

# ECOGRAPHY

## Research article

### Changes in abundance and distribution of European forest bird populations depend on biome, ecological specialisation and traits

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Forest bird abundance in Europe has remained stable overall, unlike farmland species which have declined dramatically in recent decades. However, this apparent stability may hide large variations among species and geographical regions. We aimed to determine if forest bird species with varying life histories and biome distributions show different population trends. We used functional traits and specialisation indices to study changes in abundance and distribution of European forest bird populations. For each species, we used European-level estimates of total abundance change over the last 40 years and changes in two components of spatial distribution: range change (i.e. area shrinkage or expansion) and distribution shift (i.e. latitudinal adjustments), both over the last 30 years. We also considered specialist groups of different biomes (i.e. boreal, temperate, Mediterranean and biome generalists) separately. We showed that boreal forest species have declined in abundance and range area, while Mediterranean and temperate species have increased in abundance and range, possibly as the result of warmer temperatures and forest expansion in these regions. The decline of boreal forest species may result from changes in forest structure and composition due to forestry practices, increasing temperatures and colonisation by warm-dwelling species. Among boreal species, mixed forest specialists (i.e. those preferring a mix of broadleaf and coniferous trees) declined the most in abundance and range and shifted northwards. In contrast, for vertebrate carnivores (i.e. birds of prey), we observed an increase in abundance among Mediterranean species and a southward expansion among all species. Our findings suggest that forest bird species in Europe may be influenced by the combined effects of land use and climate change, with these impacts varying across biomes. Our results highlight the need for maintaining and restoring key forest



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habitats (e.g. through increased protected areas and extensive management) and halting or limiting climate change, especially for boreal species.

Keywords: avian population, biodiversity, climate change, global change, habitat degradation, trait syndrome

## Introduction

Bird species are excellent indicators for assessing long-term biodiversity changes (Rigal et al. 2023), due to the availability of long-term monitoring in some regions (e.g. Europe, North America and Australia), their well-known biology and ecology, and their responsiveness to environmental changes (Stephens et al. 2016, Fraixedas et al. 2020, Verdon et al. 2024). In Europe and North America, overall bird abundance has declined over the last four decades, mainly due to land-use intensification in farmlands (IPBES 2019, Rosenberg et al. 2019, Burns et al. 2021, Rigal et al. 2023). In contrast, the abundance of forest and woodland birds has remained stable (Gregory et al. 2007, 2019, 2023; for updated information, see <https://pecbms.info>), although they may have declined before monitoring programs began (Rigal and Knape 2024). Consequently, discussions on bird decline have often focused on open-habitat species (Gregory et al. 2007, 2019).

The apparent stability in forest bird abundance (i.e. species occurring in wooded environments, including forest and woodland areas) conceals large differences among species (Lehikoinen and Virkkala 2018, Gregory et al. 2023).

For instance, generalist species seem to be doing well (Reif et al. 2022), while specialists have been declining in abundance (Helle and Järvinen 1986, Gregory et al. 2007, 2019). Likewise, stability in abundance may also hide major range changes (i.e. area shrinkage or expansion) and distribution shifts (i.e. latitudinal adjustment; see Fig. 1; Gil-Tena et al. 2010, Chen et al. 2011, Howard et al. 2023). The role of functional traits in these changes has yet to be fully explored for forest birds (see Gregory et al. (2007) for abundance changes) despite their potential explanatory power (Howard et al. 2023, Rigal and Knape 2024).

Temperature niche is a good predictor of temporal changes in bird communities (Devictor et al. 2012). Cold-dwellers (i.e. species related to relatively colder temperature during breeding season among European species) have declined in abundance and retreated northwards (Virkkala et al. 2008), while warm-dwellers have remained stable (Reif 2013, Rigal et al. 2023, Storch et al. 2023). Other traits like migration strategy, diet, nesting site and body mass have also influenced changes in bird abundance and distribution in Europe (Rigal et al. 2023, Santini et al. 2023). For example, Gregory et al. (2007) showed that both long-distance migrants and resident species

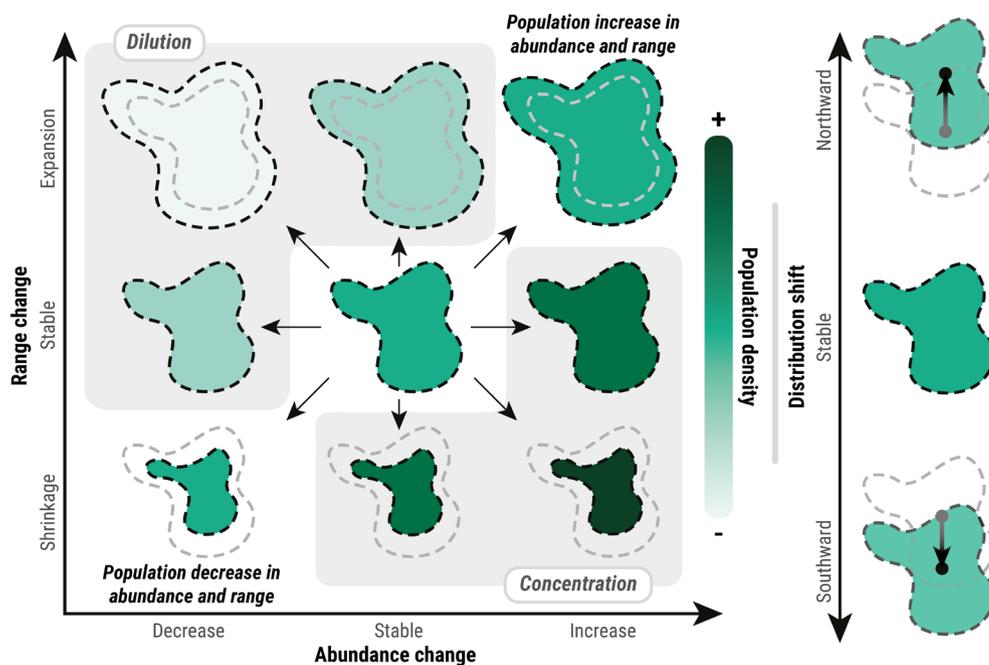


Figure 1. Schematic representation of the potential different processes behind changes in abundance and range area (left) and the potential direction of distribution shifts along the south–north gradient (right). The green gradient reflects population density levels. The *concentration* process refers to an increase in population density, while the *dilution* process refers to a decrease in density. The grey dashed line reflects previous range area. For each case of change in abundance and range (including a stable population in both dimensions), a distribution shift can occur along the latitudinal gradient.

declined in abundance, along with low-vegetation nesters and invertebrate carnivores. In a review, Reif (2013) found that over the last 40 years, large-sized bird species declined less than small-sized ones. This may be due to various reasons. For instance, in Sweden, the abundance of birds of prey (which are often the largest birds) has increased after massive declines prior to the 1970s, due to laws prohibiting hunting, trapping and poisoning of raptors (Saurola 1985), and the ban on use of the insecticide DDT (Ottvall et al. 2009).

European forests have experienced a long history of management and harvesting with major historic differences across regions (i.e. a longer history in the southern than in the northern regions). Intensive management has simplified forest structure and composition, reducing old-growth forests to only 2–3% of the total European forest area (Barredo et al. 2021). Mönkkönen and Welsh (1994) suggested that most recent changes in European forest bird populations, in terms of abundance and range, should have occurred in the boreal region due to a more recent history of human disturbance. For instance, in Finland, the loss of old-growth forests is still ongoing and seems to have contributed to the significant decline of many forest bird species (Schmiegelow and Mönkkönen 2002, Fraixedas et al. 2015, Virkkala 2016). In contrast, the deadwood volume and broadleaved trees have increased in Sweden over the last 20 years, as a direct result of legislation and certification schemes, which may have benefited forest bird abundance (Ram et al. 2017).

