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Declining population trends of European mountain birds

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Abstract

Mountain areas often hold special species communities, and they are high on the list of conservation concern. Global warming and changes in human land use, such as grazing pressure and afforestation, have been suggested to be major threats for biodiversity in the mountain areas, affecting species abundance and causing distribution shifts towards mountaintops. Population shifts towards poles and mountaintops have been documented in several areas, indicating that climate change is one of the key drivers of species' distribution changes. Despite the high conservation concern, relatively little is known about the population trends of species in mountain areas due to low accessibility and difficult working conditions. Thanks to the recent improvement of bird monitoring schemes around Europe, we can here report a first account of population trends of 44 bird species from four major European mountain

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regions: Fennoscandia, UK upland, south-western (Iberia) and south-central mountains (Alps), covering 12 countries. Overall, the mountain bird species declined significantly (−7%) during 2002–2014, which is similar to the declining rate in common birds in Europe during the same period. Mountain specialists showed a significant −10% decline in population numbers. The slope for mountain generalists was also negative, but not significantly so. The slopes of specialists and generalists did not differ from each other. Fennoscandian and Iberian populations were on average declining, while in United Kingdom and Alps, trends were nonsignificant. Temperature change or migratory behaviour was not significantly associated with regional population trends of species. Alpine habitats are highly vulnerable to climate change, and this is certainly one of the main drivers of mountain bird population trends. However, observed declines can also be partly linked with local land use practices. More efforts should be undertaken to identify the causes of decline and to increase conservation efforts for these populations.

KEYWORDS

afforestation, agriculture, alpine habitat, common bird monitoring, global warming, land use changes, loss of biodiversity, mountains, population trend, upland

1 | INTRODUCTION

Human land use changes and a changing climate are the major threats to biodiversity around the world (Root et al., 2003; Stephens et al., 2016; Travis, 2003). Habitat loss, fragmentation and degradation have affected species distribution ranges and abundances (Baillie, Hilton-Taylor, & Stuart, 2004; Fahrig, 2003). Global warming has shifted species distribution areas towards the poles and mountaintops (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Maggini et al., 2011). From a conservation point of view, it is, however, equally important to understand the effects of climate change on population densities that do not necessarily coincide with distributional changes (Chamberlain & Fuller, 2001). In general, while populations of lowland bird and butterfly species have been shown to change according to climate change scenarios in Europe and North America (Breed, Stichter, & Crone, 2013; Devictor et al., 2012; Lindström, Green, Paulson, Smith, & Devictor, 2013; Stephens et al., 2016), the population status of species in the mountain areas is generally poorly known (Chamberlain et al., 2012; Scridel et al., 2018; but see Flousek, Telenský, Hanzelka, & Reif, 2015; Lehikoinen, Green, Husby, Kålås, & Lindström, 2014).

Mountain areas often hold special species communities and are thus in the high-priority list of conservation (Rodriguez-Rodriguez, Bomhard, Butchart, & Forster, 2011). Furthermore, mountain species have been suggested to be particularly vulnerable to climate change, since it is generally more difficult for them to find new suitable habitats towards the mountaintops (low habitat availability simply because of orography, Gonzalez, Neilson, Lenihan, & Drapek, 2010; Huntley, Green, Collingham, & Willis, 2007; Sekercioglu, Schneider, Fay, & Loarie, 2008) or in other mountain ranges (low connectivity

between them, Sirami et al., 2016). The rise in temperature associated with global warming has been predicted to be two to three times higher in the 21st century than recorded during the 20th century (Nogués-Bravo, Araújo, Errea, & Martinez-Rica, 2007). In addition to climate change, mountain species, especially species breeding in uppermost open alpine areas, are also threatened by human land use changes such as altered grazing pressure, afforestation, increased disturbance of recreational activities, pollution (nitrogen and acid deposition) and their interactions (Arlettaz et al., 2007; Brambilla et al., 2010; Britton & Fisher, 2007; Herrando et al., 2016; Ims & Henden, 2012; van der Wal et al., 2003).

The use of biodiversity indicators has become an increasingly common way to monitor changes in the environment (Butchart et al., 2010; Gregory et al., 2005, 2008). Indicators, such as Biodiversity Change Index (Normander et al., 2012), Living Planet Index (Collen et al., 2009), and Red List Index (Butchart et al., 2005), gather large number of information into a single index value, which are easy to understand not only by scientists, but also policymakers and the public (Gregory et al., 2005). Recent advances in this research field have produced, for example, continental indicators of farmland birds and climate change (Gregory et al., 2005; Stephens et al., 2016), but a continental indicator for mountain areas has been lacking. To produce such indicators, large and long-term datasets are required.

From the practical side, monitoring the fate of mountain species may be particularly demanding as mountain areas are often difficult to access, the number of species sharply decrease with altitude (Zbinden et al., 2010) and population densities of species are low (Lehikoinen et al., 2014). Thanks to the recent improvements of the national bird monitoring in Fennoscandia (Norway, Sweden and

Finland), with new schemes covering also the most remote mountain areas, a first-ever regional bird indicator for the Fennoscandian mountain range was created by Lehikoinen et al., (2014). In this study, we have analysed mountain bird trends at the continental scale, with data from 11 different mountain ranges in Europe.

