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Declining population trends of European mountain birds

Running head: Decline of European mountain bird populations

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Summary

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 mountain tops. Population shifts towards poles and mountain tops 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 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 UK and Alps trends were non-significant. Temperature change or migratory behaviour were 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.

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 mountain tops (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 are 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

99 suitable habitats towards the mountain tops (low habitat availability simply because of
100 orography, Gonzalez, Neilson, Lenihan, & Drapek, 2010; Huntley, Green,
101 Collingham, & Willis, 2007; Sekercioglu, Schneider, Fay, & Loarie, 2008) or in other
102 mountain ranges (low connectivity between them, Sirami et al., 2016). The rise in
103 temperature associated with global warming has been predicted to be two to three
104 times higher in the 21st century than recorded during the 20th century (Nogués-
105 Bravo, Araújo, Errea, & Martinez-Rica, 2007). In addition to climate change,
106 mountain species, especially species breeding in uppermost open alpine areas, are also
107 threatened by human land use changes such as altered grazing pressure, afforestation,
108 increased disturbance of recreational activities, pollution (nitrogen and acid
109 deposition) and their interactions (Arlettaz et al., 2007; Brambilla et al., 2010; Britton
110 & Fisher, 2007; Herrando et al., 2016; Ims & Henden, 2012; van der Wal et al.,
111 2003).
112 The use of biodiversity indicators has become an increasingly common way to
113 monitor changes in the environment (Butchart et al., 2010; Gregory et al., 2005;
114 2008). Indicators, such as Biodiversity Change Index (Normander et al., 2012), Living
115 Planet Index (Collen et al., 2009) and Red List Index (Butchart et al., 2005) gather
116 large number of information into a single index value, which are easy to understand
117 not only by scientists, but also policy makers and the public (Gregory et al., 2005).
118 Recent advances in this research field have produced e.g. continental indicators of
119 farmland birds and climate change (Gregory et al., 2005; Stephens et al., 2016), but a
120 continental indicator for mountain areas has been lacking. To produce such indicators,
121 large and long-term datasets are required.
122 From the practical side, monitoring the fate of mountain species may be
123 particularly demanding as mountain areas are often difficult to access, the number of

124 species sharply decrease with altitude (Zbinden et al., 2010) and population densities
125 of species are low (Lehikoinen et al., 2014). Thanks to the recent improvements of the
126 national bird monitoring in Fennoscandia (Norway, Sweden and Finland), with new
127 schemes covering also the most remote mountain areas, a first-ever regional bird
128 indicator for the Fennoscandian mountain range was created by Lehikoinen et al.,
129 (2014). In this study we have analysed mountain bird trends at the continental scale,
130 with data from 11 different mountain ranges in Europe.
131 The aim of this work is (i) to investigate population trends of the common bird
132 species in Europe breeding on high altitude mountain habitats, (ii) to evaluate whether
133 population trends differ between species with different ecological characteristics,
134 which may add information on underlying causes of population changes, (iii) to
135 produce the first continental-scale biodiversity indicator for mountain bird
136 communities, and (iv) to establish four regional mountain bird indicators. The
137 continental indicator will show the overall situation, whereas the regional indicators
138 will tell more about the local conditions (Gregory et al., 2005).
139 Based on the assumption that climate and land use conditions have negatively
140 affected species inhabiting mountain habitats (Arlettaz et al., 2007; Brambilla et al.,
141 2010; Herrando et al., 2016; Ims & Hender, 2012; Lehikoinen et al., 2014), we
142 hypothesize that mountain bird species, in general, are declining in numbers. Second,
143 we hypothesize that this decline would be stronger in mountain specialists that only
144 occur in mountain areas in our study sites, whereas mountain generalists, which also
145 can be found at lower elevations are doing better because of generally higher
146 ecological flexibility (Davey, Chamberlein, Newson, Noble, & Johnston, 2012;
147 Davey, Devictor, Jonzén, Lindström, & Smith, H. G. 2013; Gough et al., 2015).
148 Third, we predict that population trends of mountain species can be influenced by the