In Mediterranean and temperate Europe, land abandonment has increased forest extent (Kuemmerle et al. 2016), creating new colonisation opportunities for forest birds (Preiss et al. 1997, Sirami et al. 2007), but also increasing fire risk (Gil-Tena et al. 2009, 2010). A changing fire regime threatens old-growth forests in Mediterranean regions (Gil-Tena et al. 2019). Moreover, global warming has intensified the frequency, extent and severity of natural disturbances, affecting forest structure and composition (Johnstone et al. 2016, Seidl et al. 2017, Senf et al. 2018, Bouget et al. 2024). Mediterranean and temperate forest bird species have experienced a multi-millennia history of human disturbance adaptation, and therefore are more suited to habitat fragmentation than boreal species (Mönkkönen and Welsh 1994) and are more ubiquitous, also using open areas (Suárez-Seoane et al. 2002). Therefore, they may be less sensitive to recent habitat changes (Matuoka et al. 2020, but see Preiss et al. 1997, Sirami et al. 2007). Consequently, given the diverse processes and the species-specific requirements across regions, biome specialisation should be considered when studying bird responses to global changes (Mönkkönen and Welsh 1994, Suárez-Seoane et al. 2002, Matuoka et al. 2020).

Most European bird studies have overlooked trait variations within ecological groups, e.g. comparing forest and farmland communities as two large, uniform groups. As an exception, Gregory et al. (2007) studied the effects of several traits on species population trends within forest bird communities. Here, we have updated and expanded the studied traits by including additional traits and calculating new habitat

specialisation indices. In addition, it is crucial to study how traits affect both abundance and distribution changes (i.e. through range area changes and distribution shifts; Fig. 1), to highlight particular demographic processes like dilution and concentration effects (Fig. 1; Tschardt et al. 2012). These insights will enhance our understanding of forest bird population dynamics, aiding conservation efforts.

In this study, we assessed changes in both abundance and spatial distribution (range area and distribution shift) of European forest bird species. Specifically, we investigated 1) whether changes in abundance are associated with range changes and distribution shifts (Fig. 1); 2) how these changes differ among species associated with the main European biomes (i.e. boreal, temperate, Mediterranean and biome generalists); and 3) how species' functional traits and specialisation indices are related to these changes. We expected a decrease in boreal bird abundance and range area, related to a decrease in cold-dweller species and, in parallel, an increase in warm-dwellers/Mediterranean species. In addition, we expected an increase for vertebrate carnivores resulting from conservation measures. We also expected a decrease in abundance and distribution for old-growth forest species, especially among the boreal species. We further expected a decrease in migrant species as they are more likely to experience threats over multiple biomes. Finally, we expected an overall decrease in specialised species (for additional information, refer to Table 1).

## Material and methods

### Selection of European forest bird species and classification of their biome preferences

We selected all species that are related to forests and woodlands based on two data sources: Storchová and Hořák (2018) and Tobias et al. (2022), resulting in 107 bird species studied (Supporting information). We defined forest bird species as those using environments ranging from closed-canopy forests to more open-canopy woodlands (Lehikoinen and Virkkala 2018, Storchová and Hořák 2018, Tobias et al. 2022). We determined their biome specialisation using breeding distribution centroids and the overall breeding distribution of each of the species, using the global map of terrestrial ecoregions from Olson et al. (2001) and range data from the European Breeding Bird Atlas 1 and 2 (Hagemeijer and Blair 1997, Keller et al. 2020). We categorised species as Mediterranean, temperate or boreal based on their predominant biogeographic region. We considered species commonly occurring over several biomes as 'generalists'. For instance, we reclassified the two typically boreal species, *Glaucidium passerinum* and *Strix uralensis*, as 'generalists' due to significant range expansions into central and southern Europe in recent decades, therefore no longer restricted to the boreal region. For the complete list of species, biome specialisation, traits and specialisation indices, refer to the Supporting information.

Table 1. List of functional traits and specialisation indices of the 107 selected forest bird species used in our study, along with data source references and the related hypotheses. 'bin.' = 'binary'.

Trait or index	Data source	Related hypothesis	Mean (min–max)
Species temperature index (STI)	<a href="#">Lehikoinen, A. et al. 2021</a>	Warm-dwelling species have tracked climate changes and moved northwards (increasing in abundance and range), while cold-dwellers have declined and shrunk northwards due to lack of colonisation opportunities	11.6 (–2.8–25) °C
Diet			
Herbivores in breeding season	<a href="#">Storchová and Hořák 2018</a>	In contrast to herbivorous species in farmland, we do not expect any significant decline in forest birds, as we do not expect overall changes in production of forest plant fruits and seeds during the last 30–40 years	bin. (0–1) 1 = 31
Invertebrate carnivores in breeding season	<a href="#">Storchová and Hořák 2018</a>	Similarly to farmland species, forest invertebrate carnivore species have experienced declines because of a general decrease of insects in Europe	bin. (0–1) 1 = 73
Vertebrate carnivores in breeding season	<a href="#">Storchová and Hořák 2018</a>	Conservation efforts (e.g. reintroductions, nesting site protection) over the last decades for birds of prey have had positive effects on population abundance and range	bin. (0–1) 1 = 20
Nesting site			
Ground nesters	<a href="#">Storchová and Hořák 2018</a>	Populations have experienced pervasive effects from forestry activities due to forest ground disturbance and global changes, mostly caused by wildfires in Mediterranean regions, and have experienced a decrease in both abundance and range	bin. (0–1) 1 = 19
Tree hole nesters	<a href="#">Pearman et al. 2014</a>	Population declined due to the scarcity of old-growth forests in European landscapes	bin. (0–1) 1 = 38
Canopy nesters	<a href="#">Pearman et al. 2014</a>	Population declined due to the development of forest diebacks	bin. (0–1) 1 = 51
Other traits			
Old-growth forest preference	Adapted from <a href="#">Mönkkönen et al. 2014</a> , <a href="#">Fraixedas et al. 2015</a>	Global forestry activities and scarcity of old-growth attributes have led to or maintained low populations and shrunk range areas	0.34 (0–1)
Migration distance	<a href="#">Howard et al. 2023</a>	Species migrating the farthest have globally experienced a stronger decline than resident species, as they have experienced changes in multiple biomes	1374 (0–5717) m(log transform)
Body mass	<a href="#">Tobias et al. 2022</a>	Threatened bird species have been shown to be larger than non-threatened species. Also, larger species might have benefited from conservation programs (e.g. birds of prey)	351 (5–9320) g (log transform)
Specialisation indices			
Climatic niche breadth	<a href="#">Reif et al. 2016</a>	Bird species with smaller climatic niche breadth have declined due to their specialisation to a specific climate	7.59 (0.28–12.96)
Diet specialisation	<a href="#">Reif et al. 2016</a>	Specialised species have declined, at least in abundance	2.2 (0.53–3.16)
Nesting specialisation	<a href="#">Morelli et al. 2019</a>	Specialised species have declined, at least in abundance	0.257 (0.09–1)
Overall specialisation	<a href="#">Morelli et al. 2019</a>	Species accumulating several aspects of specialisation have declined in abundance due to global changes (i.e. biotic homogenization)	0.321 (0–1)
Forest specialisation	Adapted from <a href="#">Storchová and Hořák 2018</a>	Specialised species have declined, at least in abundance	2.9 (1.5–4)
Broadleaf forest specialisation	Adapted from <a href="#">Storchová and Hořák 2018</a>	Replacement of broadleaf forests by high-productivity coniferous plantation in recent decades has had a negative impact on bird species associated with this habitat	0.459 (0–1)
Breeding range area	<a href="#">Reif et al. 2016</a>	Bird species occurring in larger areas have had greater distribution changes than species occupying small areas	1289 (10–2726) km <sup>2</sup> (log transform)

## Changes in abundance and distribution of European forest bird species

We assessed long-term changes in European forest bird populations through two approaches: 1) changes in estimated total

European-level species abundance over a 40-year timeframe; and 2) changes in species' spatial distribution over a 30-year timeframe ([Fig. 1](#)).