The aim of this work was (a) to investigate population trends of the common bird species in Europe breeding on high-altitude mountain habitats, (b) to evaluate whether population trends differ between species with different ecological characteristics, which may add information on underlying causes of population changes, (c) to produce the first continental-scale biodiversity indicator for mountain bird communities and (d) to establish four regional mountain bird indicators. The continental indicator will show the overall situation, whereas the regional indicators will tell more about the local conditions (Gregory et al., 2005).

Based on the assumption that climate and land use conditions have negatively affected species inhabiting mountain habitats (Arlettaz et al., 2007; Brambilla et al., 2010; Herrando et al., 2016; Ims & Hender, 2012; Lehikoinen et al., 2014), we hypothesize that mountain bird species, in general, are declining in numbers. Second, we hypothesize that this decline would be stronger in mountain specialists that only occur in mountain areas in our study sites, whereas mountain generalists, which also can be found at lower elevations, are doing better because of generally higher ecological flexibility (Davey, Chamberlein, Newson, Noble, & Johnston, 2012; Davey, Devictor, Jonzén, Lindström, & Smith, 2013; Gough et al., 2015). Third, we predict that population trends of mountain species can be influenced by the migration status of species. We hypothesize that long-distance migrants will have fared relatively poorly, as they displayed on average more negative population trends in recent years across Europe—whatever the elevation—than residents and short-distance migrants (Laaksonen & Lehikoinen, 2013; Sanderson, Donald, Pain, Burfield, & van Bommel, 2006; Vickery et al., 2014). An alternative hypothesis is that if a change in habitat quality in the mountain areas has a negative impact on species which are spending the longest time in the mountain areas, short-distance migrants and resident species should have faced stronger declines than long-distance migratory species (Lehikoinen et al., 2014). Last, we hypothesize that the decline in mountain birds is stronger at northern latitudes than at southern latitudes because temperature is expected to increase more in the north (Jacob et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Data collection

Mountain bird populations have been monitored in 11 different mountain areas distributed in 12 countries, mainly within national monitoring schemes on common breeding birds using mainly systematic sampling (Supporting Information Table S1). In the present study, we analysed data from 2002 to 2014. The data collection covered this period unless stated otherwise: Fennoscandia (Finland, Norway and Sweden), UK upland (Britain and Northern Ireland), the Giant Mountains (Czech Republic, 2002–2011), the Alps (Austria 2008–2012, France, Germany 2005–2012, Italy, Switzerland), Massif Central (France), the Pyrenees (Andorra 2011–2012, France, Spain), the Apennines (Italy), Spanish central mountains (Spain), Spanish Iberian mountain system (Spain), Baetica mountain range (Spain 2003–2012), and Cantabria mountain range (Spain; Table 1). The local census methods are explained in Supporting Information Table S1. Census methodology differed between countries, but this will unlikely introduce systematic bias into the derived trends (see, e.g., Gregory et al., 2005; Lehikoinen et al., 2014; Stephens et al., 2016).

2.2 | Site and species selection

To get enough data to calculate trends for a larger set of species, we lumped the 11 areas into four larger mountain regions: Fennoscandia, UK upland, south-western mountains (including Pyrenees and four Spanish mountain areas, hereafter called as "Iberia") and the south-central mountains (including the Alps and the surrounding smaller mountains: Giant Mountains, Massif Central and the Apennines, hereafter called as "Alps," Figure 1).

Before we could define which species to use in the study, we needed to define "mountain" monitoring sites and species in each region. Our aim was to target species that prefer open or semi-open mountain habitats. These are mainly situated on the highest altitudes of the mountains and are thus in the highest risk in terms of climate change (Gonzalez et al., 2010). Since mountaintop populations have limited places to move upwards, the expected population declines should be strongest in high-altitude habitats. Thus, we selected mountain tundra, meadows, grasslands, bare rock, sparsely vegetated areas, peat bogs and scrubland above certain altitude. We also included the, often spatially adjacent, zones of mountain birch forest

TABLE 1 The number of study sites (mean, min and max during 2002–2014) in 11 mountain areas distributed over four major mountain regions. In the Giant Mountains and the Apennines, the number of point count locations were transformed into sites dividing number of point stations by 15 (a typical number in point count routes in Italia and the Czech Republic, Giant Mountains)

