

## RESEARCH ARTICLE OPEN ACCESS

# Solar Radiation Affects Bird Distributions but Not Elevational Shifts in European Mountains

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**Keywords:** altitudinal range shift | avian community | climate adaptation | global warming | montane ecosystem | species distribution changes

## ABSTRACT

**Aim:** Climate change is driving species towards higher elevations. While local shifts in elevation are well documented, patterns across entire mountain regions are less understood. On a local scale, abiotic factors, such as topography and solar radiation relating to microclimate, affect species distributions and can thus influence the rate of elevational shifts on mountain slopes. The impact of abiotic factors on biodiversity is evident, but range shift studies have mostly focused on groups of species with low mobility, such as plants.

**Location:** Across European mountain regions of the Alps, Pyrenees, Scandinavia and the United Kingdom.

**Time Period:** 2001–2021.

**Major Taxa Studied:** One hundred seventy-seven bird species.

**Methods:** We adopted a cross-scale community approach using abundance data to quantify the impact of the amount of solar radiation (measured as potential incoming solar radiation) on the mean elevational distribution and rate of elevational shifts of bird species in four European mountain regions. We modelled the impact of the amount of solar radiation using generalised linear mixed models.

**Results:** We found that bird species inhabit higher elevations in areas receiving more solar radiation. We also found that the mean elevations at which species occur moved uphill by 0.5 m/year between the periods 2001–2004 and 2018–2021 across Europe. However, this rate of elevational shifts was similar between areas receiving low, medium and high amounts of solar

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radiation. We observed variations in the rate of elevational shifts that were fastest in Scandinavia and the Alps, while no uphill shift was observed in the UK or the Pyrenees.

**Main Conclusions:** Our findings underscore the significance of abiotic factors, including solar radiation and climate change, driving, directly or indirectly, birds' elevational distributions. They also unveil consistent patterns of uphill shifts across different solar radiation regimes at a continental scale.

## 1 | Introduction

Climate change is one of the main drivers of the ongoing biodiversity crisis (Balvanera et al. 2019). To avoid extinction, species need to either move or adapt (Parmesan 2006; Alford et al. 2007; Robinet and Roques 2010). Of these responses, latitudinal and elevational range shifts can greatly alter the composition of ecological communities (Marjakangas et al. 2023). Such shifts have been documented in various taxa, including plants, insects, mammals, birds and fish (Chen et al. 2011; Bani et al. 2019; Neate-Clegg et al. 2024). At high elevations, species attempting to shift their ranges are confronted with significant challenges due to space and habitat quality limitations (Şekercioğlu et al. 2008). Mountain topography limits land area at higher elevations (Chamberlain et al. 2023), making mountaintops climate refugia with restricted space for species to shift in search of optimal conditions (Gonzalez et al. 2010; Sirami et al. 2017; Scridel et al. 2018).

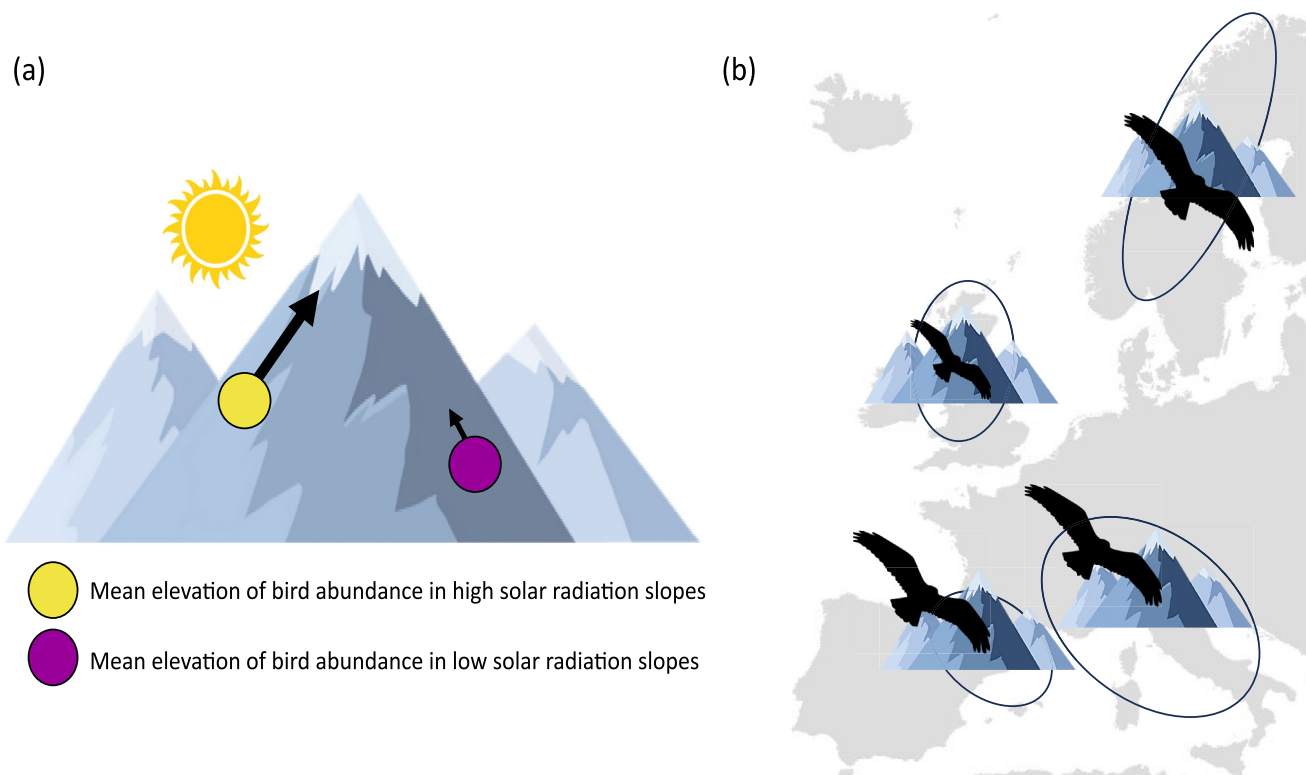
Mountains are among the most vulnerable ecosystems on Earth, facing large changes in climate (Caprio et al. 2011; Chamberlain et al. 2023). Indeed, due to their unique geological and biogeographical history, they show disproportionately more worrying signs of biodiversity loss at present and in the near future (Masson-Delmotte et al. 2018). Compared to many other ecosystems, biodiversity responses in mountain regions are understudied, with few assessments of the impacts of environmental change on their biodiversity available so far (Beniston et al. 2018; Chamberlain et al. 2023; Chan et al. 2024). Furthermore, across the world, only a few studies have reported elevational shifts of species at a broader scale, such as for entire mountain regions (Tingley et al. 2012; Couet et al. 2022) or investigated the potential spatial differences in the rate of shifts (Chen et al. 2011).

At the local scale, microclimates play a key role in shaping species' behaviour and occurrences as well as community assemblages (Lippok et al. 2014). Microclimate refers to the local climate conditions that organisms and ecosystems are exposed to (Kemppinen et al. 2024). More specifically, microclimate is a combination of local temperature, water (precipitation, air humidity, water availability), solar radiation, cloud, wind, exposition and evaporation conditions. At the ground level, temperatures are directly affected by sun exposure (i.e., amount of solar radiation), with south-facing sites being warmer and often drier than north-facing sites in the northern hemisphere (Radcliffe and Lefever 1981; Suggitt et al. 2011). This is affecting the elevational distribution of plant species and vegetation types (e.g., treeline positions), whereby species reach higher upper elevational limits on sun-facing than shadowy sites (Nagy and Grabherr 2009). The impact of solar radiation on biodiversity may be ubiquitous, but so far this impact has been studied mainly on plants at small and large spatial scales and on invertebrates and other ectotherms at small spatial scales (for plants: Opedal et al. 2015; Momberg et al. 2021; Niittynen et al. 2020; for

ectotherms: Carnicer et al. 2019; Feldmeier et al. 2020; Stickley and Fraterrigo 2023), and scarcely on other taxa (Massimino et al. 2020; Scridel et al. 2024). Moreover, it is poorly understood how variation in solar radiation (e.g., whether sites face the equator or the poles) influences variation in the rate of species elevational shifts in response to climate change, and how the rate of elevational shift varies across mountain regions at a continental scale. Here, we focus on the topographic distribution of solar radiation as it is an available proxy metric for incoming energy to local ecosystems on mountains, and thus one of the most important drivers of microclimatic conditions.

