



Elevational shifts in bird communities reveal the limits of Alpine protected areas under climate change

Riccardo Alba^{*}, Dan Chamberlain

Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Turin, Italy

ARTICLE INFO

Keywords:

Alpine birds
Alpine grasslands
CTI
Habitat conservation
Range shifts
Treeline

ABSTRACT

Mountains are global biodiversity hotspots that are increasingly vulnerable to climate change. In the European Alps, rising temperatures and land-use changes have caused shifts in vegetation, impacting bird communities, particularly alpine specialists. Protected areas (PAs) are critical for buffering climate effects and safeguarding cold-adapted species, but their effectiveness in a warming world remains unclear. This study assessed shifts in bird assemblages across the elevational gradient in the Italian Alps over 13 years, using point counts to sample bird communities, and the Community Temperature Index (CTI) as a measure of community thermal tolerance. By comparing shifts inside and outside PAs, we identified key species and elevation bands driving CTI changes and modelled species-specific elevational shifts. Results revealed a critical divergence: CTI remained stable outside PAs, but increased sharply within PAs, reflecting a 1.19 °C rise in mean annual temperature in the study area. Initially, PAs harboured cold-adapted species, but over time, their bird assemblages became more similar to those outside PAs, likely driven by a decline in high-elevation species. The most marked changes occurred near the treeline, a key zone for sensitive species. CTI increases were driven by treeline and alpine grassland species which are most vulnerable to vegetation encroachment. Our findings suggest that PAs facilitate upward shifts, but are insufficient to prevent declines in populations of high-elevation species under rapid warming. Adaptive conservation strategies, such as targeted grazing, are urgently needed to counteract vegetation shifts, preserve habitat heterogeneity, and maintain elevational connectivity. Continuous monitoring is crucial to track ecological changes and refine conservation priorities, ensuring mountain biodiversity resilience under climate change.

1. Introduction

Mountains are unique ecosystems that harbour high levels of biodiversity, and play a crucial conservation role at the global scale (Myers et al., 2000; Körner, 2004; Noroozi et al., 2018). The Alps are particularly rich in biodiversity, hosting diverse plant and animal species adapted to high elevation habitats (Nagy et al., 2003; Antonelli et al., 2018; Ramel et al., 2020). However, mountain areas face numerous threats, particularly from climate change (Beniston, 2006; Gobiet et al., 2014), with rising temperatures causing elevational shifts in vegetation zones (Theurillat and Guisan, 2001; Leonelli et al., 2011), and subsequent consequences for animal (Baur and Baur, 2013; Ferrarini et al., 2017) and plant (Greenwood and Jump, 2014) species distributions, especially at high elevations. Concurrently, land abandonment has altered traditional land-use practices, resulting in grassland degradation and vegetation encroachment (Gehrig-Fasel et al., 2007; Anselmetto

et al., 2024), with the decline of species that rely on open landscapes (Laiolo et al., 2004; Koch et al., 2015) and the rise of generalist species. The combined effects of these changes pose significant challenges to the preservation of specific Alpine habitats and their associated biodiversity.

Among the diverse taxa impacted by these changes, mountain birds are especially vulnerable (Alba et al., 2022; Chamberlain et al., 2023a). Climate change is driving many mountain bird species towards higher elevations in search of suitable habitats, as warmer temperatures render lower altitudes less hospitable (Freeman et al., 2018; Scridel et al., 2018). Additionally, the advance of shrubs and forests due to land abandonment further reduces the availability of open habitats (Laiolo et al., 2004), making alpine grassland birds one of the most threatened bird categories (Chamberlain et al., 2016). While birds at the upper limit of their range may expand their distributions towards higher elevations, they could be constrained by the topography of mountain peaks, limiting their ability to find suitable habitats (Chamberlain et al., 2013; Freeman

^{*} Corresponding author.

E-mail address: riccardo.alba@unito.it (R. Alba).

et al., 2018). Conversely, species associated with warmer climates may colonize newly available environments towards higher elevations (Scridel et al., 2017), leading to community homogenization and a loss of functional diversity, as generalist species replace high-mountain specialists (García-Navas et al., 2020). This upward shift in bird populations is not merely a response to temperature, but also reflects the complex interplay between climate and land-use changes that shape mountain habitats and consequently their elevational distributions (Neate-Clegg and Tingley, 2023). Furthermore, since birds can be easily detected and reflect well changes in their habitat, they are excellent bioindicators and thus sentinels of the changes occurring in mountain environments (Chamberlain et al., 2012; Lehikoinen et al., 2014). Understanding these dynamics is therefore essential for developing effective conservation strategies in mountains (Pearce-Higgins and Martin, 2023).

Protected areas (hereafter PAs) are key components of global conservation efforts, serving as refuges for biodiversity (Le Saout et al., 2013; Pimm et al., 2014), although their conservation role has been questioned in a climate change scenario, since PAs are static while species distributions are projected to shift (Thomas et al., 2012; Trisos et al., 2020; Lehikoinen et al., 2021b). As climate change influences ecosystems worldwide, PAs are vital for the protection of species and habitats (Hannah, 2001; Gaüzère et al., 2016). PAs in the Alps play a critical role in conserving mountain biodiversity by offering a buffer against the impacts of environmental change (Gaston et al., 2008), even though climate change is threatening the effectiveness of PAs across Europe (Araújo et al., 2011). These areas provide stable, often cooler, microhabitats that can mitigate the effects of warming temperatures, thus supporting species adapted to cold environments (Santangeli et al., 2017; Scridel et al., 2018). Alpine birds, many of which are specialized and sensitive to temperature increases, benefit from the continuity of these habitats, which help maintain suitable conditions and reduce the likelihood of upward range shifts (Hamilton, 2002). Additionally, PAs limit human disturbance (Cremer-Schulte et al., 2017) that can compound climate stressors. By safeguarding these ecologically intact landscapes, alpine PAs can promote resilience in mountain ecosystems, allowing species to adapt more gradually to changing climatic conditions. They will thus likely play a critical role in the future (Brambilla et al., 2022).

One valuable tool that has been widely used to assess the impacts of climate change on bird communities is the Community Temperature Index (CTI) (Devictor et al., 2008). This index quantifies the average temperature preferences of each species in a community through the Species Temperature Index (STI), providing insights into how species occurrence may change within communities in response to climate and environmental changes. While many studies have focused on latitudinal shifts in Europe, considering large scale surveys during the breeding (Kampichler et al., 2012; Lindström et al., 2013; Gaüzère et al., 2016; Ramón-Martínez and Seoane, 2024) or/and non-breeding season (Santangeli and Lehikoinen, 2017; Lehikoinen et al., 2021a), there remains a significant gap in research specifically addressing the upward shift of bird communities in mountain regions with this approach. Studies that have considered such elevation shifts have typically worked at relatively large scales of 1 km² or 2 km² grids (Roth et al., 2014; Gaüzère et al., 2017). Since complex topography and rough terrain in mountains often mean conditions change rapidly over short (horizontal) distances, leading to the local co-occurrence of both cold- and warm-dwelling species (Lenoir et al., 2013), large-scale studies might not capture elevation shifts accurately, and thus finer-scale studies are more appropriate (Chamberlain et al., 2013). Furthermore, the role of PAs in buffering CTI changes has been investigated at the national scale (Santangeli et al., 2017; Lehikoinen et al., 2021b), but never along elevational gradients in mountain regions, where only a few localized studies have explored elevational changes using other methodologies (e.g. Popy et al., 2010; Bani et al., 2019).

The aims of this study were: i) to investigate how bird community

thermal tolerance (as expressed by the CTI) in the Alps has shifted in elevation over the last 13 years, ii) to assess if PAs have played a role in buffering changes in CTI, iii) to identify the species that contribute most to a change in CTI, iv) to determine at which elevations has the change in CTI been most marked, and v) to analyse species-specific patterns in elevational change to test whether changes occurred in the leading or trailing edge of a given species. This research will fill a critical gap in the literature, contributing to the broader knowledge of biodiversity responses to climate change in mountain habitats, informing conservation efforts and management strategies tailored to the critical challenges faced by these high elevation ecosystems.

2. Material and methods

2.1. Study area and survey design

The study was conducted in a large area of around 2000 km² in high altitude habitats of the western Italian Alps from the Germanasca Valley in the south (44°51'31" N; 7°03'47" E) to the Lys Valley in the north (45°52'06" N; 7°48'19" E), ranging in elevation from 1700 to 3100 m (Fig. 1). In this area, the montane forest zone is dominated by larch *Larix decidua*, with shrub species such as juniper *Juniperus communis* and alpenrose *Rhododendron ferrugineum* occurring around the treeline (c. 2200 m). Open habitats consist of seasonal pastures and alpine grasslands at higher elevations above the treeline. Scree and rocky areas are found above c. 2700 m. Surveys were conducted on point counts located on elevational transects that were previously surveyed by Chamberlain et al. (2013). The original survey sites were identified based on the presence of the three main vegetation zones, larch-dominated forests, shrub-dominated ecotones above the treeline and alpine meadows, with some areas including the largely unvegetated nival zone. Sites near villages, tourist developments or ski-pistes were excluded, maintaining a minimum distance of 330 m from these features. Transects, spaced at least 1 km apart, were initially selected at random. However, due to the challenging terrain, the closest footpath to the chosen transect was often used. Point counts were located at a minimum distance of 200 m between each other, or at the first suitable location after this distance. Suitable survey areas were those free from obvious disturbances (e.g., occupied human habitation, livestock) or factors that could hinder detectability (e.g., large cliffs, noisy streams) within a 100 m radius.

