

# Short-Lived Species Move Uphill Faster Under Climate Change

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## Research Article

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# Abstract

Climate change is pushing species ranges towards poles and mountain tops. Although many studies have documented local altitudinal shifts, knowledge of general patterns at a large spatial scale, such as a whole mountain range, is very limited. From a conservation perspective, studying altitudinal shifts is particularly important as mountain regions often represent biodiversity hotspots and are among the most vulnerable ecosystems. Here, we examine whether altitudinal shifts have occurred among birds in the Scandinavian mountains over 13 years and assess whether such shifts are related to species' traits. Using abundance data, we show a clear pattern of uphill shifts in the mean altitudes of the bird species' abundances across the Scandinavian mountains, with an average speed of 0.9 m per year. Out of 77 species, 54 shifted their ranges uphill. In general, the range shift was faster when the altitudinal range within the area was wider. Importantly, the altitudinal shift was strongly related to species' longevity: short-lived species showed more pronounced altitudinal uphill shifts than long-lived species. Our results show that the altitudinal range shifts are not only driven by a small number of individuals at the range boundaries, but the overall bird abundances are on the move. This highlights the wide-ranging impact of climate change and the potential vulnerability of species with slow life-histories, as they appear unable to timely respond to rapidly changing climatic conditions.

## Introduction

During the Anthropocene, ecosystems are experiencing rapid shifts in climate. Recent climate change includes increases in temperature, changes in precipitation patterns and sea levels, decreases in snow cover, and increases in frequency and intensity of extreme events (IPCC 2014). These changes have profound impacts on life on Earth from the level of individuals to species, ecosystems, and biomes (Parmesan 2006, Scheffers *et al.* 2016). At the species level, there are three possible responses to climate change: adaptation, range shift, or/and local or global extinction (Parmesan *et al.* 2006, Alford *et al.* 2007, Robinet & Roques 2010).

Under climate change, species can shift their ranges towards higher latitudes and/or altitudes in search for suitable climatic conditions to which they are adapted (Thomas *et al.* 1999, Walther *et al.* 2002, Walther 2010). Patterns of species' range shifts are consistent with a gradient of decreasing temperatures toward higher latitudes and altitudes (Pautasso 2012). Indeed, various taxa have been observed to shift their ranges to higher latitudes at a rate of 17 km per decade and to higher elevations at a rate of 11 m per decade (Chen *et al.* 2011).

Species' ranges can be determined by the species' capacity to disperse, establish new populations, and proliferate (Pöyry *et al.* 2009, Thomas, 2010, Bateman *et al.* 2013). Such capacities depend, at least partly, on species' traits (Van der Veken *et al.* 2007). The environmental tolerances, such as the climatic conditions and the diversity of habitats that the species are able to exploit, shape species' ranges (Thompson *et al.* 1999). Various traits can affect species' potential to shift their ranges, such that species with higher dispersal capacity, reproductive rate, and degree of ecological generalization should be more

able to colonize new suitable habitats (Angert *et al.* 2011, Laube *et al.* 2013, Estrada *et al.*, 2016). Moreover, migratory species have been reported to have a small range shift potential (Forsyth *et al.* 2004, Välimäki *et al.* 2016), probably because they show higher fidelity to breeding and overwintering sites compared to resident species (Bensch 1999). Despite the above-mentioned examples, the effects of species' traits on range shift are still unclear and a recent meta-analysis concluded that the "current understanding of species' traits as predictors of range shifts is limited" (MacLean & Beissinger 2017).

Studying altitudinal range shifts is particularly relevant and timely from a conservation perspective. Mountains are among the most vulnerable ecosystems on Earth, facing disproportionate impacts of changing climate, while still harboring uniquely specialised, adapted, and range-restricted species (Thompson, 2000, Rahbek 1995, La Sorte & Jetz 2010). Compared to other ecosystems, mountaintops typically represent climate refugia that offer only limited space for species to shift in search of optimal conditions, further increasing their extinction risk (Şekercioğlu *et al.* 2008, Gonzales *et al.* 2010, Sirami *et al.* 2017, Scridel *et al.* 2018). The few available studies on altitudinal range shifts report contrasting patterns (Archaux 2004, Popy *et al.* 2010, Maggini *et al.* 2011). However, their spatial and taxonomic extents are limited and they are mainly based on presence-absence, rather than abundance data. When quantifying the speed of altitudinal range shifts, as well as the relative influence of different traits on them, the use of abundance data can greatly increase our understanding on the factors that contribute to the vulnerability of mountain species and how they can be conserved (Virkkala & Lehikoinen 2014, Folden & Young 2016).