| Mountain area	Region	Mean sites
Fennoscandia	Fennoscandia	160 (60–256)
UK upland	UK upland	99 (72–140)
Alps	"Alps"	122 (88–155)
The Giant Mountains	"Alps"	1 (0–2)
Massif Central	"Alps"	1 (0–2)
Apennines	"Alps"	20 (9–37)
Baetica mountain range	"Iberia"	6 (0–10)
Cantabria mountain range	"Iberia"	12 (4–17)
Central mountain system	"Iberia"	24 (16–29)
Iberian mountain system	"Iberia"	6 (5–7)
Pyrenees	"Iberia"	23 (11–39)
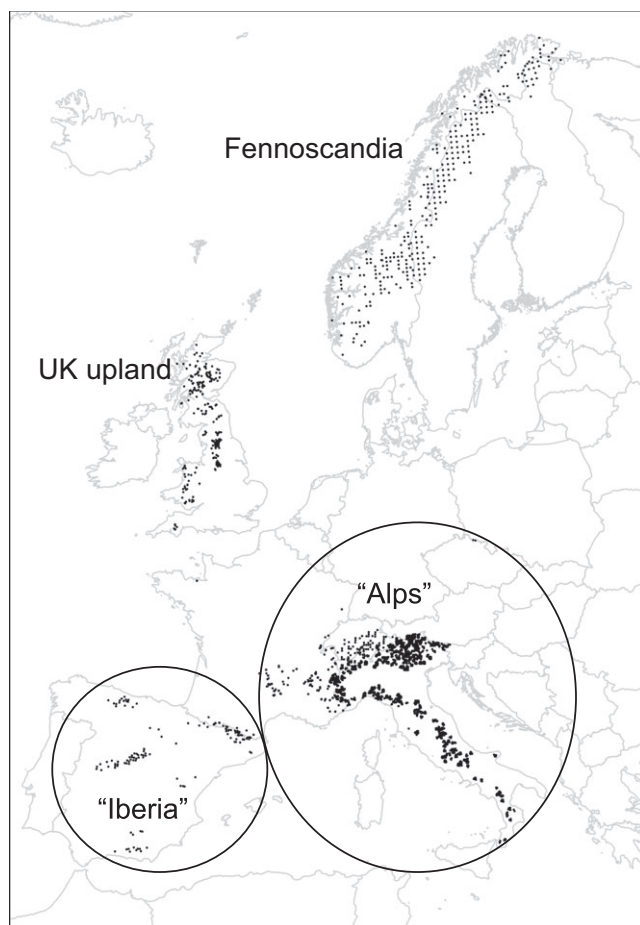
FIGURE 1 A map showing the four European mountain regions, where the data was collected. The dots show the census locations (survey route) except in Italy where each dot represents one point of a point count route

and dwarf mountain pine (for simplicity, all the mentioned habitats are generally referred to as "mountain habitat"). For latitudinal reasons (and also exposure on the western seaboard) also the altitudes where open mountain habitat occur varies and this needs to be defined separately for each mountain range. Since some of the species occur also outside the mountains—though we were only interested in the populations living in the mountain areas—we needed to use habitat information to define mountain sites from each area. For instance, due to the long north-east–south-west gradient (1,600 km) of the Fennoscandian mountain area, mountain habitats vary in altitude. For example, tundra is first found above 1,300 m altitude in the south, but at sea level in the very north (Lehikoinen et al., 2014). It should be noted though, that only four out of 289 Fennoscandian sites were situated below 100 m of altitude. In the rest of the mountain regions, "mountain sites" were set to include at least one-third open mountain habitat and to be above a certain altitude, depending on local conditions such as climate, latitude and historical land use. These altitude thresholds for mountain sites were set to 400 m for UK upland (and where the surveyed habitats were generally open), 1,100 m for the Giant Mountains and 1,200 m for all the remaining southern mountains, respectively. The UK upland have a particularly

long history of anthropogenic deforestation and in combination with high levels of extensive grazing and climatic exposure. Therefore, open habitats resembling those of montane and alpine areas exist at lower altitudes than would naturally occur (Smout, 2005; Thompson, MacDonald, Marsden, & Galbraith, 1995). Also in the southern and central European sites, open areas above the altitude limit are not necessarily caused by the natural tree line, but areas also include subalpine meadows that remain open due to grazing. The number of study sites in each area is given in Table 1.

To define species which have significant populations in high-altitude mountain habitats (so-called mountain species), we used altitude information from each larger mountain range area using data from the United Kingdom (line transects, UK upland) and Switzerland (territory mapping, the Alps) and Spain (line transects, Catalonian Pyrenees). First, we calculated relative densities based on mountain site-specific species abundances and sampling effort (birds/km line transect) in 100-m-altitude zones starting from the above-mentioned mountain thresholds of the regions. Second, based on altitude zone densities, we calculated the mean altitudes of species for each mountain region. In the United Kingdom, species whose mean altitude were above 550 m (a.s.l.; more than half of the population should be breeding above this altitude in mountain routes) and preferred open mountain habitats were included (Supporting Information Table S2). We calculated mean altitudes separately for the Swiss Alps and the Catalonian Pyrenees and used the mean of these two values for both "Iberia" and "Alps." The altitude threshold for the species in these areas was above 1800 metres (Supporting Information Table S3). In Fennoscandia, a set of 14 common mountain species were already defined by Lehikoinen et al. (2014). However, due to an increased monitoring effort in recent years, we could include nine additional, less common, mountain species for this region (Table 2).

We calculated species-specific population trends for each of the four defined mountain regions: Fennoscandia, UK upland, "Iberia" and "Alps." In addition, we pooled the counts from all regions to calculate species trends for the whole area (further details are given below). Trend analyses were conducted for species which had at least five records per year in a given area (at the regional level, maximally 1 year with a sample size below five individuals was accepted). When calculating the population trends for Europe, we also included counts from mountain regions which had lower than five records annually to maximize the total sample sizes. Mean annual sample sizes are shown in Supporting Information Table S4.