We utilized the estimated trends in European-level population size (i.e. the total number of individuals) for each

common native European bird species from 1980 to 2017, as reported by Burns et al. (2021). Three species out of the 107 studied forest species were missing in the original manuscript, so we used data generated with the same method from 1980 to 2018 from the European assessment, Article 12 (<https://nature-art12.eionet.europa.eu/article12>). These abundance trends were calculated by Burns et al. (2021) using multi-sourced annual time series. For each species, they gathered population estimates and trends from each European country as well as from European Union (EU)-level population trends. They analysed these data with a Bayesian hierarchical model to reconstruct EU-level smoothed species population time series. The model outputs include an average annual rate of abundance change and an associated 95% credible interval (Burns et al. 2021). Therefore, we did not directly use the average annual rate of abundance change, as this would have led us to consider species with low uncertainty as similar to those with high uncertainty. To account for the uncertainty, we categorised species as 1) declining, i.e. annual rates below one; 2) increasing, i.e. annual rates above one; and 3) stable, i.e. annual rate whose 95% CI overlap one, i.e. no significant change. To better acknowledge the magnitude of the abundance change, significant changes with rates below 0.98 were labelled as ‘strongly declining’ (i.e. 6.5% of the 107 species), while those above 1.02 were labelled as ‘strongly increasing’ (i.e. 11% of the 107 species). To evaluate the sensitivity of the decision to categorised abundance change data, we also analysed abundance trend as a continuous variable (Supporting information).

To determine changes in species distributions, we used a comparison of species distributions between two periods (i.e. 1985–1988 and 2013–2017) using the European Breeding Bird Atlas 1 and 2 (EBBA 1 and 2; Hagemeyer and Blair 1997, Keller et al. 2020, Howard et al. 2023). Howard et al. (2023) provided calculations of observed colonisation and extinction areas at a 50 × 50 km resolution across Europe. We measured changes in range as the difference between colonisations and extinctions of each species, with negative values indicating contracting ranges and positive values indicating expanding ranges. Additionally, we calculated the shift in the centre of gravity of the distribution range between the two periods as a distance (km) along the south–north gradient for each species (Howard et al. 2023).

### Trait and specialisation data for European forest bird species

We extracted data for six functional traits from several sources (Table 1): 1) the species temperature index (STI) represents the long-term average temperature within the species’ breeding range (Lehikoinen, A. et al. 2021); and 2) diet data during the breeding season were obtained from Storchová and Hořák (2018), classifying species into binary variables as vertebrate carnivorous, invertebrate carnivorous and herbivores (combining the leaf and seed eaters). Storchová and Hořák (2018) classified species into a diet category when the

corresponding food resource represented at least 10% of the species diet throughout the breeding season. Therefore, one species can be in several categories (i.e. omnivores). 3) We obtained nesting site data from Pearman et al. (2014), classifying species into binary variables as ground nesters, tree hole nesters or elevated nesters (> 1 m in a tree or shrub). We also included data on 4) species dependence on old-growth forests (Supporting information; mostly from Mönkkönen et al. (2014) and Fraixedas et al. (2015); if present in both references, we classified them as ‘1’ and if only in one reference as ‘0.5’); 5) migration distance (Howard et al. 2023); and 6) body mass (Tobias et al. 2022).

Finally, we extracted and developed seven species specialisation indices. 1) We used an overall specialisation index based on multiple traits (i.e. temperature, diet, foraging behaviour and substrate, habitat and nesting site); and 2) a nesting specialisation index, both obtained from Morelli et al. (2019). Both indices represent species specialisation based on the dispersion of trait preferences for each species, e.g. nesting specialism equals 0 for species that nest in all habitat types and equals 1 for species that nest in only one habitat type. They are both calculated using the Gini index of inequality, which measures overall dispersion across, for example, all traits for the overall specialisation, based on data from Pearman et al. (2014) and Storchová and Hořák (2018). For additional information, see Morelli et al. (2019). We also used 3) the diet specialisation index; (4) the species distribution range during the breeding season (hereafter ‘breeding range area’); and 5) the climatic niche breadth from Reif et al. (2016). The diet specialisation index was calculated as the coefficient of variation for diet preferences for each species, where high values denote specialised species (Reif et al. 2016). The breeding range area was evaluated as the number of 50-km squares in the distribution maps in Europe occupied by each species during the reproduction period, and is based on EBBA 1 (Hagemeyer and Blair 1997). The climatic niche breadth was calculated as the difference between the 5% hottest and the 5% coldest mean temperatures between April and June in which each species occurs, using EBBA 1 (Hagemeyer and Blair 1997, Reif et al. 2016).

Additionally, 6) we calculated a broadleaf forest specialisation index based on binary forest habitat preferences (Storchová and Hořák 2018), assigning values of one for species found only in broadleaf forests, zero for those in coniferous forests and 0.5 for those found in both. Lastly, 7) we created a forest specialisation index based on the species habitat preferences (Storchová and Hořák 2018). The forest specialisation index was calculated as the mean of species affinity across habitats. We used increasing habitat weights along a gradient of tree dominance: open habitats as 1, shrubland as 1.5, woodland as 2 (i.e. species associated with habitats structured by trees in lower density than in forest), forest generalist (found in both coniferous and broadleaf dense forests) as 3 and forest specialist (found only either in coniferous or broadleaf dense forests) as 4. For instance, the index value for species occurring either in shrubland, woodland or both broadleaf and coniferous forests is 2.167.

## Data analysis

Data analyses were conducted with R software ver. 4.4.1. ([www.r-project.org](http://www.r-project.org)). Given the non-independence of species due to their genetic relatedness, we accounted for inter-specific phylogenetic distance in all models. We constructed the phylogenetic tree for the 107 European forest bird species using the 'rotl' and 'ape' R-packages (Michonneau et al. 2022, Paradis et al. 2023). We used 'rotl' as an interface with the 'Open Tree of Life', employing the *tol\_induced\_subtree* R-function to generate the phylogenetic tree and *compute.brlen* R-function to set branch lengths using Grafen's computation. We generated separate phylogenetic trees for boreal (17), temperate (15), Mediterranean (16) and 'generalist' (59) species to perform biome-specific analysis (Supporting information).