149 migration status of species. We hypothesize that long-distance migrants will have
150 fared relatively poorly, as they displayed on average more negative population trends
151 in recent years across Europe – whatever the elevation – than residents and short-
152 distance migrants (Laaksonen & Lehikoinen, 2013; Sanderson, Donald, Pain,
153 Burfield, & van Bommel, 2006; Vickery et al., 2014). An alternative hypothesis is
154 that if a change in habitat quality in the mountain areas has a negative impact on
155 species which are spending the longest time in the mountain areas, short-distance
156 migrants and resident species should have faced stronger declines than long-distance
157 migratory species (Lehikoinen et al., 2014). Last, we hypothesize that the decline in
158 mountain birds is stronger at northern latitudes than at southern latitudes because
159 temperature is expected to increase more in the north (Jacob et al., 2014).
160
161
162 Materials and methods
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164 *Data collection*
165
166 Mountain bird populations have been monitored in 11 different mountain areas
167 distributed in 12 countries, mainly within national monitoring schemes on common
168 breeding birds using mainly systematic sampling (Table S1). In the present study we
169 analysed data from 2002 to 2014. The data collection covered this period unless stated
170 otherwise: Fennoscandia (Finland, Norway and Sweden), UK uplands (Britain and
171 Northern Ireland), the Giant Mountains (Czech Republic, 2002–2011), the Alps
172 (Austria 2008–2012, France, Germany 2005–2012, Italy, Switzerland), Massif Central
173 (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 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).

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 uplands, 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", Fig. 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 mountain top 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 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 northeast-southwest gradient (1600 km) of the Fennoscandian mountain area, mountain habitats vary in altitude. E.g. tundra is first found above 1300 m altitude in the south, but at sea level in the very north (Lehikoinen et al., 2014). It should be noted though, that only 4 out of 289 Fennoscandian sites were situated below 100 metres 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), 1100 m for the Giant Mountains, and 1200 m for all the remaining southern mountains, respectively. The UK uplands 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 UK (line transects, UK uplands) and

224 Switzerland (territory mapping, the Alps) and Spain (line transects, Catalonian
225 Pyrenees). First, we calculated relative densities based on mountain site-specific
226 species abundances and sampling effort (birds/km line transect) in 100m altitude
227 zones starting from the above mentioned mountain thresholds of the regions. Second,
228 based on altitude zone densities, we calculated the mean altitudes of species for each
229 mountain region. In the UK, species whose mean altitude were above 550 meters
230 (a.s.l.; more than half of the population should be breeding above this altitude in
231 mountain routes) and preferred open mountain habitats were included (Table S2). We
232 calculated mean altitudes separately for the Swiss Alps and the Catalonian Pyrenees
233 and used the mean of these two values for both “Iberia” and “Alps”. The altitude
234 threshold for the species in these areas was above 1800 meters (Table S3). In
235 Fennoscandia, a set of 14 common mountain species were already defined by
236 Lehikoinen et al. (2014). However, due to an increased monitoring effort in recent
237 years, we could include nine additional, less common, mountain species for this
238 region (Table 2).

239 We calculated species-specific population trends for each of the four defined
240 mountain regions: Fennoscandia, UK upland, “Iberia” and “Alps”. In addition, we
241 pooled the counts from all regions to calculate species trends for the whole area
242 (further details are given below). Trend analyses were conducted for species which
243 had at least five records per year in a given area (at the regional level, maximally one
244 year with a sample size below five individuals was accepted). When calculating the
245 population trends for Europe, we also included counts from mountain regions which
246 had lower than five records annually to maximize the total sample sizes. Mean annual
247 sample sizes are shown in 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 Schridel 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 in winter (Cramp, Simmons, & Perrins, 1977–1994; Lehikoinen et al., 2014).

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 was extracted are shown in Fig. S1.

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 i) common bird, ii) farmland and iii) 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 if 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 is 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

297 the country-specific mountain region area divided by the number of census sites
298 (average area per census sites: larger value mean lower density of census sites). Thus,
299 census sites in countries with proportionally fewer routes in mountain areas weighed
300 more in the analyses. France contributed to data of two regions ("Iberia" and "Alps")
301 and thus the weights were calculated separately for these regions. The mountain area
302 was measured using Corine land cover data (Copernicus Land Monitoring Service
303 2016), where mountain habitats were i) natural grasslands, ii) moors and heathlands,
304 iii) transitional woodland shrubs, iv) bare rock, v) sparsely vegetated areas, vi)
305 glaciers and perpetual snow and vii) peat bogs, which were above certain region-
306 specific altitude (see Table S5). Here we have used the data of the year 2012 only. We
307 believe that this represents the general situation in each country, because these habitat
308 types unlikely show large scale changes during the relatively short study period.
309 Last, we analysed a set of factors that potentially could explain the regional
310 population trends of species provided by TRIM analyses in the four major mountain
311 areas during 2002–2014, using GLMM (functions lmer and lmerTest in R). Regional
312 long-term population trends were tested against migratory behaviour (long-distance
313 migrants or other, the latter including residents, which are rare among mountain
314 birds), specialisation (mountain specialists or generalists) and short-term temperature
315 change in each region ("Alps", Fennoscandia, "Iberia" and the UK; Table 3). Species
316 was a random factor in the model to account for some species having data from
317 several mountain regions whereas some only have data from one of them. We took
318 phylogeny into account in the analyses since species with the same ancestors may
319 have more similar responses. We did this by first using various phylogenic structures
320 (order, family and genus based on del Hoyo, Collar, Christie, Elliot, & Fishpool
321 (2014) and del Hoyo et al. (2016), altogether eight combinations, see Table S6) in the