Species were classified into mountain specialists or generalists, based on their distribution areas in Europe. Species mainly restricted to mountain areas and uncommon in the lowlands were classified as mountain specialists whereas species which have substantial populations in the mountains but also commonly breed in lowlands were classified as mountain generalists (Hagemeijer & Blair, 1997, see also Scridel et al., 2018; Thompson, Kålås, & Byrkjedal, 2012; Table 2). Furthermore, species were grouped into long distance (wintering in tropical areas) and others (including both species wintering in the Western Palearctic and residents) based on their distribution ranges

TABLE 2 The average annual population growth rates (trends) and traits of 44 mountain bird species in 11 European mountain areas, as well as separate species trends for the "Alps", Fennoscandia, "Iberia" and UK upland during 2002–2014. Traits include specialization (Sp = mountain specialists, G = generalists; classification based on distribution areas of Hagemeijer and Blair (1997)) and migratory behaviour (Ld = long-distance migrant, Ot = other). Significant population change rates are in bold. "–" means that the species is not a typical mountain bird in the particular mountain region and NE means that species is a typical mountain species in the area, but there were too little data available to calculate trends (see also Supporting Information Table S4)

Species (specialization)	Traits	All areas Slope ± SE	"Alps" Slope ± SE	Fennoscandia Slope ± SE	"Iberia" Slope ± SE	UK Slope ± SE
Clangula hyemalis	Sp, Ot	−0.033 ± 0.023	–	−0.033 ± 0.023	–	–
Buteo buteo	G, Ot	−0.006 ± 0.014	–	–	–	−0.006 ± 0.014
Buteo lagopus	G, Ot	−0.041 ± 0.027	–	−0.041 ± 0.027	–	–
Falco tinnunculus	G, Ot	0.008 ± 0.007	0.011 ± 0.008	-	−0.011 ± 0.021	–
Lagopus lagopus	G, Ot	**−0.026 ± 0.006**	–	**−0.095 ± 0.010**	–	0.003 ± 0.007
Lagopus muta	Sp, Ot	**−0.018 ± 0.008**	0.013 ± 0.012	**−0.047 ± 0.013**	NE	NE
Tetrao tetrix	G, Ot	0.010 ± 0.027	0.035 ± 0.039	-	–	NE
Alectoris graeca	Sp, Ot	0.019 ± 0.021	0.019 ± 0.021	-	–	–
Charadrius hiaticula	G, Ot	**0.050 ± 0.020**	–	**0.051 ± 0.021**	–	–
Charadrius morinellus	Sp, Ot	0.012 ± 0.022	–	0.035 ± 0.024	–	NE
Pluvialis apricaria	G, Ot	**0.013 ± 0.005**	–	0.010 ± 0.005	–	0.022 ± 0.012
Calidris alpina	G, Ot	0.005 ± 0.018	–	0.009 ± 0.021	–	NE
Gallinago gallinago	G, Ot	−0.011 ± 0.012	–	–	–	−0.011 ± 0.012
Tringa totanus	G, Ot	**0.033 ± 0.010**	–	**0.033 ± 0.010**	–	–
Phalaropus lobatus	G, Ld	−0.003 ± 0.030	–	−0.003 ± 0.030	–	–
Stercorarius longicaudus	Sp, Ld	0.014 ± 0.017	–	0.014 ± 0.017	–	–
Cuculus canorus	G, Ld	**−0.053 ± 0.007**	–	**−0.053 ± 0.007**	–	–
Alauda arvensis	G, Ot	−0.001 ± 0.003	**0.016 ± 0.006**	–	**−0.033 ± 0.008**	0.004 ± 0.006
Hirundo rupestris	Sp, Ot	0.001 ± 0.009	0.012 ± 0.011	–	−0.017 ± 0.015	–
Anthus pratensis	G, Ot	**−0.008 ± 0.003**	NE	**−0.012 ± 0.005**	NE	−0.005 ± 0.004
Anthus spinoletta	Sp, Ot	−0.001 ± 0.003	0.000 ± 0.003	–	**−0.037 ± 0.013**	–
Prunella collaris	Sp, Ot	0.002 ± 0.007	0.002 ± 0.007	–	NE	–
Luscinia svecica	G, Ld	−0.001 ± 0.007	–	−0.002 ± 0.008	–	–
Phoenicurus ochruros	G, Ot	**0.008 ± 0.003**	**0.014 ± 0.003**	–	**−0.025 ± 0.007**	–
Phoenicurus phoenicurus	G, Ld	0.014 ± 0.007	–	0.014 ± 0.007	–	–
Saxicola rubetra	G, Ld	**−0.030 ± 0.008**	**−0.029 ± 0.008**	–	−0.023 ± 0.049	–
Oenanthe oenanthe	G, Ld	**0.009 ± 0.003**	**0.026 ± 0.004**	−0.005 ± 0.008	−0.013 ± 0.007	0.002 ± 0.008
Monticola saxatilis	Sp, Ld	−0.022 ± 0.013	−0.002 ± 0.017	–	**−0.059 ± 0.021**	–
Turdus torquatus	Sp, Ot	0.005 ± 0.004	0.001 ± 0.004	**0.060 ± 0.025**	0.000 ± 0.021	−0.006 ± 0.017
Turdus iliacus	G, Ot	**−0.033 ± 0.006**	–	**−0.033 ± 0.006**	–	–
Sylvia curruca	G, Ld	0.011 ± 0.006	0.011 ± 0.006	–	–	–
Phylloscopus trochilus	G, Ld	**−0.032 ± 0.003**	–	**−0.032 ± 0.003**	–	–
Pyrrhocorax graculus	Sp, Ot	−0.015 ± 0.011	−0.002 ± 0.012	–	−0.044 ± 0.025	–
Pyrrhocorax pyrrhocorax	G, Ot	**0.050 ± 0.012**	NE	–	**0.053 ± 0.014**	–
Corvus corone	G, Ot	**−0.047 ± 0.014**	–	–	–	**−0.047 ± 0.014**
Corvus corax	G, Ot	0.016 ± 0.013	–	–	–	0.016 ± 0.013
Montifringilla nivalis	Sp, Ot	**0.021 ± 0.010**	**0.021 ± 0.010**	–	NE	–
Fringilla montifringilla	G, Ot	**−0.025 ± 0.005**	–	**−0.025 ± 0.005**	–	–
Serinus citrinella	Sp, Ot	**−0.026 ± 0.013**	−0.051 ± 0.031	–	−0.023 ± 0.016	-
Carduelis cannabina	G, Ot	**0.015 ± 0.007**	0.007 ± 0.008	–	0.040 ± 0.022	-
Carduelis flammea	G, Ot	**−0.048 ± 0.005**	**−0.025 ± 0.007**	−0.052 ± 0.007	–	–

