

ARTICLE

Rapid elevational shifts of Switzerland's avifauna and associated species traits

Tyler A. Hallman  | Jérôme Guélat  | Sylvain Antoniazza | Marc Kéry | Thomas Sattler 

Swiss Ornithological Institute, Sempach, Switzerland

Correspondence

Tyler A. Hallman

Email: tyler.hallman@vogelwarte.edu

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Abstract

Global change in climate and land use has profound effects on species' geographic and elevational distributions. In European birds, while species are predicted to track their climatic niches upslope, lowland agricultural intensification and high-elevation land abandonment can drive elevational shifts. Species traits that can predict response to change in climate and land use can inform conservation, but a thorough examination of their relationships with elevational shifts in European birds is lacking. We estimate the change in the elevational distributions of 71 species from 1996 to 2016 in a region of the western Palearctic with wide elevational gradients (approximately 3000 m) and large changes in temperature. We model the relationships between elevational shifts and species traits associated with resource preference and adaptive capacity at five reference points including the cool edge, warm edge, and the core of species' elevational distributions. When intermediate reference points were removed, changes to the results were negligible, indicating that three reference points are likely sufficient. We found significant upslope and downslope shifts in 56% and 23% of our study species, respectively. Asymmetric rates of shifts in the cool and warm edges caused significant contractions in elevational extent in 30% of our study species. The effect of elevational preference (i.e., midpoint elevation) was habitat dependent. Movement in alpine birds was unidirectionally upslope, with nearly half displaying significant or apparent elevational range contractions. In woodland birds, asymmetries of shifts in reference points led to expansions in extent in low-elevation species and contractions in high-elevation species. Generally, migrants, species with smaller mass, smaller relative brain size, smaller hand-wing index, and generalists in diet, habitat, and elevation had greater upslope shifts. While elevational shifts in European birds were heterogeneous and species-specific, many were rapid, and species traits associated with resource preference and adaptive capacity were associated with common patterns of elevation.

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KEYWORDS

climate change, elevation shifts, functional traits, global change, land-use change, life history, range limits, species traits

INTRODUCTION

While evidence of climate-driven global extinctions are still relatively rare, local extinctions are widespread (Pacifi et al., 2017; Wiens, 2016). As temperatures rise, local extinctions at the warm margins of species ranges and colonizations at the cool margins are predicted to cause upward shifts in latitude and elevation as species track their shifting climatic envelopes (e.g., Wilson et al., 2005). Elevational shifts are particularly concerning in mountain species where upslope movement can be associated with declines in available area (Elsen & Tingley, 2015; Hernando et al., 2021; Rumpf et al., 2019). In summit species where further upslope expansion is impossible, declines in available area lead to population extirpations, which may eventually lead to global extinctions (Freeman, Scholer, et al., 2018; Urban, 2018). Even in species that occur below elevational summits, asymmetric rates of upslope movement between the cool and warm edges of their distributions can cause range contractions that lead to reductions in habitable area (Neate-Clegg et al., 2020; Neate-Clegg et al., 2021; Wilson et al., 2005).

Despite predictions that species will move upslope to track their shifting climatic envelopes, observed elevational shifts have been largely heterogenous, highlighted by downslope movement in substantial proportions of species (e.g., DeLuca & King, 2017; Maggini et al., 2011; Neate-Clegg et al., 2021; Rumpf et al., 2019). The interplay between the complex spatio-temporal patterns of climate change (both temperature and precipitation) and species-specific niches may explain some heterogeneity as limiting abiotic factors vary from one location to another (Tingley et al., 2012). For most birds, however, the indirect effects of climate change, such as changes to vegetation structure and composition, food availability, and predator abundance, outweigh direct effects alone (Duclos et al., 2019; Neate-Clegg et al., 2020). Lags in climate-driven, ecosystem-level changes such as afforestation and succession may contribute to heterogeneity of elevational shifts as biotic factors become limiting (Bertrand et al., 2016; Reif & Flousek, 2012). Land-use change has affected nearly one-third of the global land area over the last six decades (Winkler et al., 2021), and elevational patterns in land-cover and land-use change can simultaneously drive elevational shifts. The interactive effects of climate and land-cover change appear to drive the redistribution of species globally (Guo et al., 2018).

Across Europe, while settlement expansion and land-use intensification in the lowlands drive the decline in farmland bird communities, land abandonment and the decline in high-elevation agriculture contribute to the loss of alpine habitats through afforestation (Archaux, 2007; Donald et al., 2001; Gehrig-Fasel et al., 2007; Knaus et al., 2018; MacDonald et al., 2000; Tasser et al., 2005). In the Alps, mean temperature increased by about 1.7°C from 1975 to 2004, nearly twice the global average (Rebetez & Reinhard, 2008). European birds must contend with diverse and dramatic environmental change, and the ability of European mountains to accommodate their elevational shifts may be limited. Tools that can help us understand elevational shifts in European birds while informing conservation actions are much needed.

Species' ecological traits can be used to predict climate-driven elevational shifts, but evidence supporting theoretical predictions remain ambiguous (Estrada et al., 2016). Species with different habitat or diet preferences may show differential rates of elevation change based on elevational shifts in habitats or dietary resources (Reif & Flousek, 2012). Species' historical range limits in latitude or elevation may serve as a proxy for climatic preference, which likely plays a role in climate-induced shifts (Angert et al., 2011; MacLean & Beissinger, 2017). Traits such as body size and migratory strategy may impact a species' dispersal ability, which is essential for the colonization of new suitable habitat (Angert et al., 2011). Traits associated with increased reproductive potential, such as larger clutch size, may facilitate the establishment of viable populations in newly colonized areas (MacLean & Beissinger, 2017). Traits associated with ecological generalization in terms of habitat and diet may facilitate the colonization and establishment of populations in newly colonized areas by allowing the use of local resources (MacLean & Beissinger, 2017). Despite hypotheses, the relationships between species traits and elevational shifts in European birds remain unclear.

Here, we investigate two decades of elevational shifts and associated species characteristics for birds in a European landscape with large elevational gradients (approximately 3000 m) and high conservation responsibility for mountain species and ecosystems. Using posterior distributions of abundance models from Swiss Breeding Bird Atlases in the 1990s and 2010s (Knaus et al., 2018), we estimate change in elevation of five reference points, representing the center and edges of elevational distributions, for 71 species. We split

species traits into two categories, traits associated with specific habitats or resources that are themselves affected by elevational changes in climate and land use, and traits related to a species' adaptive capacity (i.e., the theoretical ability of a species to cope with or adapt to climatic change), which is an essential component of climatic vulnerability (Foden et al., 2019; Thurman et al., 2020). We model relationships between elevational shifts in each reference point and species traits to identify traits associated with elevational shifts in temperate birds of the western Palearctic. Additionally, with these novel methods we hope to (1) demonstrate the utility of breeding bird atlas products and the benefits of error propagation from posterior distributions of Bayesian models, (2) feature a framework in which species traits and hypotheses of their effects on elevation shifts can be attributed (i.e., resource preference and adaptive capacity), (3) assess the added benefits of including intermediate elevational reference points, and (4) highlight current conservation issues to inform conservation action.