We downloaded the shapefile of the Natura 2000 network from the European Environment Agency (EEA 2022; <https://www.eea.europa.eu>) to identify the boundaries of PAs in Italy. Using this dataset, we overlaid the Natura 2000 boundaries onto our transect locations to classify each point count as either inside a protected area (PA) or outside a protected area (non-PA). This classification was based on whether the point was contained within the spatial extent of the Natura 2000 sites. The mean and SD for point elevation in non-PAs were 2112.22 ± 256.79 m, while for points inside PAs were 2225.90 ± 270.65 m. See Table S1 for details on the PAs included in the study.

Sampling took place during 2022–2023 (hereafter the second period) by revisiting 28 transects for a total of 257 point counts that were previously surveyed in 2010–2012 (hereafter the first period, see Chamberlain et al., 2013 for more details).

2.2. Bird surveys

Point counts in the second period were carried out by the same observer (RA) according to the standard method (Bibby, 2000), using a 10 min count period. Following Chamberlain et al. (2013), surveys were preceded by a 5 min settling period. At each point, the observer recorded all birds seen and heard within a 100 m radius, noting for each individual contacted its activity using standard activity codes (Bibby, 2000). For each registration, the distance from the observer was estimated with the aid of a laser range finder. Point counts were carried out from 1 h after sunrise until midday and took place in opportune weather

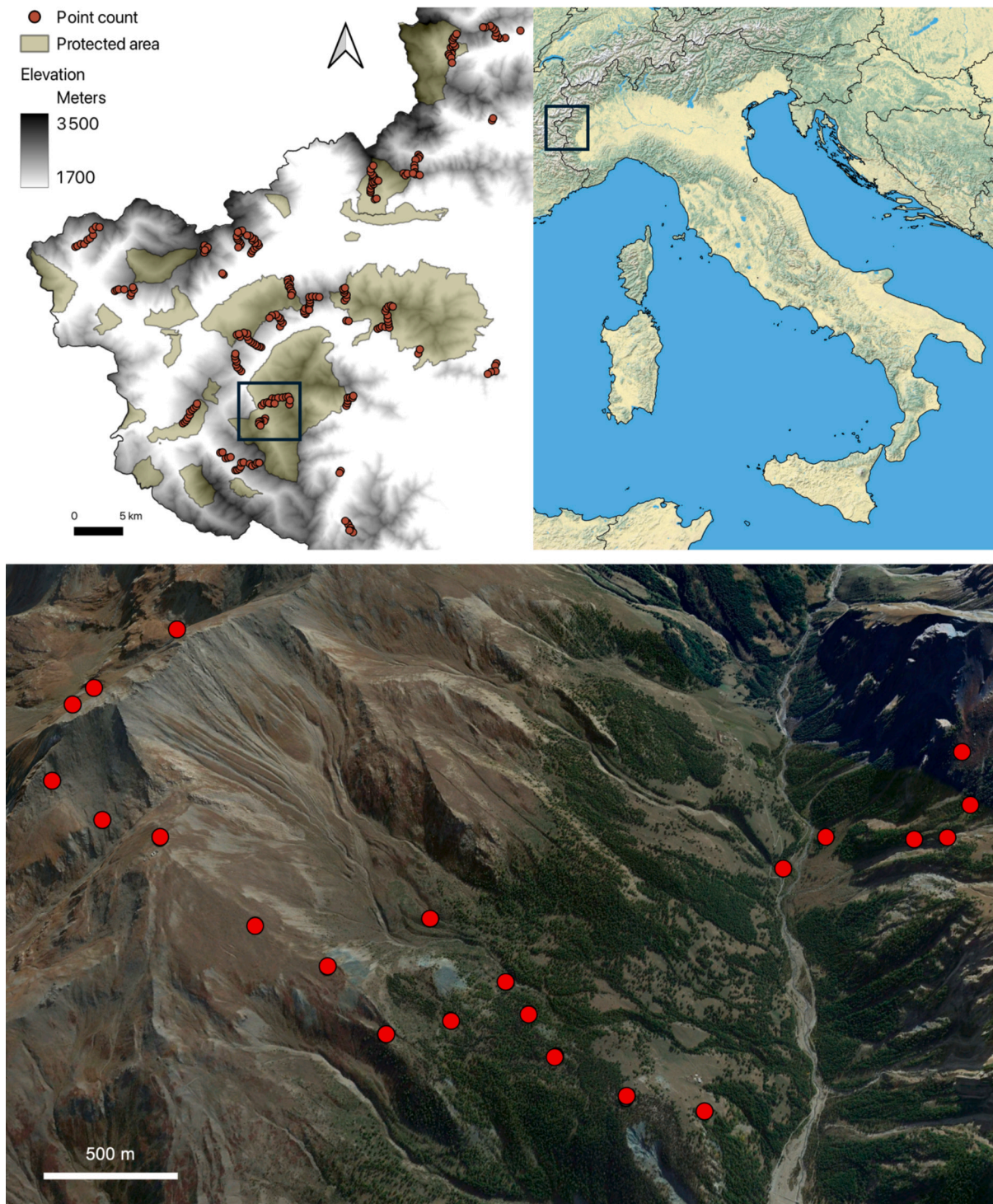


Fig. 1. Map of the study area with point counts along the elevational gradient in the Western Italian Alps. The image below shows in detail examples of two elevational transects with point counts in Val Troncea Natural Park (Pragelato, Turin province).

conditions (i.e. good visibility, no rain or strong winds). For any given point, surveys in the second period were carried out at around the same date as the first period, within a 7-day period of the survey date of the first period, to control for potential seasonal effects.

Since the observer (RA) that revisited the point counts was different from the one of the first period (DC), a subset of 41 point counts (> 15 % of the total sample) was carried out simultaneously in the second period, but independently by the two observers, to test for differences in detectability between them (see Statistical Analyses). These surveys

were carried out on the same day by both observers, but at slightly different times, the second observer waiting for a period of c. 30 min after the first observer had set out on a given transect before setting out themselves. In this way, the surveys were independent, but were subject to the same seasonal and meteorological conditions.

2.3. Climate data and community temperature index (CTI)

We retrieved climate data for the Piemonte region from Arpa

Piemonte (Arpa Piemonte, 2021) to assess trends in temperature in the period 1990–2020 across the study area. Although our data extended to 2023, we limited our analysis to 2020 due to the unavailability or incompleteness of data for subsequent years. We used mean annual temperature, calculated as the mean of average daily temperature across the year, measured at eight weather stations scattered across the Piemonte region in north-western Italy (Arpa Piemonte, 2021).

To assess potential elevational shifts in bird communities between the two periods, we calculated the Community Temperature Index (CTI) for each bird community in each point count. The CTI represents a weighted mean of species-specific temperature niches within a community, based on the Species Temperature Index (STI) (Devictor et al., 2008; Devictor et al., 2012a, b). The CTI was calculated as:

$$CTI = \frac{\sum (STI_i \times Abundance_i)}{\sum Abundance_i}$$

where STI_i and $Abundance_i$ are the Species Temperature Index and abundance of a given species i respectively.

The European breeding range of each species, retrieved from BirdLife International (BirdLife International, 2023), was used as the geographic range from which the STI was calculated (Devictor et al., 2008). Since these range polygons derived from BirdLife International were found to overestimate the actual extent of suitable habitats compared to habitat suitability models (Brambilla et al., 2020), we refined these polygons to achieve greater accuracy. Specifically, we adjusted each species' range by incorporating its documented elevational limits in Europe, obtained from Birds of the World (Billerman et al., 2022). This correction ensured that the geographic ranges used for the STI calculation more accurately reflected the species' actual ecological and habitat preferences. When elevational range was not clearly defined, we defined it or corrected it based on expert opinion. Subsequently, we superimposed each range with the mean temperatures of the breeding season months (May–July) downloaded from WorldClim version 2.1 climate data for 1970–2000 (<http://www.worldclim.org>), and then calculated the STI. It is important to underline that the STI is not an absolute measure of the species temperature niche because it does not take into account the niche breadth, yet it can be considered a reliable index of a species' temperature affinity (Devictor et al., 2012a, b). Therefore, a high CTI for a given bird community represents a community dominated by warm-dwelling species, whereas a low CTI represents a community dominated by cold-dwelling species.

2.4. Statistical analysis

2.4.1. Temperature changes

We tested for significant changes in mean annual temperature in our study area by fitting a Linear Mixed Model (LMM) using the R package *lme4* (Bates et al., 2003) with annual temperature as the response variable and year as a predictor. The weather station where data were collected was fit as random term with eight-levels.