(Continues)

TABLE 2 (Continued)

Species (specialization)	Traits	All areas Slope ± SE	"Alps" Slope ± SE	Fennoscandia Slope ± SE	"Iberia" Slope ± SE	UK Slope ± SE
Calcarius lapponica	Sp, Ot	−0.026 ± 0.008	–	−0.026 ± 0.008	–	–
Plectrophenax nivalis	Sp, Ot	−0.041 ± 0.014	–	−0.042 ± 0.014	–	NE
Emberiza cia	Sp, Ot	−0.031 ± 0.006	−0.024 ± 0.012	–	−0.033 ± 0.008	–

in winter (Cramp, Simmons, & Perrins, 1977–1994; Lehikoinen et al., 2014).

2.3 | Weather data

We used European weather data (available at European Climate Assessment & Dataset http://www.ecad.eu/download/ensembles/download.php in 0.25 degree grids across the continent) to calculate changes in the temperature of the breeding season April–August. We tested rate of change in the mean temperature in each region in the long term (1980–2014) and short term (1995–2014) using linear regression. We first calculated region-specific annual mean temperatures from weather sites situated in the mountain region and then conducted the linear regression. The locations from where the data were extracted are shown in Supporting Information Figure S1.

2.4 | Statistical analyses

Log-linear population trends and annual indices were calculated for each species separately using the software TRIM (Pannekoek & Van Strien, 2005). TRIM is a commonly used tool in bird monitoring in Europe that accounts for overdispersion and serial correlation and interpolates missing observations using a Poisson general log-linear model (European Bird Census Council, 2018). TRIM produces annual growth rate as well as annual abundance indices, including their standard errors. Long-term annual growth rates and annual abundance indices were calculated for Europe using aggregated data from all regions and separately for each of the four major mountain regions. We compared the change in the overall mountain bird indicator to the corresponding magnitude of change in European (a) common bird, (b) farmland and (c) forest bird indicators during 2002–2014 provided by European Bird Census Council (2018).

The calculation of the indicators was done using a new statistical tool, which has not been used earlier in continental analyses. We combined annual population indices of species as multi-species indicators using the R-package tool (Soldaat, Pannekoek, Verweij, van Turnhout, & van Strien, 2017). The package calculates annual multi-species indicator values and their standard errors as well as a long-term change of the indicator using Monte Carlo simulation method and the species-specific indices and their standard errors provided by TRIM. We used TREND_DIFF-function of the package to test whether the indicators differed from each other (specialist vs. generalists, or regional indicators).

Spatial differences in sampling network could lead into a situation where trends are more driven by areas where number of census sites are dense compared to areas where the network is sparse. We therefore, per each contributing country, weighted the trend analyses by the spatial coverage of the national network. As weight, we used the country-specific mountain region area divided by the number of census sites (average area per census sites: larger value mean lower density of census sites). Thus, census sites in countries with proportionally fewer routes in mountain areas weighed more in the analyses. France contributed to data of two regions ("Iberia" and "Alps"), and thus, the weights were calculated separately for these regions. The mountain area was measured using Corine land cover data (Copernicus Land Monitoring Service, 2016), where mountain habitats were (a) natural grasslands, (b) moors and heathlands, (c) transitional woodland shrubs, (d) bare rock, (e) sparsely vegetated areas, (f) glaciers and perpetual snow and (g) peat bogs, which were above certain region-specific altitude (see Supporting Information Table S5). Here, we have used the data of the year 2012 only. We believe that this represents the general situation in each country, because these habitat types unlikely show large-scale changes during the relatively short study period.

Last, we analysed a set of factors that potentially could explain the regional population trends of species provided by TRIM analyses in the four major mountain areas during 2002–2014, using GLMM (functions lmer and lmerTest in R). Regional long-term population trends were tested against migratory behaviour (long-distance migrants or other, the latter including residents, which are rare among mountain birds), specialization (mountain specialists or generalists) and short-term temperature change in each region ("Alps," Fennoscandia, "Iberia" and the United Kingdom; Table 3). Species was a random factor in the model to account for some species having data from several mountain regions whereas some only have data from one of them. We took phylogeny into account in the analyses since species with the same ancestors may have more similar responses. We did this by first using various phylogenic structures (order, family and genus based on del Hoyo, Collar, Christie, Elliot, and Fishpool (2014) and del Hoyo et al. (2016), altogether eight combinations, see Supporting Information Table S6) in the random part of the full model. We ranked these models based on AICc (Burnham & Anderson, 2004). Second, we used the best phylogenic structure in the final analyses, where we constructed 12 model combinations, and where the full model included the two-way interactions temperature*migration and temperature*specialization. The inclusion of an interaction between temperature and migration was based on the hypothesis that species that spend most of the time in the mountain areas (short-distance migrants and residents) may face the largest declines in areas where the temperature increase has

been highest. The interaction between temperature and specialization relates to the hypothesis that specialists would be declining fastest in the area with high temperature increase. The model combinations are shown in Table 3. These 12 models were ranked based on AIC corrected for small sample sizes (Burnham & Anderson, 2004). Finally, we took the uncertainty of the population trends into account in the analyses using the reciprocal of the standard errors of the trends as weights. We used R (version 3.4.1) in all the analyses (R Core Development Team, 2017).