To investigate the effects of functional traits and specialisation indices on abundance, range changes and distribution shift, we used two regression methods. All methods were based on the relationships between a measure of *change* and a *functional trait* or *specialisation index*. Our sample unit is an individual forest bird species (i.e. one value for each species, either abundance or range change, or distribution shift). Abundance change was a categorical variable (i.e. strong decline – decline – stable – increase – strong increase), while range change (i.e. difference between colonisation and extinction) and distribution shift (i.e. south–north shift) were continuous variables. Therefore, to study abundance changes, we used proportional-odds linear mixed effects model using the (Phylo)*clmm* R-function from the 'ordinal' R-package (Christensen 2022). Interspecific phylogenetic relatedness was included as a random effect, reflecting the correlation between species based on phylogenetic distances (Seibold et al. 2015, Haggé et al. 2021). For distribution changes, we employed phylogenetic generalised least squares regression (PGLS) using the *gl* R-function from the 'nlme' R-package (Pinheiro et al. 2023). The phylogenetic correlation structure was integrated into PGLS using Pagel's lambda parameter ( $\lambda$ ; Pagel 1999), a widely used measure of phylogenetic signal strength (Triviño et al. 2013, Haggé et al. 2021).

Furthermore, we included latitude, a key driver of bird communities at broad scales (Luoto et al. 2007), as a fixed covariable (centroid latitude of the species' breeding distribution) in all global models (i.e. species from all biomes together), except for the STI model due to strong correlation. For biome-specific analysis, we included latitude only in boreal species models for range change and distribution shift, as it significantly improved model fit ( $\Delta\text{AIC} < -2$ ). We did not include latitude for models specific to temperate, Mediterranean and generalist species since it did not improve model fits ( $\Delta\text{AIC} > -2$ ). Additionally, we included breeding range area in range change and distribution shift models, assuming that species with larger ranges would exhibit larger shifts. We scaled predictors to a mean of 0 and a standard deviation of 1 to facilitate effect size comparisons. We adjusted p-values using the Holm method (for  $n=3$ ) to account for multiple testing of traits and specialisation indices on three response variables.

## Results

### Species changes in abundance and range, and distribution shifts

The 107 forest bird species were categorized into 17 boreal, 15 temperate, 16 Mediterranean and 59 generalist species (Fig. 2–3). There was a significant positive relationship between species abundance and range changes ( $p < 0.001$ ,  $R^2 = 12.8\%$ ; Fig. 2): species with declining abundance generally had shrinking ranges, and vice versa. Among species declining in abundance, 76% also experienced range shrinkage, predominantly boreal species (32% of all species declining in both abundance and range). Conversely, 85% of species that increased in abundance also expanded their range area (Fig. 1). However, exceptions existed, such as the redpoll *Acanthis flammea*, which strongly decreased in abundance but increased in range (Fig. 1–2).

Abundance and range changes significantly varied among biome preference groups (Fig. 3a–3b). Approximately one-third of temperate and biome generalist species, and one-half of Mediterranean species, have increased in abundance (Fig. 3a). Boreal forest species showed a higher proportion of declines (47%, 8 species) compared to temperate and Mediterranean species, with only two and zero species, respectively, declining in abundance (Fig. 3a). Boreal species also experienced more range shrinkages (i.e. negative range change, 70.5% of species) compared to other biome preferences, with a significant difference only with temperate species (Fig. 3b). Most temperate and Mediterranean species showed positive range changes (60 and 71%, respectively; Fig. 2–3b). Boreal species have mostly experienced declines in both abundance and range, while temperate species have shown opposite trends (Fig. 2). Regarding distribution shifts, there was no significant difference among biomes, but a large variability in responses was observed across all groups (Fig. 3c). Overall, more species have shifted northwards than southwards, with 62.5% of boreal and temperate species and 69.0% of the Mediterranean species shifting northwards.

### Response of species' functional traits and specialisation

Warm-dwellers tended to increase in abundance and cold-dwellers have declined (i.e. positive effect of STI; 724 200 individuals lost per year for cold-dwellers;  $p < 0.01$ ; Fig. 3a). Hereafter, for continuous traits, low (and high) values refer to the 1st (and 3rd) quartile of the trait distribution, cold-dwellers being the low values in the present example. Meanwhile, the range area of warm-dwelling boreal species shrank (189 500 km<sup>2</sup> lost on average for boreal warm-dwellers,  $p < 0.001$ ; Fig. 4a, Supporting information). In terms of diet, herbivores and invertebrate carnivores showed no significant changes in abundance or range. However, Mediterranean vertebrate carnivores, such as the short-toed eagle *Circus gallicus*, have increased in abundance (429 new individuals per year on average,  $p < 0.05$ ; Fig. 4a–5c). In addition, all vertebrate carnivores expanded their ranges (186 500 km<sup>2</sup> on

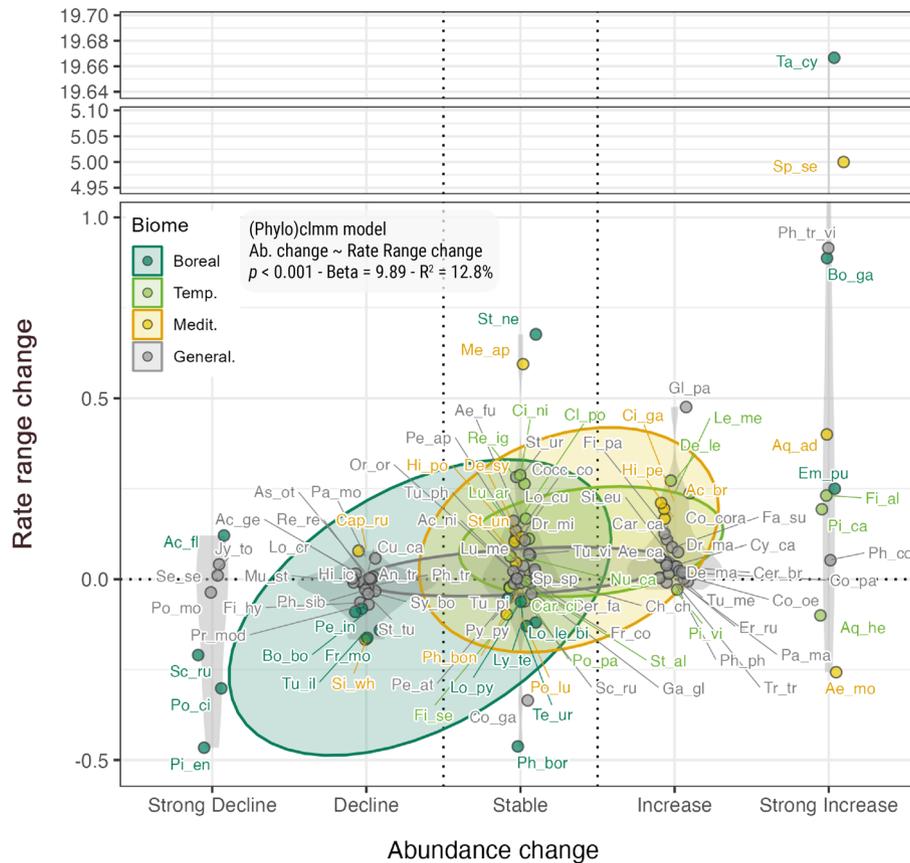


Figure 2. Species range change as a function of an ordinal gradient of abundance change. Negative values for range change rate denote shrinkage and positive values expansion. Rate is calculated as range change divided by breeding range area in the 1980s. In subsequent models, we directly used values of range change as response variables and added breeding range area in the 1980s as a covariable. Each point represents a species (jitter effect added to points for clarity). Ellipses contain 50% of points for each biome, and are drawn to illustrate point density for each biome specialisation. Point labels refer to species name initials (Supporting information). Dotted lines are used to separate no changes (stable), positive and negative changes in range area and abundance. ‘Beta’ = ‘Beta-coefficient from the (Phylo)cmm model’. A similar illustration of the relationship conducted with abundance change as a continuous variable is available in the Supporting information.

average,  $p < 0.05$ ), particularly biome generalists (279 175 km<sup>2</sup> on average,  $p < 0.01$ ; Fig. 4a), while they all shifted southwards (42 km on average,  $p < 0.01$ ; Fig. 4a). Nesting preferences, affinity for old-growth forests, migration distance and body size did not influence changes in abundance, range or distribution (Fig. 4a).