Birds are highly mobile, which likely increases their potential to respond more rapidly to climate change via range shifts when compared to more sessile taxa, such as plants. As a result, any bird species could respond to climate change by moving at least part of its population uphill, including species that have historically mainly been found in the lowlands. To capture the resulting reorganisation in the bird community compositions across elevations, in this paper, we consider all bird species with sufficient data occurring along the full elevational gradient of mountain regions. Although the coverage of bird monitoring networks through citizen science has improved significantly in many continents, the number of surveys in mountain ecosystems is still limited due to challenging accessibility. Globally, the survey networks with the best coverage in mountain areas are located in Europe and North America (Chamberlain et al. 2023), allowing detailed assessments of solar radiation amount effects on species' climate change responses in mountain ecosystems at an unprecedented spatiotemporal scale and resolution.

Here, we adopted a unique cross-scale community approach using these long-term large-scale datasets of bird abundances across four European mountain regions (Pyrenees, Scandinavian mountains, UK uplands and Alps and its neighbouring mountainous areas, including Massif Central and the Apennines) to study patterns of elevational distributions and elevational shifts at a continental scale. Most studies on climate change so far have used presence-absence, that is, range margin data (Pearce-Higgins and Green 2014). However, typically local extinctions and colonisations are preceded by changes in abundance under a perturbation event, such as climate change (Ashcroft et al. 2017). Therefore, using abundance data, rather than presence-absence, enables unveiling early signs of bird species redistributions before these result in local extinctions and/or colonisation (Dirzo et al. 2014). Using abundances enables assessing where the majority of the bird individuals are, which is an important measure for the continued functioning of mountain ecosystems under climate change. To improve the understanding of bird species' responses to climate change in mountain ecosystems, we study (1) the impact of solar radiation amount (measured as



**FIGURE 1** | Schematic illustration of the hypotheses. Panel (a): The mean elevation of bird species abundance is hypothesised to be higher in sites with high amounts of solar radiation (Hypothesis 1) and to have faster shifts uphill than in sites with low solar radiation (Hypothesis 3). Panel (b): Faster shifts are hypothesised in mountain regions that experienced faster rates of warming (Hypothesis 2), illustrated with different sizes of common buzzard symbols.

the potential incoming solar radiation) on bird abundances along the elevational gradient, (2) the variation in the rate of elevational shifts of bird abundances among mountain regions and (3) the variation in the rate of elevational shifts of bird abundances under different solar radiation regimes at the European scale and within individual mountain regions.

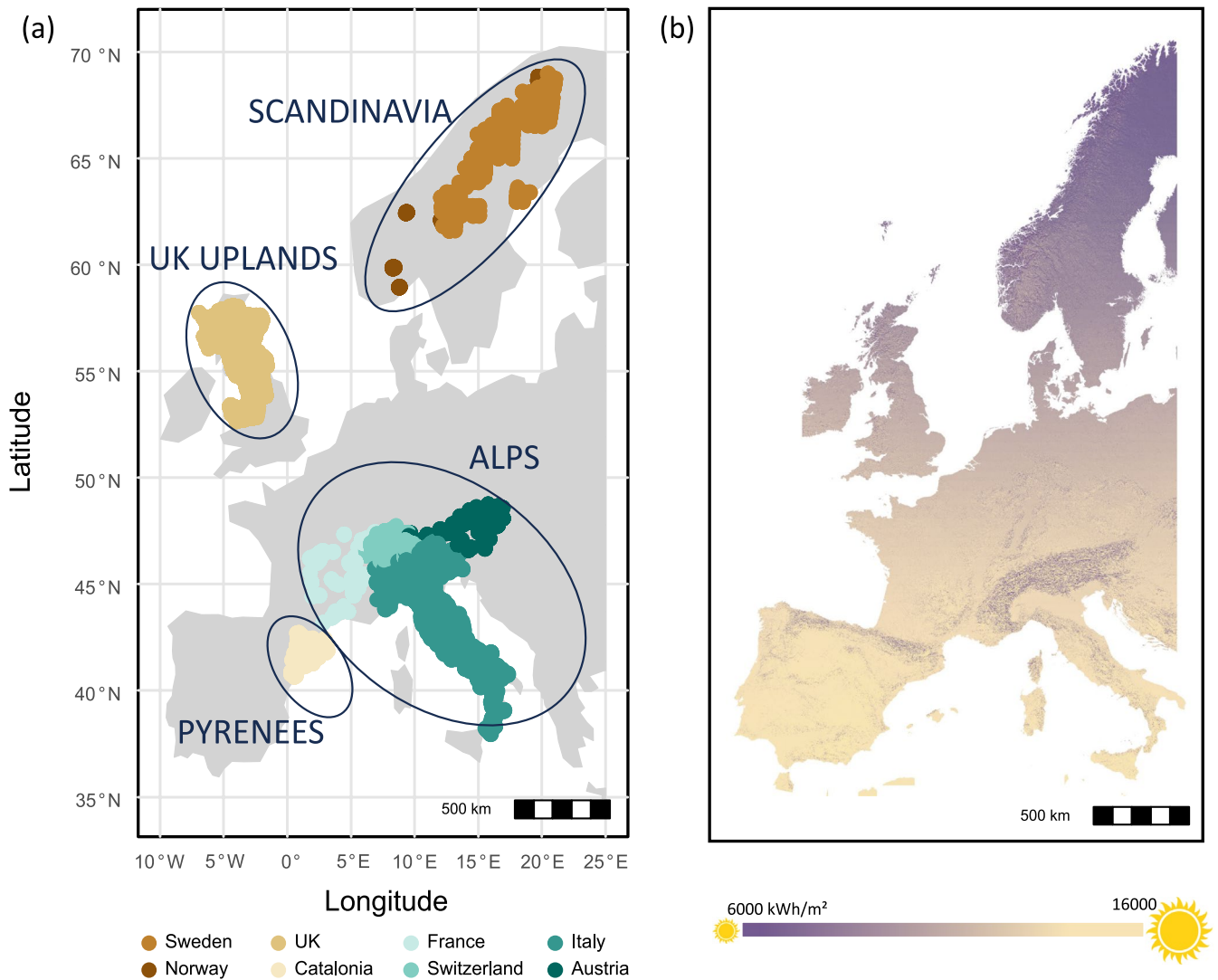
As solar radiation is known to shape the spatial distributions of species (Lippok et al. 2014), we expect birds to occur at higher elevations in areas receiving more intense solar radiation, which tend to be south-facing in the northern hemisphere (Geiger et al. 2009). That is, we expect elevational ranges of birds to align with the elevational variation observed in vegetation zones and ectothermic animals that many bird species depend on for habitat and food resources (Fekedulegn et al. 2003; Feldmeier et al. 2020) (Figure 1a). Thus, here we seek correlative evidence on the relationship between solar radiation and bird abundance, which may be driven by direct links, or indirectly by, for example, solar radiation effects on lower trophic levels (plants and/or insects) that in turn affect birds. We also expect bird communities to shift their mean elevations uphill over time across Europe and within mountain regions, despite the documented rate of change having been slow (0.33–1.1 m/year in reviews; Chen et al. 2011; Pearce-Higgins and Green 2014; Lenoir and Svenning 2015). However, we expect differences in the rates of shift among mountain regions. Specifically, we expect shifts to be faster in areas with high solar radiation (Moore 2008) (Figure 1a) and in mountain regions that have experienced the fastest increases in annual temperatures (Lehikoinen et al. 2019, Appendix S1) (Figure 1b). We expect that areas of high solar radiation show

faster range shifts, because occurrence shifts of plant species towards mountaintops have been faster in areas with more intense solar radiation and earlier snowmelt (Cannone et al. 2007; Nagy and Grabherr 2009; Devictor et al. 2012).

