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1 Declining population trends of European mountain birds

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3 Running head: Decline of European mountain bird populations

4

5

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44

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47

48

49 Summary

50

51 Mountain areas often hold special species communities, and they are high on the list
52 of conservation concern. Global warming and changes in human land use, such as
53 grazing pressure and afforestation, have been suggested to be major threats for
54 biodiversity in the mountain areas, affecting species abundance and causing
55 distribution shifts towards mountain tops. Population shifts towards poles and
56 mountain tops have been documented in several areas indicating that climate change
57 is one of the key drivers of species' distribution changes. Despite the high
58 conservation concern, relatively little is known about the population trends of species
59 in mountain areas due to low accessibility and difficult working conditions. Thanks to
60 the recent improvement of bird monitoring schemes around Europe we can here report
61 a first account of population trends of 44 bird species from four major European
62 mountain regions: Fennoscandia, UK upland, south-western (Iberia) and south-central
63 mountains (Alps), covering 12 countries. Overall the mountain bird species declined
64 significantly (-7%) during 2002–2014, which is similar to the declining rate in
65 common birds in Europe during the same period. Mountain specialists showed a
66 significant -10% decline in population numbers. The slope for mountain generalists
67 was also negative, but not significantly so. The slopes of specialists and generalists
68 did not differ from each other. Fennoscandian and Iberian populations were on
69 average declining, while in UK and Alps trends were non-significant. Temperature
70 change or migratory behaviour were not significantly associated with regional
71 population trends of species. Alpine habitats are highly vulnerable to climate change
72 and this is certainly one of the main drivers of mountain bird population trends.
73 However, observed declines can also be partly linked with local land use practices.

74 More efforts should be undertaken to identify the causes of decline and to increase
75 conservation efforts for these populations.

76

77

78 Introduction

79

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

95 Mountain areas often hold special species communities and are thus in the high
96 priority list of conservation (Rodriguez-Rodriguez, Bomhard, Butchart, & Forster,
97 2011). Furthermore, mountain species have been suggested to be particularly
98 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

163

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),

174 Spanish central mountains (Spain), Spanish Iberian mountain system (Spain), Baetica
175 mountain range (Spain 2003–2012), and Cantabria mountain range (Spain; Table 1).
176 The local census methods are explained in Table S1. Census methodology differed
177 between countries, but this will unlikely introduce systematic bias into the derived
178 trends (see e.g. Gregory et al., 2005; Lehtikoinen et al., 2014; Stephens et al., 2016).

179

180 *Site and species selection*

181

182 To get enough data to calculate trends for a larger set of species, we lumped the 11
183 areas into four larger mountain regions: Fennoscandia, UK uplands, south-western
184 mountains (including Pyrenees and four Spanish mountain areas, hereafter called as
185 “Iberia”) and the south-central mountains (including the Alps and the surrounding
186 smaller mountains: Giant Mountains, Massif Central and the Apennines, hereafter
187 called as “Alps”, Fig. 1).

188 Before we could define which species to use in the study, we needed to define
189 “mountain” monitoring sites and species in each region. Our aim was to target species
190 that prefer open or semi-open mountain habitats. These are mainly situated on the
191 highest altitudes of the mountains and are thus in the highest risk in terms of climate
192 change (Gonzalez et al., 2010). Since mountain top populations have limited places to
193 move upwards, the expected population declines should be strongest in high altitude
194 habitats. Thus we selected mountain tundra, meadows, grasslands, bare rock, sparsely
195 vegetated areas, peat bogs and scrubland above certain altitude. We also included the,
196 often spatially adjacent, zones of mountain birch forest and dwarf mountain pine (for
197 simplicity all the mentioned habitats are generally referred to as ‘mountain habitat’).
198 For latitudinal reasons (and also exposure on the western seaboard) also the altitudes