2.4.2. Detectability

Before the analyses on bird communities, we tested for differences in bird detection between observers by comparing the communities sampled simultaneously, but independently, by both observers. We carried out two Generalized Linear Mixed Models (GLMMs) with a Poisson family and log link function using species richness and bird abundance for each point as response variables and observer as a two-level categorical predictor. Point identity and site were specified as nested random factors to account for spatial correlation in the analysis. Furthermore, we performed a Non-metric Multidimensional Scaling (NMDS) using the *metaMDS* function from the *vegan* R package (Oksanen et al., 2024) using the Bray-Curtis dissimilarity index to quantify differences in species composition among sites. The NMDS was conducted with two dimensions ($k = 2$) and a maximum of 100 random

starts (trymax = 100) to ensure convergence to a stable solution. To formally test for significant differences in community composition between observers, we conducted a Permutational Multivariate Analysis of Variance (PERMANOVA) using the *'adonis2'* function. The community matrix was analysed with respect to the observer factor and a total of 999 permutations were used to assess the significance of observed differences. We checked for homogeneity of dispersion among groups using the *'betadisper'* function, which assesses the variability of communities in multivariate space.

When including all birds (i.e. singing, calling, seen with no vocal activity), the analyses revealed significant differences in bird abundance (Chisq = 7.90, p value = 0.005) and species richness (Chisq = 4.60, p value = 0.032) between observers. We subsequently repeated the analyses by removing records of calling birds, as calls are more prone to identification errors between observers compared to songs. In these cases, there were no significant differences in bird abundance (Chisq = 10.15, p value = 0.312) or species richness (Chisq = 0.48, p value = 0.489). In both cases (i.e. including all records, or discarding calling birds), there were no differences in community structure ($F_{(1,115)} = 0.97$, p value = 0.438, Fig. S1) meaning that the bird communities were equally sampled by the two observers (i.e. the observers had similar detection rates in surveying bird communities). Therefore, for all subsequent analyses, we discarded all records of birds that were identified only by their calls to compare the two periods without any bias in detection rates. Moreover, we excluded birds that were flying over the point, but did not show evidence of interacting with it (e.g. soaring birds of prey and aerial foragers such as martins and swifts, which can move long distances between breeding sites and foraging areas and thus cannot be reliably associated with the habitat and climate of a given point).

2.4.3. Changes in CTI

We tested for significant changes in CTI by including period (first or second, i.e. 2010–2012 and 2022–2023), a factorial variable PA status (iPA or non-PA) and their interaction, in a Linear Mixed Model (LMM). We specified the CTI of each point as the response variable. Significance was assessed using chi-squared tests on change in deviance with the *anova* function from the *car* package (Fox et al., 2012). Point identity and site were used as nested random factors to account for spatial correlation in the analysis (because there were multiple observations per point and multiple points per transect). We checked goodness-of-fit by visually inspecting residual plots and qq-norm plots using *DHARMA* package (Hartig, 2018), without any indication of poor model fit.

2.4.4. Sensitivity analyses

To explore which species may have driven the changes in CTI in the bird communities, and at which elevation along the elevational gradient the changes occurred, we conducted two sensitivity analyses. First, we fit a LMM with the CTI of each point as the response variable, using period as two-level categorical predictor and point identity and site as nested random factors as previously. Using the model's parameter estimates, we calculated the overall CTI change ($\Delta CTI_{\text{general}}$) between the two periods. We then repeated this process, each time removing one species from the dataset and recalculating ΔCTI ($\Delta CTI_{\text{species } i}$ where i is a given species), allowing us to assess the contribution of individual species to CTI changes. Subsequently, we subtracted each $\Delta CTI_{\text{species } i}$ from $\Delta CTI_{\text{general}}$ and plotted the overall results in a random forest plot. If removing a given species produced positive values (i.e. $\Delta CTI_{\text{species } i} < \Delta CTI_{\text{general}}$), that species would have contributed to an increase of CTI in the second period. On the contrary, if removing a species produced negative values (i.e. $\Delta CTI_{\text{species } i} > \Delta CTI_{\text{general}}$), that species would have contributed to a decrease of CTI. Note that, for this analysis, we used only species that were contacted during both periods in order to assess the change in elevation; species that were contacted only in one period are addressed at the beginning of Results.

We adopted a similar framework to the above analysis to assess at

which elevation the changes in CTI had occurred. We divided our elevational range into five elevational categories and categorized them in habitat categories to help visualize the results (1700–2000 = montane forest, 2000–2300 = treeline ecotone, 2300–2600 = alpine grasslands, 2600–2900 = rocky scree, 2900–3100 = nival zone). In a similar way to the species sensitivity analysis, we removed from the general dataset one interval at a time and re-calculated the ΔCTI ($\Delta\text{CTI}_{\text{interval } i}$ where i is a given interval), subtracting it from $\Delta\text{CTI}_{\text{general}}$. If removing a given interval produced positive values (i.e. $\Delta\text{CTI}_{\text{interval } i} < \Delta\text{CTI}_{\text{general}}$), that interval contributed to increasing the CTI of the overall community, suggesting that an increase in warm-dwelling species, or a decrease in cold-dwelling species, had occurred at those elevations. On the contrary, if removing an interval produced negative values (i.e. $\Delta\text{CTI}_{\text{interval } i} > \Delta\text{CTI}_{\text{general}}$), an increase in cold-dwelling species or a decrease in warm-dwelling species had occurred.

2.4.5. Shifts in individual species

As a final analysis, we carried out Linear Models (LMs) for species with a reasonable sample size (n points > 20) using the elevations of the points where the species was contacted as a response variable and period as a two-level categorical predictor. Site was initially used as random factor to account for spatial correlation in the analysis in an LMM, but was subsequently dropped due to convergence problems. As an alternative, we included the spatial coordinates (latitude and longitude) as covariates in our models to account for potential spatial autocorrelation. We then plotted the results using the mean elevations and first and third quartiles as error bars for the first and second period to highlight the species' distribution shifts. We deliberately opted for quartiles instead of 95 % confidence intervals as we were interested in showing changes in trailing and leading edges of the distributions (i.e. quartiles are not symmetrical in contrast to confidence intervals). We grouped species into habitat categories based on the mean elevation derived from model parameters to visually aid interpretation. All analyses were performed using R software version 4.4.1 (R Core Team, 2024).

3. Results

During the first period (i.e. 2010–11–12), 59 species were contacted, while during the second (i.e. 2022–2023) we recorded 66 species. The mean species richness during the first period was 4.86 ± 2.73 (min = 1, max = 15) while during the second it was 4.88 ± 2.68 (min = 1, max = 14). PAs had a mean species richness of 7.59 ± 3.73 (min = 1, max = 18), while non-PAs had 7.41 ± 3.73 (min = 1, max = 19). There was a significant increase in mean annual temperature over time across the region in the period 2010–2020 (Chisq = 55.51, $p < 0.001$; Fig. S2), the mean temperature being 12.78 ± 0.29 °C in 2010 and 13.97 ± 0.29 °C in 2020. In the first period, PAs showed lower CTI values compared to non-PAs, but during the second visit, CTI values were approximately equal between PA and non-PA sites, meaning that CTI significantly increased inside, but not outside, PAs over time (Chisq = 5.47, $p = 0.019$; Fig. 2). There was a non-significant overall increase in CTI between the two periods (Chisq = 1.74, $p = 0.187$; Fig. S3a), and CTI differed significantly between PAs and non-PAs (Chisq = 8.12, $p = 0.004$; Fig. S3b, see Table S2 for full results).

Sensitivity analyses showed that the species contributing the most to an increase in CTI were generally species tied to alpine grasslands (e.g. alpine chough *Pyrrhocorax pyrrhocorax*, water pipit *Anthus spinoletta*, skylark *Alauda arvensis*) and species characteristic of shrubby habitats typical of the treeline ecotone (e.g. rock bunting *Emberiza cia*, wren *Troglodytes troglodytes*, linnet *Linaria cannabina*), but also montane forest species (e.g. coal tit *Periparus ater*, see Fig. 3a). Furthermore, the greatest increases were shown for the elevational intervals between 2000 and 2300 m around the treeline ecotone, and to a lesser extent in montane forest. By contrast, there were smaller changes towards higher elevations (Fig. 3b). See Table S3 for full results.

Species-specific models in elevational change highlighted that most of the distribution changes occurred at the treeline, with species such as dunnock *Prunella modularis*, crossbill *Loxia curvirostra*, and cuckoo *Cuculus canorus* showing a significant increase in elevation over the last decade. Notable upward shifts were also observed in alpine grassland species, including water pipit *Anthus spinoletta*, northern wheatear *Oenanthe oenanthe*, and black redstart *Phoenicurus ochruros*. In montane