## 2 | Methods

### 2.1 | Data

We used species and topographic data from the following European mountain regions: the Alps and its neighbouring mountainous areas (including Massif Central and Apennines; hereafter, the Alps), the Pyrenees, Scandinavian mountains (hereafter, Scandinavia) and the United Kingdom uplands (hereafter, UK uplands) (Figure 2a). Over the last 20 years, the annual temperatures have increased overall in the study area by  $+0.81^{\circ}\text{C}$  ( $\pm 0.03$ ) but at different rates in the different mountain regions (Alps =  $+1.00^{\circ}\text{C} \pm 0.02^{\circ}\text{C}$ , Pyrenees =  $+0.88^{\circ}\text{C} \pm 0.03^{\circ}\text{C}$ , Scandinavia =  $+0.63^{\circ}\text{C} \pm 0.03^{\circ}\text{C}$ , UK uplands =  $+0.15^{\circ}\text{C} \pm 0.03^{\circ}\text{C}$ ) (for more details, see Appendix S1 ‘Additional Methods and Sensitivity analysis’, Figure S1). Across Europe, we obtained bird abundance data from eight monitoring schemes carried out in the Alps (Austria, France, Italy and Switzerland), Pyrenees (Catalonia, NE Spain), UK uplands (UK) and Scandinavia (Norway and Sweden). These monitoring schemes follow either the point count method (Austria, Italy, France and Norway), the line transect method (Catalonia, UK, and Sweden) or the territory mapping method

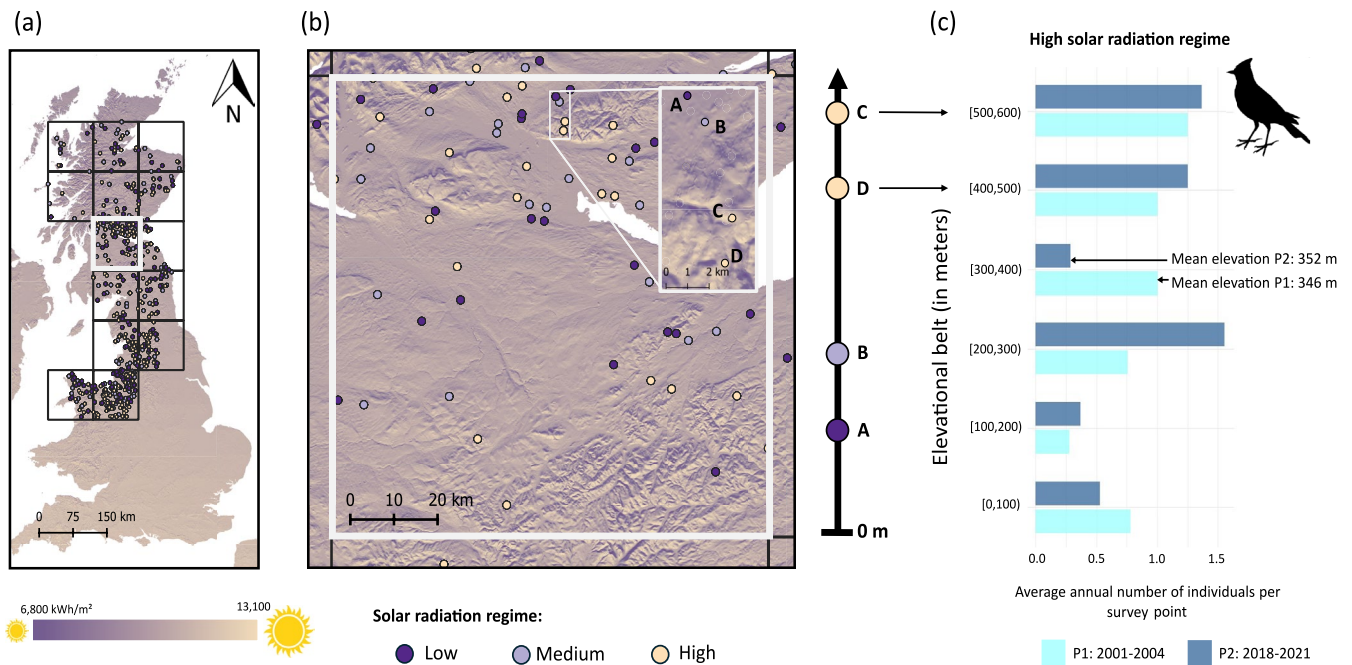


**FIGURE 2** | Overview of the study region. Panel (a): Locations of the survey points ( $N=14,484$ ) included in the analyses after data selection. The different colours show the different monitoring schemes. The dark blue circles represent our four study regions. Panel (b): Map of the estimated potential incoming solar radiation averaged between March and August.

(Switzerland) (for more details see Appendix S1, Table S1). For each year, all individual birds/pairs of birds seen and/or heard were reported. As the survey scheme designs differ, we harmonised the data set to have similar spatial resolutions and hierarchical designs (Appendix S1, Table S1 and methods below). As a result, the finest scale unit of each survey scheme corresponds to 'survey point' in the subsequent analyses. The elevational range of the study area based on the minimum elevation and the maximum elevation of all survey points was 3200 m (elevational range<sub>Alps</sub> = 3200 m; elevational range<sub>Pyrenees</sub> = 2548 m; elevational range<sub>Scandinavia</sub> = 1536 m; elevational range<sub>UK uplands</sub> = 1178 m).

We investigated elevational shifts that occurred between two 4-year study periods (Period 1: 2001–2004 and Period 2: 2018–2021), for which there was adequate data for all countries and regions. At minimum, each country needed to have 3 years of surveys conducted during each 4-year study period. Compiling data into study periods of 4 years allowed us to reduce the potential effect of environmental stochasticity among monitoring seasons (Lehikoinen and Virkkala 2016; Couet

et al. 2022). Within each country, we selected those survey sites that were surveyed in at least 1 year during both study periods. As interest in mountain biodiversity and the survey effort at higher elevations have increased in recent years (Chamberlain et al. 2023), selecting the same survey points allowed us to account for a potential sampling bias towards the high elevation areas in the second study period. We divided the selected survey points into grid cells of  $100 \times 100$  km. For the Norwegian data, we used the locations of the survey areas as they were already organised in spatially distinct clusters. Since we were interested in the elevational abundance shifts, we included only those grid cells that comprised a minimum elevational range (i.e., difference between the minimum and the maximum elevation within the grid cell) of 500 m (European Union, Copernicus Land Monitoring Service 2020, <https://land.copernicus.eu/en>) and contained at least 10 survey points spanning an elevational range of 300 m. For the Alps and Pyrenees, we used the same grid; therefore the same grid cell could contain surveys from multiple countries. In total, there were 14,484 survey points surveyed in both study periods across mountain regions ( $N_{\text{Alps}} = 6592$ ,  $N_{\text{Pyrenees}} = 797$ ,



**FIGURE 3** | Overview of the hierarchical study design. Panel (a) shows the distribution of the 14 grid cells within the UK uplands study region. Panel (b) shows the central points of the surveyed sites within one grid cell of 100×100 km. The inset highlights four example survey points classified into solar radiation regimes based on within-grid cell 33% quantiles: A = low, B = medium, and C & D = high solar radiation. The vertical arrow indicates their relative positions along the elevational gradient of the grid cell. The horizontal arrows linking survey points C and D to the elevational belts of panel (c) indicate which elevational belts these survey points have been assigned. Panel (c) shows the average annual number of individuals per survey point in each elevational belt for the Eurasian skylark (*Alauda arvensis*) in the selected grid cell, shown for the high solar radiation regime across the two study periods. The mean elevation is also shown for this specific species in both periods in high solar radiation regime within the grid cell (= response variable of the study).