199 where open mountain habitat occur varies and this needs to be defined separately for
200 each mountain range. Since some of the species occur also outside the mountains -
201 though we were only interested in the populations living in the mountain areas - we
202 needed to use habitat information to define mountain sites from each area. For
203 instance, due to the long northeast-southwest gradient (1600 km) of the
204 Fennoscandian mountain area, mountain habitats vary in altitude. E.g. tundra is first
205 found above 1300 m altitude in the south, but at sea level in the very north
206 (Lehikoinen et al., 2014). It should be noted though, that only 4 out of 289
207 Fennoscandian sites were situated below 100 metres of altitude. In the rest of the
208 mountain regions, “mountain sites” were set to include at least one-third open
209 mountain habitat and to be above a certain altitude, depending on local conditions
210 such as climate, latitude and historical land use. These altitude thresholds for
211 mountain sites were set to 400 m for UK upland (and where the surveyed habitats
212 were generally open), 1100 m for the Giant Mountains, and 1200 m for all the
213 remaining southern mountains, respectively. The UK uplands have a particularly long
214 history of anthropogenic deforestation and in combination with high levels of
215 extensive grazing and climatic exposure. Therefore, open habitats resembling those of
216 montane and alpine areas exist at lower altitudes than would naturally occur (Smout,
217 2005; Thompson, MacDonald, Marsden, & Galbraith, 1995). Also in the southern and
218 central European sites open areas above the altitude limit are not necessarily caused
219 by the natural tree line, but areas also include subalpine meadows that remain open
220 due to grazing. The number of study sites in each area is given in Table 1.

221 To define species which have significant populations in high altitude mountain
222 habitats (so called mountain species), we used altitude information from each larger
223 mountain range area using data from the UK (line transects, UK uplands) and

224 Switzerland (territory mapping, the Alps) and Spain (line transects, Catalanian
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 Catalanian 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 Lehtikoinen 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.

248 Species were classified into mountain specialists or generalists, based on their
249 distribution areas in Europe. Species mainly restricted to mountain areas and
250 uncommon in the lowlands were classified as mountain specialists whereas species
251 which have substantial populations in the mountains but also commonly breed in
252 lowlands were classified as mountain generalists (Hagemeijer & Blair, 1997, see also
253 Schridel et al., 2018; Thompson, Kålås, & Byrkjedal, 2012; Table 2). Furthermore,
254 species were grouped into long-distance (wintering in tropical areas) and others
255 (including both species wintering in the Western Palearctic and residents) based on
256 their distribution ranges in winter (Cramp, Simmons, & Perrins, 1977–1994;
257 Lehtikoinen et al., 2014).

258

259 *Weather data*

260

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

269

270 *Statistical analyses*

271

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

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

293 Spatial differences in sampling network could lead into a situation where trends
294 are more driven by areas where number of census sites is dense compared to areas
295 where the network is sparse. We therefore, per each contributing country, weighted
296 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 phylogenetic 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 phylogenetic 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

339

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.

347 -10%). The mountain generalist slope was also negative ($n = 28$ species, -0.46% /
348 year), but not significantly so (95% CI -1.06 to 0.17 ; Fig. 2b). The slopes of
349 specialists and the generalists did not differ from each other (trend difference =
350 0.0040 , $se = 0.0051$, $P > 0.05$, see also Table 3). Among the specialists, five out of 16
351 species showed negative and one showed positive trends. Among the generalists, nine
352 out of 28 species declined and seven increased (Table 2). Despite the fact that many
353 mountain bird species have a wide distribution in Europe, it is important to note that
354 only for two out of 44 species (northern wheatear and ring ouzel) were there enough
355 data to calculate trends in all four mountain areas. In addition, for about half of the
356 species, population trends were only calculated for one of the four regions, because
357 the species were too rare in other regions (Table 2).

358 The indicator of “Alps” showed no significant trends during 2002–2014 ($n = 20$
359 species, $+0.29\%$ / year, 95% CI -0.59 to 1.17 , Fig. 3a). Four species showed positive
360 and three species showed negative trends during 2002–2014 (Table 2). The
361 Fennoscandian and “Iberian” indicators showed significant negative trends during
362 2002–2014 (Fennoscandia, $n = 23$ species, -1.20% / year, 95% CI -2.04 to -0.36 ,
363 overall decline -13% ; “Iberia”, $n = 14$ species, -1.94% , 95% CI -3.61 to -0.27 , overall
364 decline -21% ; Fig. 3b–c). In Fennoscandia and “Iberia”, respectively, ten and five
365 species showed negative, and three and one showed positive trends (Table 3). The
366 indicator of UK Upland showed no significant trend during 2002–2014 ($n = 10$
367 species, -0.29% / year, 95% CI -1.13 to 0.55 , Fig. 3d). In UK uplands one species
368 declined (carrion crow) and none increased in 2002–2014 (Table 2). According to
369 bootstrapping simulations the slopes of Fennoscandian and “Iberian” indicators
370 differed significantly from slopes in the “Alps” (trend difference between “Alps” and
371 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 phylogenetic 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 0.81–1.55°C 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