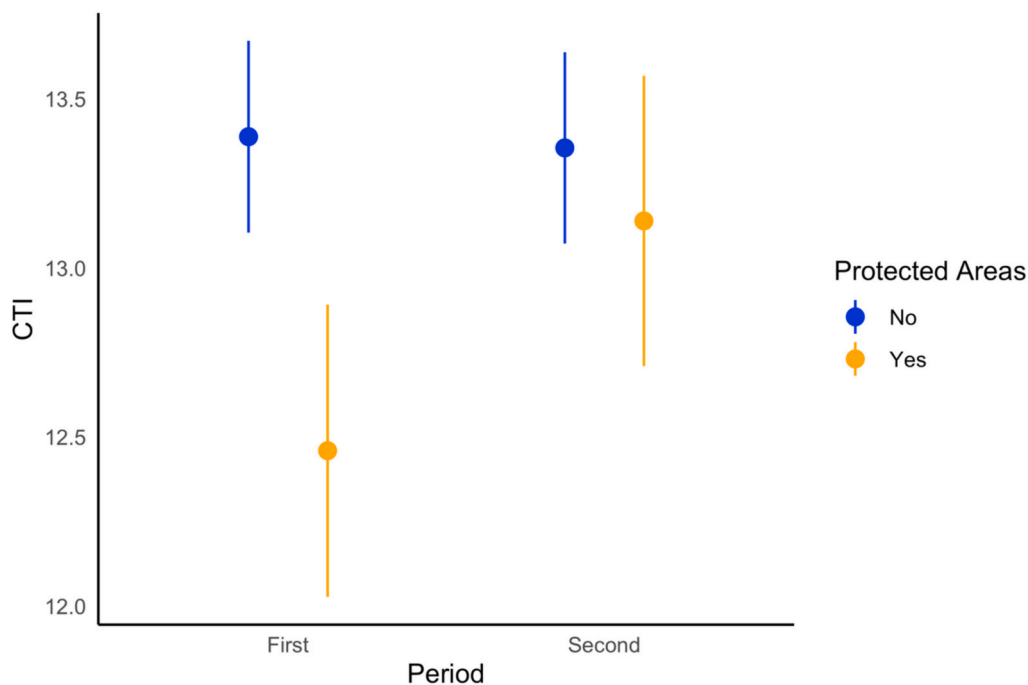


Fig. 2. Changes in CTI between the first and second periods and between sites included ($n = 78$) or not included ($n = 176$) in protected areas, specifying an interaction term. Mean and 95 % confidence intervals are shown. See Table S2 for full results.

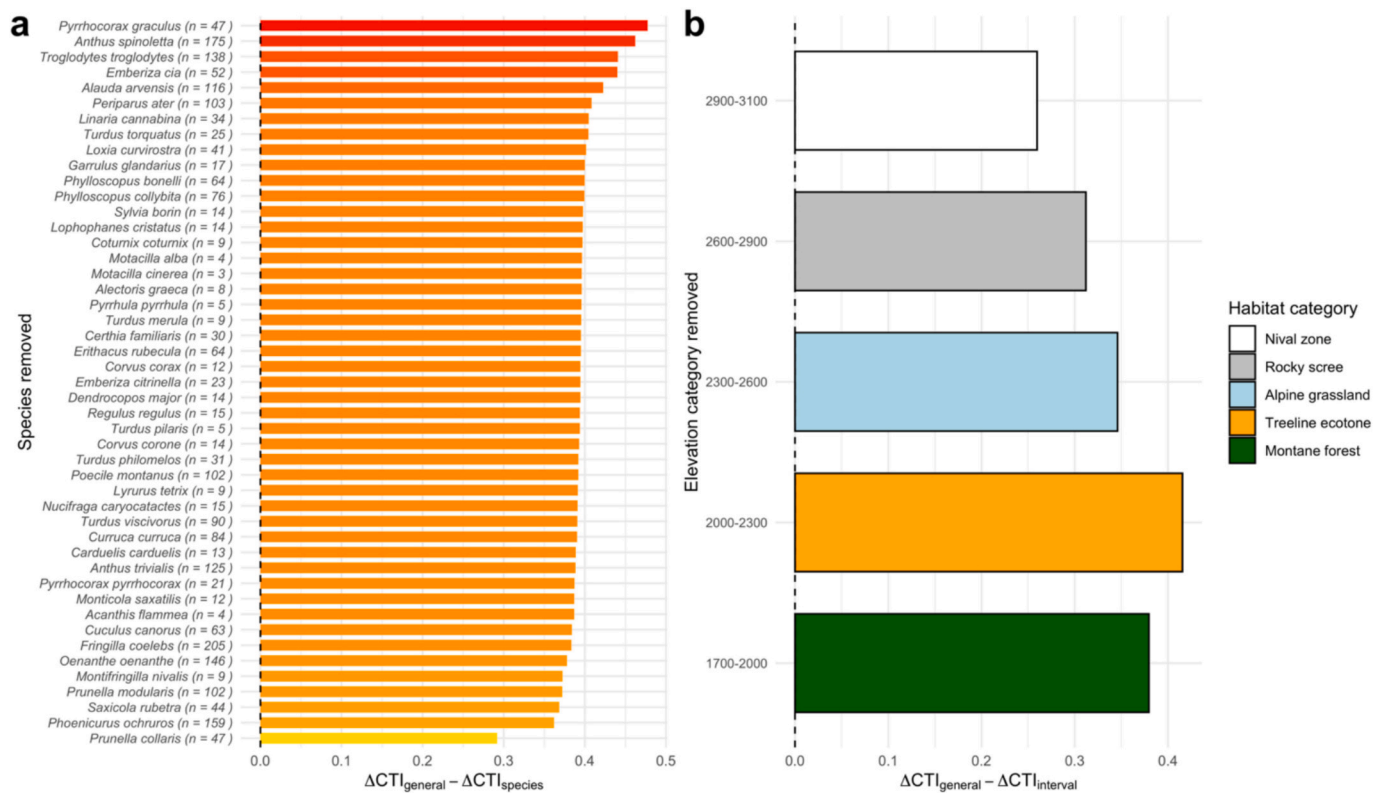


Fig. 3. Differences between $\Delta CTI_{general}$ (i.e. with all species included) and $\Delta CTI_{species}$ (i.e. with a given species removed, see y-axis for species and sample size) (a) and differences between $\Delta CTI_{general}$ (i.e. with all elevation intervals included) and $\Delta CTI_{interval}$ (i.e. with a given elevation interval removed, see y-axis) (b). Species bars range from yellow to red based on the contribution to an increase in CTI. Note that the plot shows only species contacted in both periods. Elevational intervals were categorized in habitat categories to aid visualization, starting from lower elevations and going upwards: montane forest (green), treeline ecotone (orange), alpine grasslands (light blue) and nival zone (white). See Table S3 for full results. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

forest habitats, the coal tit *Periparus ater* showed a significant increase in elevation, while the wren *Troglodytes troglodytes* transitioned from montane forest habitat into the treeline ecotone. While most species appeared to shift both their trailing and leading edges upslope, the leading edge showed a more pronounced change for some species (Fig. 4). See Table S4 for full results.

4. Discussion

This study has highlighted significant shifts in bird communities along the elevational gradient in the Alps over the past decade with different species-specific responses, emphasizing the role of climate change and protected areas in shaping these dynamics. While the overall CTI did not change, the observed patterns of CTI changes within protected areas offer critical insights into species responses to environmental change and underline the importance of targeted conservation strategies in mountain ecosystems.

The significant rise in mean annual temperature (1.19 °C) observed over the study period aligns with global warming trends, which are particularly pronounced in mountain regions (Pepin et al., 2022). This warming likely drives species towards higher elevations, as has been documented in other mountain systems (Freeman et al., 2018; Van Der Hoek et al., 2020). However, the non-significant overall change in CTI suggests that community-level shifts are complex and might be shaped by factors beyond temperature alone, such as changes in precipitation patterns (Tingley et al., 2012), competition (Lenoir et al., 2010), species-specific tolerances (Moritz et al., 2008; Pöyry et al., 2009) and grazing management (Chiffard et al., 2023).

Species-specific models suggested that species are expanding into higher elevations more rapidly at their upper range limits, driven by

habitat availability and climate factors. Furthermore, most distribution shifts occurred in the treeline ecotone, highlighting this zone as a hot-spot for ecological transformations. The treeline represents a transition zone where species turnover is particularly dynamic, yet it remains relatively understudied in mountain ecology (Chamberlain et al., 2023a, 2023b). While this ecotone is often characterized by a sharp shift in dominant functional groups—from montane forest to alpine open-habitat species—our results suggest that treeline habitats may also facilitate range shifts for species associated with shrublands. Dunnock, wren and cuckoo all showed significant increases in elevational distribution over the last decade, reinforcing the sensitivity of treeline habitats to climate-induced change (Chamberlain et al., 2023a, 2023b). Notably, wren even expanded from montane forests into the treeline zone, likely reflecting the upward colonization of shrubs into higher elevations. In alpine grasslands, water pipit, northern wheatear and black redstart demonstrated substantial upward shifts, potentially signalling vegetation encroachment and forest upshift as key drivers of open habitat species distribution shifts. Within montane forest habitats, fewer changes were evident, although coal tit exhibited a marked increase in elevation. Species turnover between the two periods further highlighted the dual impacts of climate change and land-use alterations. The appearance of species such as blackcap *Sylvia atricapilla* and firecrest *Regulus ignicapilla*, typically associated with warmer and more forested habitats, that were not contacted in the first period supports the hypothesis that warming temperatures and associated vegetation encroachment enable thermophilic species to expand their ranges.

