively small and medium-range areas, as these species in our study had both very narrow and very broad climatic niches. A similar relationship has been found in a multi-taxa study carried out across North and South America, showing both a clear general trend while also highlighting idiosyncratic results between species (Dallas and Kramer 2022) and providing further evidence that climatic niche breadth should not be treated as synonymous with distributional size. Moreover, while rare species are frequently thought to be the most prone to population declines (Vincent et al. 2020), rarity has previously been found not to be an important variable explaining species population trends (Daskalova et al. 2020). A possible reason for this could be that small-ranged species are commonly focal species for conservation actions, and therefore, targeted management may potentially buffer or delay the negative effects of environmental change (Gaget et al. 2024). This, combined with our results, highlights that using range size alone may oversimplify our understanding of species environmental tolerance, and the climatic niche to range area index is likely a useful tool in anticipating the effects of climate change.

The drivers behind species with broader niches being more likely to have increasing population trends are likely multifaceted and complex. Species with broader climatic niches, that is, those experiencing a wider range of climatic conditions, are likely to have broader physiological limits, enabling them to adapt and persist in areas with greater climatic variability (e.g. Jiguet et al. 2006). This in turn could mean that changes in climatic conditions may be less likely to extend past their physiological thresholds, making the species with a broader climatic niche more resilient, and therefore, less likely to experience population declines (Carrera et al. 2022). Furthermore, the effects of climate change are likely to vary spatially (e.g. Antão et al. 2022); hence, species with broader climatic niches may also be better able to sustain populations across their current range, while species with narrow climatic niches may be more vulnerable to local extinctions and disappear from parts of their range, therefore, experiencing greater population declines (Grinder and Wiens 2023).

The links between climatic exposure and climate resilience have been previously investigated at local scales; for example, willow flycatcher (*Empidonax traillii*) populations in North America with relatively narrower climatic niches are declining more rapidly than populations with broader niches (Ruegg et al. 2021). Similarly, the level of vulnerability to climate change has also been shown to vary depending on the extent to which species or populations have encountered climatic changes, regardless of whether the species possessed characteristics classified as particularly under threat (Bailey et al. 2022). Moreover, populations exposed to higher levels of climatic variability may be better able to respond to environmental extremes, as shown in damselflies (*Ischnura elegans*), where individuals from populations experiencing greater climatic variability were faster at recovering from exposure to extreme cold compared to populations inhabiting less climatically heterogeneous areas (Lancaster et al. 2015). Finally, climatic niches, and particularly a relatively narrow range of temperature tolerances, have been associated with the occurrence of northward distributional shifts during



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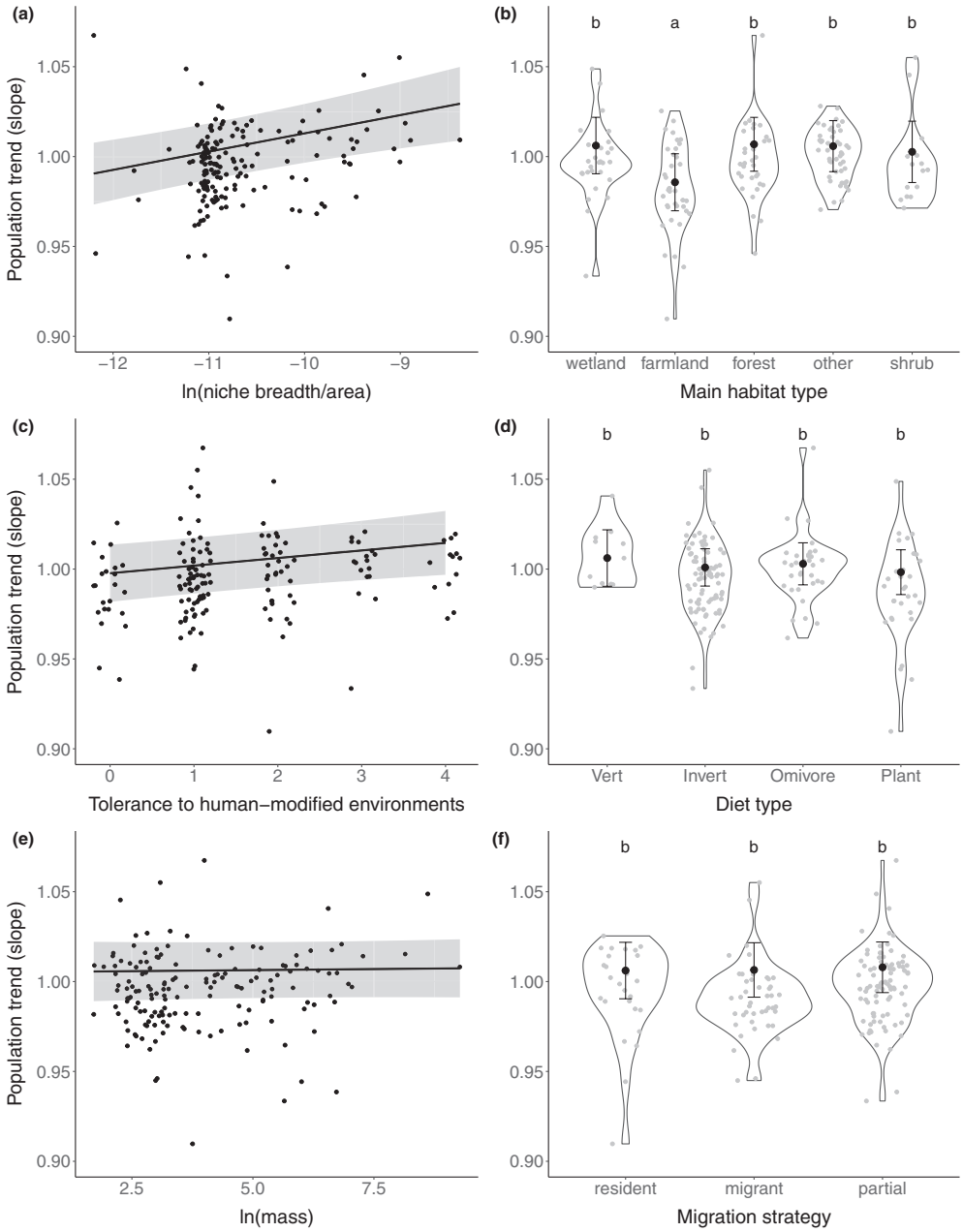