METHODS

Study area

Switzerland and Liechtenstein ("Switzerland" herein) have a combined area of 41,460 km², about 69% of which is mountainous, with elevations reaching up to 4618 m. Of the 82 peaks above 4000 m in the Alps, more than half are in Switzerland. Patterns in land-cover and land-use change in the region mirror broader patterns across Europe (Gehrig-Fasel et al., 2007; Knaus et al., 2018; MacDonald et al., 2000; Tasser et al., 2005). The lowlands, which range in elevation from 260 to 960 m, are heavily cultivated and densely populated (Gonseth et al., 2001). Settlements, which account for about 8% of the total area, expanded by 23% from 1985 to 2009. In the mid-1990s, intensive agricultural practices already common in the lowlands started to increase at midpoint elevation (800–1400 m) in the 1990s. The large elevational gradient, high proportion of mountain habitat, increasing mean temperatures, and elevational patterns of land-use change that are common at a much broader scale make Switzerland an ideal area to study elevational shifts in species distributions.

Avian data and atlas abundance modeling

Our analyses of elevational change were based on abundance models previously developed for two Swiss Breeding Bird Atlases (Knaus et al., 2018; Knaus et al., 2021; Schmid et al., 1998), which covered 1993–1996 (herein 1996) and 2013–2016 (herein 2016). For detailed information about

study design, data collection, validation, and modeling, see atlases. In short, territory mapping (Bibby et al., 2000) was conducted by volunteers during the breeding season (mid-April to early July) in preselected 1-km squares. In each square, an observer conducted three surveys (two above the tree line) within a breeding season, recording the locations of all birds detected by sight or sound. Surveys were conducted in the morning during good conditions and lasted between 2 and 5 h. In total, volunteers surveyed 2943 and 2318 squares for the 1996 and 2016 atlases, respectively, walking approximately 46,440 km in the squares and recording 745,428 territories. Volunteers resurveyed 1600 of the 1996 squares for the 2016 atlas. Locations of species detected across visits were used to deduce the locations of territories within each square. The total number of territories observed within each square was used for atlas abundance modeling. Within these atlases, the abundance of 71 common bird species was modeled with 16 environmental variables at a 1-km² resolution (Appendix S1: Table S1) using Poisson generalized linear mixed models. Penalized 2D splines were used to account for spatial autocorrelation in abundance as regional differences not accounted for by the environmental variables have an effect (Crase et al., 2014; Guélat & Kéry, 2018). Edge effects were avoided by including squares from across the Swiss border in models. Both time periods were modeled separately and final models were used to predict spatially explicit abundance throughout Switzerland. All abundance analyses were conducted with JAGS (Plummer, 2003), using Bayesian inference.

Quantifying elevational shifts

For 71 species, we used predicted abundance throughout Switzerland to calculate change at five reference points along species' abundance-weighted elevational distributions: the warm edge (10th quantile), warm central border (25th quantile), center (50th quantile, i.e., the median), cool central border (75th quantile), and cool edge (90th quantile) (Figure 1; DeLuca & King, 2017; Maggini et al., 2011). Warm edge refers to the lower elevation edge or warm margin, while cool edge refers to the higher elevation or cool margin of species' elevational distributions. In the calculation of all reference points, error was propagated from abundance model estimates by using samples from the posterior predictive distributions of abundance obtained in Knaus et al. (2018). To alleviate the computational burden, for each species, we thinned the available 6000 Markov chain Monte Carlo draws of the posterior distribution of the abundance to 1500 per square for both 1996 and 2016. For each of the 1500 draws, we rounded values with predicted

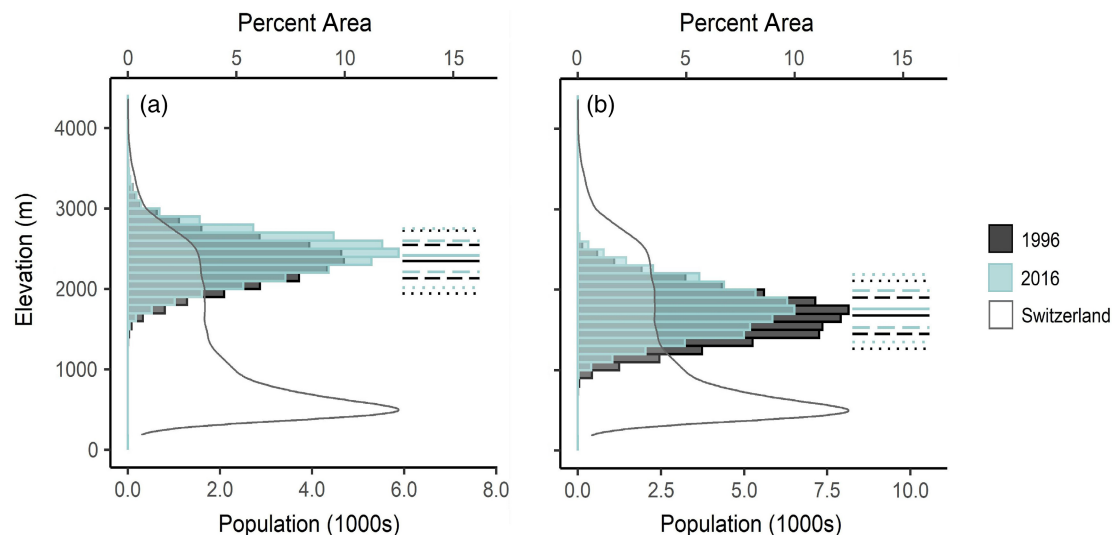


FIGURE 1 Examples of elevational distributions and reference points in 1996 and 2016 for (a) Alpine Accentor (*Prunella collaris*) and (b) Ring Ouzel (*Turdus torquatus*). The cool and warm edges are indicated by dotted lines, the cool and warm central borders are indicated by dashed lines, the center is indicated by a solid line, and the solid black line indicates the elevations available in the study area. For all 71 species analyzed, see Appendix S1: Figure S1.

abundances of less than 0.1–0 and reduced unrealistically high abundances (those above the 99th quantile from the distribution of abundance for a species) to the value of the 99th quantile. We used these censored abundances and the mean elevation in each square to calculate the abundance-weighted elevational distribution of each species, which we used to calculate reference points (i.e., 10th, 25th, 50th, 75th, and 90th quantiles).

After estimating elevational distributions and reference points for each period, we calculated the draw-wise change of each reference point from 1996 to 2016. We computed the elevational extent as the draw-wise difference between the reference point at the cool edge (i.e., 90th quantile) and warm edge (i.e., 10th quantile) of the elevational distribution and similarly estimated change in elevational extent from 1996 to 2016. We calculated 95% credible intervals for each reference point and elevational extent to assess the “significance” (analogous to the frequentist variant of a significance test by comparing a 95% CI with the null hypothesis) of change, then used patterns of significance in reference points to categorize shifts in each species elevational distribution into overall upslope, neutral, or downslope patterns (Maggini et al., 2011). Ultimately, the warm and cool central borders provided little additional insight into patterns of change and were removed for increased clarity. See Appendix S1 for results and discussion of these two reference points. To roughly examine the relationships between population change and observed shifts, we used independent estimates of percent change in population from 1996 to 2016 and used linear regressions of the association between population change and change in the

central reference point and between population change and change in elevational extent. For these post hoc analyses, we used the mean of posterior distributions.