391

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

397 differed from the slope of the corresponding indicator in the “Alps”. Based on
398 European common bird monitoring the magnitude of the decline is the same as all
399 common birds in Europe during the same study period. More specifically the trends of
400 bird indicators in two important habitats, farmland and forests, were -13% and -1%,
401 during the study same period, respectively (European Bird Census Council, 2018).
402 Thus, in general mountain birds are doing less bad than farmland birds, but clearly
403 worse than forest birds in Europe. The severe declines of farmland birds are mainly
404 driven by intensification of agriculture rather than climate change (Butler, Boccacio,
405 Gregory, Voříšek, & Norris 2010; Eglinton & Pearce-Higgins, 2012; Jørgensen et
406 al., 2016). However, in case of mountain birds, climate change can have a larger
407 impact as the climatic niche of especially mountain specialists is shrinking,
408 highlighted by the relatively fast declines of mountain species.

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

420 We got no support for our third main hypothesis, that long-distance migrant
421 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, & Martínez-Rica,
450 2007). These can cause considerable effects on biodiversity even though the direct
451 impacts can be difficult to measure (Araújo, Errea, & Martínez-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).

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

514

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516

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776 Table 1. The number of study sites (mean, min and max during 2002–2014) in 11
777 mountain areas distributed over four major mountain regions. In the Giant Mountains
778 and the Apennines, the number of point count locations were transformed into sites
779 dividing number of point stations by 15 (a typical number in point count routes in
780 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)

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783 Table 2. The average annual population growth rates (trends) and traits of 44

784 mountain bird species in 11 European mountain areas, as well as separate species

785 trends for the “Alps”, Fennoscandia, “Iberia” and UK upland during 2002–2014.

786 Traits include specialisation (Sp = mountain specialists, G = generalists; classification

787 based on distribution areas of Hagemeyer & Blair (1997)) and migratory behaviour

788 (Ld = long-distance migrant, Ot = other). Significant population change rates are in

789 bold. ‘-’ means that the species is not a typical mountain bird in the particular

790 mountain region and NE means that species is a typical mountain species in the area,

791 but there were too little data available to calculate trends (see also Table S4).

Species (specialisation)	Traits	All areas Slope ± SE	“Alps” Slope ± SE	Fennoscandia Slope ± SE	“Iberia” Slope ± SE	UK Slope ± SE
<i>Clangula hyemalis</i>	Sp, Ot	-0.033 ± 0.023	-	-0.033 ± 0.023	-	-
<i>Buteo buteo</i>	G, Ot	-0.006 ± 0.014	-	-	-	-0.006 ± 0.014
<i>Buteo lagopus</i>	G, Ot	-0.041 ± 0.027	-	-0.041 ± 0.027	-	-
<i>Falco tinnunculus</i>	G, Ot	0.008 ± 0.007	0.011 ± 0.008	-	-0.011 ± 0.021	-
<i>Lagopus lagopus</i>	G, Ot	-0.026 ± 0.006	-	-0.095 ± 0.010	-	0.003 ± 0.007
<i>Lagopus muta</i>	Sp, Ot	-0.018 ± 0.008	0.013 ± 0.012	-0.047 ± 0.013	NE	NE
<i>Tetrao tetrix</i>	G, Ot	0.010 ± 0.027	0.035 ± 0.039	-	-	NE
<i>Alectoris graeca</i>	Sp, Ot	0.019 ± 0.021	0.019 ± 0.021	-	-	-
<i>Charadrius hiaticula</i>	G, Ot	0.050 ± 0.020	-	0.051 ± 0.021	-	-
<i>Charadrius morinellus</i>	Sp, Ot	0.012 ± 0.022	-	0.035 ± 0.024	-	NE
<i>Pluvialis apricaria</i>	G, Ot	0.013 ± 0.005	-	0.010 ± 0.005	-	0.022 ± 0.012
<i>Calidris alpina</i>	G, Ot	0.005 ± 0.018	-	0.009 ± 0.021	-	NE
<i>Gallinago gallinago</i>	G, Ot	-0.011 ± 0.012	-	-	-	-0.011 ± 0.012
<i>Tringa totanus</i>	G, Ot	0.033 ± 0.010	-	0.033 ± 0.010	-	-
<i>Phalaropus lobatus</i>	G, Ld	-0.003 ± 0.030	-	-0.003 ± 0.030	-	-
<i>Stercorarius longicaudus</i>	Sp, Ld	0.014 ± 0.017	-	0.014 ± 0.017	-	-