322 random part of the full model. We ranked these models based on AICc (Burnham &
323 Anderson, 2004). Second we used the best phylogenic structure in the final analyses,
324 where we constructed 12 model combinations, and where the full model included the
325 two-way interactions temperature*migration and temperature*specialisation. The
326 inclusion of an interaction between temperature and migration was based on the
327 hypothesis that species that spend most of the time in the mountain areas (short-
328 distance migrants and residents) may face the largest declines in areas where the
329 temperature increase has been highest. The interaction between temperature and
330 specialisation relates to the hypothesis that specialists would be declining fastest in
331 the area with high temperature increase. The model combinations are shown in Table
332 3. These 12 models were ranked based on AIC corrected for small sample sizes
333 (Burnham & Anderson, 2004). Finally, we took the uncertainty of the population
334 trends into account in the analyses using the reciprocal of the standard errors of the
335 trends as weights. We used R (version 3.4.1) in all the analyses (R Development Core
336 Team, 2017).
337
338 Results
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340 Because the results of the weighted analyses according to the national area per census
341 sites ratio were almost identical to the non-weighted analyses (Table S6), we decided
342 to show only the un-weighted results in the main results section (Table 2).
343 The European mountain bird indicator showed a significant negative decline
344 during 2002–2014 (44 species; -0.61% / year, 95% CI -1.14 to -0.08, overall decline
345 c. -7%; Fig. 2a). The European mountain specialist indicator also declined
346 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; Fig. 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 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, Fig. 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%; Fig. 3b–c). In Fennoscandia and "Iberia", respectively, ten and five species showed negative, and three and one showed positive trends (Table 3). 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, Fig. 3d). In UK uplands 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

372 0.022 ± 0.010 se, $P < 0.05$). Slopes of the other regions did not differ from each other
373 (all $P > 0.05$).
374 The species only was the best random structure compared to more complicated
375 phylogenic structures (Table S7) and thus species only was used in the latter analyses.
376 The best model explaining the regional population trends of species during 2002–
377 2014 was the null model. Although two other more complex models were within 2
378 AIC units, additional variables of those models can be considered as uninformative
379 parameters (*sensu* Arnold, 2010). Thus this modelling approach was not able to find
380 that region, specialisation or migratory behaviour were linked with the regional
381 population trends (Table 3). The intercept of the null model was significantly below
382 zero (-0.0072 ± 0.0035, $t = 2.0$, $P < 0.05$), suggesting in general negative regional
383 population trends during this particular period.
384 Annual temperatures during the breeding season (April–August) increased
385 significantly in all four regions in the long-term (rate of increase 0.81–1.55ºC during
386 1980–2014; Table 4). During the last 20 years (1995–2014) the temperature increase
387 was only significant in Fennoscandia (Table 4).
388
389
390 Discussion
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392 We set out to test three hypotheses regarding the recent population trends in European
393 mountain birds. We got unequivocal support for the first hypothesis regarding a
394 negative trend of European mountain bird populations since we found that the
395 indicator has an overall decline of -7% during 2002 – 2014 (-0.61 %/year).
396 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 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 non-significant 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