PAs showed a limited capacity to mitigate climate change effects, as evidenced by the significant interaction between PA status and period in determining CTI values. Initially, PAs exhibited lower CTI values compared to non-PAs, indicating communities more dominated by cold-

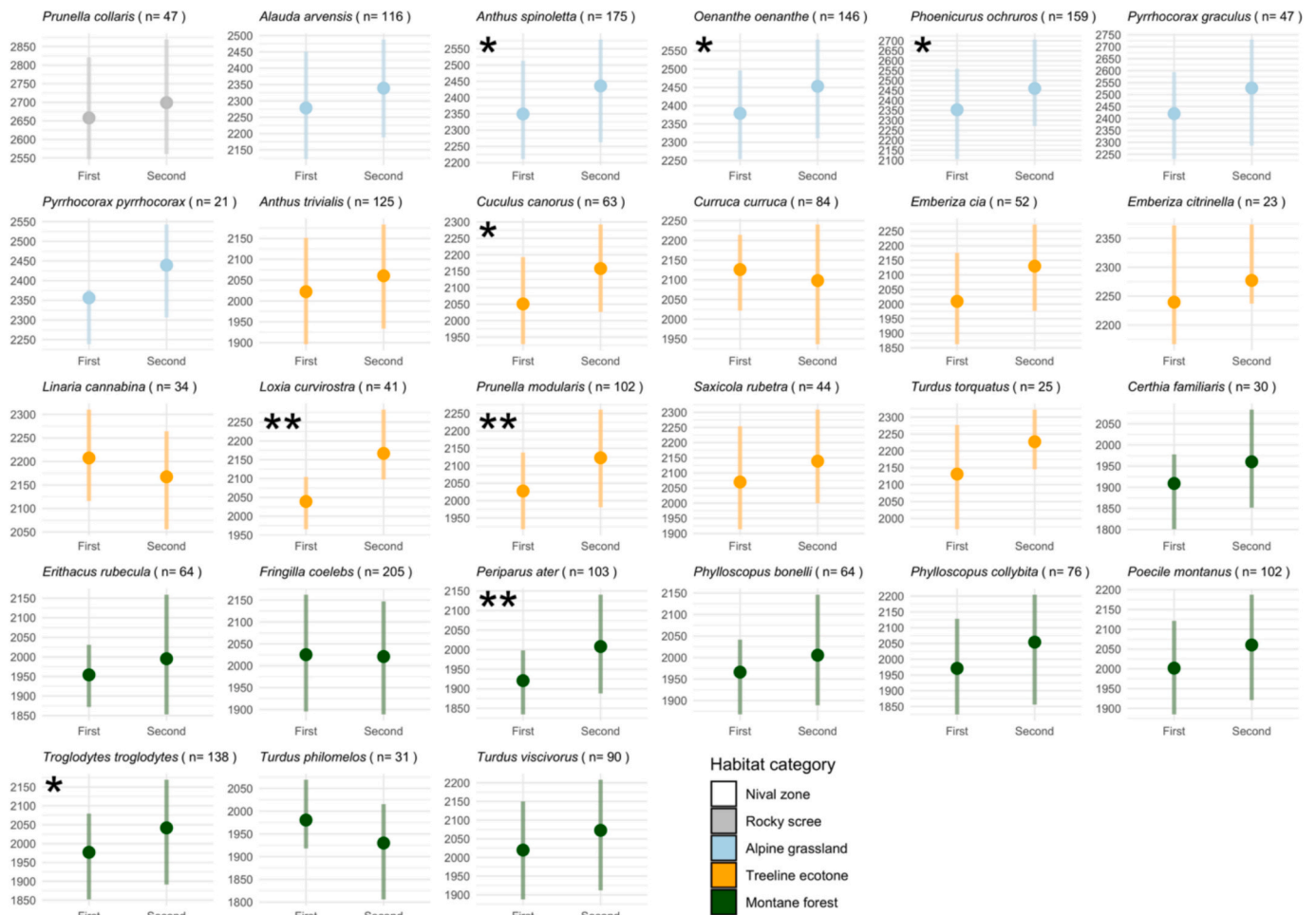


Fig. 4. Changes in elevation between the first and second period for individual species. Points show the mean while error bars show first and third quartiles, representing trailing and leading edges of a given species distribution. Note that only species with $n > 20$ were used in the analysis. ‘***’ $P < 0.01$ ‘**’ $P < 0.05$. See Table S4 for full model results.

adapted species. This pattern may reflect the generally higher ecological quality of PAs and their capacity to support habitat specialists, including species with cold-climate affinities. In mountainous regions, PAs often encompass higher elevations or less disturbed areas, which may help maintain conditions favourable to cold-adapted birds (Cremer-Schulte et al., 2017). In contrast, non-PAs appeared to harbour more depauperate “cold communities” possibly reflecting greater historical pressures such as land-use changes, grazing, or recreational activities like skiing, which limited the presence of cold-adapted species (Rolando et al., 2007; Patthey et al., 2008). In fact, most cold-adapted species tend to be ground nesters and to avoid shrub or tree cover, making them particularly vulnerable to vegetation changes while many warm-adapted species are shrub or tree nesters and may benefit from climate change-induced shifts in vegetation structure.

Over the last decade, CTI values within PAs have risen, converging with those of non-protected areas. This pattern may indicate a dual dynamic: on one hand, PAs might facilitate colonization by warmer-adapted species due to climate-driven upward shifts; on the other hand, these areas may also be losing their characteristic cold-adapted species, a trend consistent with broader warming effects observed across ecosystems (Scridel et al., 2018). This loss in cold-adapted species within PAs may reflect their reduced ability to mitigate the rapid pace of warming, despite their role in maintaining higher-quality habitats compared to non-PAs. Notably, points located within PAs were, on average, about 100 m higher in elevation than those in non-PAs. This difference may partly explain the initially lower CTI values in PAs, as

they hosted more cold-dwelling species in the first period. However, the current convergence in CTI between the two area types—despite this elevation difference—suggests that PAs are disproportionately losing cold-adapted species and/or gaining warm-adapted ones, further reinforcing our interpretation. Non-PAs, by contrast, showed minimal change in CTI values, likely due to their already lower representation of cold-adapted species during the initial period. In these areas, further shifts might be constrained by limited availability of suitable habitat for new colonizers or localized extinction events of cold-adapted species capable of persisting under warming conditions.

The combined trends suggest that while PAs can act as refuges for biodiversity, they also face significant challenges in retaining cold-adapted species, especially under scenarios of ongoing climate change (Araújo et al., 2011; Brambilla et al., 2022). These findings highlight the need for enhanced conservation strategies that account for the dual role of PAs as both refuges for cold-adapted species and facilitators of range shifts for warm-adapted species, emphasizing their critical importance in supporting biodiversity under future warming scenarios (Virkkala et al., 2014). One key strategy to achieve these dual conservation goals would be the establishment of elevational habitat corridors that connect lower and higher-altitude habitats within and beyond PAs. Such corridors could enhance species connectivity, ensuring that cold-adapted species have access to suitable higher-elevation refugia while also allowing species tracking climate change to move more easily across the landscape. Additionally, adaptive habitat management—such as regulating grazing pressure and afforestation in key alpine areas—could help

maintain open habitats critical for species undergoing elevational shifts. Implementing these measures within PAs could improve their resilience to climate change while balancing the conservation needs of both cold-adapted and expanding warm-adapted species.

The significant increase in CTI within PAs could also reflect habitat changes driven by land abandonment. In many alpine regions, reduced grazing has led to shrub encroachment and forest expansion, particularly near the treeline ecotone, where we registered the biggest changes (Tremblé et al., 2016; Bebi et al., 2017). These dynamics may create suitable habitats for thermophilic and forest species, thus contributing to the upward shift in CTI. The sensitivity analysis revealed that species contributing most to CTI changes spanned multiple habitat types, including alpine grasslands, the treeline ecotone and montane forests. This suggests that shifts in CTI are not restricted to a single habitat type, but represent a broader reorganization of bird communities across the elevational gradient. Abandonment of grazing alone is thus unlikely to be the factor driving these changes, although it could act in tandem with vegetation shifts due to climate change (Gehrig-Fasel et al., 2007). The marked increase in CTI around the 2000–2300 m elevational band, corresponding to the treeline ecotone, underscores the importance of this transitional zone as a hotspot of ecological change (Altamirano et al., 2020; Martin et al., 2021). This zone is particularly sensitive to warming, as it represents the upper limit for tree growth and a critical interface between forested and open habitats. Conservation efforts should prioritize this zone, as it is likely to experience the greatest shifts in species composition and habitat structure (Jähnig et al., 2018; Chamberlain et al., 2023a, 2023b).

These findings highlight the urgent need for adaptive conservation strategies that account for the dynamic nature of alpine ecosystems under climate change. PAs should be managed not only to preserve current biodiversity, but also to facilitate species adaptation to changing conditions in the near future. One key approach is maintaining habitat heterogeneity (Brambilla et al., 2017), which ensures that species with different ecological requirements can find suitable conditions within PAs. This can be achieved by preventing the homogenization of alpine landscapes through targeted management of vegetation succession, particularly in areas experiencing shrub encroachment due to climate change (Anthelme et al., 2021). As mentioned above, supporting connectivity between elevational zones is also crucial, as it allows species to track suitable climatic conditions as they shift upslope (Heller and Zavaleta, 2009), and can be promoted through the establishment of elevational habitat corridors that link lowland and alpine zones, reducing fragmentation and enabling species to disperse more effectively (Scridel et al., 2018). Conservation planning should prioritize these corridors by integrating them into existing PAs and ensuring that land-use policies in surrounding areas facilitate, rather than hinder, range shifts. Additionally, active management practices are needed to counteract vegetation encroachment and maintain open alpine habitats, which are critical for cold-adapted species (Hof et al., 2017). Strategies such as selective grazing, controlled burning, and mechanical removal of shrubs have been proposed to slow the encroachment of forests into alpine meadows, preserving habitat mosaics that support a diverse avifauna (Jähnig et al., 2018). Finally, monitoring shifts in Community Temperature Index (CTI) and species distributions can provide early warnings of ecological disruptions, guiding conservation interventions (Santangeli et al., 2017). Birds serve as sensitive bioindicators in mountain systems, reflecting both climate-driven and habitat-related changes (Martin et al., 2023). Long-term monitoring programs, combined with predictive modelling, should be integrated into conservation planning to identify priority areas for protection and management under future climate scenarios.