**FIGURE 2** | Full average model predictions from linear model of the long-term population trends across species (from PECBMS) in relation to index of niche breadth to range size (area; a), main habitat type used by species (farmland, forest, other, shrub and wetland; b), level of tolerance to human-modified environments (0 = no tolerance, 4 = able to tolerate all human-modified environments; c), diet type (invertebrate, omnivore, plant/seed, vertebrate/fish/scavenging; d), natural logarithm-transformed body mass (non-significant effect, Table 2; e) and migration strategy (migrant, partial, resident; f). Predictions for each variable were calculated using average values of the remaining continuous predictors, for tolerance to human-modified environments a value of 2 and for the following levels of categorical variables: Migration status = resident, diet = VertScav, habitat = wetland. Shaded area and error bars show 95% confidence intervals. Black (in a, c, e) and grey points show the raw data distribution.

the last 20 years across over 80 bird species in Finland (Hällfors et al. 2024). Our findings complement these studies with larger-scale evidence across a wider species pool, further emphasising the importance of climatic niches for understanding population trends.

As expected, species that occur in human-modified habitats were less likely to be declining. Species associated with more natural habitats, by contrast, are more vulnerable to habitat disturbance, fragmentation and loss (Matuoka et al. 2020; Storch et al. 2023), the effects of which may be amplified by climate change (Khelifa et al. 2022). There are trade-offs to using human-disturbed sites, as proximity to humans might reduce predation intensity or increase food availability but induce high levels of disturbance within such habitats and have a detrimental effect on individual performance (Reynolds et al. 2019). Hence, with increasing urbanisation and heightened levels of anthropogenic disturbances to natural environments over the last several decades, it is unsurprising that species able to utilise human-modified habitats are showing growing population trends.



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While the population trends were relatively similar across species associated with most habitat types, farmland species were more likely to be declining, which has also been described by recent research (Lees et al. 2022; Storch et al. 2023). This negative trend has been attributed to particularly high levels of disturbance due to the increasing intensity of agricultural activities (Donald et al. 2001; Rigal et al. 2023). Furthermore, the highly detrimental impact of land use change on bird species may be intensified by climate change (Srinivasan and Wilcove 2021), highlighting the complexity of the impacts of global environmental change on species population trends.

We found no overall effect of diet type on long-term population trends. All diet groups were expected to have similar trend slopes. Previous studies looking at population trends within Europe found a negative population trend in species feeding on seeds as well as on invertebrates (Bowler et al. 2019). Similarly, within the island bird species in Panama, insectivorous species were shown to be most prone to extinction (Curtis et al. 2021). The lack of any significant difference observed in our study might be due to diet and habitat being linked and, therefore, the effect of diet may have been diluted by the presence of habitat type within the model (Bowler et al. 2019). Indeed, the extent of declines in insectivorous species varied across different farmland habitat types and has been linked to increased levels of disturbance and agricultural activity (Reif and Hanzelka 2020).