422 birds, finding no significant differences between migratory groups on the regional
423 level. Therefore the diminishing mountain bird populations are not only driven by
424 general declines of long-distance migrants (e.g. Sanderson et al., 2006; Vickery et al.,
425 2014), but also species wintering in Europe are contributing to the decline in
426 mountain birds. This could indicate that mountain species have also problems in their
427 breeding areas (Lehikoinen et al., 2014). More work needs to be done to understand,
428 what are the valid traits to evaluate the vulnerability of mountain species in the face of
429 climate change (see also MacLean & Beissinger, 2017).
430 The reason why there seem to be no universal patterns explaining species-
431 specific variation in responses to climate change could be that regional circumstances,
432 such as land use practices, differ between areas. In one area, impacts of climate
433 change may be more important than changes in land use and *vice versa*. Agro-pastoral
434 land use practices have become less intense or have been abandoned completely
435 allowing forest cover to increase again, especially in the low altitude mountains of the
436 southern mountain regions ("Alps" and "Iberia"; Brambilla et al., 2010; Herrando et
437 al., 2016; Maggini et al., 2014). Interactions with agricultural abandonment and forest
438 expansion can be complex and offer both threats and opportunities depending on the
439 ecological requirements of species and assemblages involved (Calladine, Bielinski, &
440 Shaw, 2013; Gillings, Fuller, & Henderson, 1998; Herrando et al., 2016).
441 The April–August temperatures have increased substantially in recent decades
442 in all four mountain areas. Although the temperature increase has been significant
443 only in Fennoscandia over the last two decades, the temperatures are nowadays above
444 the long-term mean in all regions (Lehikoinen et al., 2014). Climate change may
445 affect bird populations in a different manner depending on the region (Sæther &
446 Engen, 2010). Furthermore, temperatures are expected to rise faster in higher northern

447 latitude mountains than in mountains located in temperate and tropical zones, and the
448 rate of warming in mountain systems can be two to three times higher than that
449 recorded during the 20th century (Nogués-Bravo, Araújo, Errea, & Martinez-Rica,
450 2007). These can cause considerable effects on biodiversity even though the direct
451 impacts can be difficult to measure (Araújo, Errea, & Martinez-Rica, 2007). Although
452 we could not link the population dynamics with the observed climate change, the
453 observed declines are in line with the population predictions in relation to climate
454 change (Huntley et al., 2007). Human induced land use changes are not as extensive
455 in Fennoscandian mountains (Lehikoinen et al., 2014) compared to "Iberia"
456 (Herrando et al., 2016), and several Fennoscandian studies have revealed changes in
457 plant community due to climate change (Kullman & Öberg, 2009; Michelsen,
458 Syverhuset, Pedersen, & Holten, 2011; Vuorinen et al., 2017). One should also keep
459 in mind that especially in Fennoscandia some mountain species are nomadic to some
460 extent (Lindström, 1987) and both plant and animal communities are strongly
461 influenced by multi-annual cyclic fluctuation of small rodents (Hanski, Hansson, &
462 Henttonen, 1991; Turchin, Oksanen, Ekerholm, Oksanen & Henttonen, 2000). Even
463 animal species that are not using rodents in their diet, are influenced by the cycles due
464 to predator-prey interactions (Lehikoinen et al., 2016). Despite these kinds of
465 fluctuations, we were able to detect a negative long-term trend in Fennoscandia.
466 We must stress that the methods of the monitoring schemes and their intensity
467 showed spatial variation within the overall study area. However, we do not believe
468 that this has biased the analysis. First, the magnitude of the trend should be
469 comparable independently of whether it is based on point count, line transect or
470 territory mapping (Gregory et al., 2005). Second, we tried to compensate for the
471 potential biases in the sampling by using country-specific weights. The use of weights

472 did not influence the main results. We believe that there are two reasons why our
473 weighting did not influence the population trends: (1) Many of the species data is only
474 available from one of the study regions and thus weighting between regions have no
475 importance; and (2) population trends of nearby countries are similar. As the
476 monitoring schemes have improved in many countries in recent years including
477 systematic sampling, future analyses of monitoring data will be even more reliable
478 due to increased sample sizes.

479 Modelling work on the future effects of climate and land use change have
480 suggested that species-specific conservation measures aiming at improving habitat to
481 counteract the negative influence of climate change can only deliver minor
482 improvements of the future fate of mountain birds (Braunisch et al., 2014). Even if
483 high mountains may provide refuges for threatened mountain species currently
484 populating lower altitudes, in the long term, climate change can be expected to have a
485 strong impact on alpine species (Freeman, Scholer, Ruiz-Gutierrez & Fitzpatrick,
486 2018). Alpine habitats are expected to be reduced and become more fragmented and
487 isolated due to rise of the tree line where species have increasing limited dispersal
488 possibilities. Our findings also emphasize that local studies are needed to understand
489 the mechanisms and drivers of the population changes of individual species and
490 species communities in mountains including information about species habitat
491 selection and changes in the amount of preferred habitat. Despite international actions
492 to halt climate change, climate will change in the near future (EEA, 2012). To
493 mitigate the potential impacts of climate change, it is important to take measures that
494 can improve connectivity between suitable mountain habitats and to minimize the
495 effects of other threats such as non-sustainable tourism and afforestation of grasslands
496 (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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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)

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 specialisation (Sp = mountain specialists, G = generalists; classification based on distribution areas of Hagemeijer & 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 Table S4).