Species traits

We compiled species trait information from existing literature to investigate their relationships with elevational shifts (García-Navas et al., 2020; Sheard et al., 2020; Storchová & Hořák, 2018; Swiss Ornithological Institute, 2021; Tsuboi et al., 2018; Wilman et al., 2014). We selected species characteristics based on two sets of hypotheses: (1) characteristics that might be associated with the specific changes in habitat and resources in Switzerland (herein resource preference hypotheses); and (2) characteristics associated with a species’ adaptive capacity (i.e., their theoretical ability to respond to environmental change herein adaptive capacity hypotheses) (Thurman et al., 2020). In cases where any species characteristics across both hypothesis sets were correlated at a 0.5 threshold, we omitted the characteristic for which we found weaker evidence in the literature. Ultimately, for the resource preference hypotheses, we included variables for preferred habitat, diet, midpoint elevation, and foraging strata (Table 1). For the adaptive capacity hypotheses, we included four life history variables (body mass, relative brain size, annual fecundity, and hand-wing index), three specialization variables (habitat specialization, dietary specialization, and elevational breadth), and migratory strategy (Table 1). Although Hooded Crow (*Corvus cornix*) and Carrion Crow (*Corvus*

TABLE 1 Species characteristics, by hypothesis set (resource preference and adaptive capacity), used in models of effects on change in elevation and change in elevational range.

Variable	Type/levels	Variable description	Source
Resource preference			
Habitat	Categorical: other, farmland, woodland, alpine	Primary habitat reduced to four categories due to sample size	Swiss Ornithological Institute (2021)
Diet	Categorical: other, seeds and plants, invertebrates	Primary diet reduced to three categories due to sample size	García-Navas et al. (2020)
Midpoint elevation	Continuous	Median abundance-weighted elevation in 1996	Calculated in this study
Hand-wing index	Continuous	Index of wing shape as a proxy for dispersal ability	Sheard et al. (2020)
Foraging strata	Continuous	Weighted average rank of foraging strata calculated on the proportion of use for ranks 1:5 for ground to aerial	García-Navas et al. (2020)
Adaptive capacity			
Body mass	Continuous	Mass	García-Navas et al. (2020)
Relative brain size	Continuous	Brain mass divided by body mass	García-Navas et al. (2020)
Annual fecundity	Continuous	Clutch size multiplied by no. broods	Swiss Ornithological Institute (2021)
Habitat specialization	Continuous	Gini coefficient of the habitats in which the species occurs	Storchová and Hořák (2018)
Dietary specialization	Continuous	Gini coefficient from the percent contribution of 10 dietary categories	García-Navas et al. (2020)
Elevational breadth	Continuous	90th minus 10th quantile from 1996 elevation	Calculated in this study
Migratory strategy	Categorical: sedentary, facultative, short-distance, long-distance		Simplified from Storchová and Hořák (2018)

corone) were modeled separately in the atlases, available species trait information did not differentiate between the two. We therefore removed Hooded Crow from these analyses as Carrion Crow had far more data.

For both sets of hypotheses, we modeled the relationship between species characteristics and elevational shifts in each reference point and elevational extent. As species traits can explain overlapping variance, we included all traits from our resource preference hypotheses in a full resource preference model and all traits from our adaptive capacity hypotheses in a full adaptive capacity model. Due to our limited sample size, and because we were interested in comparing variables within but not across hypothesis sets, we analyzed hypothesis sets separately. To avoid issues of limited sample size in these analyses (e.g., 70 species), we included only additive linear effects in our initial models. As we did not believe that different habitats in the resource preference hypotheses should necessarily share a slope, we included an interaction

between habitat preference and elevation. Due to the presence of outliers, we used robust linear models throughout. To propagate error from the original abundance models and reference point calculation to these analyses, we conducted regressions for each of the 1500 posterior draws of change, resulting in posterior distributions of all model parameters. We calculated 95% credible intervals for each model coefficient. We used the MASS package in R version 4.0.3 for all analyses (R Core Team, 2020; Venables & Ripley, 2002).

RESULTS

Elevational shifts

We found significant elevational shifts (i.e., 95% credible intervals of change in the center or edges did not include 0) in 60 (85%) of our 71 study species (Figures 1 and 2;

Appendix S1: Figure S1). Of those with significant elevational shifts, 40 (56%) moved unidirectionally upslope and 16 (23%) moved unidirectionally downslope, and four (6%) exhibited bidirectional, neutral patterns. Overall, the center and warm edge moved upslope significantly in more species than the cool edge. The cool edge moved downslope significantly in more species than the warm edge. When assessed visually, there was no obvious taxonomic signal in elevational shifts (Appendix S1: Figures S1 and S2).

In the 40 species with significant upslope shifts, the center of species' elevational distributions moved upslope at a mean rate of 3.7 m/year for a total shift of about 75 m over the 20-year period. The center of Willow Warbler's (*Phylloscopus trochilus*) elevational distribution moved by far the fastest, at a rate of 16.6 m/year, for a total shift of about 332 m. The cool and warm edges of these species' elevational distributions moved at mean rates of 3.1 and 1.9 m/year, respectively. In alpine birds, five of seven species (71%) moved upslope (Figure 2). The cool edge, center, and warm edge of alpine birds moved at mean rates of 1.9, 2.8, and 3.1 m/year, respectively. In the five species of alpine birds with a significant upslope

movement, the cool edge, center, and warm edge moved at mean rates of 2.5, 3.5, and 3.8 m/year, respectively. In woodland birds, 21 of 37 species (57%) moved upslope. The cool edge, center, and warm edge of their elevational distributions moved upslope at mean rates of 2.5, 3.6, and 2.1 m/year, respectively. In farmland birds, 7 of 13 species (54%) moved upslope. The cool edge, center, and warm edge of their elevational distributions moved upslope at mean rates of 2.9, 2.3, and 1.3, respectively.

In the 16 species with significant downslope shifts, the center of species' elevational distributions moved downslope at a rate of -2.3 m/year. The cool and warm edges of these species' elevational distributions moved downslope at mean rates of -3.4 and -0.5 , respectively. No alpine birds moved downslope (Figure 2). In woodland birds, 8 of 37 species (22%) moved downslope. The cool edge, center, and warm edge of their elevational distributions moved at mean rates of -3.6 , -2.6 , and -0.5 m/year, respectively. In farmland birds, 3 of 13 species (23%) moved downslope. The cool edge, center, and warm edge of their elevational distributions moved at mean rates of -5.5 , -3.8 , and -1.2 m/year, respectively. Change in the central reference point was negatively