Population trends were similar across the three migratory strategies: resident, partial and full migrants. This result differed from previous studies that highlighted considerable declines in migratory species populations, for example (Gilroy et al. 2016; Howard et al. 2020; Vickery et al. 2023). The discrepancy between the findings of these studies and our results may stem from these studies focusing exclusively on migratory species (Howard et al. 2020; Vickery et al. 2023) or considering a different and greater number of species (Gilroy et al. 2016). Furthermore, the factors driving population changes of migratory species have been shown to differ between breeding and wintering parts of their range (Howard et al. 2020) and trends varied even within the migratory species group depending on the location of wintering grounds (Vickery et al. 2023). Coupled with our relatively broad classification of migratory strategy, this variability may explain why the differences in population trends between full and partial migrants and resident species have not been captured here.

We did not find any difference in population trend in relation to species body size. This was unexpected, as generation turnover is generally faster in smaller-bodied species, and, therefore, changes may be more noticeable in those populations. Furthermore, the effects of climate change have been frequently shown to differ depending on either lifespan or body size e.g. (Mason et al. 2019; Storch et al. 2023; Gregory et al. 2023). This is true not only when considering the overall population trend but, e.g. in breeding and nesting success, where as temperatures increase, offspring production in species with relatively larger body sizes was expected to decrease. In contrast, the opposite was predicted to be true for smaller species (Halupka et al. 2023).

This study treated bird species ranges in Europe as static distributions and there was a temporal mismatch between the climate and species distribution data used here. The historical annual average climate data used in this study covered the years 1970–2000, while the species distribution data was collated from 1980 to the year 2020. We adopted this simplified approach because this temporal mismatch is unlikely to affect the results at the spatial scale this study was conducted, and due to the speed at which bird species respond to climate change (Pearce-Higgins and Green 2014). The events potentially impacting population trends, such as climate change or disturbances, tend to occur or progress rapidly, while species responses may not always be instantaneous (Menéndez et al. 2006). Furthermore, species respond to extremes rather than to changes in mean climate, but the effect of extremes is better captured by long-term population trends and changes in distribution.

Our definition of the realised climatic niche and the inferences that can be made need to be approached with caution. The metric obtained provides the range of conditions a species experiences, that is, it exists within such combinations of climatic conditions and can maintain viable populations. However, the spatial locations where a species is found are determined by a variety of interacting variables, including biotic and abiotic interactions, and thus the fundamental niche may be broader than the realised niche (Hutchinson 1953). If these biotic interactions change, which could occur due to the speed at which different species respond to climate changes (Parmesan and Yohe 2003), the realised climatic niche breadth may also change; hence the hypervolume that characterises the species climatic niche may be different in the presence of new species interactions.

## 5 | Conclusion

This study highlights the importance of understanding the level of exposure to climatic variability when assessing vulnerability to population declines. We show that for a given distribution area, species with a broader climatic niche are less likely to be declining than species within narrower climatic conditions. In agreement with previous studies, we found that species associated with farmland habitats were more likely to be declining, while those able to tolerate human-modified environments were expected to have an increasing population trend.

However, changes in climatic conditions within the extent of this study, as well as shifts in species distributions across the temporal scale considered here, were not included in the models, presenting a static view of the exposure to climatic variability based on average variable values. This approach is largely useful for multi-species large-scale overviews such as this study; however, caution should be taken if our results were to be used for planning specific conservation action, as in that case, a more dynamic approach to modelling species niches may be more appropriate.

### Author Contributions

K.Z.: conceptualization, methodology, data curation, formal analysis, visualization, writing – original draft, review and editing; J.J.G.: funding acquisition, methodology, supervision, writing – review and editing; I.C.: funding acquisition, methodology, supervision, writing – review and editing; P.W.A.: funding acquisition, methodology, supervision; A.K.: data provision, writing – review and editing; A.M.A.F.: conceptualization, funding acquisition, methodology, supervision, writing – review and editing.



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## Ethics Statement

The authors have nothing to report.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data used for the analysis presented in this manuscript relies on previously published datasets, a list of which is available in the Supporting Information (Table S1), and are freely available either upon request to data owners or from a repository. We provide the full dataset used in the analysis in the Supporting Information (Table S4).

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.



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