Here, we use a comprehensive temporal dataset of bird abundances in Northern Europe to 1) quantify the overall speed and extent of altitudinal abundance shifts of the bird community over the past decade under climate change, and 2) assess whether species' altitudinal shifts are related to their traits. Given the high rates of climate warming in the study region (IPCC 2014) and in mountain areas more generally (Thompson 2000, Brunetti *et al.* 2009), we expected that the mean altitude of the bird species' abundances has moved uphill during the study period. We also expected species-specific abundance shifts to have varied along four trait gradients: (1) fastness-slowness of species' life-history (body mass, clutch size, and longevity), (2) ecological niche (habitat association, diet specialization, and climatic niche), (3) migration behaviour (migration strategy), and (4) population dynamics (population trend). We expected species with faster life-histories and wider habitat niche to respond more rapidly to changing climatic conditions (as reported by Välimäki *et al.* 2016), thus showing faster uphill shifts. Moreover, we expected resident and short-distance migrant species to respond faster, and show more pronounced uphill shifts, as they overwinter at higher latitudes where climate change is most rapid (Auer & King 2014, Välimäki *et al.* 2016). Finally, we expected a larger shift in mean altitude of abundances for species with preference for colder climatic niches, as they may be more forced to seek optimal conditions (Tayleur *et al.* 2016), and for species with positive population trend, as this means that more individuals are available for colonizing higher altitude areas (Koschová & Reif 2015, Ralston *et al.* 2017, Flousek *et al.* 2015).

# Materials And Methods

## Data

We used species and topographic data from the Scandinavian mountains (Figure 1). We obtained the altitudinal information at 25 m resolution (European Union, Copernicus Land Monitoring Service 2020) for all survey points using QGIS software (version 3.4.14.). In addition, we obtained the monthly temperature data for all Swedish survey points. Data from all weather stations around Sweden (approximately 300 stations spread evenly over the country) has been interpolated to a 4 x 4 km grid of virtual weather stations, using geo-statistic interpolation (Johansson 2000). For the analyses, we selected the virtual site nearest each mountainous site.

We obtained abundance data of bird communities from two monitoring schemes carried out in Norway and Sweden. The Norwegian data span from 1990 to present, with seven survey locations distributed randomly across the country to cover a wide range of climatic conditions. Each survey location has 200 survey points situated along eight to ten survey routes each with 20–25 survey points. The distance between the survey points within a survey route is 200–300 m (Solbu *et al.* 2018) (Figure 1A), totalling 1400 point counts across an altitudinal range from 200 to 1350 m. At each point count location, five minute recording of all birds seen and heard were carried out yearly from late May to early July (one day visit per year). The Swedish data follow the “fixed routes” (Lindström *et al.* 2013), and span from 1996 to present. A total of 716 routes are distributed across the country and across a 25 km grid. Each route consists of an eight km line transect that forms a 2 \* 2 km square (Figure 1B), which includes eight point count locations (one per km). Thus, the total number of surveyed points is 5728. The altitude varies from 0 to 1207 meters. The surveys were carried out yearly from mid-May (southern Sweden) to early July (northern Sweden). All individual birds seen and heard during a survey were recorded.

We used eight species’ traits as explanatory variables in the analysis of the role of species-specific differences in altitudinal range shifts: clutch size (Storchová & Hořák 2018), longevity (De Magalhaes & Costa 2009), body mass (Wilman *et al.* 2014), main habitat (Lehikoinen & Virkkala 2016), diet specialization (modified from Wilman *et al.* 2014), migration strategy (Laaksonen & Lehikoinen 2013), species thermal index (STI, Devictor *et al.* 2008), and population trend (Svensk Fågeltaxering 2019) (for more details, see Table S1).

## Data selection

We investigated altitudinal shifts that occurred between two four-year study periods (period 1: 1999-2002 and period 2: 2015-2018), for which there are adequate data for both countries. Compiling data into study periods of four years allows reducing the potential effect of random environmental stochasticity among monitoring seasons. We selected survey points that have been surveyed during at least one year during both study periods. In total, there were 4835 survey points in common between study periods (1400 Norwegian points and 3435 Swedish points). We divided the selected survey points into grid cells. For the Norwegian data, we used the location of the seven survey areas as they were distant from each other

(Figure 1). For the Swedish data, we divided the country into grid cells of 100 \* 100 km<sup>2</sup>. Since we were interested in the altitudinal shifts, we included only those grid cells that comprised a minimum altitudinal range (i.e., difference between the minimum and the maximum altitude) of 300 m and contained at least 10 survey points. Thereby, we excluded from the analyses the lowlands of Sweden and focused on the more hilly regions, and not least the Scandinavian mountain range that runs along the Swedish-Norwegian border (Figure 1). In total, there were seven grid cells in Norway, where each grid cell had 200 survey points. In Sweden, there were 30 grid cells with 13 to 118 survey points (Figure 1).

Because we were interested in the general pattern of birds' altitudinal shifts, we removed observations of very rare species to ensure reliable estimates of range shift speed. We included in the analyses those species that were observed in at least three grid cells. In addition, we calculated the annual mean number of bird individuals in each survey point in each study period and included in the analyses only those species for which the mean was at least five within a grid cell and study period. We excluded non-native Canada goose (*Branta canadensis*) from the analyses, because its range expansion is not necessarily driven by climatic factors but by human-induced introduction programs. Thus, we included 77 bird species in the analyses (for the full list of species, see Table S2). To validate the robustness of the species selection procedure, we repeated the analyses with varying selection thresholds and did not find major differences in the speeds of species' range shifts depending on the threshold (Table S3).