3 | RESULTS

Because the results of the weighted analyses according to the national area per census sites ratio were almost identical to the non-weighted analyses (Supporting Information Table S6), we decided to show only the unweighted results in the main results section (Table 2).

The European mountain bird indicator showed a significant negative decline during 2002–2014 (44 species; −0.61%/year, 95% CI −1.14 to −0.08, overall decline c. −7%; Figure 2a). The European mountain specialist indicator also declined significantly (n = 16 species, −0.88%/year, 95% CI −1.66 to −0.10, overall decline c. −10%). The mountain generalist slope was also negative (n = 28 species, −0.46%/year), but not significantly so (95% CI −1.06 to 0.17; Figure 2b). The slopes of specialists and the generalists did not differ from each other (trend difference = 0.0040, se = 0.0051, p > 0.05, see also Table 3). Among the specialists, five out of 16 species showed negative and one showed positive trends. Among the generalists, nine out of 28 species declined and seven increased (Table 2). Despite the fact that many mountain bird species have a wide distribution in Europe, it is important to note that only for two out of 44 species (northern wheatear and ring ouzel) were there enough data

TABLE 3 AICc differences, AIC weights (w) and evidence ratios (ER) of models explaining regional population trends of mountain birds during 2002–2014. Spe is specialization (mountain specialist or generalist), Mig is migratory behaviour (short- or long-distance migrant) and Mt is mountain region

Model	ΔAICc	w	ER
Intercept only	0.00	0.276	1.0
Temp	0.96	0.171	1.6
Spe	1.53	0.128	2.2
Mig	2.05	0.099	2.8
Spe + Temp	2.35	0.085	3.2
Spe + Temp + Spe*Temp	3.13	0.057	4.8
Mig + Temp	3.22	0.055	5.0
Mig + Spe	3.43	0.050	5.5
Mig + Spe + Temp	4.53	0.029	9.5
Mig + Spe + Temp + Spe*Temp	5.45	0.018	15.3
Mig + Temp + Mig*Temp	5.46	0.018	15.3
Mig + Spe + Temp + Mig*Temp	6.87	0.009	30.7

to calculate trends in all four mountain areas. In addition, for about half of the species, population trends were only calculated for one of the four regions, because the species were too rare in other regions (Table 2).

The indicator of "Alps" showed no significant trends during 2002–2014 (n = 20 species, +0.29%/year, 95% CI −0.59 to 1.17, Figure 3a). Four species showed positive, and three species showed negative trends during 2002–2014 (Table 2). The Fennoscandian and "Iberian" indicators showed significant negative trends during 2002–2014 (Fennoscandia, n = 23 species, −1.20%/year, 95% CI −2.04 to −0.36, overall decline −13%; "Iberia", n = 14 species, −1.94%, 95% CI −3.61 to −0.27, overall decline −21%; Figure 3b–c). In Fennoscandia and "Iberia," respectively, 10 and five species showed negative, and three and one showed positive trends (Table 2). The indicator of UK upland showed no significant trend during 2002–2014 (n = 10 species, −0.29%/year, 95% CI −1.13 to 0.55, Figure 3d). In UK upland, one species declined (carrion crow) and none increased in 2002–2014 (Table 2). According to bootstrapping simulations, the slopes of Fennoscandian and "Iberian" indicators differed significantly from slopes in the "Alps" (trend difference between "Alps" and Fennoscandia 0.015 ± 0.006 se, p < 0.05, trend difference between "Alps" and Iberia 0.022 ± 0.010 se, p < 0.05). Slopes of the other regions did not differ from each other (all p > 0.05).

The species only was the best random structure compared to more complicated phylogenic structures (Supporting Information Table S7), and thus, species only was used in the latter analyses. The best model explaining the regional population trends of species during 2002–2014 was the null model. Although two other more complex models were within two AIC units, additional variables of those models can be considered as uninformative parameters (sensu Arnold, 2010). Thus, this modelling approach was not able to find that region, specialization or migratory behaviour was linked with the regional population trends (Table 3). The intercept of the null model was significantly below zero (−0.0072 ± 0.0035, t = 2.0, p < 0.05), suggesting in general negative regional population trends during this particular period.

Annual temperatures during the breeding season (April–August) increased significantly in all four regions in the long term (rate of increase 0.81–1.55°C during 1980–2014; Table 4). During the last 20 years (1995–2014), the temperature increase was only significant in Fennoscandia (Table 4).