Species (specialisation)	Traits	All areas	"Alps"	Fennoscandia	"Iberia"	UK
		Slope ± SE	Slope ± SE	Slope ± SE	Slope ± SE	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**	-	-
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**	-

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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 specialisation (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

Table 4. Annual changes in temperature (in ºC 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

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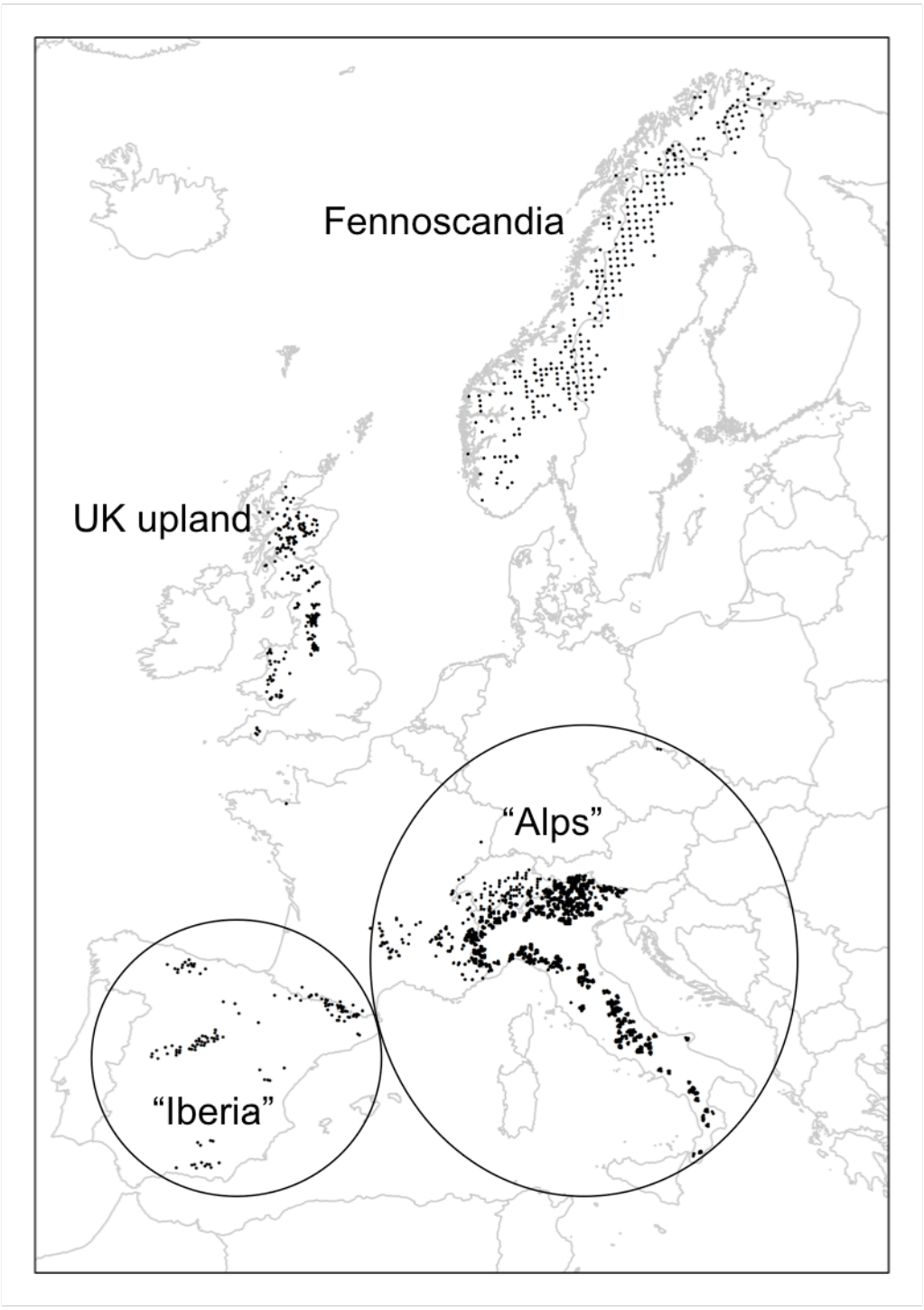

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807 Fig. 1. A map showing the four European mountain regions, where the data was

808 collected. The dots show the census locations (survey route) except in Italy where

809 each dot represents one point of a point count route.