## Statistical analyses

To assess the altitudinal shift of a bird species, we estimated the mean altitude of each species for each grid cell and each study period in four steps.

1. We calculated the average number of individuals ( $A$ ) of a species per survey point per period:

$$A = \frac{\sum \text{observations}}{N}$$

where  $N$  is the number of years for which the point was surveyed in a given period. Some points were not surveyed in all years within a period, so we weighed the grid cell-specific abundances with the number of years surveyed.

2. We created an altitudinal gradient for each grid cell from 325 to 1400 m by 50 m intervals and aggregated the average number of observations along this gradient.
3. We estimated the relative abundance  $R$  of species  $i$  in each altitudinal interval of each grid cell:

$$Ri = \frac{\sum A}{np}$$

where  $np$  is the number of points inside the altitudinal interval of the grid cell.

4. We estimated the mean altitude of each species ( $M_{alt}$ ) in a grid cell and period:

$$Ri = \frac{\sum A}{np}$$

where  $\frac{Ri}{\sum Ri}$  is the relative abundance of a species in each grid cell and  $Mi$  the mean altitude of the survey points within an altitudinal interval of a grid cell.

We performed a linear mixed effect model to test for changes in the mean altitude of the 77 study species between the two study periods using packages *lme4* (Bates *et al.* 2015) and *lmerTest* (Kuznetsova *et al.* 2017) in R software (version 3.6.1, R Core Team 2020). The response variable was the mean altitude of species in each period and grid cell (N = 1812). First, we investigated if there has been any general change in the altitude of species. Here we included three topographical and spatial variables as fixed effects in the model: the study period (as a continuous variable: period 1 and 2), the altitudinal range within the survey sites inside the grid, and the mean longitude of the grid cell. We excluded latitude due to its strong correlation with longitude (N = 37,  $r_s = 0.739$ ,  $p < 0.001$ ) and altitudinal range (N = 37,  $r_s = 0.408$ ,  $p = 0.010$ ). Inclusion of longitude allowed us to account for potential spatial autocorrelation. We included the identities of country, grid cell, and species as random factors. Second, we wanted to investigate whether the potential altitudinal changes were affected by the interaction of the study period with the longitude and altitudinal range of the grid cell. For this, we used the above-mentioned model and added the interactions between period and longitude, and period and altitudinal range.

To validate the robustness of our results, we performed several sensitivity analyses. Firstly, we visually inspected spatial correlograms of the model residuals for a maximal distance of 500 km using package *ncf* (Bjornstad 2020) for R software. We found no sign of spatial autocorrelation in the residuals at any distance (Figure S1). Then, we fitted the same linear mixed model with different data selection criteria (e.g. by varying selection criteria for number of grid cells, number of species, and number of individuals) (Table S3). Finally, we confirmed the temperature trend across the study area by using the grid cell-specific monthly temperatures from Sweden to calculate the mean temperature for each study period. More specifically, we averaged the monthly temperatures of March and April (early spring) and May and June (late spring – early summer) in each year and then averaged those yearly means across the years within the study period. We used paired t-test (function *t.test* in R program)

To identify those species' traits that may drive the speed of the altitudinal shift, we considered as a response variable the average species-specific change in the mean altitude between periods across grid cells and as explanatory variables species' traits. The order and the family of the species were included as random factors to control for phylogenetic relatedness. We excluded common raven (*Corvus corax*) from this analysis because its longevity trait value was recorded for a captive individual, whereas longevity trait values of other species were recorded for wild individuals. Due to strong correlations with clutch size ( $N = 76$ ,  $r_s = -0.440$ ,  $p < 0.001$ ) and longevity ( $N = 76$ ,  $r_s = 0.616$ ,  $p < 0.001$ ), we excluded body mass from the analysis. Before fitting the models, we rescaled all numerical explanatory variables (standardized to zero mean and unit variance). Then, we fitted generalized linear mixed models using packages *lme4* and *lmerTest* in R software (Bates *et al.* 2015, Kuznetsova *et al.* 2017) to test all the possible combinations of hypotheses, totalling 16 models (Table 3). We performed model selection using Akaike information criterion for small sample sizes (AICc) using package *MuMIn* in R software (Barton, 2019). In the case of several equally good models, we performed model averaging of all the models within 2 AICc units (Burnham & Anderson, 2004).

## Results

### Temperature changes

The temperatures were significantly warmer (mean difference  $+0.6^\circ\text{C}$ ,  $t = -10.8$ ,  $df = 35$ ,  $P < 0.001$ ) during the second study period in March-April, but significantly colder in May-June (mean difference  $-0.3^\circ\text{C}$ ,  $t = 3.99$ ,  $df = 35$ ,  $P < 0.001$ ) across the Swedish part of the study region.