Regarding specialisation indices, climatic niche breadth did not relate to any indicators of change (Fig. 4b). Among Mediterranean species, nest specialists have expanded their ranges (337 500 km<sup>2</sup> on average,  $p < 0.05$ ; Fig. 4b). Among all species, diet generalists showed shifts northwards, while nest specialists showed shifts southwards (28 km on average,  $p < 0.05$ , and 7 km on average,  $p < 0.05$ , respectively; Fig. 4b). For nest specialists, boreal species and, to a lesser extent, biome generalists drove the observed southward distribution shift (73 km on average,  $p < 0.001$ , and 33 km on average,  $p < 0.05$ , respectively; Fig. 4b). Overall, specialised species have shifted southwards (30 km on average,  $p < 0.05$ ), driven mainly by boreal species (82 km on

average,  $p < 0.01$ ; Fig. 4b). Forest specialists among biome generalists have expanded in range area (151 120 km<sup>2</sup> on average,  $p < 0.01$ ; Fig. 4b), and Mediterranean forest generalists have shifted northwards (68 km on average,  $p < 0.05$ ; Fig. 4b). Boreal species associated with mixed forests (i.e. a mix of broadleaf and coniferous trees, since all boreal species are also associated with coniferous forests) have declined in abundance (509 000 individuals lost per year,  $p < 0.05$ ) and range (−103 750 km<sup>2</sup> on average,  $p < 0.05$ ), and shifted northwards (65 km on average,  $p < 0.05$ ; Fig. 4b). Examples include the pine grosbeak *Pinicola enucleator* and Siberian tit *Poecile cinctus* (Fig. 5a–b). The same pattern was also observed for breeding range area (abundance: 289 900 individuals lost per year,  $p < 0.05$ ; range: 114 375 km<sup>2</sup> lost on average,  $p < 0.05$ ; and distribution shifts: 69 km on average,  $p < 0.05$ ; Fig. 4b). Lastly, biome generalists with the smallest breeding range area have shifted southwards (i.e. a positive effect of breeding range area on distribution shift, 47 km southwards on average,  $p < 0.01$ ; Fig. 4b, Supporting information).

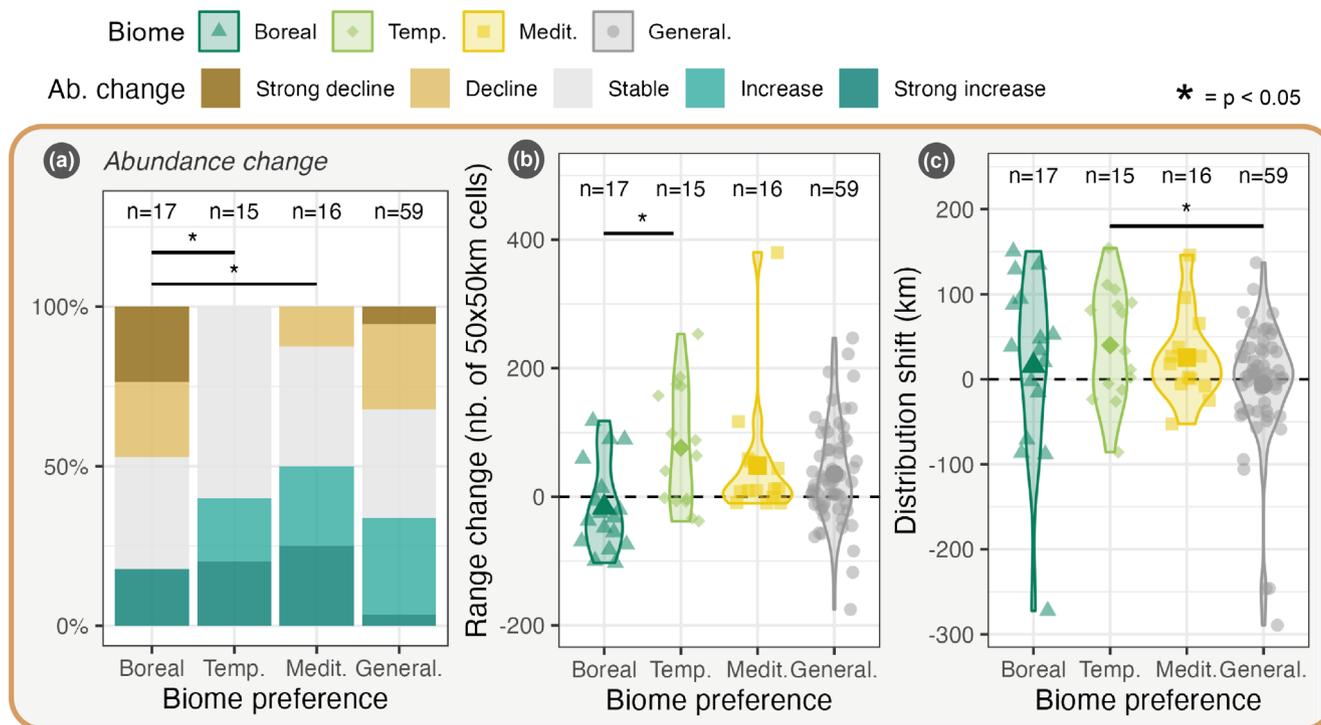


Figure 3. (a) Abundance change, (b) range change and (c) distribution shift according to species biome specialisation. 'General' relates to the biome generalist species with wide European distribution. 'n' = number of species included in each biome specialisation group. Values above 0 indicate range extension (b) and a northward shift (c). P-values from pairwise comparisons were adjusted using the Tukey method, based on *clmm* and *gls* regressions.

## Discussion

In this study, we examined how functional traits and specialisation have influenced changes in both abundance and distribution among European forest birds across different biomes. Despite the overall apparent stability of forest birds, our study found significant changes at the species level, highlighting species decreasing both in abundance and range (and vice versa) and shifting their distribution in Europe. Our findings reveal that changes in bird populations are significantly biome-dependent, with a general decline of boreal species. We observed diverse responses in species across all biomes, influenced significantly by both functional traits and specialisation indices. Specialisation indices emerged as stronger explanatory factors compared to functional traits in understanding these population dynamics. Therefore, species' distribution across biomes and their level of specialisation on key resources appear particularly important to understand the population changes of European forest bird species in the last four decades.