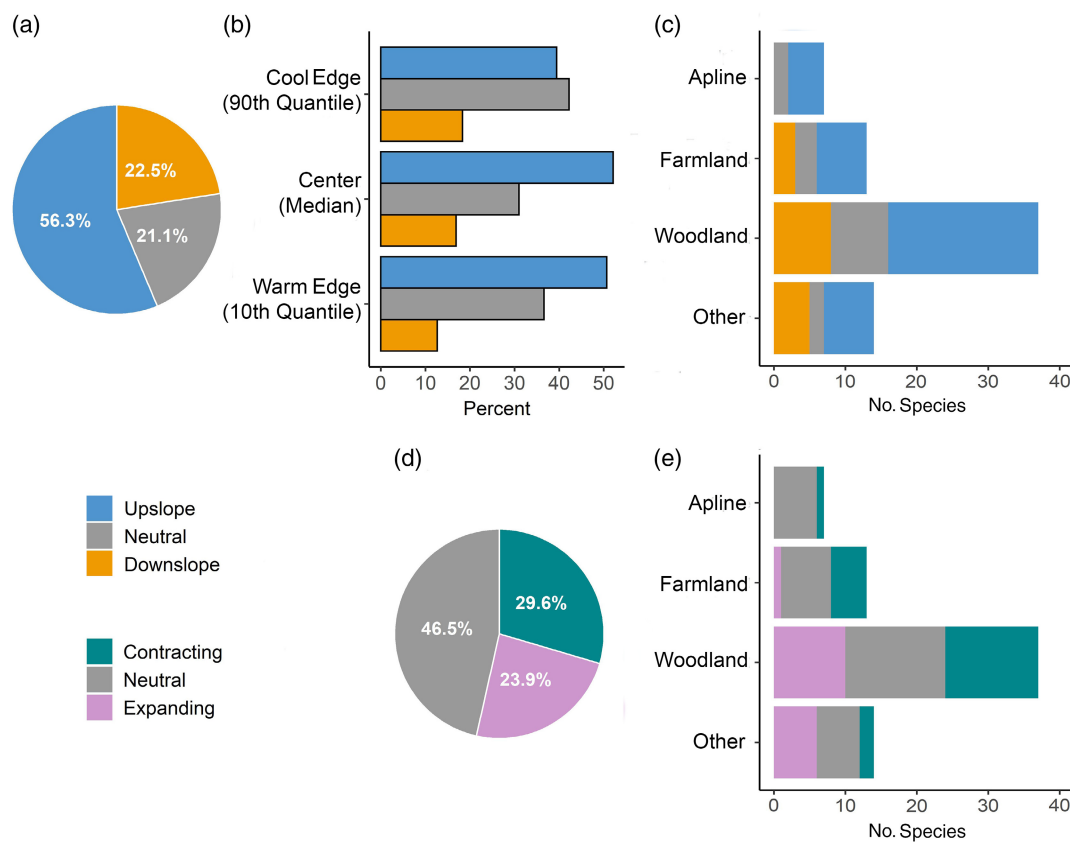


FIGURE 2 Elevational movement in 71 study species (a) overall upslope and downslope patterns, (b) upslope and downslope patterns at each reference point in species' elevational distributions, and (c) overall upslope and downslope patterns grouped by habitat, and (d) overall patterns in elevational extent and (e) overall patterns of elevational extent grouped by habitat.

associated with rough population change ($R^2 = 0.14$, $F = 12.0$, $df = 64$, $p < 0.00$).

Based on the outermost reference points (i.e., cool and warm edge), elevational extent significantly contracted in 30% and expanded in 24% of our study species (Figure 2). Significant contractions occurred at a mean rate of -4.0 m/year, with maximum rates between -8.0 and -11.3 m/year. Significant expansions occurred at a mean rate of 4.6 m/year, with a maximum rate of about 11.3 m/year. As with directional shifts, when assessed visually, there was no clear taxonomic signal in change in elevational extent (Appendix S1: Figure S2). While no alpine species ($n = 7$) had expanding extents, contractions in extent were significant in one species and apparent, but nonsignificant at the 0.05 level in two others (Figure 1). In farmland birds, five species had significantly contracting extents, while expanding extents were significant in one and apparent but nonsignificant in four others. In woodland birds, nearly equal numbers of species had expanding ($n = 10$) and contracting ($n = 13$) extents with slightly more contractions, while in

uncategorized other habitats, more species had significantly expanding ($n = 6$) than contracting ($n = 2$) extents. Rough population change was negatively associated with change in elevational extent ($R^2 = 0.08$, $F = 6.8$, $df = 64$, $p = 0.01$).

Resource preference hypotheses

While the effects of foraging strata and diet were negligible, midpoint elevation and habitat preference had strong interactive effects on change in elevation at every reference point in the resource preference models (Figure 3; Appendix S1: Table S2). The strength and direction of the effects of midpoint elevation and habitat preference were reference point dependent. In alpine birds, while the effect of midpoint elevation was negligible at the warm edge and center, there was a negative effect of midpoint elevation at the cool edge, indicating that the cool edge of lower elevation species moved more rapidly than higher elevation species in this habitat. In farmland birds, the

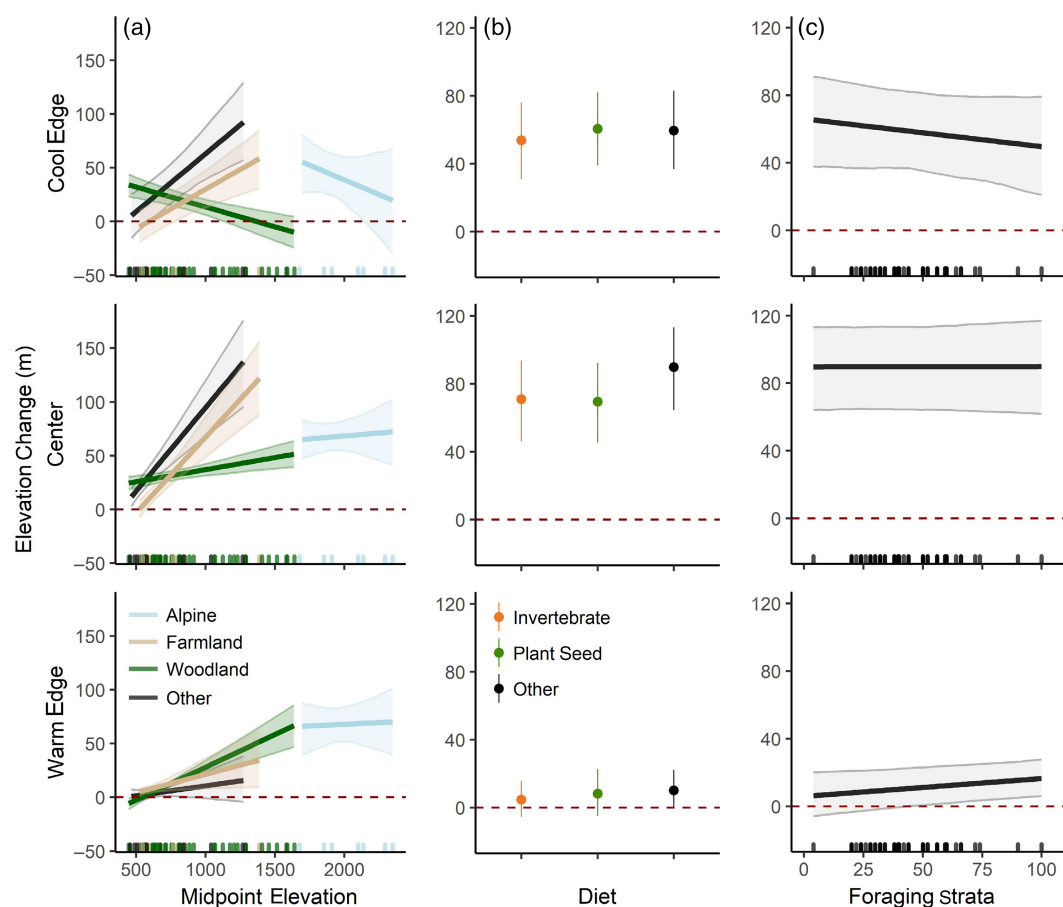


FIGURE 3 Predicted effects of (a) an interaction between midpoint elevation and habitat, (b) diet, and (c) foraging strata, on change in elevation for three reference points along a species' elevational distribution in the resource preference models. Tick marks on the x-axis represent datapoint values for that independent variable. Red dashed line indicates no predicted change in elevational extent.

effect of midpoint elevation was always positive, indicating that higher elevation species moved upslope more rapidly than lower elevation species in this habitat. The strongest effects in farmland birds were at the center of their elevational distributions. In woodland birds, the effects of midpoint elevation were positive at the warm edge and center, but negative at the cool edge. For woodland birds, while the warm edge moved upslope more quickly in higher elevation species than lower elevation species, the cool edge appeared to do the opposite, with much faster upslope movement in lower elevation species and no upslope movement in higher elevation species.