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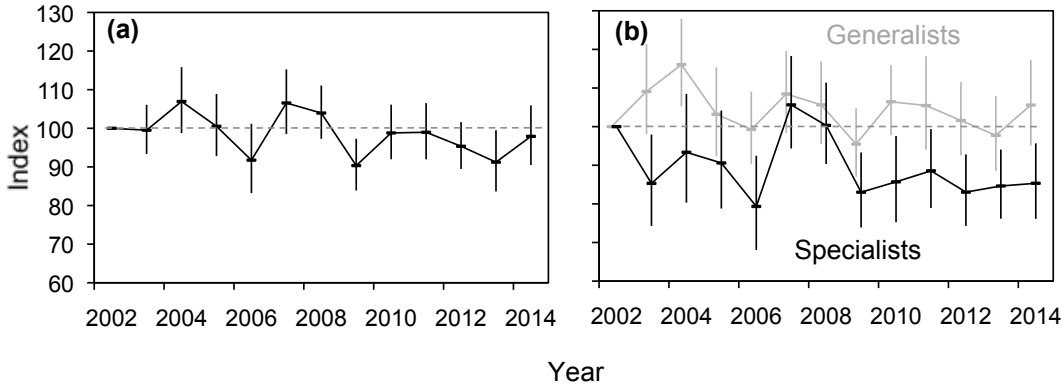

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812 Fig. 2. (a) The mountain bird indicator for Europe and (b) the separate indicators for

813 specialists and generalists, during 2002–2014. Calculated mean of the indices and

814 their 95% CIs are given.

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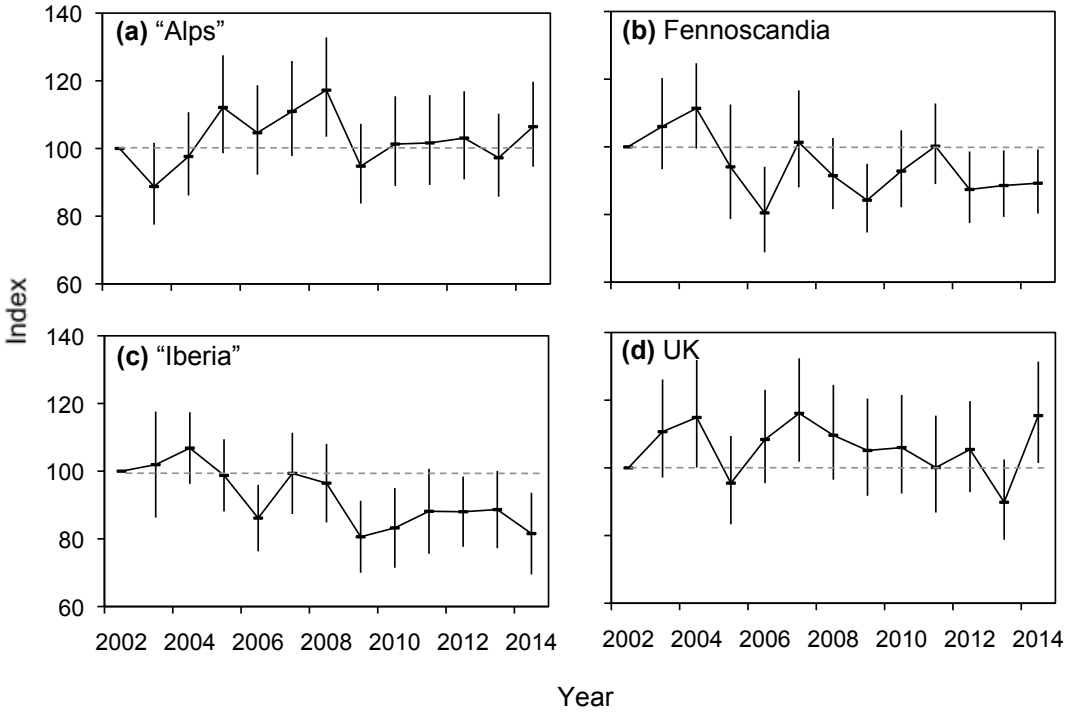

Fig. 3. Regional mountain bird indicators during 2002–2014 from (a) "Alps", (b) Fennoscandia, (c) "Iberia" and (d) UK. Calculated mean of the indices and their 95% CIs are given.