### Matching changes in bird species abundance and range

We found a significant correlation between changes in abundance and range area among bird species: increases in abundance were typically associated with range expansion, and vice versa (Fig. 1). For instance, both pine grosbeak and Siberian

tit populations showed marked declines in abundance while shrinking in range area (Fig. 2, 5). The decline in abundance and range shrinkage were most pronounced for boreal forest species, probably resulting from the combined effects of intensive forest management, and rapid climate change at high latitudes (Mönkkönen and Welsh 1994, Loarie et al. 2009, Mönkkönen et al. 2022). Nonetheless, changing habitat conditions and climate change can also act independently. For example, the creation of protected areas and species reintroduction can improve both abundance and distribution (e.g. with the Spanish imperial eagle *Aquila adalberti*; Burfield 2008, BirdLife International 2021), and climate change can make new areas available for colonisation where climate was the only former limiting condition (e.g. with the European bee-eater *Merops apiaster*; Stiels et al. 2021).

We also observed discrepancies between changes in abundance and range area. Several species have declined or remained stable in abundance, while maintaining the same geographic range or even expanding it (e.g. redpoll), suggesting a dilution process with decreasing individual densities (Fig. 1). This phenomenon may be caused by a reduction in habitat quality (e.g. the decreased availability of suitable habitats or resources), where habitats support fewer individuals per unit area, causing populations to disperse more widely (Fig. 1). Nomadic bird species, such as the redpoll, may be particularly affected by such processes, as they are well known for foraging over large distances in search of food from year to year (Newton 2006, Lehikoinen et al. 2014). The dilution

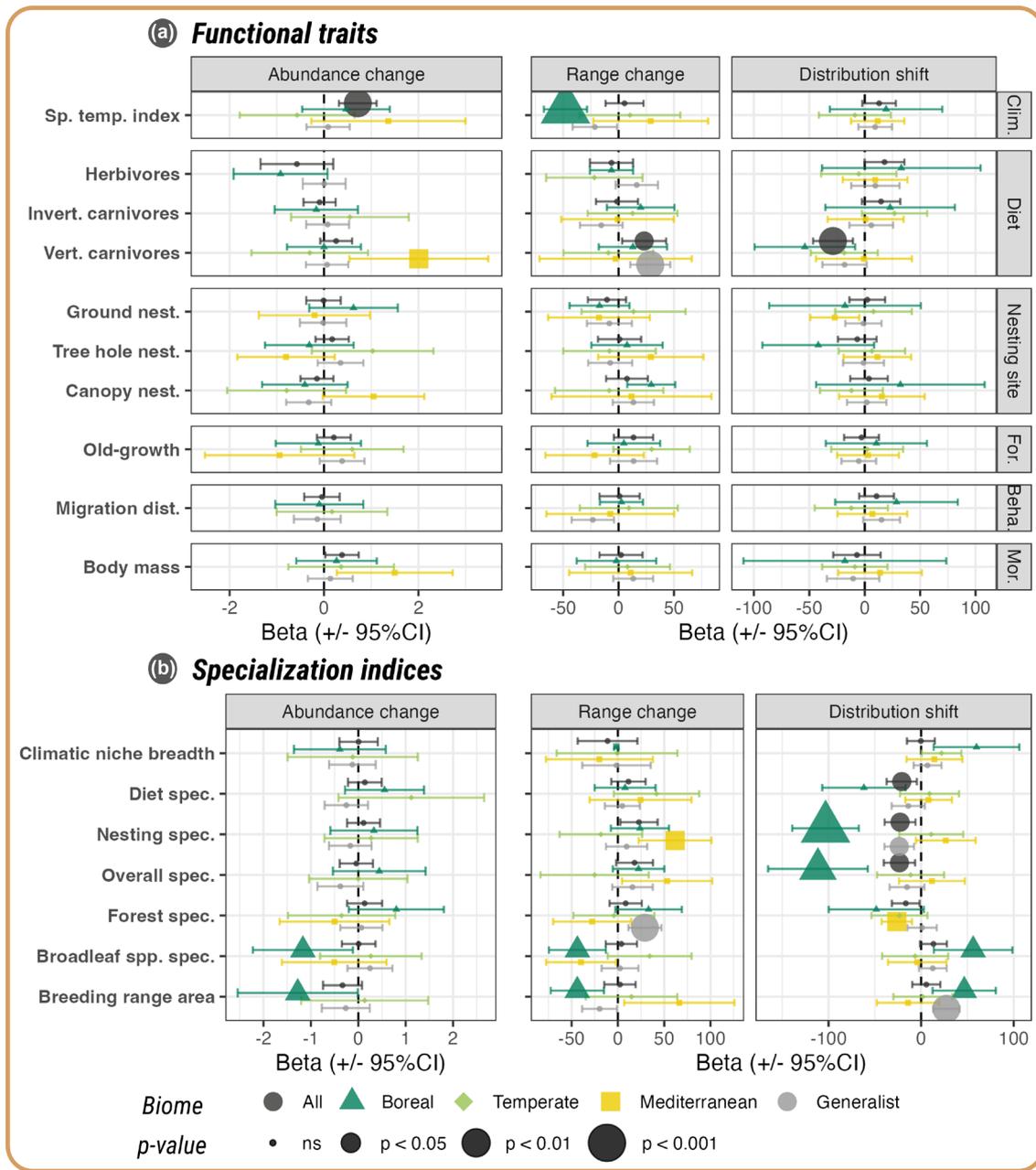


Figure 4. Effect of (a) functional traits and (b) specialisation indices on European forest bird long-term abundance change, range change (i.e. negative (positive) value indicates range shrinkage (expansion)), and distribution shift (i.e. along the south–north gradient). Results are provided for all species (black circles) and groups based on their biome specialisation: boreal (dark green triangles), temperate (light green diamonds), Mediterranean (yellow squares) and generalist (grey circles) species. Each relationship is tested separately with a ‘change/shift ~ trait’ model integrating phylogenetic correlation or distance (either *Phyloclmm* for abundance changes or *gls* for distribution changes). Beta-coefficients indicate the effect strength of the tested relationships while symbol size increased gradually with adjusted p-value. 95% confidence intervals before multiple comparison adjustment show uncertainty level of each beta-coefficient. A missing point means that the model has not converged and therefore no results can be presented. See the Supporting information for more detailed information. ‘Sp. Temp. Index’=‘Species temperature index’, ‘Invert.’=‘Invertebrate’, ‘Vert.’=‘Vertebrate’, ‘For.’=‘Forest’, ‘Beha.’=‘Behaviour’, ‘Mor.’=‘Morphology’, ‘Spec.’=‘Specialisation’. See the Supporting information for the results of the analyses performed with abundance change as a continuous variable.

effect may also reflect an ongoing distribution shift, where populations established in recently colonized areas are still building, while the populations in the original range are decreasing due to modified conditions.