$N_{\text{Scandinavia}} = 2003$ ,  $N_{\text{UK uplands}} = 5092$ ), divided into 110 grid cells ( $N_{\text{Alps}} = 68$ ,  $N_{\text{Pyrenees}} = 7$ ,  $N_{\text{Scandinavia}} = 21$ ,  $N_{\text{UK uplands}} = 14$ , example of the grid for the UK uplands in Figure 3a).

As we were interested in the general pattern of bird elevational abundance shifts, and also to ensure reliable estimates of elevational shifts, we excluded observations of very rare species. That is, we calculated the mean annual number of individuals at each survey point in each study period in each solar radiation regime in each grid cell and country and in each mountain region. Then, we included in the analyses only those species for which the mean annual number of individuals was at least three records within a grid cell, country, solar radiation and period. We kept species associated with aquatic ecosystems as solar radiation can influence their distribution indirectly through water temperatures, evapotranspiration which can in turn impact food abundance and nesting habitat (Wetzel and Likens 2000). As a final step, we also excluded (1) species that are non-native or do not breed in the area (*Anser brachyrhynchus*, *Branta canadensis*), (2) marine species (*Larus marinus*, *Phalacrocorax carbo*, *Somateria mollissima*, *Sterna sandvicensis*) and (3) hybrids (*Passer italiae* × *Passer domesticus*). The marine species are not expected to show elevational shifts due to their inherent associations with marine environments, while non-native species' range expansions may not be driven by climatic factors but by human-induced introductions. In total, we included 177 bird species across the European mountain regions ( $N_{\text{Alps}} = 125$ ,  $N_{\text{Pyrenees}} = 99$ ,  $N_{\text{Scandinavia}} = 57$ ,  $N_{\text{UK uplands}} = 95$ ). For the full list of species, see Appendix S1, Table S2.

We obtained the elevational information from a 25-m resolution digital elevation model (European Union, Copernicus Land Monitoring Service 2020) for all survey points using QGIS software (version 3.16.16). We estimated the potential incoming solar radiation (hereafter, solar radiation) for each survey point based on a model that includes the local aspect, slope, latitude and the shadowing effect of the surrounding topography (Figure 2b). The potential incoming solar radiation is a proxy metric for incoming energy to local ecosystems on mountains available across large areas at high spatial resolution. We used the Potential Incoming Solar Radiation tool in the SAGA-GIS software (version 7.6.2; [http://www.saga-gis.org/saga\\_tool\\_doc/7.6.2/ta\\_lighting\\_2.html](http://www.saga-gis.org/saga_tool_doc/7.6.2/ta_lighting_2.html)).

We calculated the potential incoming solar radiation as a radiation sum of every 15 days in the period between March 1st and August 31st with a 1-h interval. For each survey point, we created a buffer of 100 m inside which we extracted the mean elevation and the solar radiation. To facilitate comparisons across mountain regions with varying solar radiation baselines, and to ensure an adequate and representative sample size, we classified solar radiation into three categories (low, medium and high) based on the 33rd and 66th percentiles of the distribution across all grid cells. This approach allowed us to identify and compare species' elevational responses in areas that are relatively more or less exposed to solar radiation, rather than relying on absolute values that are not directly comparable across regions (higher solar radiation with decreasing latitude; Figure 2b). For each grid cell, we included species that were observed in at least two out of the three solar radiation regimes. We also calculated

the anomaly between the mean elevation of each solar radiation regime in the grid cell and the mean elevation in the same grid cell. We compared survey point steepness (slope) and elevation across solar radiation regimes using linear models (*lm()* function, R package *stats*; R Core Team 2012), with slope or elevation as the response variable and solar radiation category as a fixed factor. Medium solar radiation regimes occurred more often at low elevations and slopes than both low and high radiation regimes (Appendix S1, Figure S2a,b). Thus, these solar radiation regime- and grid cell-specific anomalies capture biases in the selection of survey points along the elevational gradient and abiotic conditions. Indeed, the mean elevation of bird abundances could appear to occur at lower elevations in medium solar radiation regimes if only lower elevation sites have been surveyed for the regime.

In total, we had a sample size of 20,638, where the unit is the mean elevation of one species in one solar radiation regime in one country in one grid cell during one study period ( $N_{\text{Alps}} = 12,956$ ,  $N_{\text{Pyrenees}} = 1906$ ,  $N_{\text{Scandinavia}} = 1760$ ,  $N_{\text{UK uplands}} = 4016$ ). The full workflow of data processing and selection procedures for each mountain region is summarised in supplementary flowcharts (Appendix S1, Figures S3–S6).

## 2.2 | Statistical Analyses

We used the harmonised and filtered abundance data to assess the elevational abundances and shifts of birds. For this, we estimated the mean elevation of each species' abundance for each solar radiation regime in each grid cell and each study period. This was done by clustering the survey points in 100-m elevational belts, where we calculated the mean abundance of each species per survey point in each belt in each solar radiation regime within each grid cell in each country (Figure 3c). The number of survey points per elevational belt decreased with elevation, resulting in scarcer coverage of high-elevation areas (see the distributions of the survey points per elevational belt in Appendix S1, Figure S7). This clustering process produced relative abundances for each surveyed elevational belt where the mean elevation of a species' abundance was calculated using a method presented by Couet et al. (2022). The mean elevation of a species corresponds to the elevation at which the mean abundance of this species is located along the elevational gradient (Couet et al. 2022, see Appendix S1 for detailed equations).

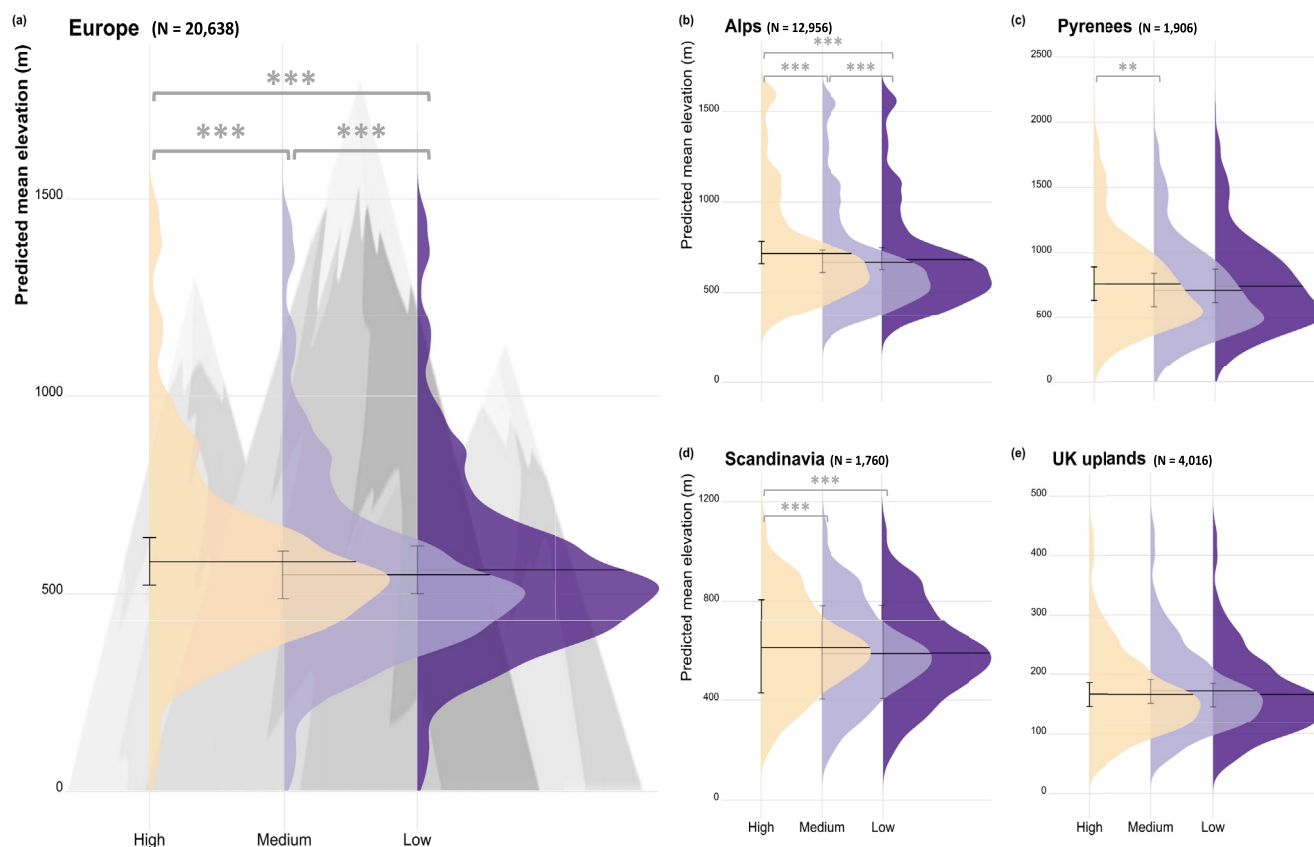
To answer our first two study questions investigating (1) the effect of solar radiation on the mean elevations of bird species abundances and (2) the variation in the rate of elevational shifts across and among different mountain regions, we modelled the mean elevation of species as a function of the study period (fixed factor with two levels), the solar radiation regime (fixed factor with three levels), the mean elevation of the grid cell (fixed continuous numeric variable), the solar radiation-specific mean elevation anomaly (fixed continuous numeric variable), species identity (random factor with 177 levels for the European model, 125 for Alps, 99 for Pyrenees, 57 for Scandinavia and 95 for UK uplands), grid cell identity (random factor with 110 levels for the European model, 68 for Alps, 7 for Pyrenees, 21 for Scandinavia and 14 for UK uplands) and the country (random factor with 8 levels for the European