<i>Cuculus canorus</i>	G, Ld	-0.053 ± 0.007	-	-0.053 ± 0.007	-	-
<i>Alauda arvensis</i>	G, Ot	-0.001 ± 0.003	0.016 ± 0.006	-	-0.033 ± 0.008	0.004 ± 0.006
<i>Hirundo rupestris</i>	Sp, Ot	0.001 ± 0.009	0.012 ± 0.011	-	-0.017 ± 0.015	-
<i>Anthus pratensis</i>	G, Ot	-0.008 ± 0.003	NE	-0.012 ± 0.005	NE	-0.005 ± 0.004
<i>Anthus spinoletta</i>	Sp, Ot	-0.001 ± 0.003	0.000 ± 0.003	-	-0.037 ± 0.013	-
<i>Prunella collaris</i>	Sp, Ot	0.002 ± 0.007	0.002 ± 0.007	-	NE	-
<i>Luscinia svecica</i>	G, Ld	-0.001 ± 0.007	-	-0.002 ± 0.008	-	-
<i>Phoenicurus ochruros</i>	G, Ot	0.008 ± 0.003	0.014 ± 0.003	-	-0.025 ± 0.007	-
<i>Phoenicurus phoenicurus</i>	G, Ld	0.014 ± 0.007	-	0.014 ± 0.007	-	-
<i>Saxicola rubetra</i>	G, Ld	-0.030 ± 0.008	-0.029 ± 0.008	-	-0.023 ± 0.049	-
<i>Oenanthe oenanthe</i>	G, Ld	0.009 ± 0.003	0.026 ± 0.004	-0.005 ± 0.008	-0.013 ± 0.007	0.002 ± 0.008
<i>Monticola saxatilis</i>	Sp, Ld	-0.022 ± 0.013	-0.002 ± 0.017	-	-0.059 ± 0.021	-
<i>Turdus torquatus</i>	Sp, Ot	0.005 ± 0.004	0.001 ± 0.004	0.060 ± 0.025	0.000 ± 0.021	-0.006 ± 0.017
<i>Turdus iliacus</i>	G, Ot	-0.033 ± 0.006	-	-0.033 ± 0.006	-	-
<i>Sylvia curruca</i>	G, Ld	0.011 ± 0.006	0.011 ± 0.006	-	-	-
<i>Phylloscopus trochilus</i>	G, Ld	-0.032 ± 0.003	-	-0.032 ± 0.003	-	-
<i>Pyrhcorax graculus</i>	Sp, Ot	-0.015 ± 0.011	-0.002 ± 0.012	-	-0.044 ± 0.025	-
<i>Pyrhcorax pyrrhcorax</i>	G, Ot	0.050 ± 0.012	NE	-	0.053 ± 0.014	-
<i>Corvus corone</i>	G, Ot	-0.047 ± 0.014	-	-	-	-0.047 ± 0.014
<i>Corvus corax</i>	G, Ot	0.016 ± 0.013	-	-	-	0.016 ± 0.013
<i>Montifringilla nivalis</i>	Sp, Ot	0.021 ± 0.010	0.021 ± 0.010	-	NE	-
<i>Fringilla montifringilla</i>	G, Ot	-0.025 ± 0.005	-	-0.025 ± 0.005	-	-
<i>Serinus citrinella</i>	Sp, Ot	-0.026 ± 0.013	-0.051 ± 0.031	-	-0.023 ± 0.016	-
<i>Carduelis cannabina</i>	G, Ot	0.015 ± 0.007	0.007 ± 0.008	-	0.040 ± 0.022	-
<i>Carduelis flammea</i>	G, Ot	-0.048 ± 0.005	-0.025 ± 0.007	-0.052 ± 0.007	-	-
<i>Calcarius lapponica</i>	Sp, Ot	-0.026 ± 0.008	-	-0.026 ± 0.008	-	-
<i>Plectrophenax nivalis</i>	Sp, Ot	-0.041 ± 0.014	-	-0.042 ± 0.014	-	NE
<i>Emberiza cia</i>	Sp, Ot	-0.031 ± 0.006	-0.024 ± 0.012	-	-0.033 ± 0.008	-