Similarly, while effects of foraging strata and diet were negligible, habitat and midpoint elevation appeared to have strong interactive effects on change in elevational extent (Figure 4). In alpine birds, there was a negative relationship between midpoint elevation and change in elevational extent, indicating that higher elevation species have more strongly contracting elevational extents. In woodland birds, there was a strong negative

relationship with expansions of elevational extent in low-elevation species and contractions in high-elevation species. In contrast, farmland birds, showed no relationship between midpoint elevation and change in elevational extent and the relationship was positive for species in uncategorized habitats, indicating that higher elevation species had greater expansions to elevational extent.

Adaptive capacity hypotheses

Many adaptive capacity hypotheses had significant effects. Generally, where significant, the effects of habitat specialization, diet specialization, and elevational breadth indicated that more generalized species moved upslope more rapidly than more specialized species (Figure 5; Appendix S1: Table S2). Greater habitat generalization was associated with greater elevational shifts at the center and cool edge of species' elevational distributions. Greater elevational generalization, represented by

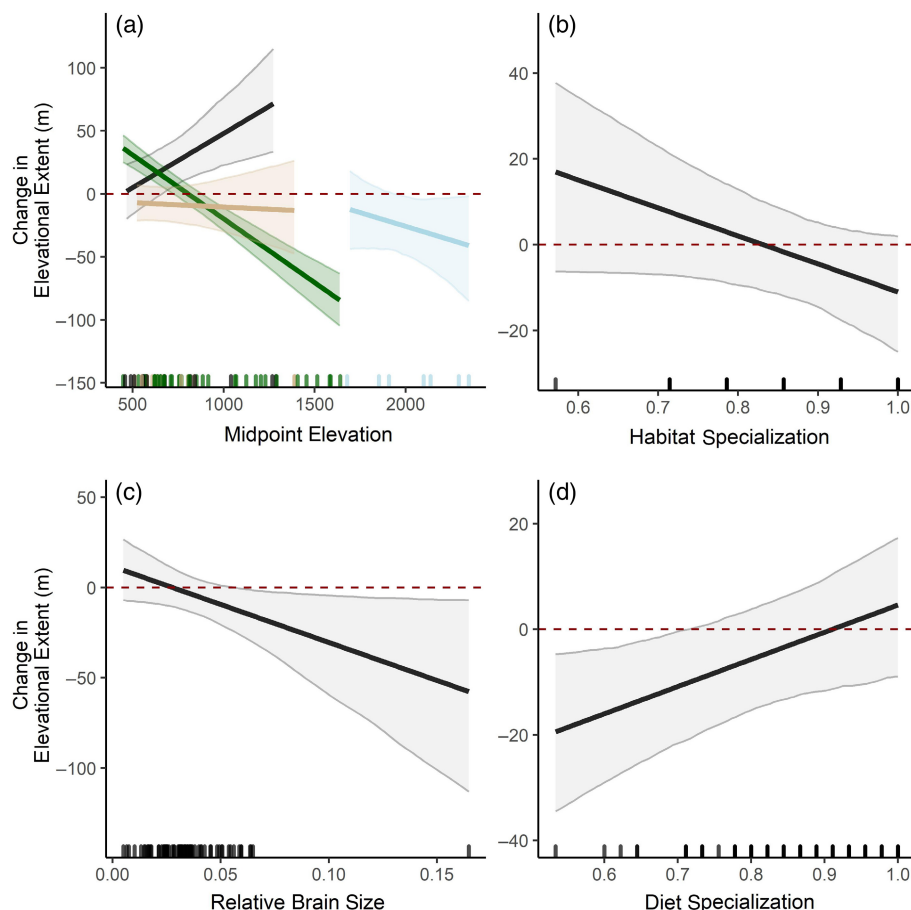


FIGURE 4 Predicted effects of (a) an interaction between midpoint elevation and habitat in the resource preference models and (b) habitat specialization, (c) relative brain size, and (d) diet specialization in the adaptive capacity models on change in elevational extent. In panel a, green indicates forest, tan indicates farmland, blue indicates alpine, and black indicates other habitat preferences. Tick marks on the x-axis represent datapoint values for that independent variable. Red dashed line indicates no predicted change in elevational extent.

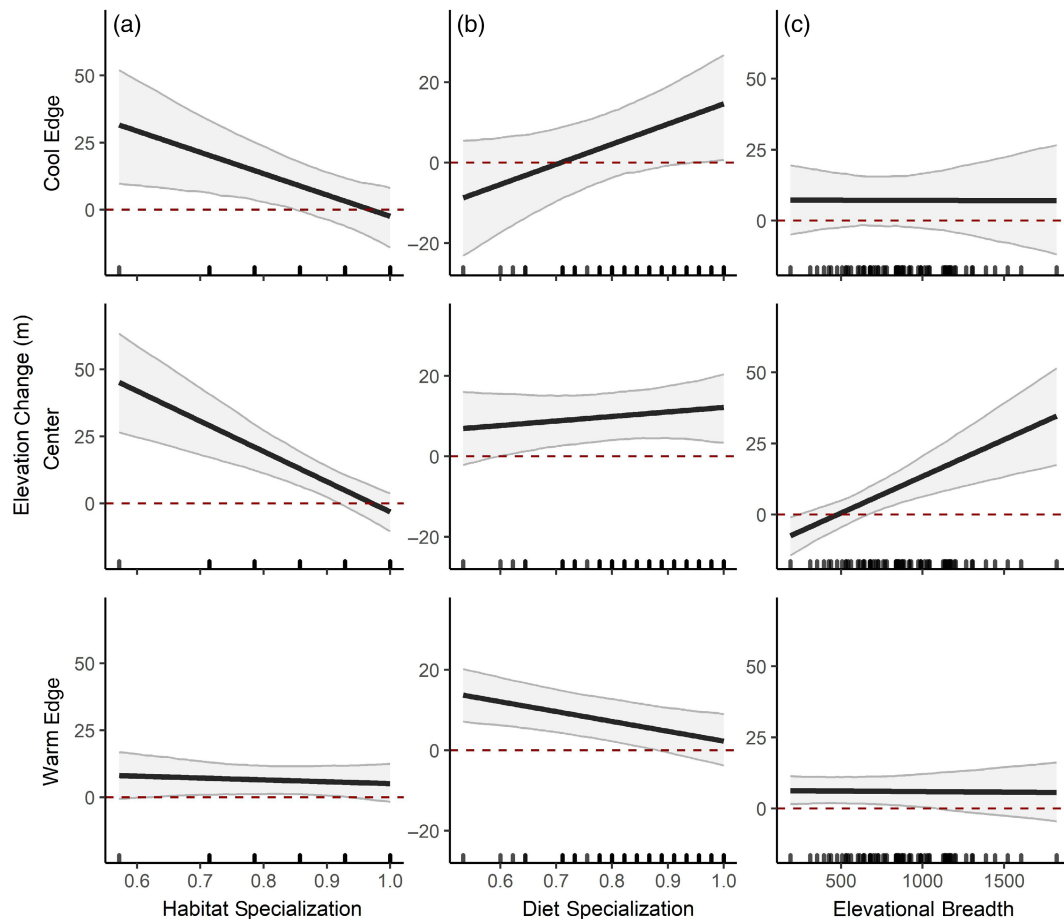


FIGURE 5 Predicted effects of (a) habitat specialization, (b) diet specialization, and (c) elevational breadth on change in elevation for three reference points along a species' elevational distribution in the adaptive capacity models. Tick marks on the x-axis represent datapoint values for that independent variable. Red dashed line indicates no predicted change in elevational extent.