model, 4 for Alps and 2 for Scandinavia; for mountain regions that encompassed survey data from more than one country). We used this model structure for the whole of Europe and for each mountain region separately, which resulted in five models. To study pairwise differences among solar radiation regimes, we performed post hoc tests using the package 'emmeans' (Lenth 2024). To answer our third study question investigating the variation in the rate of elevational shifts of bird abundances under different solar radiation regimes, we modelled the mean elevation of species as a function of the study period (fixed factor) in interaction with the solar radiation regime, the mean elevation of the grid cell (fixed continuous numeric variable) and the solar radiation-specific mean elevation anomaly (fixed continuous numeric variable), species identity (random factor), grid cell identity (random factor) and the country (random factor) for mountain regions that encompassed survey data from more than one country. Both model equations are provided in the Appendix S1. We again used this model structure for all of Europe and for each mountain region separately, which resulted in five models. For all modelling, we used Generalised Linear Mixed Models (GLMMs) with Gaussian distribution using function *lmer* from R packages 'lme4' and 'lmerTest' (Bates et al. 2015; Kuznetsova et al. 2017) in R software (R Core Team 2012, version R-4.1.2).

## 2.3 | Sensitivity Analyses

To validate the robustness of the results, we first visually inspected spatial correlograms of the model residuals for a maximum distance of 500 km for Europe, Alps, Scandinavia and UK uplands and a maximum distance of 300 km for Pyrenees (maximum distance between survey points) using package 'nccf' (Bjornstad 2020). We found no strong sign of spatial autocorrelation in the residuals at any distance (Appendix S1, Figure S8). Second, to validate the robustness of the species selection procedure, we repeated the analyses with varying selection thresholds and did not find major differences in the species abundances and shifts (Appendix S1, Tables S3 and S4). Additionally, we performed the same analyses by removing the aquatic and wetland species (belonging to the families of *Laridae*, *Ardeidae* and *Anatidae*) because these species are not expected to show strong elevational shifts due to their inherent associations with wetlands. We did not find any major differences in the results when excluding aquatic and wetland species (Appendix S1, Tables S5 and S6). We also validated the selected buffer size of the mean elevation and solar radiation values for each survey point by extracting values at two alternative buffer sizes: 0 and 250 m. Using the R package 'psych' (Revelle 2017), we created a correlation plot of mean solar radiation in the different buffer sizes and did not find significant differences (Appendix S1, Figure S9). Additionally, to validate the solar radiation regime categorisation, we repeated the analyses using the threshold (low: lowest 25% of sites, high: highest 75% of sites and medium between 25% and 75% of the solar radiation sites), following the method used by Hinneberg et al. (2025). We did not find any major differences than with the 33% quantiles (Appendix S1, Tables S7 and S8).

To validate the robustness of the results to sample size balance across mountain regions, we fitted both European models



**FIGURE 4** | Predicted distribution of mean elevations of bird species abundances according to the different solar radiation regimes (High, Medium, Low) for (a) all studied European mountain regions, and separately for (b) the Alps, (c) the Pyrenees, (d) Scandinavia and (e) UK uplands. The y-axis scale differs between panels. The black horizontal lines represent the predicted means of the distributions. The error bars represent the 95% confidence intervals. 'N' refers to the sample sizes where the unit is the mean elevation of one species in one solar radiation regime in one country in one grid cell during one period. Asterisks (\*) represents the significance of the difference between study periods (\*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ ). No asterisk represents a nonsignificant difference between solar radiation regimes.

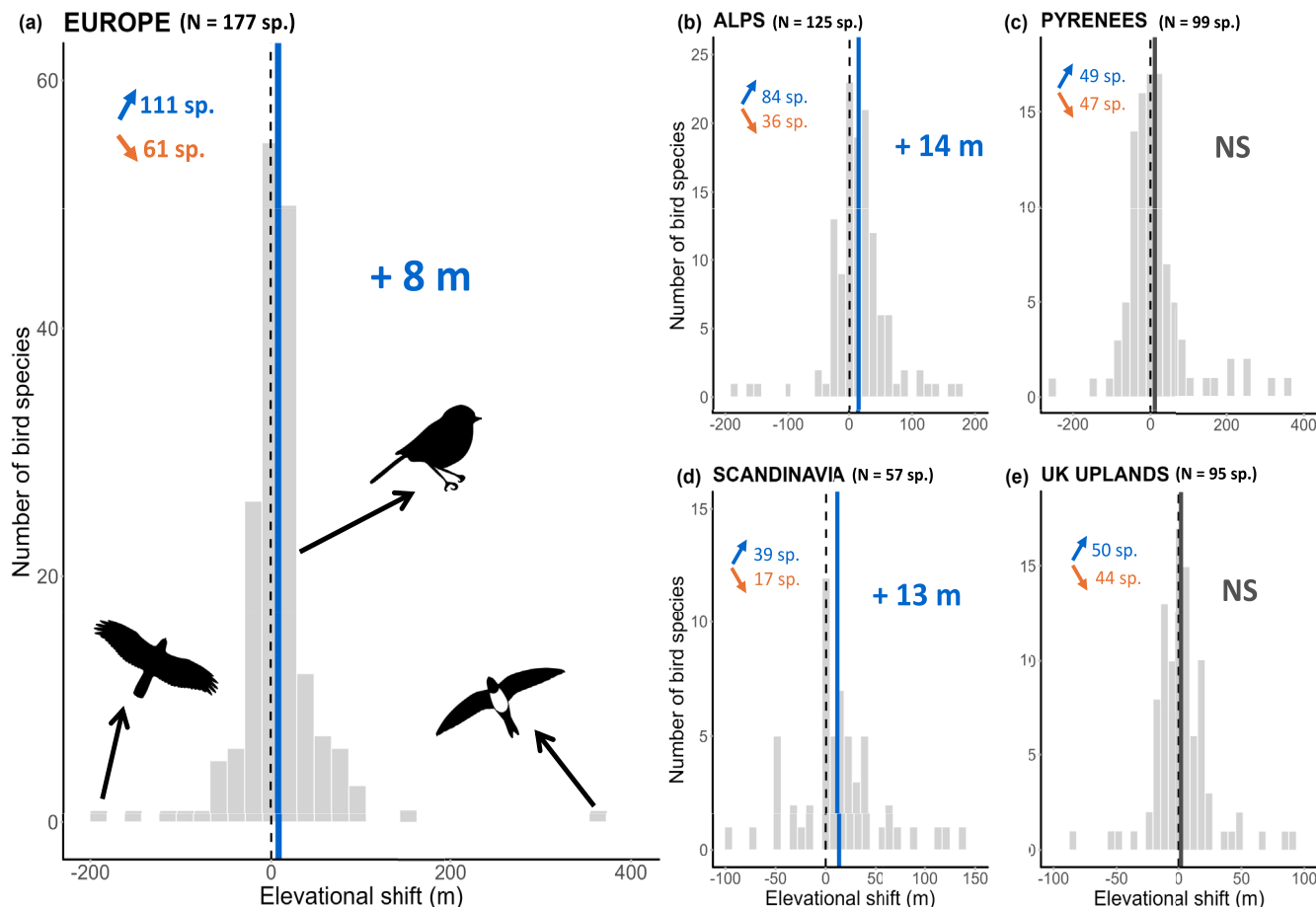
(without and with interaction terms) with weights using centred reciprocal values for the different mountain regions. The resulting pattern was similar to the model without weights (Appendix S1, Table S9). To test whether slope alone (not solar radiation) determines bird species abundances and shifts, we extracted the slope values of each survey point (using function 'slope' in QGIS, version 3.16.16) and created three regimes of slope based on quantiles: flat, medium, and steep. Then, we performed the exact same analyses as we did with solar radiation and found that the mean elevation of birds was significantly lower in the flatter areas and highest in the steeper areas (for detailed results, see Appendix S1, Table S10). Finally, to test whether the phylogenetic relationships of the species influenced the observed elevational shifts, we performed phylogenetic generalised linear mixed models (PGLMM) with Gaussian distribution and did not find significant differences compared with the main analyses (Appendix S1, Tables S11 and S12). For this, we used a consensus of 100 phylogenetic trees (Jetz et al. 2012) and R packages 'phyr' and 'ape' (Paradis and Schliep 2019; Li et al. 2020).