793
 794 Table 3. AICc differences, AIC weights (w) and evidence ratios (ER) of models
 795 explaining regional population trends of mountain birds during 2002–2014. Spe is
 796 specialisation (mountain specialist or generalist), Mig is migratory behaviour (short-
 797 or long-distance migrant) and Mt is mountain region.
 798

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

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801 Table 4. Annual changes in temperature (in °C from April to August) in four

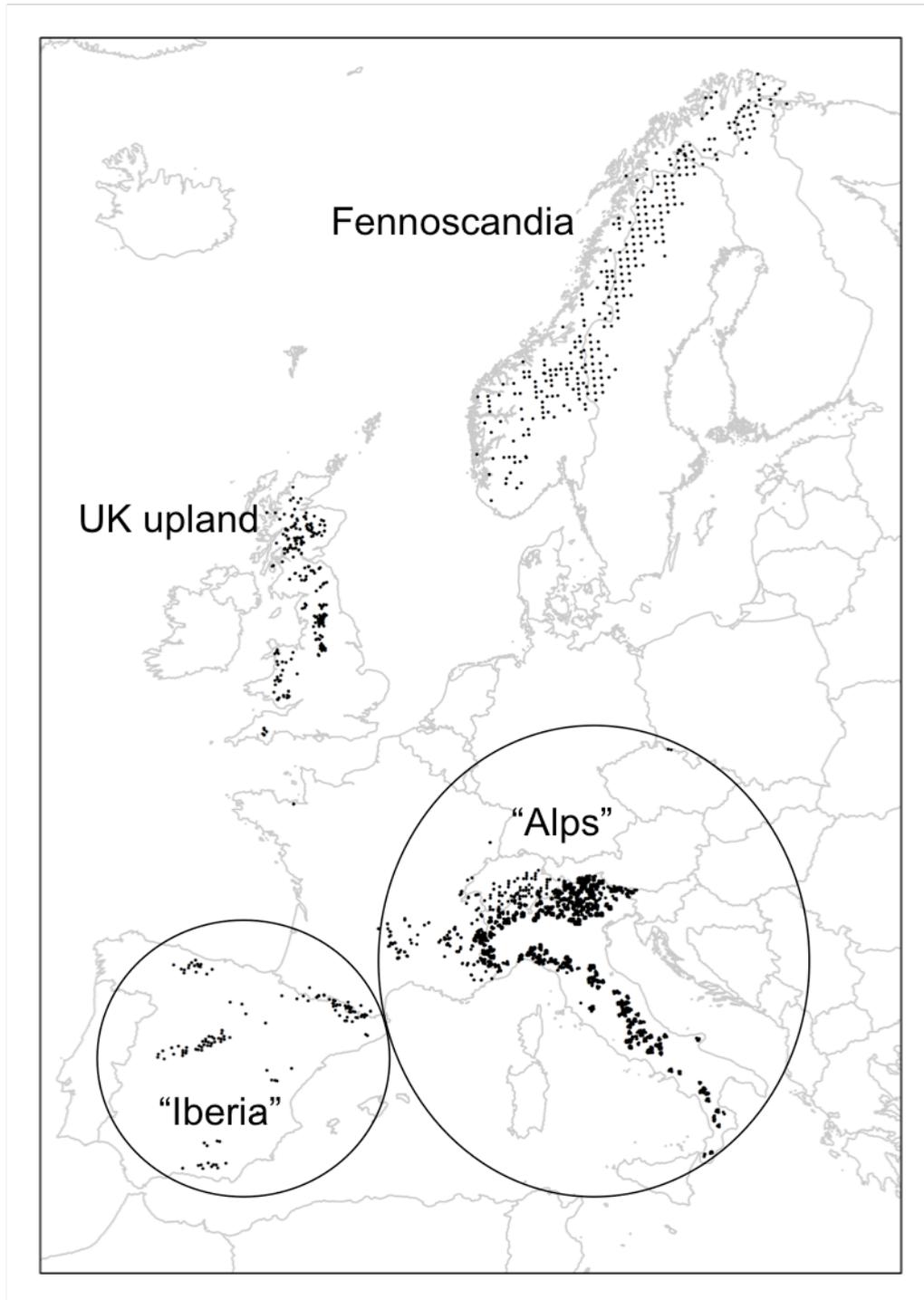
802 mountain regions in Europe during 1980–2014 and 1995–2014. Significant