elevational breadth, was associated with greater shifts at the center of species' elevational distributions. Greater diet generalization was associated with greater shifts at the warm edge, but smaller shifts or potentially downward shifts in the cool edge of species' elevational distributions. In our life history variables, body mass, relative brain size, and hand-wing index had fairly consistent negative effects, indicating that species with higher body mass, larger relative brain size, and a larger hand-wing index had smaller or even negative shifts in elevation (Figure 6). Smaller birds with smaller relative brain size and smaller hand-wing index had larger upslope shifts. While these results should be interpreted with some degree of caution, given the small number of data points with large values in each of these variables (e.g., few large birds, birds with large relative brain size, and birds with large hand-wing index), post hoc checks of the impact of removing extreme values indicated little change in the effect of body size, brain size, and hand-wing index on elevational shifts. This provides some confidence that

the relationships are not driven by extreme values. Annual fecundity had somewhat varied nonsignificant effects across species' elevational distributions (Figure 7). Migratory strategy had strong effects on elevational shifts as sedentary species consistently moved less than short- and long-distance migrants. At the warm edge and center, short-distance migrants had much larger shifts than sedentary species and facultative migrants. This effect was smaller at the cool edge of species' elevational distributions. While long-distance migrants had greater shifts than sedentary species and facultative migrants across reference points, the effect was strongest at the cool edge of species' elevational distributions. At the cool edge of species' elevational distributions, even facultative migrants had larger elevational shifts than sedentary species.

Habitat specialization, relative brain size, and diet specialization all had significant effects on change in elevational extent (Figure 4). Species with larger relative brain size and greater habitat specialization had stronger contractions in elevational extent. Species with greater

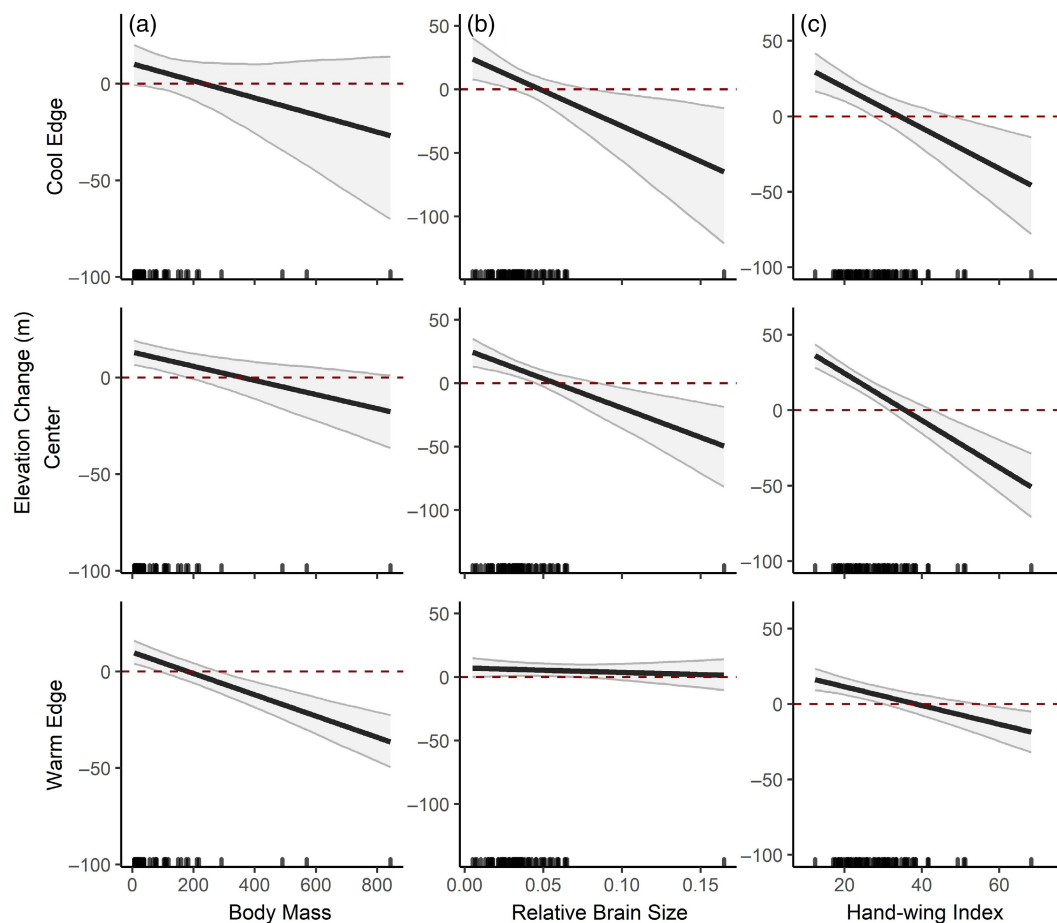


FIGURE 6 Predicted effects of (a) body mass, (b) relative brain size, and (c) hand-wing index on change in elevation for three reference points along a species' elevational distribution in the adaptive capacity models. Tick marks on the x-axis represent datapoint values for that independent variable. Red dashed line indicates no predicted change in elevational extent.

dietary specialization, contrastingly, had less change in elevational extent (e.g., smaller contractions).

DISCUSSION

Elevational distributions of Swiss birds were highly dynamic, with shifts in the outer edges or center of 79% of species from 1996 to 2016. While the variability in elevational shifts suggests considerable complexity in species' response to environmental change, more than twice as many species shifted upslope than downslope, matching basic climate-based predictions. Upslope shifts in the central reference point were associated with recent declines in population, highlighting the importance of elevation change research in Europe. Furthermore, as expansions in elevational extent were weakly associated with declining populations, it is unlikely that observed shifts were simply a product of population-level processes as opposed to response to environmental change. Overall, shifts were strongly associated with species traits. Of the

resource preference hypotheses, habitat and elevational preference had the strongest associations with elevational shifts and changes in elevational extent. While all adaptive capacity hypotheses were associated with elevational shifts, few were associated with changes in elevational extent.

Resource preference hypotheses

The risk of persistent climate-driven elevational shifts is greatest for high-elevation species where the potential for upslope movement is limited (Freeman, Lee-Yaw, et al., 2018; Urban, 2018). The preponderance of upslope movement in our study was particularly defined in alpine habitats (i.e., above the tree line), where the directionality of elevational shifts was entirely upslope. The consistent positive association of alpine habitat preference in our models showed that alpine birds are moving upslope across their elevational distributions (Figure 3). In alpine birds, the warm edge moved more quickly than the cool