### 3 | Results

Related to our first study question investigating the effect of solar radiation on the mean elevations of bird species abundances, we found that mean elevations of bird abundances varied depending

on solar radiation regime: mean elevations were higher on average in the high solar radiation regime compared with the low (estimate = +21.5 m; 95% CI [15.52, 27.45];  $t = +7.1$ ;  $p < 0.001$ ) and the medium solar radiation regimes (estimate = +34.2; 95% CI [27.61, 40.79];  $t = -10.17$ ;  $p < 0.001$ ) (Figure 4a, Appendix S2 'Additional results', Table S1). In the Alps, we also found that the differences in mean elevations among solar radiation regimes were similar (Figure 4b), such that the mean elevation of bird abundances was significantly lowest in the medium solar radiation regime (estimate = -48.3 m; 95% CI [-56.50, -40.10];  $t = -11.55$ ;  $p < 0.001$ ). In the Pyrenees, we did not find significant differences between high and low solar radiation regimes but the mean elevations of bird abundances in the medium solar radiation regime were significantly lower (estimate = -48.5 m; 95% CI [-78.74, -18.36];  $t = -3.2$ ;  $p < 0.001$ ; Figure 4c). In Scandinavia, the mean elevations were lowest in the medium solar radiation regime but did not significantly differ from the mean elevations in the low solar radiation regime (Figure 4d). In UK uplands, we did not find differences in the mean elevations of bird abundances among the solar radiation regimes (Figure 4e; for detailed tables, see Appendix S2, Table S1; for post hoc test results, see Appendix S2 'Additional results', Table S2).

Related to our second study question investigating the variation in the rate of elevational shifts across and among different



**FIGURE 5** | Distribution of the rates of elevational shift (in meters) between study periods (2001–2004 and 2018–2021) for (a) the four European mountain regions combined, and separately for (b) the Alps, (c) the Pyrenees, (d) Scandinavia and (e) UK uplands. The y- and x-axis scale differs between panels. Dashed vertical line corresponds to an absence of shift between study periods ( $x=0$  m). The negative values indicate downhill shifts, and the positive values indicate uphill shifts. The bold vertical line corresponds to the average elevational shift across the species: Blue for significant average shift and dark grey for nonsignificant average shift. The values are obtained by averaging the elevational shift per species within all grids. In each panel, blue and orange arrows indicate the number of species showing uphill and downhill shifts, respectively.

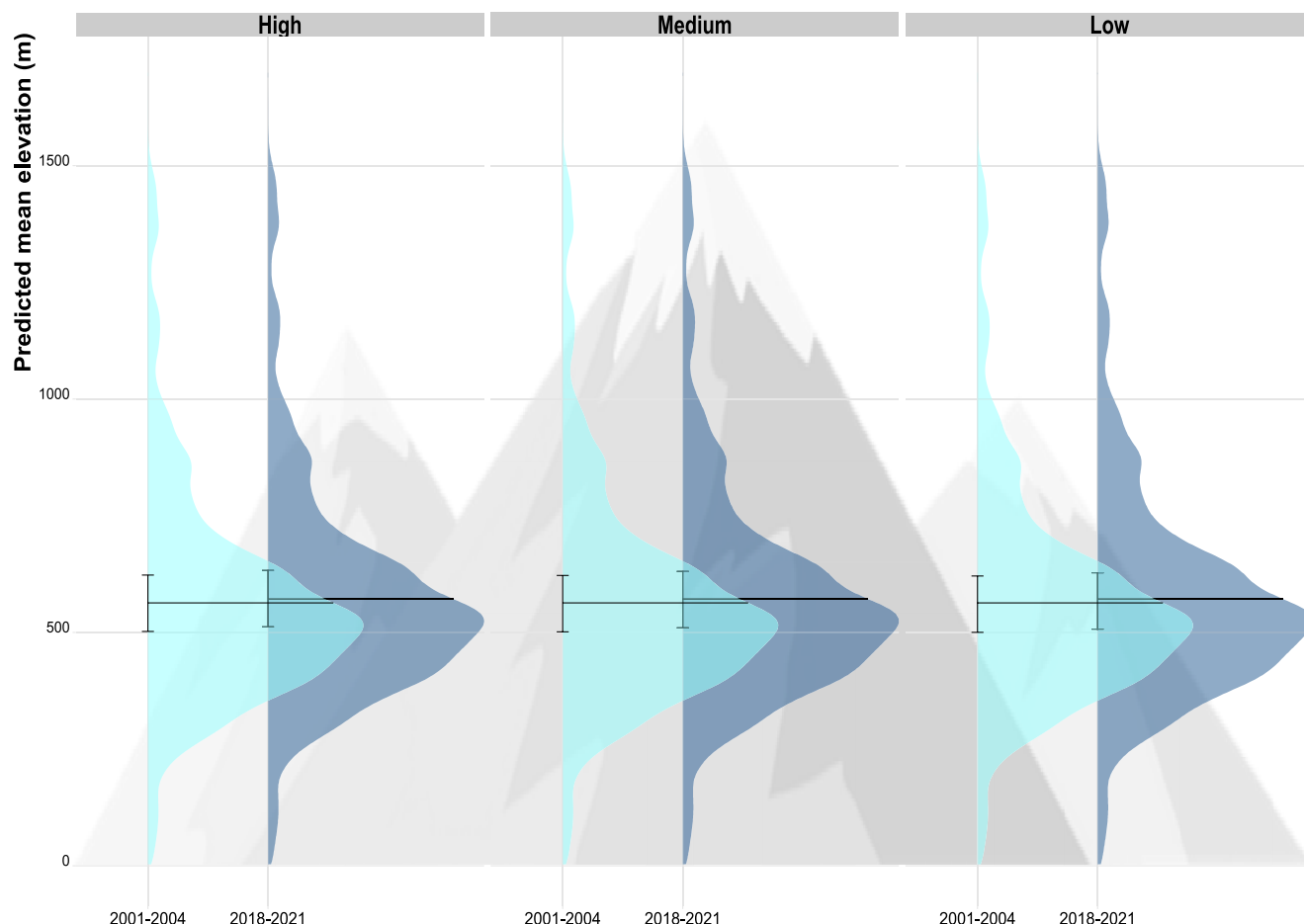
mountain regions, we found variations between species' responses. Of the 177 species included in the analysis, 111 species exhibited uphill shifts in their mean elevations and 61 species exhibited downhill shifts (Figure 5a; for the elevational shift values of each species, see Appendix S1, Table S2). These shifts varied widely across species, ranging from a 188 m downhill shift for the honey buzzard (*Pernis apivorus*) to a 366 m uphill shift for the alpine swift (*Tachymarptis melba*). On average, birds shifted uphill by 8.4 m between 2001–2004 and 2018–2021 (i.e., 0.5 m/year; 95% CI [3.69, 13.22];  $t=3.5$ ;  $p<0.001$ ) across all four mountain regions studied (Figure 5a, Appendix S2, Table S1). We found similar uphill shifts in the Alps (estimate = +11.6 m; 95% CI [5.54, 17.62];  $t=3.8$ ;  $p<0.001$ ) and Scandinavia (estimate = +12.1 m; 95% CI [4.64, 19.57];  $t=3.18$ ;  $p<0.01$ ) in the analyses at mountain region scale (Figure 5b,d, Appendix S2, Table S1). Uphill shifts were not significant in the Pyrenees or UK uplands. The rates and the extents of bird species' elevational shifts did not differ from the overall shift and when looking specifically within solar radiation regimes (Appendix S2, Figures S1–S5).