### Shift in the mean altitude

According to our first altitudinal shift model, bird species moved uphill on average by 12.3 m from 1999-2002 to 2015-2018 (Figure 2A, Table 1), which corresponds approximately to 0.9 m per year. For 54 species, we estimated an uphill shift while 23 species had a downhill shift (Table S4). The mean altitude of bird species was higher in the east and in grid cells with a larger altitudinal range (Table 1). Our interaction model showed that altitudinal shifts of species were dependent on topography of the grid, being faster in grid cells with a large altitudinal range (Table 2, Figure 2B, Figure S3).

### Role of species' traits

The model selection procedure identified two best-supported models explaining the species-specific speed in altitudinal shifts that were within two AICc units from each other (Table 3). After averaging these two models, the mean altitudinal shift of birds' ranges was best explained by the fastness-slowness life-history continuum (Table 4), whereby short-lived species showed significant uphill shifts in their mean altitude of abundances (Figure 3). Conversely, population tendency was not significantly related to mean altitude shift (Table 4).

## Discussion

In this study, we showed that bird species' abundances across the Scandinavian mountains shifted uphill over the past decade. Moreover, we showed that the magnitude of the altitudinal shifts is uneven in space and largely mediated by species' traits, species' longevity in particular. At the same time the early spring temperatures have increased whereas the late spring – early summer temperatures have slightly cooled down.

The mean altitude of bird species' ranges has moved uphill at an average speed of 12.3 m within 13 years. This highlights that the altitudinal range shifts are not only driven by a small number of individuals at the range boundaries, but the overall bird abundances are on the move. The observed uphill shift aligns with our expectations under increased temperatures in the study region (IPCC 2014), and with earlier studies reporting bird distributions to be sensitive to temperatures (Böhning-Gaese & Lemoine 2004). The observed uphill shifts in abundances are also in line with earlier studies using presence-absence data that have documented uphill shifts in Southeast Asia (Peh 2007), North America (DeLuca & King 2017), and Europe (Maggini *et al.* 2011, Reif & Flousek 2012). The uphill shifts reported in our study were consistently associated with an increasing temperature trend, indicating that birds are able to shift their ranges rapidly, even in just 13 years, to track suitable climatic niches.

Our findings also illustrate that species' altitudinal shifts are faster in areas that have a wider altitudinal range. These areas of high altitudinal heterogeneity may also hold more space available uphill, which may in turn facilitate a more rapid shift of species. This suggests, at least partly, that species' movement uphill may be limited, to some extent, by the topography of the landscape (Elsen *et al.* 2020).

Out of 77 species, 54 shifted their ranges uphill. Importantly, we found that short-lived species shifted their ranges along the altitudinal gradient more than long-lived species. Longevity is strongly associated with body size and reproduction rate (Angert *et al.* 2011). Thus, long generation lengths may cause the species to have a lower potential for responding fast to changing circumstances and subsequently lead to limited altitudinal or latitudinal range shifts compared to short-lived species (Brommer 2008, Auer & King 2014, Välimäki *et al.* 2016, Böhm *et al.* 2016, Pacifici *et al.* 2020). Our result can be interpreted in two ways. On the one hand, species with a slow turnover of generations can be more vulnerable to climate change (Folden & Young 2016), because they are less capable of rapidly responding to climate change via range shifts to higher altitudes or latitudes (Brommer 2008, Auer & King 2014, Välimäki *et al.* 2016). Furthermore, species with slow life-histories are also more extinction prone (Sodhi *et al.* 2009). The high extinction risk of slow species is also related to their particular niche properties: large and slow species typically occur at low densities and require larger areas that may become a limited resource under climate change, particularly in mountain areas where space shrinks further up. Thus, on top of all other drivers of extinction risk, climate change may exert a particularly strong pressure on slow species. On the other hand, even if small sized species seem to be more capable of expanding their range to higher altitudes (as shown in our study) and latitudes (e.g. Välimäki *et al.* 2016), those species that are already occurring in the mountaintops may be highly vulnerable to climate change. The common mountain bird monitoring in Fennoscandia has shown that high altitude passerines, like snow bunting (*Plectrophenax nivalis*) and Lapland bunting (*Calcarius lapponicus*), are already declining (Lehikoinen *et al.* 2019). Thus, the

vulnerability of a mountain species is not necessarily dependent on its range shift speed, but also on the mean altitude at which it occurs. Based on our results, cold-dwelling passerines, such as bluethroat (*Luscinia svecica*), northern wheatear (*Oenanthe oenanthe*) and common redpoll (*Acanthis flammea*), show faster altitudinal shifts than all species on average (Table S4) and may be under the largest threat.

Beyond longevity, species' traits did not significantly affect altitudinal range shifts. This might be explained by the strong link between species' need to find suitable climatic conditions and their capacity to colonise new areas (Angert *et al.* 2011). Indeed, as the rate of warming is particularly high in the study area (Thompson 2000, Brunetti *et al.* 2009, IPCC, 2014), species may move uphill to cooler habitats to survive, even if it means reaching their niche limits in terms of food or other resources. It is also possible that by excluding some uncommon species due to data limitations, we may have excluded particular trait values. That could further lead to the absence of relationship between the other traits and altitudinal range shifts.