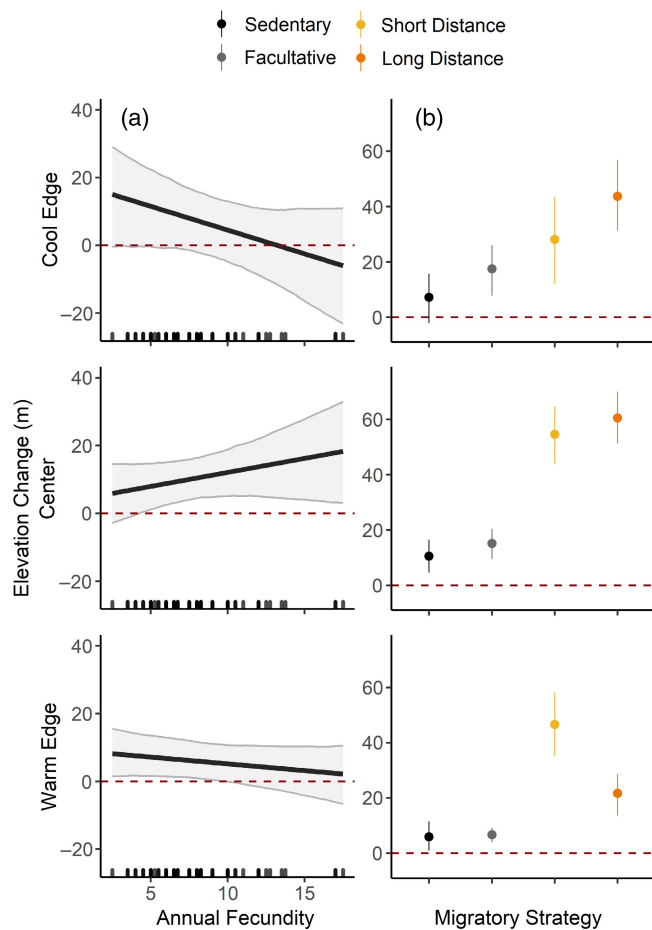


FIGURE 7 Predicted effects of (a) annual fecundity and (b) migratory strategy on change in elevation for three reference points along a species' elevational distribution in the adaptive capacity models. Tick marks on the x-axis represent datapoint values for that independent variable. Red dashed line indicates no predicted change in elevational extent.

edge, an asymmetry that increased at higher elevations, and commonly causes contractions of elevational extent in mountain birds (Neate-Clegg et al., 2020; Neate-Clegg et al., 2021; Wilson et al., 2005). In Switzerland, the abandonment of high-elevation pastures and changing climatic conditions simultaneously promote high-elevation afforestation and the reduction of open habitats (Gehrig-Fasel et al., 2007), likely forcing upslope movement in their warm edge. In our study, contractions in elevational extent were significant for Water Pipit (*Anthus spinoletta*), and apparent, but nonsignificant in Common Redpoll (*Acanthis flammea*) and Alpine Accentor (*Prunella collaris*), which together comprise three of the seven alpine species examined. With a combined rate of -2.8 m/year across these three species and a maximum rate of -4.5 m/year for Water Pipit, contractions in extent may soon warrant conservation concern. In contrast to birds in other habitats, no alpine birds had

significant or apparent expansions in elevational extent, which, combined with the unidirectional movement, highlights the sensitivity of alpine species to the current global change.

Upslope elevational shifts in mountain species are especially concerning when available area decreases with increasing elevation (Urban, 2018). Though not universal in mountains globally, this decrease in area with increased elevation is true in the Alps (Elsen & Tingley, 2015). In Switzerland, between 1000 and 2500 m, the available area remains relatively constant (Figure 1). Above 2500 m, however, the available area declines precipitously with further increases in elevation. Assuming climate tracking of suitable habitat, for species below 2500 m, such as the Common Redpoll, Lesser White-throat (*Sylvia curruca*), and Ring Ouzel (*Turdus torquatus*), the Alps may provide a temporary buffer against the negative effects of climate-driven elevational shifts. For higher elevation species such as the Alpine Accentor, further upslope shifts in the center or warm edge of their distributions will lead to a decrease in available area (Figure 1). Despite elevation shifts, of the seven alpine species here, only Ring Ouzel experienced dramatic population declines in Switzerland over this period (Knaus et al., 2018; Strebel et al., 2019). Rarer species, not included here, often have smaller, more isolated populations, and the conservation implications of upslope shifts may be much more severe. Our findings suggest that risks associated with continued climate- and land-use-induced elevational shifts apply to temperate regions as well as the tropics (Freeman, Scholer, et al., 2018; Lehikoinen et al., 2019; Maggini et al., 2014; Urban, 2018).

For farmland birds, there was a strong relationship between midpoint elevation and elevational shifts, with greater shifts in higher elevation species (Figure 3). Across reference points there was little elevational movement in low-elevation farmland birds, whereas higher elevation farmland birds moved upslope rapidly, especially in the center and cool edge of their distributions. Despite somewhat asymmetric rates of upslope movement, there appeared to be little to no relationship between elevation and the contraction or expansion of elevational extent (Figure 4). Although previous studies have found range expansions in lowland species and contractions in high-elevation species, we found no such pattern in farmland birds (Freeman, Lee-Yaw, et al., 2018). In the lowlands, upslope movement in the warm edge of elevational distributions of farmland birds is presumably driven by agricultural intensification, a factor implicated in the declines of farmland specialists across Europe (Archaux, 2007; Chamberlain et al., 2000; Donald et al., 2001; Guerrero et al., 2012). Differential sensitivities to agricultural

intensification likely play a role in the disparity between lower and higher elevation farmland birds. Species still occurring in the lowlands are likely less sensitive to agricultural intensification as they seem able to persist where intensity is high (in 1996, agricultural use was already intense in the Swiss lowlands). As intensification moves upslope, farmland species sensitive to intensification are pushed further upslope to more suitable conditions. Although changes appear small for these species as a group, changes for individual species were sometimes quite large. Tree Pipit (*Anthus trivialis*), for example, had a yearly increase in the warm edge of their distribution of 6.8 m/year, by far the fastest rate of any species in this group, and a corresponding increase of 2.9 m/year in the cool edge. This species may be particularly sensitive to the upslope movement of agricultural intensification as it breeds primarily in low-intensity pastures and meadows with scattered bushes and conifers, which are now mainly restricted to mountain areas (Knaus et al., 2018). Lowland population declines in Common Linnet (*Linaria cannabina*) and Eurasian Skylark (*Alauda arvensis*) are similarly attributed to agricultural intensification. For some farmland birds, high-elevation meadows (e.g., above tree line) will play an important role in mitigating the effects of lowland agricultural intensification.

Woodland birds had the strongest and most dynamic relationship between midpoint elevation and elevational shifts (Figure 3). The strong positive relationship between midpoint elevation and elevational shifts in the warm edge was reversed in the cool edge. The resulting asymmetric rates of elevational movement caused a strong negative relationship between elevation and change in elevational extent, with expansions in extent in low-elevation species and contractions in high-elevation species (Figure 4), fitting previously described patterns (Freeman, Lee-Yaw, et al., 2018). For coniferous woodland birds such as Dunnock (*Prunella modularis*), Coal Tit (*Periparus ater*), and Northern Nutcracker (*Nucifraga caryocatactes*), greater rates of upslope movement in the warm than the cool edge of their distributions are likely tied to habitat loss at low elevations (Guo et al., 2018; Neate-Clegg et al., 2018; Rumpf et al., 2019). Mixed coniferous forests at low elevations are mainly a result of man-made plantations of Norway spruce (*Picea abies*), a common practice in the last three centuries. In the last few decades, however, the area of lowland coniferous stands has declined dramatically as this forest practice was replaced by natural, site-appropriate, forest regeneration (Rigling & Schaffer, 2015), while simultaneously, land abandonment in the Alps has led to forest regrowth in elevations between 1000 and 2200 m (Federal Statistical Office, 2015). At higher elevations, however, woodland specialists can only shift as quickly as their woodland habitats, and lags in climate-driven forest

expansion and maturation cause cascading lags in elevational shifts in the cool edge of species distributions (Bertrand et al., 2016; Rehm & Feeley, 2015). Tree lines act as barriers with further upslope expansion limited by the absence of suitable habitat. The commonly observed decoupling of climatic change and upslope movement in birds (Archaux, 2004; Neate-Clegg et al., 2020; Popy et al., 2010) may be a result of such lags and cause woodland species to move more slowly than other groups (Reif & Flousek, 2012). In contrast, lower elevation deciduous woodland species, such as the Hawfinch (*Coccothraustes coccothraustes*) and Eurasian Blue Tit (*Cyanistes caeruleus*), had higher rates of upslope movement in the cool than warm edge, which likely indicates increasing elevation in the cool edge of deciduous woodlands and climate-induced increases in the suitability of higher elevation forests.