More severe habitat loss may lead to a concentration process, as individuals would need to relocate and ‘concentrate’ within a decreasing number of suitable ‘refuge’ areas (Fig. 1; Tschamtko et al. 2012). The concentration effect is

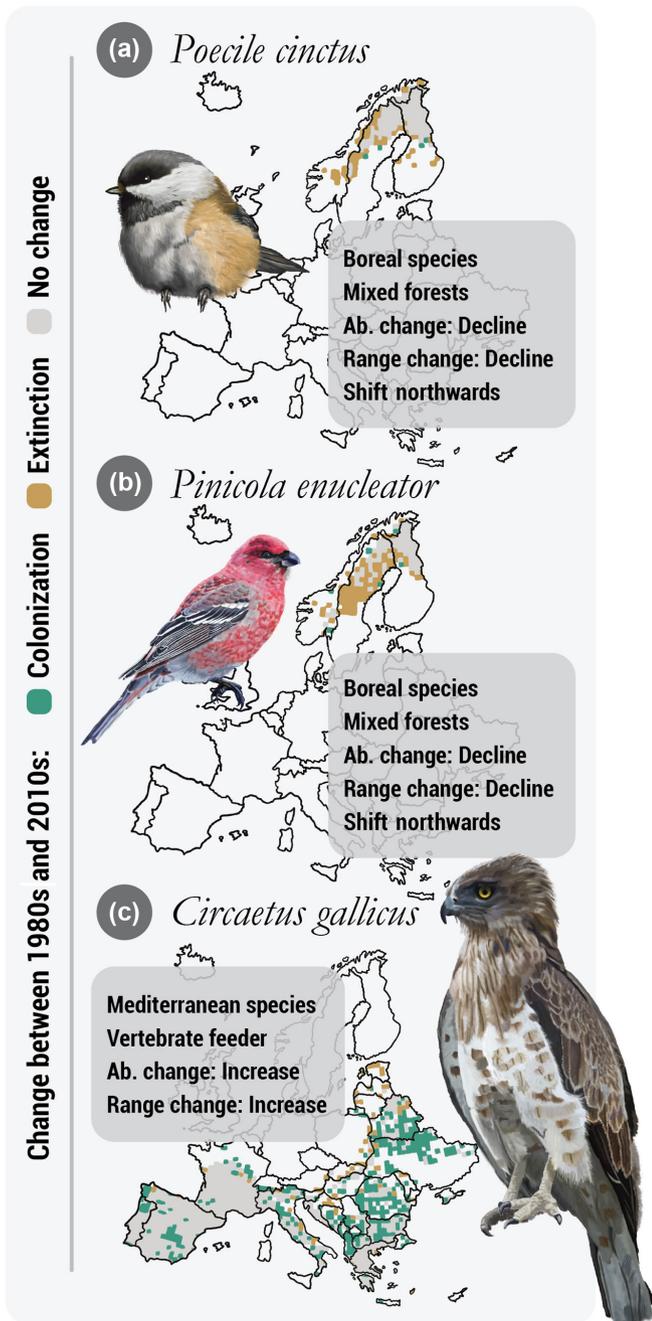


Figure 5. Examples of population dynamics for three species, including two boreal species (a) *Poecile cinctus* and (b) *Pinicola enucleator*, whose abundance and range area have declined, and a Mediterranean bird of prey (c) *Circaetus gallicus*, whose abundance and range area have increased. Occurrence data from European Breeding Bird Atlas atlases (Keller et al. 2020), see Material and methods. 'Ab.' = 'abundance'.

particularly concerning, as it could result in an extinction debt – a transient increase in population density within a smaller area followed by a decline due to resource shortages. Several species showed signs of concentration with increased population densities (Fig. 1–2). For instance, we detected

strong population increases combined with range shrinkage for two raptor species: the cinereous vulture *Aegypius monachus* and the eastern imperial eagle *Aquila heliaca*. These patterns could be attributed to habitat destruction in certain landscapes, concurrent with conservation measures elsewhere. As a result, the positive effects of conservation actions, such as those implemented in protected areas, outweigh the negative impacts of habitat destruction in unprotected landscapes. While the observed increase in abundance for these two species is encouraging, their range contraction should remain a cause for concern. Therefore, our approach demonstrates that changes in population abundance alone may be insufficient to accurately assess the level of conservation effort required for a species.

### Response differences between biome preference groups: a question of traits and specialisation indices?

We found that boreal forest species exhibited declines in both abundance and range area compared to temperate and Mediterranean species, which generally increased. Similarly, species adapted to cold temperatures (i.e. cold-dwellers, or low STI) have declined in abundance, whereas those adapted to warm temperatures (i.e. warm-dwellers, or high STI) have increased. These findings align with previous studies that have documented declines among cold-dwellers and concurrent increases among warm-dwellers across Europe (Virkkala et al. 2008, Lehikoinen and Virkkala 2018, Rigal et al. 2023). Notably, northern latitudes in Europe experienced most of the increases in bird community temperature index (i.e. averaged STI at the community level), reflecting a shift towards warmer-dwelling species expanding their distribution ranges northwards and replacing cold-dwellers (referred to as community thermophilization; Devictor et al. 2012, Lehikoinen, A. et al. 2021).

Surprisingly, climatic niche breadth showed no significant influence on either abundance or distribution patterns, contrasting with our expectation that species with broader climatic niches would be better adapted to changing conditions. In comparison, Hällfors et al. (2024) reported that, in Finland, bird species with narrower climatic niches shifted northwards more rapidly than species with wider niches. Their study also indicated that migration strategy was always in the best model in addition to climatic niche breadth, potentially explaining why we did not detect this relationship (since we did not test both simultaneously). Moreover, in Finland, the northward shifts we tested for have primarily involved farmland birds; instead, forest species have predominantly shifted eastwards (Bosco et al. 2022). National-scale shifts might also be different to the large-scale shifts we tested.

### The decline of boreal forest species

Habitat degradation and loss from forest management practices (e.g. thinning and clearcut) significantly constrain European boreal forest birds (Mönkkönen and Welsh

1994, Lehikoinen and Virkkala 2018). Boreal species associated with mixed forests have sharply declined in both abundance and range – e.g. the Siberian tit and pine grosbeak (Fig. 2, 5; Virkkala et al. 2008, 2013, Lehikoinen and Virkkala 2018). Range shrinkages were mostly concentrated at the southern edges of their distributions, where forestry is most intense, leading to northward shifts (i.e. northward shrinkage; Virkkala et al. 2014, Keller et al. 2020). This shift has also affected nest generalists due to correlated traits (Supporting information). Over the past century, European boreal forests have increasingly replaced old-growth, broadleaf and mixed forests with young coniferous production stands (Lindbladh et al. 2014, Kouki et al. 2019, Mönkkönen et al. 2022). Similar processes behind forest bird decline were observed in boreal North America (Betts et al. 2022). Therefore, the decline in mixed forest bird species is likely due to intensive forest management (Lehikoinen and Virkkala 2018), compounded by climate change and colonisation by warm-dwellers.

Boreal species favouring higher temperatures (measured by STI), and larger breeding ranges typically found at the southern limits of boreal regions, have experienced major range shrinkages. Species with the largest breeding ranges have also experienced abundance declines compounded by northward distribution shifts. These species are particularly vulnerable to intensive forestry, and possibly competition from colonising warm-dwellers (Virkkala and Rajasärkkä 2010, 2011, Virkkala et al. 2013, 2014, Grinde and Niemi 2016, Tayleur et al. 2016) in a warming climate (Callaghan et al. 2004). Consequently, boreal species seem to face a synergistic challenge of habitat degradation, rising temperatures and competitive exclusion.

We observed no declines in boreal old-growth forest specialists. These species are also mostly conifer forest specialists and, therefore, represent a different ecological group than the mixed forests specialists (nonetheless, we noticed that both Siberian tit and pine grosbeak are old-growth forest specialists; Supporting information). Stability among old-growth forest specialists may stem from earlier declines in old-growth forests preceding the study time frame (i.e. before 1980; Mönkkönen et al. 2022); thus, bird populations have remained degraded. In contrast, broadleaf forest reductions are more recent (Mönkkönen et al. 2022).