Contrary to our expectation, 23 of the 77 species shifted their ranges downhill (Table S4). This may be due to multiple reasons such as sink-source dynamics or e.g. random variation in fluctuation in food resources such rodents or seeds of trees (Gallego Zamorano *et al.* 2018, Sundell *et al.* 2004).

At a general level, species may respond to climate change in three ways: shift their range or abundance in search for climatically optimal areas, adapt locally for example via shifts in phenology, or decline in numbers and eventually go extinct locally or globally (Parmesan 2006). Typically, species that have been shown to shift fastest under climate change have been classified as winners, and those shifting slowest as losers (e.g., Tayleur *et al.* 2016). However, in mountain areas, the amount of suitable habitat typically shrinks towards higher altitudes. Therefore, species that are shifting faster, and potentially occupy already high altitudes at present, may in fact appear as winners at present, but be losers in the long run. This is because such rapidly shifting species, such as the short-lived species in our study, when occurring at already high altitudes, may face much faster reductions in the overall range, as shifts in the leading range edge will inevitably be hindered by physical constraints, such as by reaching the mountaintop (Elsen *et al.* 2020). Conversely, species shifting slower will take longer to reach the mountaintop and thus may preserve their range extent for longer. However, such species will persist in potentially suboptimal climatic niches, which may hamper their survival and reproduction. Ultimately, assessing the relative importance of stressors, such as human-induced range contractions and species' adaptation capacity, will be key to assessing population persistence under climate change and identify losers and winners at present, but also in the near and far future.

The altitudinal range shifts are complex because they can depend on various underlying processes. In our study, we observed clear shifts uphill despite only early spring temperatures have increased. Importantly, microclimatic conditions differ strongly between slopes, particularly between northern and southern slopes, and may be mediated by the land cover type. Similarly, changes in land use and in species' interactions may be important in further explaining altitudinal range shifts (Heikkinen *et al.* 2007, Bateman *et al.* 2015, Reino *et al.* 2018). For example, the temperature-driven changes in availability of

prey species may affect breeding success of predator species and lead into species-specific changes in the speed of range shift (Pearce-Higgins *et al.* 2010, Pearce-Higgins & Green 2014). It is still poorly understood how these different abiotic and biotic factors interact in affecting the speed of altitudinal range shifts. Furthermore, understanding the complex microclimatic effects on range shifts is important for conservation as the colder northern slopes could serve as microclimatic refugia for cold-dwelling species. Therefore, future research should assess the fine-scale differences in altitudinal range shifts to understand the role of microclimate in range shift speed.

Ultimately, our results emphasize that altitudinal shifts are occurring at large spatial scales and affect species differently, with long-lived species showing the weakest responses. These results are thus particularly important for facilitating future assessments of species vulnerability to climate change, and to furthering our understanding on species' adaptation and persistence under global change.

## Declarations

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**Availability of data and material:** The data is available upon a request.

**Code availability:** The code of the analyses is available upon a request.

**Conflict of interest:** The authors declare that they have no conflict of interest.

**Author contributions:** JC, ELM, AS and AL contributed to the study conception and design. JAK and ÅL provided the data. Data analysis were performed by JC. All authors contributed to the writing of the manuscript. JC, ELM, AS and AL wrote the manuscript; other authors provided editorial advice.

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## Tables

**Table 1.** Results of mixed model analysis on the mean altitude of bird species. Period refers to the categorical variable, whereby the statistics relate to the most recent study period (2015–2018), and the more distant study period (1999–2002) is set as the reference study period. Mean longitude is mean longitude of the grid and altitudinal range is altitudinal range of the grid.

Variable	Estimate	Standard error	df	t value	p-value
Intercept	465.79	52.66	0.78	8.84	0.112
Period	12.29	2.90	1695.7	4.23	< 0.001
Mean longitude	-70.08	24.15	26.4	-2.90	0.007
Altitudinal range	106.75	19.90	33.5	5.37	< 0.001

**Table 2.** Results of mixed model analysis on the mean altitude of bird species including interaction between period and spatial variables: study period, mean longitude of the grid and altitudinal range of the grid. Period refers to the categorical variable, whereby the statistics relate to the most recent study period (2015–2018), and the more distant study period (1999–2002) is set as the reference study period.

Variable	Estimate	Standard error	df	t value	p-value
Intercept	465.74	52.52	0.78	8.87	0.112
Period	12.29	2.90	1693.73	4.24	<0.001
Mean longitude	-68.47	24.53	28.18	-2.79	<0.01
Altitudinal range	97.47	20.36	36.84	4.79	<0.0001
Period * Mean longitude	-1.09	2.90	1693.73	-0.3788	0.705
Period * Altitudinal range	6.18	2.90	1693.73	2.13	<0.05

**Table 3.** Summary of model selection showing  $\Delta$ AICc values of linear mixed effects models explaining variation in the extent of the altitudinal shift according to the species' trait hypotheses tested. The rows are ordered according to the increasing  $\Delta$ AICc values.