4 | DISCUSSION

We set out to test three hypotheses regarding the recent population trends in European mountain birds. We got unequivocal support for the first hypothesis regarding a negative trend of European mountain bird populations since we found that the indicator has an overall decline of −7% during 2002–2014 (−0.61%/year). Fennoscandian and "Iberian" mountain bird indicators declined significantly and differed from the slope of the corresponding indicator in the "Alps". Based on European common bird monitoring, the magnitude of the decline is the same as all common birds in Europe during the same
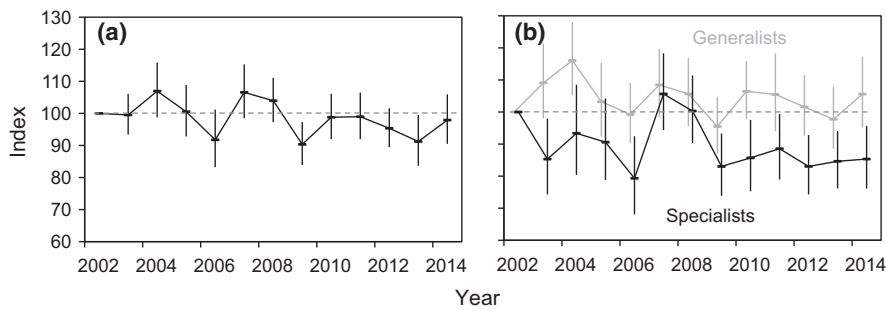
FIGURE 2 (a) The mountain bird indicator for Europe and (b) the separate indicators for specialists and generalists, during 2002–2014. Calculated mean of the indices and their 95% CIs are given
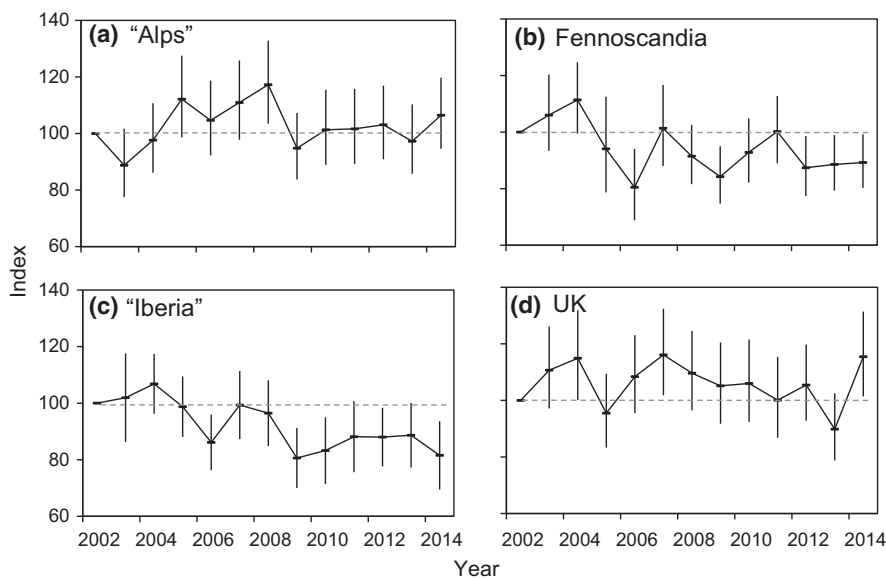

FIGURE 3 Regional mountain bird indicators during 2002–2014 from (a) "Alps", (b) Fennoscandia, (c) "Iberia" and (d) United Kingdom. Calculated mean of the indices and their 95% CIs are given

TABLE 4 Annual changes in temperature (in °C from April to August) in four mountain regions in Europe during 1980–2014 and 1995–2014. Significant temperature changes are marked in bold

Mountain area	1980–2014	1995–2014
"Alps"	0.045 ± 0.012	0.016 ± 0.026
Fennoscandia	0.035 ± 0.012	0.067 ± 0.031
"Iberia"	0.037 ± 0.010	0.013 ± 0.026
UK upland	0.024 ± 0.008	0.007 ± 0.019

study period. More specifically, the trends of bird indicators in two important habitats, farmland and forests, were −13% and −1%, during the study same period, respectively (European Bird Census Council, 2018). Thus, in general mountain birds are doing less bad than farmland birds, but clearly worse than forest birds in Europe. The severe declines of farmland birds are mainly driven by intensification of agriculture rather than climate change (Butler, Boccacio, Gregory, Voříšek, & Norris, 2010; Eglington & Pearce-Higgins, 2012; Jørgensen et al., 2016). However, in case of mountain birds, climate change can have a larger impact as the climatic niche of especially mountain specialists is shrinking, highlighted by the relatively fast declines of mountain species.

As far as our second hypothesis is concerned, that the decline would be stronger in mountain specialists than in mountain generalists, the outcomes of our tests are less straightforward to interpret. Numerically, the decline was indeed larger among the specialists (−0.88%/year vs. −0.46%/year). However, the two slopes were not statistically different from each other, nor is the generalist slope statistically significant in itself. We believe that the nonsignificant difference between these two groups is at least partly caused by small sample sizes, which increase uncertainty in the trend estimates and reduce statistical power. The topic should be re-evaluated in the future with longer time series. In general, we should be more worried about mountain specialists, since this group of species showed already significant population declines.

We got no support for our third main hypothesis that long-distance migrant mountain birds have fared worse than resident and short-distance migrant mountain birds, finding no significant differences between migratory groups on the regional level. Therefore, the diminishing mountain bird populations are not only driven by general declines of long-distance migrants (e.g., Sanderson et al., 2006; Vickery et al., 2014), but also species wintering in Europe are contributing to the decline in mountain birds. This could indicate that mountain species have also problems in their breeding areas (Lehikoinen et al., 2014). More work needs to be done to understand, what are the valid traits to evaluate the vulnerability of mountain species in the face of climate change (see also MacLean & Beissinger, 2017).