Adaptive capacity hypotheses

Adaptive capacity, the ability of a species to cope with or adapt to climatic change, is an essential component of species vulnerability (Foden et al., 2019; Thurman et al., 2020). The ability to use species traits to predict sensitivity and response to climate change would be valuable to conservation, but evidence supporting their effects remains elusive (Estrada et al., 2016). Generally, migration distance is positively associated with dispersal distance (Dawideit et al., 2009; Sheard et al., 2020), an important component of adaptive capacity (Thurman et al., 2020), so migration distance is predicted to be positively associated with elevational shifts. In our study, short- and long-distance migrants had significantly greater elevational shifts than nonmigrants at every reference point (Figure 7). In avian communities in North America, faster upslope shifts in migrants than residents likely account for differential rates of increasing species richness at high elevations (i.e., migrant species richness is increasing more rapidly than resident species richness) and decreasing species richness at low elevations (i.e., migrant species richness is decreasing more rapidly than resident species richness) (Furnas, 2020). The relationship between migratory strategy and range shifts in past studies has been fairly heterogeneous, with more studies showing smaller shifts in long-distance migrants than short-distance migrants or nonmigrants (MacLean & Beissinger, 2017). In our study, at the warm edge of their distributions, short-distance migrants moved upslope at a much greater rate than long-distance migrants. At the cool edge, however, the pattern was reversed, with long-distance migrants shifting more quickly than short-distance migrants. The inconsistency in the relationship between migratory strategy and

elevational shifts may be in part based on the diversity of reference points used across studies. Furthermore, although migratory strategy here is being used as a proxy for dispersal ability, there are many other aspects of migratory strategy that might influence elevational shifts. For example, long-distance migrants also generally show higher site fidelity (Estrada et al., 2016), which would be associated with smaller range shifts. Such associations work in opposition to common hypotheses and add heterogeneity to the relationship between migratory strategy and elevational shifts.

While three of our life history characteristics had significant negative relationships with elevation shifts (Figure 6), these results should be interpreted with some caution, as very few species had high values for these variables. Negative associations of elevational shifts with body mass and hand-wing index, both of which are correlates of dispersal distance, contradicted the predictions that larger birds and birds with higher hand-wing index will move upslope more rapidly (Jenkins et al., 2007; MacLean & Beissinger, 2017), but support findings of faster upslope elevation shifts in smaller birds in the tropics (Neate-Clegg et al., 2020; Neate-Clegg et al., 2021). The negative relationship between elevation shifts and relative brain size contradicted the prediction that greater generalization based on greater relative brain size would drive faster elevation shifts in species with larger brains (Brommer & Møller, 2010). The associations between body mass, hand-wing index, and relative brain size, with slow life history characteristics such as clutch size, lifespan, and developmental time, likely add heterogeneity to their relationships with elevation shifts. Clutch size, which is highly correlated with annual fecundity, has been associated with stronger upslope movement (Auer & King, 2014), but we found no relationship between annual fecundity and elevation shifts (Figure 7).

Generally, greater degrees of ecological generalization are predicted to be associated with increased elevational shifts as species are more able to take advantage of the changing conditions in newly suitable habitat (MacLean & Beissinger, 2017). Whereas habitat generalization appears to have consistent positive effects on range shifts in the literature, the relationships with diet generalization have been mixed (Angert et al., 2011; Auer & King, 2014; MacLean & Beissinger, 2017). In our study, greater degrees of generalization of any kind, including habitat, diet, and elevation, were mostly associated with faster upslope shifts (Figure 5). The type of generalization with the strongest association was reference point dependent. Whereas there were significant relationships between diet specialization and elevational shifts at the warm edge of species' distributions, the relationship between elevational breadth and elevational shifts was

strongest toward the center. The relationship between elevational shifts and habitat specialization was strongest at the center, with no relationship at the warm edge. Selective pressures and limiting factors may differ across a species' elevational distribution, altering the relative importance and significance of specific traits within species' adaptive capacity. Based on our results, dietary generalization may be more adaptive at the warm edge, while habitat generalization is more adaptive at the center and cool edge of species' elevational distributions. Habitat generalists may be able to shift their cool edges more quickly than specific habitats, which may lag behind changes in climatic conditions (e.g., shift in tree line). The relationship between diet specialization and elevational shifts is likely complicated by tight tracking between specialized species and their food resources.

Conclusions and broader context

In Switzerland, species inhabiting coniferous forest and alpine habitats are predicted to have significantly higher vulnerability to climate and land-use change than species in other habitats (Maggini et al., 2014). Our results over two decades show consistent upslope elevational shifts in alpine birds and contractions in their elevational extents. In the Alps, upslope elevational shifts and contractions in elevational extent lead to reduced available area, a particularly pronounced problem for high-elevation species. By simultaneously examining multiple reference points and basing analyses on density, which generally responds more quickly to environmental change than occurrence, we were able to identify significant relationships between species traits associated with adaptive capacity and elevational shifts over a relatively short period.

The factors influencing elevation shifts in Switzerland mirror those of mountainous regions at a much broader scale. Across Europe, lowlands are facing the expansion of settlements and agricultural intensification, increasingly upslope, while high elevations experience agricultural abandonment, which contributes to tree encroachment and the loss of alpine meadows (Archaux, 2007; Donald et al., 2001; MacDonald et al., 2000). Species must respond to this elevational asymmetry in rates of land-use change while European temperatures continue to rise between 1.4 and 6.2°C by 2100 (European Environment Agency, 2021). For many species, the disconnect between suitable climatic and suitable habitat conditions may continue to grow. For high-elevation forest species, for example, tree lines that form the cool edge of many distributions take time to expand, grow, and age into the appropriate habitat, so elevational extents may continue to contract. For some lowland species, as habitats at low elevations

become less suitable due to development and intensification, higher elevations may serve as refugia. For alpine species, further upslope shifts are nearly certain. While high-elevation mountains may serve as refugia, their ability to buffer the effects of global change is finite. Species traits associated with adaptive capacity can be used to inform conservation prioritization by identifying species that cannot effectively respond to global change. Migrants and generalists, for example, move upslope more quickly than residents and specialists, indicating a greater adaptive capacity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No new data were collected for this study. All data used in this study are from previously published sources. Thinned MCMC samples of the posterior distributions for the Swiss Breeding Bird Atlas abundance models are available on Zenodo (Knaus et al., 2021): <https://doi.org/10.5281/zenodo.5734916>. R scripts, compiled species characteristics, and other files used in these analyses are also available on Zenodo (Hallman et al., 2022): <https://doi.org/10.5281/zenodo.5769118>.

ORCID

Tyler A. Hallman  <https://orcid.org/0000-0003-2604-0548>

Jérôme Guélat  <https://orcid.org/0000-0003-1438-4378>

Thomas Sattler  <https://orcid.org/0000-0001-5359-6387>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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