Hypothesis	Explanatory variables	$\Delta AICc$
Fastness-slowness + population dynamics	~ Clutch size + Longevity + Population tendency	0
Fastness-slowness	~ Clutch size + Longevity	0.37
Fastness-slowness + migratory behaviour + population dynamics	~ Clutch size + Longevity + Migration strategy + Population tendency	2.48
Fastness-slowness + migratory behaviour	~ Clutch size + Longevity + Migration strategy	3.24
Null model	~ 1	4.92
Population dynamics	~ Population tendency	5.33
Migratory behaviour	~ Migration strategy	5.76
Migratory behaviour + population dynamics	~ Migration strategy + Population tendency	5.82
Fastness-slowness + ecological niche	~ Clutch size + Longevity + Habitat + Diet + STI	8.39
Fastness-slowness + ecological niche + population dynamics	~ Clutch size + Longevity + Habitat + Diet + STI + Population tendency	10.54
Ecological niche	~ Habitat + Diet + STI	12.08
Fastness-slowness + ecological niche + migratory behaviour	~ Clutch size + Longevity + Habitat + Diet + STI + migration strategy	13.47
Ecological niche + population dynamics	~ Habitat + Diet + STI + Population tendency	14.42
Ecological niche + migratory behaviour	~ Habitat + Diet + STI + Migration strategy	15.13
Full model	~ Clutch size + Longevity + Habitat + Diet + STI + Migration strategy + Population tendency	15.45
Ecological niche + migratory behaviour + population dynamics	~ Habitat + Diet + Migration strategy + Population tendency + STI	17.38

**Table 4.** Results of the averaged models of altitudinal shifts as a function of species' traits. The best models within two AICc units (Table 3) were averaged, i.e. the explanatory variables included in fastness-slowness continuum (longevity of species) and population dynamics hypotheses (population trend of species).

Variable	Estimate	Standard error	df	t value	p-value
Intercept	4.825	7.362	7.429	0.650	0.516
Clutch size	-3.276	2.912	2.964	1.105	0.269
Longevity	-9.839	2.884	2.935	3.353	< 0.001
Population tendency	2.727	3.306	3.332	0.818	0.413