5. Conclusions

This study highlights the urgent need for adaptive conservation strategies in alpine ecosystems facing rapid climate and land-use

changes. While PAs remain essential for safeguarding biodiversity, their capacity to buffer cold-adapted species is increasingly challenged. Observed shifts in bird communities—especially near the treeline—underscore the importance of managing habitat heterogeneity, preventing vegetation homogenization, and maintaining connectivity along elevational gradients. Active management interventions, such as controlling shrub encroachment, are crucial to preserve open alpine habitats. Conservation planning should integrate long-term monitoring and predictive tools to guide restoration and support species adaptation. To remain effective under climate change, PAs must act both as refuges and as corridors enabling range shifts, supported by forward-looking, coordinated policies that account for dynamic ecological processes.

CRediT authorship contribution statement

Riccardo Alba: Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **Dan Chamberlain:** Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization, Writing – review & editing.

Funding

The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgements

We are thankful to the Ente di Gestione delle Aree Protette delle Alpi Cozie for help during the fieldwork and to Davide Scridel for the suggestions provided about the CTI.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111267>.

Data availability

Data and R code used in this study are available from the corresponding author on reasonable request.

References

- Alba, Riccardo, Kasoar, Tim, Chamberlain, Dan, Buchanan, Graeme, Thompson, Des, Pearce-Higgins, James W., 2022. Drivers of change in mountain and upland bird populations in Europe. *Ibis* 164 (3), 635–648. <https://doi.org/10.1111/ibi.13043>.
- Altamirano, T.A., de Zwaan, D.R., Ibarra, J.T., Wilson, S., Martin, K., 2020. Treeline ecotones shape the distribution of avian species richness and functional diversity in south temperate mountains. *Sci. Rep.* 10 (1), 18428. <https://doi.org/10.1038/s41598-020-75470-2>.
- Anselmetto, Nicolò, Weisberg, Peter J., Garbarino, Matteo, 2024. Global change in the European Alps: a century of post-abandonment natural reforestation at the landscape scale. In: *Landscape and Urban Planning*, 243 (March), p. 104973. <https://doi.org/10.1016/j.landurbplan.2023.104973>.
- Anthelme, Fabien, Cauvy-Fraunié, Sophie, Francou, Bernard, Cáceres, Bolívar, Dangles, Olivier, 2021. Living at the edge: increasing stress for plants 2–13 years after the retreat of a tropical glacier. *Frontiers in Ecology and Evolution* 9, 584872. <https://doi.org/10.3389/fevo.2021.584872>.
- Antonelli, Alexandre, Kissling, W. Daniel, Flantua, Suzette G.A., Bermúdez, Mauricio A., Mulch, Andreas, Muellner-Riehl, Alexandra N., Kreft, Holger, et al., 2018. Geological and climatic influences on mountain biodiversity. *Nat. Geosci.* 11 (10), 718–725. <https://doi.org/10.1038/s41561-018-0236-z>.
- Araújo, Miguel B., Alagador, Diogo, Cabeza, Mar, Nogués-Bravo, David, Thuiller, Wilfried, 2011. Climate change threatens European conservation areas: climate change threatens conservation areas. *Ecol. Lett.* 14 (5), 484–492. <https://doi.org/10.1111/j.1461-0248.2011.01610.x>.