In contrast, three boreal species have strongly increased in abundance and expanded their ranges (Fig. 2, i.e. the Bohemian waxwing *Bombycilla garrulus*, the little bunting *Emberiza pusilla* and the red-flanked bush robin *Tarsiger cyanurus*). They only shared one characteristic – they have a smaller breeding range area than stable and decreasing species, and have expanded southwards (Keller et al. 2020). The strong increase in Bohemian waxwing can be related to the increase in berry production by rowan *Sorbus aucuparia*. Indeed, rowan berries are very important for waxwings during the winter, especially at the southern end of their distribution (Virkkala et al. 2014). Red-flanked bush robin expansion and population increase seems to result from a longer-term expansion from the Ural mountains in Siberia

reported in the 1950s, and seemingly resulting from warming spring temperatures (Helminen 1958).

The nomadic redpoll and great grey owl *Strix nebulosa* have expanded their ranges as well. Their ranges could have changed partly as a result of irruptive migration behaviour, where individuals have poor site fidelity and mostly follow food resources from one year to another (Newton 2006). In that case, food resource expansion might explain the range expansions of these species, as it has been observed for waxwings. The great grey owl is a vole-eating bird of prey, and vole peaks have happened in the southern boreal region, explaining the southern expansion for this species (Virkkala et al. 2014). In addition, the great grey owl has also disappeared from its northern distribution, possibly also due to nesting habitat degradations or fluctuating food availability in northern latitudes (Sulkava and Huhtala 1997, Ławicki et al. 2013, Mysterud 2016, Keller et al. 2020).

Southward shifts in diet among boreal nest specialists involve the great grey owl, with climate change impacting winter conditions for boreal owls by altering snow cover and hardness, which in turn affects hunting success and prey availability (Lehikoinen et al. 2011, Mysterud 2016). The Ural owl *Strix uralensis* and the pygmy owl *Glaucidium passerinum*, two biome generalist species with large populations in European boreal regions, have significantly expanded their distribution ranges southwards, i.e. toward temperate central Europe, while losing territories in the north (Lehikoinen and Virkkala 2018, Keller et al. 2020). The Ural owl has contributed significantly to the southward shift of nesting specialists, species with small breeding territories among biome generalists and diet specialists.

### The increase of Mediterranean and temperate forest species

Unlike boreal species, Mediterranean and temperate species generally maintained or increased their abundances while expanding their ranges. Mediterranean vertebrate carnivores like the short-toed eagle *Circus gallicus*; Fig. 5c), have increased in abundance, potentially due to targeted conservation efforts since the 1970s, following their critical decrease beforehand. Similarly, vertebrate carnivores among biome generalist species have expanded their ranges across Europe. Nonetheless, many birds of prey remain threatened by poisoning (Mateo 2009, IUCN 2023) and habitat degradation (Derlink et al. 2018). For instance, the Spanish imperial eagle is still classified as ‘vulnerable’ on the European Red List, since the species still has a very small population and faces many threats (BirdLife International 2021). Moreover, these rapid increases following a demographic bottleneck could lead to reduced genetic diversity (but for some non-forest raptors, see Hailer et al. 2006, Graciá et al. 2015). Also, despite an increase in abundance, cinereous vultures and eastern imperial eagles have experienced range shrinkage (Keller et al. 2020). For temperate species, despite abundance increases and range expansions, no clear influence of traits and specialisation indices were detected.

Mediterranean species' range changes were linked to several specialisation indices, which seem to be mainly caused by global warming, i.e. warmer temperatures and altered rainfall patterns. For instance, the range expansion of nest specialists was mainly explained by one species: the European bee-eater. The range expansion and northward distribution shifts of forest generalists was mainly explained by the same species. The European bee-eater has colonised many new territories northwards (Keller et al. 2020), most likely due to warming temperatures (Stiels et al. 2021). Conversely, the generalist nesting species western Bonelli's warbler *Phylloscopus bonelli* has shrunk southwards, most likely due to biotic interactions (i.e. competition with willow warblers *Phylloscopus trochilus*) and moister breeding conditions in the north (Olioso et al. 2020). Additionally, the overall increase of Mediterranean and temperate species may reflect rural land abandonment and subsequent forest expansion in these regions (Gil-Tena et al. 2010, Kuemmerle et al. 2016).

### Variations among generalist species

Among biome generalist species, we identified relationships with various traits and specialisation indices. Vertebrate carnivores and forest specialists have expanded their ranges, while ranges of forest generalists either did not respond or shrank (Supporting information). Forest generalists include species that occur in both open areas and forest areas. Forest generalists, mainly the European roller *Coracias garrulus*, the dunnock *Prunella modularis* and the European turtle dove *Streptopelia turtur*, have seen their ranges shrink, possibly due to the reduction in open woodlands from intensive agricultural practices (e.g. loss of hedgerows and their large trees bearing cavities), or due to forest encroachment (Sirami et al. 2007, Regos et al. 2016, Kiss et al. 2020, Rigal et al. 2023). In contrast, five forest specialists including the pygmy owl, the hawfinch *Coccothraustes coccothraustes*, the red crossbill *Loxia curvirostra*, the boreal owl *Aegolius funereus* and the common raven *Corvus corax*, have expanded their ranges, possibly benefiting from overall forest expansion in temperate Europe.

### Conclusions

Our study integrates species abundance and distribution data, revealing both similarities and differences between them, underpinned by a demographic framework (Fig. 1). We emphasize two key findings: 1) declines in abundance and range area of boreal forest species over the past 3–4 decades, and a northward distribution shift observed for mixed-forest species, possibly due to forestry-driven changes in forest composition, rising temperatures and colonisation by warm-dwelling species; and 2) increases in abundance and northward range expansion of Mediterranean and temperate species, possibly driven by warmer temperatures and forest expansion in these regions.

In Europe, our findings align with broader trends indicating declines in forest cold-dwellers, and increases in

warm-dwellers, consistent with studies on all bird species (Rigal et al. 2023). Similar declines in forest birds in North American boreal regions due to forestry practices have been documented (Betts et al. 2022). Therefore, different geographic regions might adopt different conservation strategies. Protected areas have shown promise in mitigating declines of forest and/or cold-dwelling bird species in Europe (Lehikoinen et al. 2019, Lehikoinen, P. et al. 2021, Santangeli et al. 2023) and North America (Hintsanen et al. 2023). Alternative forest management practices, e.g. extensive management, can help support bird diversity as well (Blattert et al. 2023, Triviño et al. 2023). However, the current network of protection areas and extensive management practices may not suffice to safeguard boreal forest bird species against climate change impacts (Bakx et al. 2023, Hintsanen et al. 2023, Santangeli et al. 2023, Mönkkönen et al. 2024). In the temperate and Mediterranean regions, measures targeting specific declining species (such as raptors), limiting the development of industrial forestry and protecting remaining large trees may be more relevant. Addressing climate change alongside habitat degradation is crucial to mitigate synergistic pressures on bird populations (Virkkala et al. 2023), demanding immediate and effective actions.

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### Author contributions

**Jérémy Cours:** Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Merja Elo:** Resources (supporting); Writing – review and editing (equal). **Joséphine Pithon:** Writing – review and editing (equal). **María Triviño:** Writing – review and editing (equal). **Mikko Mönkkönen:** Writing – review and editing (equal). **Jonas Haggé:** Resources (supporting); Writing – review and editing (equal). **Aleksi Lehikoinen:** Writing – review and editing (equal). **Rémi Duflot:** Funding acquisition (lead); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

### Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07582>.

## Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.14845055> (Cours et al. 2025).

## Supporting information

The Supporting information associated with this article is available with the online version.

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