## Figures

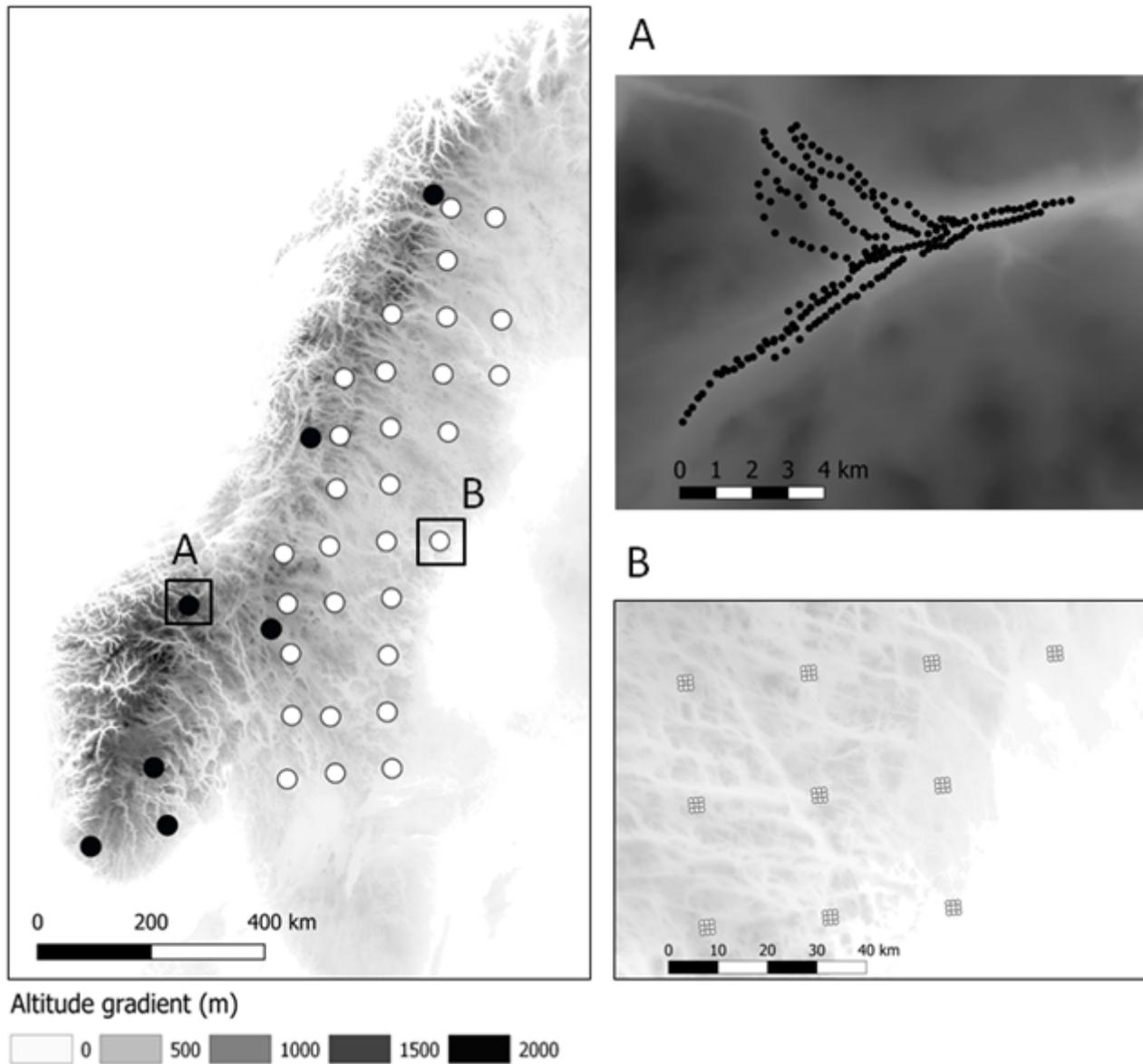
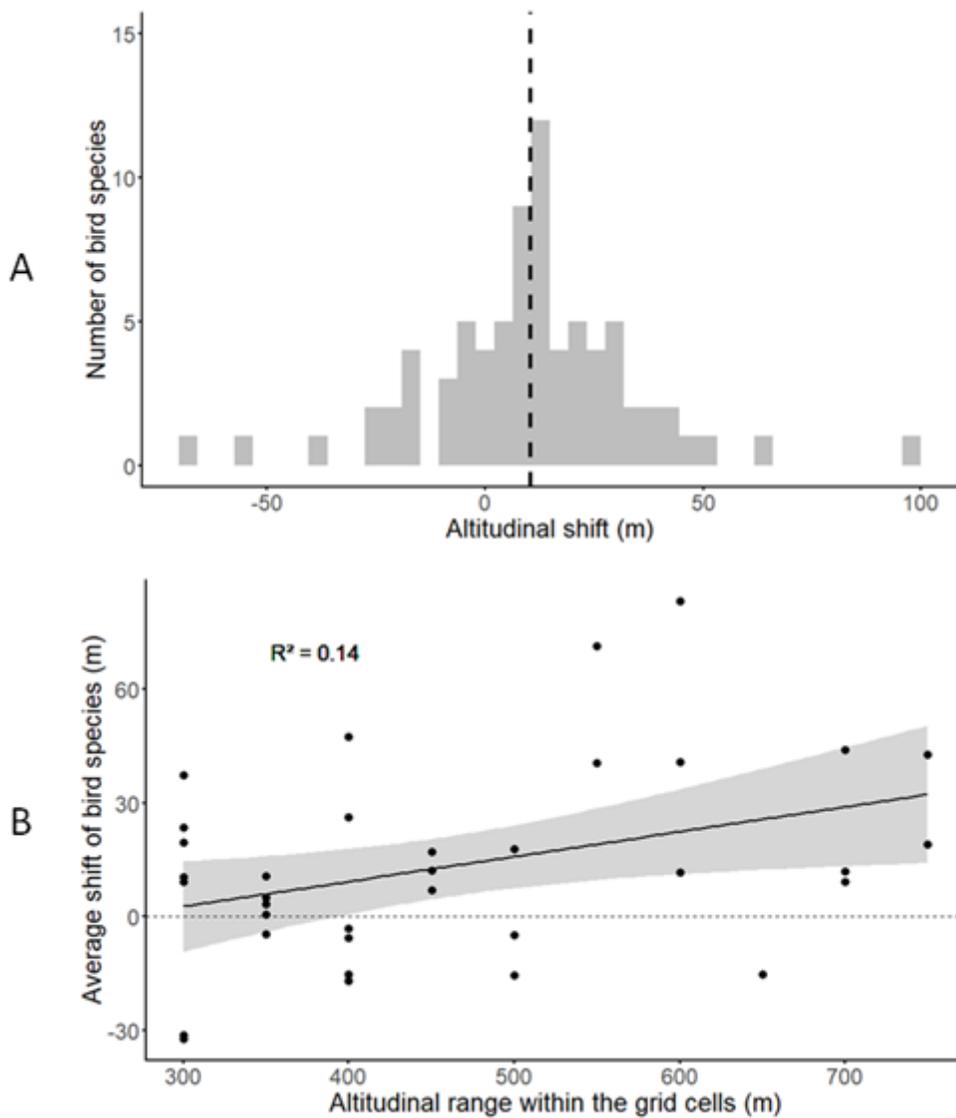


Figure 1

The locations of the geographical centroids of the grid cells included in the analyses. Black dots represent Norwegian centroids of grid cells and white dots represent Swedish centroids of grid cells.

Altitude of the study locations varied between 325 and 1225 meters. Maps (A) and (B) show examples of study design within grid cells in Norway and in Sweden, respectively. Each dot on maps (A) and (B) represents a surveyed point within a route.