Related to our third study question investigating the variation in the rate of elevational shifts of bird abundances under different

solar radiation regimes, bird abundances shifted uphill independently of the amount of solar radiation. That is, the interaction term including study period and solar radiation regime was not statistically significant in any of the models (Figure 6, Appendix S2, Tables S1 and S4).

#### 4 | Discussion

We found that bird abundances across and within European mountain regions are centred at a higher elevation in areas receiving more solar radiation and at a lower elevation in areas receiving a medium amount of solar radiation. Moreover, at the European scale, we found that on average the bird abundances in mountain regions have shifted uphill over the past two decades. This pattern was seen when considering all studied mountain regions together but was only observed individually for the Alps and Scandinavia. While the Alps provided most of the data, additional analyses with regionally weighted models confirmed that our general findings were not exclusively driven by this region. Although microclimate (i.e., solar radiation) is an important determinant of elevational distributions of birds in European mountain regions, it did not mediate the rate of



**FIGURE 6** | Differences in predicted distribution of mean elevations of bird species among solar radiation regimes and between study periods (2001–2004 and 2018–2021) across the four European mountain regions studied ( $N=20,638$ ). The black horizontal lines represent the means of the distributions. The error bars represent the 95% confidence intervals.

long-term elevational shifts. That is, rates are similar regardless of the incoming energy regimes. Our data covered a large proportion of all breeding bird species occurring along the entire elevational gradient and allowed us to detect elevational shifts in the abundances of breeding birds as a whole across European mountain regions. Our results highlight that the responses of animal communities to abiotic conditions are complex when considering the full elevational gradient (Figure 6).

#### 4.1 | Amount of Solar Radiation Effects on the Elevational Distribution of Bird Abundances

The observed patterns of the mean elevations of bird species align with our hypothesis that solar radiation (and consequently local thermal conditions) plays a significant role in determining the elevational distribution of bird abundances within and across European mountain regions. Specifically, we observed that bird abundances are distributed on average at higher elevations on more exposed sites that receive more intense solar radiation. These patterns likely reflect both direct and indirect effects of solar radiation. Directly, warmer microclimates on exposed slopes can reduce thermoregulatory costs for birds, allowing species to persist at higher elevations (McKechnie and Wolf 2019). Indirectly, higher amounts of solar radiation

influence vegetation structure, that is, treeline being higher, and productivity, leading to greater plant biomass and higher abundance of insects and other invertebrate prey (Newton 2020; Schumm et al. 2020). Moreover, these high solar radiation sites tend to experience less snow cover and earlier snowmelt in the spring (Kormos et al. 2014), increasing the availability of higher-elevation habitats earlier in the season. This may allow birds to occupy these higher-elevation areas for breeding sooner. However, the mean elevation of bird species was lowest in areas in the medium solar radiation regime in the Alps and Pyrenees. Our topography analyses show that areas with a medium solar radiation amount are significantly flatter and at lower elevations than high or low radiation areas. Flat areas with medium radiation are typically in lowlands or mountain valleys. This likely explains the low mean elevation of the bird species' abundances found in areas receiving medium solar radiation as it is easier for bird species to colonise such areas. It is also possible that this is linked to land-use practices, as flat areas are easier for humans to manage than steep ones (Malek and Verburg 2020), offering more available habitats for example for the species associated with farmlands. However, confirming such an effect would require more detailed research that goes beyond the scope of this study. As we found consistent effects of solar radiation intensity on bird abundances along the elevational gradient in the different mountain regions separately and in all our sensitivity

analyses, we believe these patterns are universal. Differences in the abiotic conditions and the subsequent microhabitats likely create distinct ecological niches that shape birds' abundances along elevational ranges across mountain regions.

## 4.2 | Continental-Scale Uphill Shifts Driven by Strong Regional Responses

Across the four European mountain regions considered here, the mean elevation of bird species abundances has moved uphill at an average rate of 0.5 m per year, which is similar to rates that have been found in earlier studies and on also other species composition and taxa (Chen et al. 2011; Pearce-Higgins and Green 2014; Lenoir and Svenning 2015; Neate-Clegg et al. 2024). In practice, this means that a large portion of individual birds is shifting uphill consistently at a continental scale and that elevational shifts are not only driven by some individual occurrences at the range boundaries (Freeman et al. 2018; Couet et al. 2022). Presumably species are shifting to higher elevations to track cooler and wetter conditions as temperatures rise (Chen et al. 2011; Pecl et al. 2017). Indeed, warmer annual temperatures have been documented across Europe and are likely driving these shifts (Schär et al. 2004; Blunden and Arndt 2019). These uphill shifts also follow the uphill shifts of plants that have been observed in the different mountain regions (Frei et al. 2010). Contrary to our expectations, at the mountain region scale, birds only shifted uphill in the Scandinavian region and the Alps and their neighbouring areas. Given that climate warming has been strongest in Scandinavia and the Alps (Lehikoinen et al. 2019, Figure S1-1), this result indicates that climate warming is a strong driver of birds' elevational shifts. Another possible explanation for the observed uphill shifts is the spatial variation in land-use history and change in Europe. Indeed, southern European mountain regions (Pyrenees and Alps) have experienced recent land abandonment at high elevations, while land use has remained relatively stable in northern European mountain regions (MacDonald et al. 2000; Sitzia et al. 2010).