803 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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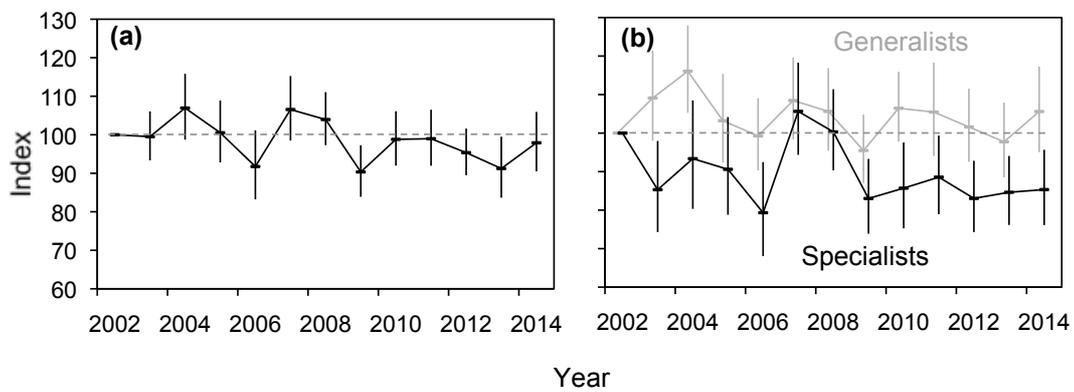
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807 Fig. 1. A map showing the four European mountain regions, where the data was
808 collected. The dots show the census locations (survey route) except in Italy where
809 each dot represents one point of a point count route.

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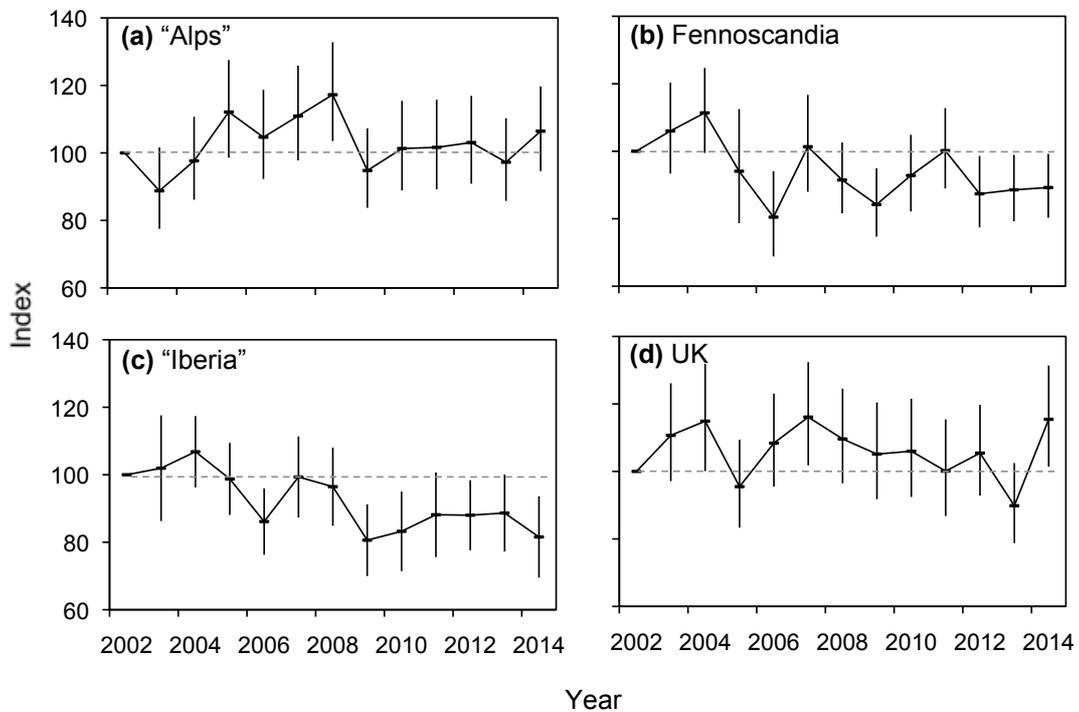


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 812 Fig. 2. (a) The mountain bird indicator for Europe and (b) the separate indicators for
 813 specialists and generalists, during 2002–2014. Calculated mean of the indices and
 814 their 95% CIs are given.
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819 Fig. 3. Regional mountain bird indicators during 2002–2014 from (a) “Alps”, (b)

820 Fennoscandia, (c) “Iberia” and (d) UK. Calculated mean of the indices and their 95%

821 CIs are given.

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