- Arpa Piemonte, 2021. Average Annual Temperature, Piedmont Region. https://old-stati.c.arpa.piemonte.it/reporting/indicatori-on_line/componenti-ambientali/clima/clima_temperatura-media.html.
- Bani, Luciano, Luppi, Massimiliano, Rocchia, Emanuel, Dondina, Olivia, Orioli, Valerio, 2019. Winners and losers: how the elevational range of breeding birds on alps has varied over the past four decades due to climate and habitat changes. *Ecol. Evol.* 9 (3), 1289–1305. <https://doi.org/10.1002/ece3.4838>.
- Bates, Douglas, Maechler, Martin, Bolker, Ben, Walker, Steven, 2003. lme4: Linear Mixed-Effects Models Using “Eigen” and S4. <https://doi.org/10.32614/CRAN.package.lme4>.
- Baur, Bruno, Baur, Anette, 2013. Snails keep the pace: shift in upper elevation limit on mountain slopes as a response to climate warming. *Can. J. Zool.* 91 (8), 596–599. <https://doi.org/10.1139/cjz-2013-0036>.
- Bebi, P., Seidl, R., Motta, R., Fuhr, M., Firm, D., Krumm, F., Kulakowski, D., 2017. Changes of forest cover and disturbance regimes in the mountain forests of the Alps. *For. Ecol. Manage.* 388, 43–56. <https://doi.org/10.1016/j.foreco.2016.10.028>.
- Beniston, Martin, 2006. Mountain weather and climate: a general overview and a focus on climatic change in the alps. *Hydrobiologia* 562 (1), 3–16. <https://doi.org/10.1007/s10750-005-1802-0>.
- Bibby, C.J. (Ed.), 2000. *Bird Census Techniques*, 2nd ed. Academic, London; San Diego.
- Billerman, M.S., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S., 2022. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA. <https://birds.oftheworld.org/bow/home>.
- BirdLife International, 2023. Handbook of the Birds of the World. n.d. ‘Bird Species Distribution Maps of the World. Version 2023.1. Available at <http://Datazone.Birdlife.org/Species/Requestdis>.
- Brambilla, Mattia, Cortesi, Matteo, Capelli, Federico, Chamberlain, Dan, Pedrini, Paolo, Rubolini, Diego, 2017. Foraging habitat selection by Alpine White-winged Snowfinches *Montifringilla nivalis* during the nestling rearing period. *Journal of Ornithology* 158, 277–286. <https://doi.org/10.1007/s10336-016-1392-9>.
- Brambilla, Mattia, Resano-Mayor, Jaime, Arlettaz, Raphaël, Bettega, Chiara, Binggeli, Anaïs, Bogliani, Giuseppe, Braunsch, Veronika, et al., 2020. Potential distribution of a climate sensitive species, the white-winged snowfinch *Montifringilla Nivalis* in Europe. *Bird Conserv. Intl.* 30 (4), 522–532. <https://doi.org/10.1017/S0959270920000027>.
- Brambilla, Mattia, Rubolini, Diego, Appukuttan, Ojan, Calvi, Gianpiero, Karger, Dirk Nikolaus, Kmecl, Primož, Mihelič, Tomaž, et al., 2022. Identifying climate refugia for high-elevation alpine birds under current climate warming predictions. *Glob. Chang. Biol.* 28 (14), 4276–4291. <https://doi.org/10.1111/gcb.16187>.
- Chamberlain, Dan, Arlettaz, Raphaël, Caprio, Enrico, Maggini, Ramona, Pedrini, Paolo, Rolando, Antonio, Zbinden, Niklaus, 2012. The altitudinal frontier in avian climate impact research. *Ibis* 154 (1), 205–209. <https://doi.org/10.1111/j.1474-919X.2011.01196.x>.
- Chamberlain, Dan E., Negro, Matteo, Caprio, Enrico, Rolando, Antonio, 2013. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biol. Conserv.* 167 (November), 127–135. <https://doi.org/10.1016/j.biocon.2013.07.036>.
- Chamberlain, Dan E., Pedrini, Paolo, Brambilla, Mattia, Rolando, Antonio, Girardello, Marco, 2016. Identifying key conservation threats to alpine birds through expert knowledge. *PeerJ* 4 (February), e1723. <https://doi.org/10.7717/peerj.1723>.
- Chamberlain, Dan, Lehikoinen, Aleks, Martin, Kathy, 2023a. Ecology and conservation of mountain birds. In: *Ecology, Biodiversity and Conservation*. Cambridge university press, Cambridge, United Kingdom.
- Chamberlain, Dan, Melikhova, Evgeniya, Jähniq, Susanne, Sevillano-Ríos, C. Steven, 2023b. Birds of Treeline ecotones. In: Chamberlain, Dan, Lehikoinen, Aleks, Martin, Kathy (Eds.), *Ecology and Conservation of Mountain Birds*. Dan Chamberlain, Aleks Lehikoinen, Kathy Martin, Cambridge, United Kingdom, pp. 137–175.
- Chiffard, J., Bentaleb, I., Yoccoz, N.G., Fourel, F., Blanquet, E., Besnard, A., 2023. Grazing intensity drives a trophic shift in the diet of common alpine birds. *Agr Ecosyst Environ* 348, 108418.
- Cremer-Schulte, Dominik, Rehnus, Maik, Duparc, Antoine, Perrin-Malterre, Clémence, Arneodo, Letizia, 2017. Wildlife disturbance and winter recreational activities in alpine protected areas: recommendations for successful management. *Eco. Mont. (Journal on Protected Mountain Areas Research)* 9 (2), 66–73. <https://doi.org/10.1553/eco.mont-9-2s66>.
- Devictor, Vincent, Julliard, Romain, Couvet, Denis, Jiguet, Frédéric, 2008. Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B Biol. Sci.* 275 (1652), 2743–2748. <https://doi.org/10.1098/rspb.2008.0878>.
- Devictor, Vincent, Van Swaay, Chris, Brereton, Tom, Brotons, Lluís, Chamberlain, Dan, Heliölä, Janne, Herrando, Sergi, Julliard, Romain, Kuussaari, Mikko, Lindström, Åke, Reif, Jirí, Roy, David B., Schweiger, Oliver, Settele, Josef, Stefanescu, Constant, Van Strien, Arco, Van Turnhout, Chris, Vermouzek, Zdenek, De Vries, Michiel Wallis, et al., 2012a. Uncertainty in thermal tolerances and climatic debt. *Nature Clim. Change* 2 (9), 638–639. <https://doi.org/10.1038/nclimate1668>.
- Devictor, Vincent, Van Swaay, Chris, Brereton, Tom, Brotons, Lluís, Chamberlain, Dan, Heliölä, Janne, Herrando, Sergi, Julliard, Romain, Kuussaari, Mikko, Lindström, Åke, Reif, Jirí, Roy, David B., Schweiger, Oliver, Settele, Josef, Stefanescu, Constant, Van Strien, Arco, Van Turnhout, Chris, Vermouzek, Zdenek, WallisDeVries, Michiel, et al., 2012b. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* 2 (2), 121–124. <https://doi.org/10.1038/nclimate1347>.
- European Environment Agency (EEA), 2022. Natura 2000 Network: Spatial Data for Italy. <https://www.eea.europa.eu>.
- Ferrarini, Alessandro, Alatalo, Juha M., Gustin, Marco, 2017. Climate change will seriously impact bird species dwelling above the Treeline: a prospective study for the Italian Alps. *Sci. Total Environ.* 590–591 (July), 686–694. <https://doi.org/10.1016/j.scitotenv.2017.03.027>.
- Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Heiberger, R., 2012. Package ‘car’. Vienna: R Foundation for Statistical Computing 16 (332), 333.
- Freeman, Benjamin G., Scholer, Micah N., Ruiz-Gutiérrez, Viviana, Fitzpatrick, John W., 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc. Natl. Acad. Sci.* 115 (47), 11982–11987. <https://doi.org/10.1073/pnas.1804224115>.
- García-Navas, V., Sattler, T., Schmid, H., Ozgul, A., 2020. Temporal homogenization of functional and beta diversity in bird communities of the Swiss Alps. *Divers. Distrib.* 26, 900–911. <https://doi.org/10.1111/ddi.13076>.
- Gaston, Kevin J., Jackson, Sarah F., Nagy, Arnold, Cantú-Salazar, Lisette, Johnson, Mark, 2008. Protected areas in Europe: principle and practice. *Ann. N. Y. Acad. Sci.* 1134 (1), 97–119. <https://doi.org/10.1196/annals.1439.006>.
- Gaüzère, Pierre, Jiguet, Frédéric, Devictor, Vincent, 2016. Rapid adjustment of bird community compositions to local climatic variations and its functional consequences. *Glob. Chang. Biol.* 21 (9), 3367–3378. <https://doi.org/10.1111/gcb.12917>.
- Gaüzère, Pierre, Princé, Karine, Devictor, Vincent, 2017. Where do they go? The effects of topography and habitat diversity on reducing climatic debt in birds. *Glob. Chang. Biol.* 23 (6), 2218–2229. <https://doi.org/10.1111/gcb.13500>.
- Gehrig-Fasel, Jacqueline, Guisan, Antoine, Zimmermann, Niklaus E., 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *J. Veg. Sci.* 18 (4), 571–582. <https://doi.org/10.1111/j.1654-1103.2007.tb02571.x>.
- Gobiet, Andreas, Kotlarski, Sven, Beniston, Martin, Heinrich, Georg, Rajczak, Jan, Stoffel, Markus, 2014. 21st century climate change in the European Alps—a review. *Sci. Total Environ.* 493 (September), 1138–1151. <https://doi.org/10.1016/j.scitotenv.2013.07.050>.
- Greenwood, Sarah, Jump, Alistair S., 2014. Consequences of treeline shifts for the diversity and function of high altitude ecosystems. *Arct. Antarct. Alp. Res.* 46 (4), 829–840. <https://doi.org/10.1657/1938-4246-46.4.829>.
- Hamilton, Lawrence S., 2002. *Conserving mountain biodiversity in protected areas. In: Mountain Biodiversity: A Global Assessment*. CRC Press, Boca Raton, Fla.
- Hannah, Lee, 2001. The role of a global protected areas system in conserving biodiversity in the face of climate change. In: Visconti, Guido, Beniston, Martin, Iannorelli, Emilio D., Barba, Diego (Eds.), *Global Change and Protected Areas, Advances in Global Change Research*, 9. Springer Netherlands, Dordrecht, pp. 413–422. https://doi.org/10.1007/0-306-48051-4_38.
- Hartig, F., 2018. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. <https://CRAN.R-project.org/package=DHARMA>.
- Heller, Nicole E., Zavaleta, Erika S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological conservation* 142 (1), 14–32. <https://doi.org/10.1016/j.biocon.2008.10.006>.
- Hof, Anouschka R., Rodríguez-Castañeda, Geneveva, Allen, Andrew M., Jansson, Roland, Nilsson, Christer, 2017. Vulnerability of Subarctic and Arctic breeding birds. *Ecological Applications* 27 (1), 219–234. <https://doi.org/10.1002/eap.1434>.
- Jähniq, Susanne, Alba, Riccardo, Vallino, Cristina, Rosselli, Domenico, Pittarello, Marco, Rolando, Antonio, Chamberlain, Dan, 2018. The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an alpine forest-shrub ecotone. *J. Ornithol.* 159 (3), 747–759. <https://doi.org/10.1007/s10336-018-1549-9>.
- Kampichler, Christian, Turnhout, Van Chris A.M., Devictor, Vincent, Jeugd, Van Der Henk P., 2012. Large-scale changes in community composition: determining land use and climate change signals. Edited by Adam Siepielski *PLoS One* 7 (4), e35272. <https://doi.org/10.1371/journal.pone.0035272>.
- Koch, Bärbel, Edwards, Peter J., Blanckenhorn, Wolf U., Walter, Thomas, Hofer, Gabriela, 2015. Shrub encroachment affects the diversity of plants, butterflies, and grasshoppers on two Swiss subalpine pastures. *Arct. Antarct. Alp. Res.* 47 (2), 345–357. <https://doi.org/10.1657/AAAR0013-093>.
- Körner, Christian, 2004. ‘Mountain biodiversity, its causes and function’. *AMBIO: a journal of the human environment* 33 (sp13), 11. <https://doi.org/10.1007/0044-7447-33.sp13.11>.
- Laiolo, Paola, Dondero, Francesca, Ciliento, Enza, Rolando, Antonio, 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J. Appl. Ecol.* 41 (2), 294–304. <https://doi.org/10.1111/j.0021-8901.2004.00893.x>.
- Le Saout, Soizic, Hoffmann, Michael, Shi, Yichuan, Hughes, Adrian, Bernard, Cyril, Brooks, Thomas M., Bertzy, Bastian, et al., 2013. Protected areas and effective biodiversity conservation. *Science* 342 (6160), 803–805. <https://doi.org/10.1126/science.1239268>.
- Lehikoinen, Aleks, Green, Martin, Husby, Magne, Kälås, John Atle, Lindström, Åke, 2014. Common montane birds are declining in northern Europe. *J. Avian Biol.* 45 (1), 3–14. <https://doi.org/10.1111/j.1600-048X.2013.00177.x>.
- Lehikoinen, Aleks, Lindström, Åke, Santangeli, Andrea, Sirkiä, Päivi M., Brotons, Lluís, Devictor, Vincent, Elts, Jaanus, et al., 2021a. Wintering bird communities are tracking climate change faster than breeding communities. *J. Anim. Ecol.* 90 (5), 1085–1095. <https://doi.org/10.1111/1365-2656.13433>.
- Lehikoinen, Petteri, Tiusanen, Maria, Santangeli, Andrea, Rajasärkkä, Ari, Jaatinen, Kim, Valkama, Jari, Virkkala, Raimo, Lehikoinen, Aleks, 2021b. Increasing protected area coverage mitigates climate-driven community changes. *Biol. Conserv.* 253 (January), 108892. <https://doi.org/10.1016/j.biocon.2020.108892>.
- Lenoir, Jonathan, Gégout, Jean-Claude, Guisan, Antoine, Vittoz, Pascal, Wohlgemuth, Thomas, Zimmermann, Niklaus E., Dullinger, Stefan, Pauli, Harald, Willner, Wolfgang, Svenning, Jens-Christian, 2010. Going against the flow: potential

- mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33 (2), 295–303. <https://doi.org/10.1111/j.1600-0587.2010.06279.x>.
- Lenoir, Jonathan, Graae, Bente Jessen, Aarrestad, Per Arild, Alsos, Inger Greve, Armbruster, W. Scott, Austrheim, Gunnar, Bergendorff, Claes, et al., 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Glob. Chang. Biol.* 19 (5), 1470–1481. <https://doi.org/10.1111/gcb.12129>.
- Leonelli, Giovanni, Pelfini, Manuela, Di Cella, Umberto Morra, Garavaglia, Valentina, 2011. Climate warming and the recent treeline shift in the European Alps: the role of geomorphological factors in high-altitude sites. *AMBIO* 40 (3), 264–273. <https://doi.org/10.1007/s13280-010-0096-2>.
- Lindström, Åke, Green, Martin, Paulson, Göran, Smith, Henrik G., Devictor, Vincent, 2013. Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography* 36 (3), 313–322. <https://doi.org/10.1111/j.1600-0587.2012.07799.x>.
- Martin, K., Altamirano, T.A., de Zwaan, D.R., Hick, K.G., Vanderpas, A., Wilson, S., 2021. Avian ecology and community structure across elevation gradients: the importance of high latitude temperate mountain habitats for conserving biodiversity in the Americas. *Glob. Ecol. Conserv.* 30, e01799. <https://doi.org/10.1016/j.gecco.2021.e01799>.
- Martin, Kathy, Chamberlain, Dan, Lehikoinen, Aleks, 2023. Priorities for information, research and conservation of birds in high mountains. In: Chamberlain, Dan, Lehikoinen, Aleks, Martin, Kathy (Eds.), *Ecology and Conservation of Mountain Birds*. United Kingdom, Cambridge, pp. 372–406.
- Moritz, Craig, Patton, James L., Conroy, Chris J., Parra, Juan L., White, Gary C., Beissinger, Steven R., 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322 (5899), 261–264. <https://doi.org/10.1126/science.1163428>.
- Myers, Norman, Mittermeier, Russell A., Mittermeier, Cristina G., Da Fonseca, Gustavo A. B., Kent, Jennifer, 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 (6772), 853–858. <https://doi.org/10.1038/35002501>.
- Nagy, Laszlo, Grabherr, Georg, Körner, Christian, Thompson, Desmond B.A., 2003. *Alpine biodiversity in Europe*. 1st ed. 2003. In: *Ecological Studies, Analysis and Synthesis*, 167. Springer Berlin Heidelberg, Berlin, Heidelberg. <https://doi.org/10.1007/978-3-642-18967-8>.
- Neate-Clegg, Montague H.C., Tingley, Morgan W., 2023. Building a mechanistic understanding of climate-driven elevational shifts in birds. *Jamie Males PLoS Climate* 2 (3), e0000174. <https://doi.org/10.1371/journal.pclm.0000174>.
- Noroozi, Jalil, Talebi, Amir, Doostmohammadi, Moslem, Rumpf, Sabine B., Linder, Hans Peter, Schneeweiss, Gerald M., 2018. Hotspots within a global biodiversity hotspot - areas of endemism are associated with high mountain ranges. *Sci. Rep.* 8 (1), 10345. <https://doi.org/10.1038/s41598-018-28504-9>.
- Oksanen, Jari, Simpson, Gavin L., Blanchet, F. Guillaume, Kindt, Roeland, Legendre, Pierre, Minchin, Peter R., O'Hara, R.B., et al., 2024. *Vegan: Community Ecology Package*. <https://doi.org/10.32614/CRAN.package.vegan>.
- Patthey, Patrick, Wirthner, Sven, Signorell, Natalina, Arlettaz, Raphaël, 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. *J. Appl. Ecol.* 45 (6), 1704–1711. <https://doi.org/10.1111/j.1365-2664.2008.01547.x>.
- Pearce-Higgins, James W., Martin, Kathy, 2023. Climate change impacts on mountain birds. In: Chamberlain, Dan, Lehikoinen, Aleks, Martin, Kathy (Eds.), *Ecology and Conservation of Mountain Birds*. Cambridge university press, Cambridge, UK.
- Pepin, N.C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., et al., 2022. Climate changes and their elevational patterns in the mountains of the world. *Rev. Geophys.* 60 (1), e2020RG000730. <https://doi.org/10.1029/2020RG000730>.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P. H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344 (6187), 1246752. <https://doi.org/10.1126/science.1246752>.
- Popy, Simon, Bordignon, Lucio, Prodon, Roger, 2010. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. *J. Biogeogr.* 37 (1), 57–67. <https://doi.org/10.1111/j.1365-2699.2009.02197.x>.
- Pöyry, Juha, Luoto, Miska, Heikkinen, Risto K., Kuussaari, Mikko, Saarinen, Kimmo, 2009. Species traits explain recent range shifts of Finnish butterflies. *Glob. Chang. Biol.* 15 (3), 732–743. <https://doi.org/10.1111/j.1365-2486.2008.01789.x>.
- R Core Team, 2024. *R: A Language and Environment for Statistical Computing*.
- Ramel, Cindy, Rey, Pierre-Louis, Fernandes, Rui, Vincent, Claire, Cardoso, Ana R., Broennimann, Olivier, Pellissier, Loïc, et al., 2020. Integrating ecosystem services within spatial biodiversity conservation prioritization in the Alps. *Ecosyst. Serv.* 45 (October), 101186. <https://doi.org/10.1016/j.ecoser.2020.101186>.
- Ramón-Martínez, D., Seoane, J., 2024. Changes in thermal niche position and breadth of bird assemblages in Spain in relation to increasing temperatures. *J. Biogeogr.* 51 (5), 783–796. <https://doi.org/10.1111/jbi.14779>.
- Rolando, Antonio, Caprio, Enrico, Rinaldi, Enrico, Ellena, Ivan, 2007. The impact of high-altitude ski-runs on alpine grassland bird communities. *J. Appl. Ecol.* 44 (1), 210–219. <https://doi.org/10.1111/j.1365-2664.2006.01253.x>.
- Roth, Tobias, Plattner, Matthias, Amrhein, Valentin, 2014. Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. *Francesco De Bello PLoS One* 9 (1), e82490. <https://doi.org/10.1371/journal.pone.0082490>.
- Santangeli, Andrea, Lehikoinen, Aleks, 2017. Are winter and breeding bird communities able to track rapid climate change? Lessons from the high north. *Diederik Strubbe Divers. Distrib.* 23 (3), 308–316. <https://doi.org/10.1111/ddi.12529>.
- Santangeli, Andrea, Rajasärkkä, Ari, Lehikoinen, Aleks, 2017. Effects of high latitude protected areas on bird communities under rapid climate change. *Glob. Chang. Biol.* 23 (6), 2241–2249. <https://doi.org/10.1111/gcb.13518>.
- Scridel, D., Bogliani, G., Pedrini, P., Iemma, A., Von Hardenberg, A., Brambilla, M., 2017. Thermal niche predicts recent changes in range size for bird species. *Climate Res.* 73 (3), 207–216. <https://doi.org/10.3354/cr01477>.
- Scridel, Davide, Brambilla, Mattia, Martin, Kathy, Lehikoinen, Aleks, Iemma, Aaron, Matteo, Anderle, Jähnig, Susanne, et al., 2018. A review and meta-analysis of the effects of climate change on Holarctic Mountain and upland bird populations. *Ibis* 160 (3), 489–515. <https://doi.org/10.1111/ibi.12585>.
- Theurillat, Jean-Paul, Guisan, Antoine, 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Clim. Change* 50 (1/2), 77–109. <https://doi.org/10.1023/A:1010632015572>.
- Thomas, Chris D., Gillingham, Phillipa K., Bradbury, Richard B., Roy, David B., Anderson, Barbara J., Baxter, John M., Bourn, Nigel A.D., et al., 2012. Protected areas facilitate species' range expansions. *Proc. Natl. Acad. Sci.* 109 (35), 14063–14068. <https://doi.org/10.1073/pnas.1210251109>.
- Tingley, Morgan W., Koo, Michelle S., Moritz, Craig, Rush, Andrew C., Beissinger, Steven R., 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* 18 (11), 3279–3290. <https://doi.org/10.1111/j.1365-2486.2012.02784.x>.
- Tremli, Václav, Šenfeldr, Martin, Chuman, Tomáš, Ponocná, Tereza, Demková, Katarína, 2016. Twentieth century Treeline ecotone advance in the Sudetes Mountains (Central Europe) was induced by agricultural land abandonment rather than climate change. *Beverly Collins J. Veg. Sci.* 27 (6), 1209–1221. <https://doi.org/10.1111/jvs.12448>.
- Trisos, Christopher H., Merow, Cory, Pigot, Alex L., 2020. The projected timing of abrupt ecological disruption from climate change. *Nature* 580 (7804), 496–501. <https://doi.org/10.1038/s41586-020-2189-9>.
- Van Der Hoek, Yntze, Faida, Emmanuel, Musemakweli, Valens, Tuyisingize, Deogratias, 2020. Living the high life: remarkable high-elevation records of birds in an east African mountain range. *Ecology* 101 (1), e02866. <https://doi.org/10.1002/ecy.2866>.
- Virkkala, Raimo, Pöyry, Juha, Heikkinen, Risto K., Lehikoinen, Aleks, Valkama, Jari, 2014. Protected areas alleviate climate change effects on northern bird species of conservation concern. *Ecol. Evol.* 4 (15), 2991–3003. <https://doi.org/10.1002/ece3.1162>.