## 4.3 | Differences in Rate of Shift Among Europeans Mountain Regions

The rate of elevational shifts varied among the four European mountain regions studied. In the UK uplands, we observed no significant shift. This pattern is consistent with the findings of Massimino et al. (2015), who studied elevational shifts for 80 species in Great Britain. The absence of a measurable uphill shift in species elevational abundance may be attributed to the low annual rate of warming and to factors related to topography or the oceanic climate, which could mitigate general temperature increases in the UK uplands (Pearce-Higgins et al. 2009). Concerning the Pyrenees, the limited number of grid cells may pose a challenge for detecting a clear, consistent general pattern of shift. Furthermore, the lack of elevational shift in the Pyrenees is also consistent with the results of Franch et al. (2021) using presence-absence data for a set of 120 species in Catalonia. For Scandinavia and the Alps, we found elevational shifts of 0.7 m per year. A similar general pattern with an elevational shift of 0.9 m per year has already been found in Scandinavia (Couet et al. 2022). The slight deviation in

elevational shift rates between this study and the earlier study by Couet et al. (2022) may be attributed to the slight difference in the composition of studied species. Although uphill shifts have been found in earlier studies in the Alps, for example, repeated atlas surveys in Switzerland and Austria (Knaus et al. 2018; Teufelbauer et al. 2017), our results show lower average rates of uphill shifts compared to some fine-scale studies previously conducted in the region. For instance, Hallman et al. (2022) reported an average shift of +3.7 m per year based on abundance data, while Roth et al. (2014) found a rate of +5.3 m per year in Switzerland using occurrence data. These differences may reflect variations in study design, spatial scale or species composition. In particular, the inclusion of alpine specialist species in the Swiss studies, species that are underrepresented in our data set due to low sample sizes, could partly explain the higher shift rates observed. Alpine specialists are known to be more sensitive to climate change and may respond more rapidly by moving uphill (Hock et al. 2019). Moreover, the use of different types of data (occurrence vs. abundance data), metrics (median vs. mean) and lengths of study periods may further induce small differences in observed elevational shift rates in our study compared to earlier ones.

It is also possible that land-use change explains why the Alps are experiencing a faster shift than the other mountain regions. More precisely, in the Alps and its neighbouring ranges, natural afforestation after land abandonment may have increased the area of suitable habitat for forest species at higher elevations, leading to range expansions towards the mountain tops (Lasanta et al. 2015; Bani et al. 2019; Teufelbauer et al. 2017). At the same time, human encroachment into natural habitats at lower elevations is progressing fast. Both recreation, such as skiing or hiking, and land use, such as agriculture and livestock farming, are sprawling across most of these areas (Chamberlain et al. 2023). This may have reduced abundances and even caused local bird extinctions in the lowlands, shifting the overall distribution of the bird community uphill. The effects of land use and its complex interaction with climate change are still largely understudied and require more investigation to understand the relative importance of these two drivers (Howard et al. 2015, 2020; Santangeli 2024).

## 4.4 | Rate of Shift Is Unaffected by the Intensity of Solar Radiation

Contrary to our hypothesis, the rate of elevational shift in bird species abundance was independent of the amount of solar radiation, meaning that bird abundances shifted uphill at a similar pace in low, medium and high solar radiation areas. Ecologically, this suggests that bird distributional changes are responding uniformly to broader climatic pressures rather than being mediated by localised differences in abiotic conditions. Previous studies at fine spatial scales have shown that vegetation moves uphill faster on south-facing sites due to higher solar radiation and earlier snowmelt (Cannone et al. 2007; Nagy and Grabherr 2009; Devictor et al. 2012). Moreover, the uniform rates in abundance shifts might reflect that birds are experiencing spatially constant pressures to move to higher elevations across all microclimatic areas, possibly due to shrinking habitat suitability at lower elevations as temperatures

rise and/or increasing suitability at higher elevations (Rumpf et al. 2018).

#### 4.5 | Species-Level Variations

Finally, as with most community-level studies, we observed variations in species-level responses, with the majority of species having exhibited uphill shifts. Variations in elevational shifts between species likely reflect both species traits and local context (Warmer et al. 2025). Traits such as dispersal ability, habitat specialisation or longevity influence the capacity to track climate change, with mobile or generalist species shifting more readily than specialists or long-lived species (Couet et al. 2022; Hallman et al. 2022). At the same time, responses are strongly context-dependent. The local context dependency hypothesis suggests that regional conditions, such as habitat availability, land-use intensity or microclimatic heterogeneity, mediate how species respond (Platts et al. 2019). Species in heterogeneous landscapes may persist in microrefugia, while those in more uniform environments may be forced to shift. These interactions explain why even ecologically similar species can exhibit contrasting elevational shifts across regions.

#### 5 | Conclusions

Mountain regions represent relict ecosystems preserved from the ancient past to the present. As such, they harbour unique biodiversity, often warranting their listing as biodiversity hotspots (La Sorte and Jetz 2010; Antonelli et al. 2018; Rahbek et al. 2019). In the face of global change, mountain ecosystems and their unique remaining biodiversity are becoming progressively more threatened, mainly from climate and land-use change (Chan et al. 2024). Our findings underscore the universal nature of climate forcing on bird communities shifting uphill at the continental level. This in itself presents challenges for conservation, highlighting the need for multiscale conservation actions that integrate both climate adaptation and mitigation strategies. To this end, abiotic conditions may offer a nuanced understanding for prioritising conservation efforts (Kempainen et al. 2024). Though the rate of uphill shift proved to be uniform regardless of solar radiation regime, bird communities are distributed higher up on sites receiving higher solar radiation, usually south-facing. This leaves them less space to move further uphill before reaching the summit, highlighting the urgency for their conservation. The scientific evidence provided here can help achieve effective conservation planning in mountain ecosystems and underscores the important role of microhabitat factors driving biodiversity distributions between and within mountain regions at a continental scale.

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#### Conflicts of Interest

The authors declare no conflicts of interest.

#### Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.17292549>. The raw data cannot be shared due to data protection regulations but are available upon request from the national data providers.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **APPENDIX S1:** Additional methods and sensitivity analyses. **FIGURE S1:** Spatial distribution of annual temperature trends over the study period (2001–2021) in Europe. **TABLE S1:** Table of the monitoring schemes in different European countries and mountain regions. **TABLE S2:** Species list and averaged estimated elevational shifts. **FIGURE S2:** Steepness (in degrees) and elevation (in meters) of survey points according to the different solar radiation regimes. **FIGURE S3:** Flowchart illustrating the steps of data handling and selection for the Alps study region. **FIGURE S4:** Flowchart illustrating the steps of data handling and selection for the Pyrenees study region. **FIGURE S5:** Flowchart illustrating the steps of data handling and selection for the Scandinavian study region. **FIGURE S6:** Flowchart illustrating the steps of data handling and selection for the UK uplands study region. **FIGURE S7:** Distribution of the survey points along the 100-m elevational belts. **EQUATIONS.** Detailed equations for the mean elevation estimations of each species abundance. **MODEL EQUATIONS.** Detailed equations of the linear mixed-effects model without and with interaction. **FIGURE S8:** Spatial autocorrelations of the linear mixed model residuals. **TABLE S3: and S4** Results of the sensitivity mixed model analyses for different combinations of the data selection criteria. **TABLE S5: and S6** Results of the mixed model analysis on the mean elevation of bird species abundances without the aquatic species. **FIGURE S9:** Correlation plot between the different solar radiation buffer sizes. **TABLE S7: and S8** Results of the mixed model analysis on the mean elevation of bird species abundances using 25% and 75% quantiles for the solar radiation categorisation. **TABLE S9:** Results of the European weighted mixed model analysis on the mean elevation of bird species abundance. **TABLE S10:** Results of the European mixed model analysis on the mean elevation of bird species abundances in relation to the steepness of the slope. **TABLE S11: and S12** Results of the phylogenetic mixed model analysis on the mean elevation of bird species abundance. **APPENDIX S2:** Additional results. **TABLE S1:** Full results of the European mixed model analysis on the mean elevation of bird species abundance. **TABLE S2:** Results of the post hoc tests on the mean elevation of bird species abundance. **TABLE S3: and S4** Results of the mixed model analysis on the mean elevation of bird species abundance for the different mountain regions. **FIGURE S1:** Distribution of the rates of elevational shift among 177 bird species between study periods (2001–2004 and 2018–2021).

**FIGURE S2:** Distribution of the rates of elevational shift among 177 bird species between study periods (2001–2004 and 2018–2021) for the Alps. **FIGURE S3:** Distribution of the rates of elevational shift among 177 bird species between study periods (2001–2004 and 2018–2021) for the Pyrenees. **FIGURE S4:** Distribution of the rates of elevational shift among 177 bird species between study periods (2001–2004 and 2018–2021) for Scandinavia. **FIGURE S5:** Distribution of the rates of elevational shift among 177 bird species between study periods (2001–2004 and 2018–2021) for the UK uplands.

## Biography

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