**Figure 2**

Distribution of the speed of altitudinal shift among 77 bird species between study periods (1999-2002 and 2015-2018). Panel A illustrates the number of species per altitudinal shift bin (y-axis). The speed of the altitudinal shift is shown on the x-axis such that the negative values indicate downhill shift and the positive values indicate uphill shift. Dashed vertical line corresponds to the average altitudinal shift across the species. The values are obtained from the raw data. Panel B illustrates the relationship between the average altitudinal shift across bird species and the altitudinal range within grid cells. Each black dot represents one grid cell. Black line represents the linear regression relationship of the variables, while the dark grey area represents the 95% confidence interval. The average speed of the altitudinal shift across species is shown on the y-axis such that the negative values indicate an average downhill shift

and the positive values indicate an average uphill shift in the bird community within the grid cell. Altitudinal range within the grid cell, shown on the x-axis, is measured as the difference between the minimum and the maximum altitude of any location within the grid cell.

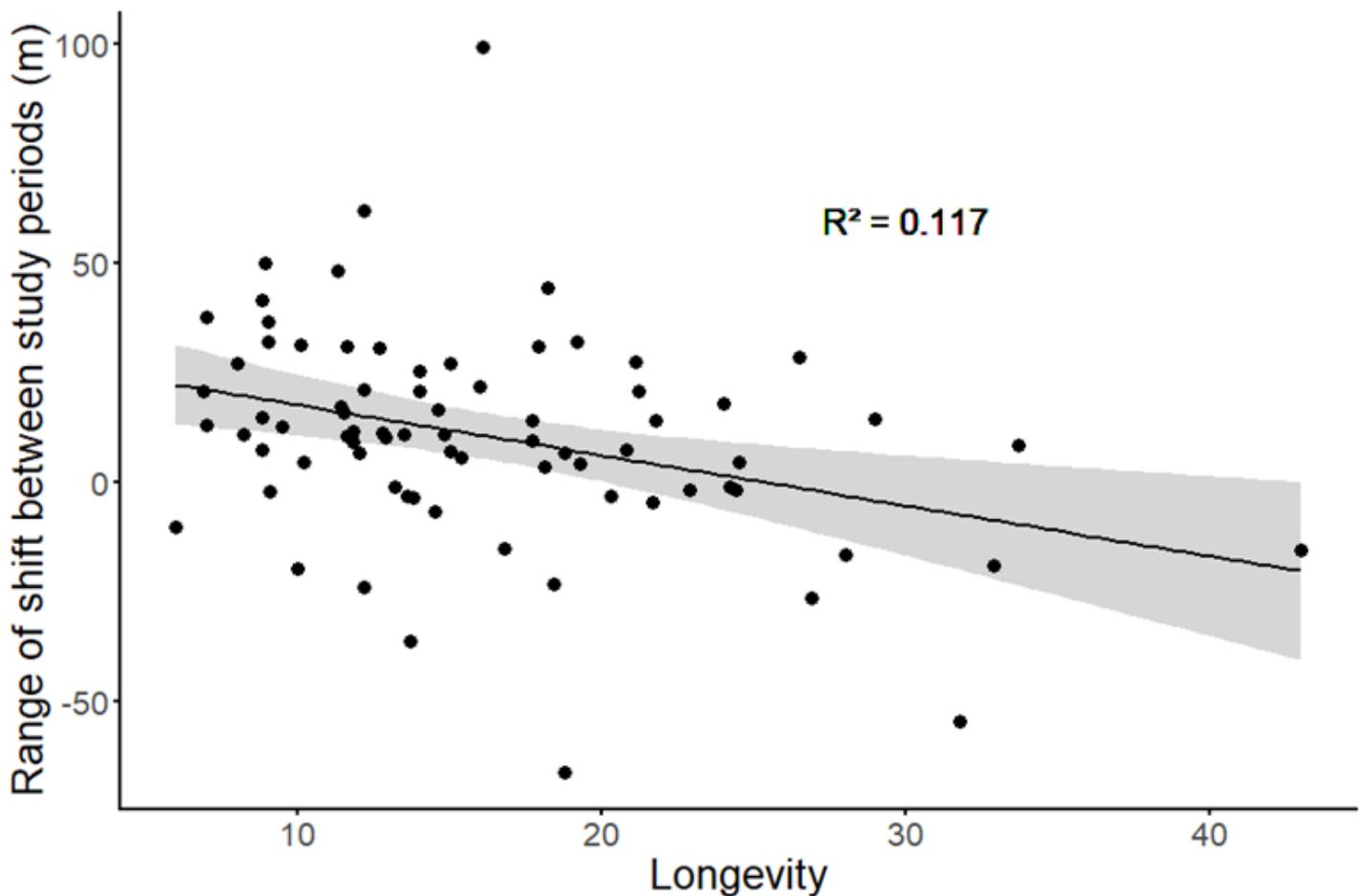


Figure 3

Relationship of the altitudinal range shifts between the two study periods (1999-2002 and 2015-2018) and species' longevity in years. Each black dot represents one species (N = 76). Fitted line represents the least square regression line and dark grey area is the 95% confidence interval. The explanatory power of the linear relationship is shown within the panel.

## Supplementary Files

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