The reason why there seem to be no universal patterns explaining species-specific variation in responses to climate change could be that regional circumstances, such as land use practices, differ between areas. In one area, impacts of climate change may be more important than changes in land use and *vice versa*. Agro-pastoral land use practices have become less intense or have been abandoned completely allowing forest cover to increase again, especially in the low-altitude mountains of the southern mountain regions ("Alps" and "Iberia"; Brambilla et al., 2010; Herrando et al., 2016; Maggini et al., 2014). Interactions with agricultural abandonment and forest expansion can be complex and offer both threats and opportunities depending on the ecological requirements of species and assemblages involved (Calladine, Bielinski, & Shaw, 2013; Gillings, Fuller, & Henderson, 1998; Herrando et al., 2016).

The April–August temperatures have increased substantially in recent decades in all four mountain areas. Although the temperature increase has been significant only in Fennoscandia over the last two decades, the temperatures are nowadays above the long-term mean in all regions (Lehikoinen et al., 2014). Climate change may affect bird populations in a different manner depending on the region (Sæther & Engen, 2010). Furthermore, temperatures are expected to rise faster in higher northern latitude mountains than in mountains located in temperate and tropical zones, and the rate of warming in mountain systems can be two to three times higher than that recorded during the 20th century (Nogués-Bravo et al., 2007). These can cause considerable effects on biodiversity even though the direct impacts can be difficult to measure (Araújo, Errea, & Martinez-Rica, 2007). Although we could not link the population dynamics with the observed climate change, the observed declines are in line with the population predictions in relation to climate change (Huntley et al., 2007). Human-induced land use changes are not as extensive in Fennoscandian mountains (Lehikoinen et al., 2014) compared to "Iberia" (Herrando et al., 2016), and several Fennoscandian studies have revealed changes in plant community due to climate change (Kullman & Öberg, 2009; Michelsen, Syverhuset, Pedersen, & Holten, 2011; Vuorinen et al., 2017). One should also keep in mind that especially in Fennoscandia some mountain species are nomadic to some extent (Lindström, 1987) and both plant and animal communities are strongly influenced by multi-annual cyclic fluctuation of small rodents (Hanski, Hansson, & Henttonen, 1991; Turchin, Oksanen, Ekerholm, Oksanen, & Henttonen, 2000). Even animal species that are not using rodents in their diet are influenced by the cycles due to predator–prey interactions (Lehikoinen et al., 2016). Despite these kinds of fluctuations, we were able to detect a negative long-term trend in Fennoscandia.

We must stress that the methods of the monitoring schemes and their intensity showed spatial variation within the overall study area. However, we do not believe that this has biased the analysis. First, the magnitude of the trend should be comparable independently of whether it is based on point count, line transect or territory mapping (Gregory et al., 2005). Second, we tried to compensate for the potential biases in the sampling by using country-specific weights. The use of weights did not influence the main results. We believe that there are two reasons why our weighting did not influence the population trends: (a) Many of the species data are only available from one of the study regions and thus weighting between regions have no importance; and (b) population trends of nearby countries are similar. As the monitoring schemes have improved in many countries in recent years including systematic sampling, future analyses of monitoring data will be even more reliable due to increased sample sizes.

Modelling work on the future effects of climate and land use change have suggested that species-specific conservation measures aiming at improving habitat to counteract the negative influence of climate change can only deliver minor improvements of the future fate of mountain birds (Braunisch et al., 2014). Even if high mountains may provide refuges for threatened mountain species currently populating lower altitudes, in the long term, climate change can be expected to have a strong impact on alpine species (Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick, 2018). Alpine habitats are expected to be reduced and become more fragmented and isolated due to rise of the tree line where species have increasing limited dispersal possibilities. Our findings also emphasize that local studies are needed to understand the mechanisms and drivers of the population changes of individual species and species communities in mountains including information about species habitat selection and changes in the amount of preferred habitat. Despite international actions to halt climate change, climate will change in the near future (EEA, 2012). To mitigate the potential impacts of climate change, it is important to take measures that can improve connectivity between suitable mountain habitats and to minimize the effects of other threats such as non-sustainable tourism and afforestation of grasslands (Lloret, 2017).

Last, to understand the big picture on the continental and global scale we also need to continue existing monitoring work in the mountain areas and expand both the taxonomic and spatial coverage of monitoring schemes. Monitoring should preferably be based on systematic sampling design with a reasonable number of study sites covered on annual basis. One reason why we did not observe significant differences in trends between specialization groups could be the still relatively small sample sizes and thus larger uncertainties in our trend estimates. Nevertheless, our European mountain bird indicator and regional indicators provide an important tool to measure and monitor the changes in mountain biodiversity with regular updates in the future and the spatial coverage of the indicator can easily be expanded when suitable monitoring data become available. Given that climate and land use changes in the uplands are likely to manifest themselves into the loss of open mountain habitats and expansion of shrubland/forest, we suggest that future work should also look at mechanistic reasons behind the declines. More and important information may come from comparing potential differences in trends between mountain and lowland population of the mountain generalists, where the land use pressures can differ between the areas.

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SUPPORTING INFORMATION

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

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