



Declining population trends of European mountain birds

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Keywords:	alpine habitat, agriculture, afforestation, common bird monitoring, global warming, land use changes, loss of biodiversity, mountain population
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 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

	<p>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 potential 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.</p>

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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

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

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50 Summary

51

52 Mountain areas often hold special species communities, and they are high on the list
53 of conservation concern. Global warming and changes in human land use, such as
54 grazing pressure and afforestation, have been suggested to be major threats for
55 biodiversity in the mountain areas, affecting species abundance and causing
56 distribution shifts towards mountain tops. Population shifts towards poles and
57 mountain tops have been documented in several areas indicating that climate
58 change is one of the key drivers of species' distribution changes. Despite the high
59 conservation concern, relatively little is known about the population trends of
60 species in mountain areas due to low accessibility and difficult working conditions.
61 Thanks to the recent improvement of bird monitoring schemes around Europe we
62 can here report a first account of population trends of 44 bird species from four
63 major European mountain regions: Fennoscandia, UK upland, south-western
64 (Iberia) and south-central mountains (Alps), covering 12 countries. Overall the
65 mountain bird species declined significantly (-7%) during 2002–2014, which is
66 similar to the declining rate in common birds in Europe during the same period.
67 Mountain specialists showed a significant -10% decline in population numbers. The

68 slope for mountain generalists was also negative, but not significantly so. The slopes
69 of specialists and generalists did not differ from each other. Fennoscandian and
70 Iberian populations were on average declining, while in UK and Alps trends were
71 non-significant. Temperature change or migratory behaviour were not significantly
72 associated with regional population trends of species. Alpine habitats are highly
73 vulnerable to climate change and this is certainly one of the potential main drivers
74 of mountain bird population trends. However, observed declines can also be partly
75 linked with local land use practices. More efforts should be undertaken to identify
76 the causes of decline and to increase conservation efforts for these populations.

77

78

79 Introduction

80

81 Human land use changes and a changing climate are the major threats to
82 biodiversity around the world (Root et al., 2003; Stephens et al., 2016; Travis, 2003).
83 Habitat loss, fragmentation and degradation have affected species distribution
84 ranges and abundances (Baillie, Hilton-Taylor, & Stuart, 2004; Fahrig, 2003). Global
85 warming has shifted species distribution areas towards the poles and mountain tops
86 (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Maggini et al., 2011). From a
87 conservation point-of-view, it is, however, equally important to understand the
88 effects of climate change on population densities, that do not necessarily coincide
89 with distributional changes (Chamberlain & Fuller, 2001). In general, while
90 populations of lowland bird and butterfly species have been shown to change

91 according to climate change scenarios in Europe and North America (Breed,
92 Stichter, & Crone, 2013; Devictor et al., 2012; Lindström, Green, Paulson, Smith, &
93 Devictor, 2013; Stephens et al., 2016), the population status of species in the
94 mountain areas are generally poorly known (Chamberlain et al., 2012; Scridel et al.,
95 2018; but see Flousek, Telenský, Hanzelka, & Reif, 2015; Lehikoinen, Green, Husby,
96 Kålås, & Lindström, 2014).

97 Mountain areas often hold special species communities and are thus in the
98 high priority list of conservation (Rodriguez-Rodriguez, Bomhard, Butchart, &
99 Forster, 2011). Furthermore, mountain species have been suggested to be
100 particularly vulnerable to climate change, since it is generally more difficult for them
101 to find new suitable habitats towards the mountain tops (low habitat availability
102 simply because of orography, Gonzalez, Neilson, Lenihan, & Drapek, 2010; Huntley,
103 Green, Collingham, & Willis, 2007; Sekercioglu, Schneider, Fay, & Loarie, 2008) or in
104 other mountain ranges (low connectivity between them, Sirami et al., 2016). The
105 rise in temperature associated with global warming has been predicted to be two to
106 three times higher in the 21st century than recorded during the 20th century
107 (Nogués-Bravo, Araújo, Errea, & Martinez-Rica, 2007). In addition to climate change,
108 mountain species, especially species breeding in uppermost open alpine areas, are
109 also threatened by human land use changes such as altered grazing pressure,
110 afforestation, increased disturbance of recreational activities, pollution (nitrogen
111 and acid deposition) and their interactions (Arlettaz et al., 2007; Brambilla et al.,
112 2010; Britton & Fisher, 2007; Herrando et al., 2016; Ims & Henden, 2012; van der
113 Wal et al., 2003).

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

124 From the practical side, monitoring the fate of mountain species may be
125 particularly demanding as mountain areas are often difficult to access, the number
126 of species sharply decrease with altitude (Zbinden et al., 2010) and population
127 densities of species are low (Lehikoinen et al., 2014). Thanks to the recent
128 improvements of the national bird monitoring in Fennoscandia (Norway, Sweden
129 and Finland), with new schemes covering also the most remote mountain areas, a
130 first-ever regional bird indicator for the Fennoscandian mountain range was created
131 by Lehikoinen et al., (2014). In this study we have analysed mountain bird trends at
132 the continental scale, with data from 11 different mountain ranges in Europe.

133 The aim of this work is (i) to investigate population trends of the common bird
134 species in Europe breeding on high altitude mountain habitats, (ii) to evaluate
135 whether population trends differ between species with different ecological
136 characteristics, which may add information on underlying causes of population

137 changes, and (iii) to produce the first continental-scale biodiversity indicator for
138 mountain bird communities. In addition, we establish four regional mountain bird
139 indicators. The continental indicator will show the overall situation, whereas the
140 regional indicators will tell more about the local conditions (Gregory et al., 2005).

141 Based on the assumption that climate and land use conditions have negatively
142 affected species inhabiting mountain habitats (Arlettaz et al., 2007; Brambilla et al.,
143 2010; Herrando et al., 2016; Ims & Hender, 2012; Lehikoinen et al., 2014), we
144 hypothesize that mountain bird species, in general, are declining in numbers.
145 Second, we hypothesize that this decline would be stronger in mountain specialists
146 that only occur in mountain areas in our study sites, whereas mountain generalists,
147 which also can be found at lower elevations are doing better because of generally
148 higher ecological flexibility (Davey, Chamberlein, Newson, Noble, & Johnston, 2012;
149 Davey, Devictor, Jonzén, Lindström, & Smith, H. G. 2013; Gough et al., 2015). Third,
150 we predict that population trends of mountain species can be influenced by the
151 migration status of species. We hypothesize that long-distance migrants will have
152 fared relatively poorly, as they displayed on average more negative population
153 trends in recent years across Europe – whatever the elevation – than residents and
154 short-distance migrants (Laaksonen & Lehikoinen, 2013; Sanderson, Donald, Pain,
155 Burfield, & van Bommel, 2006; Vickery et al., 2014). An alternative hypothesis is that
156 if a change in habitat quality in the mountain areas has a negative impact on species
157 which are spending the longest time in the mountain areas, short-distance migrants
158 and resident species should have faced stronger declines than long-distance
159 migratory species (Lehikoinen et al., 2014). Last, we hypothesize that the decline in

160 mountain birds is stronger at northern latitudes than at southern latitudes because
161 temperature is expected to increase more in the north (Jacob et al., 2014).

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164 Material and methods

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166 *Data collection*

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

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184 Table 1. The number of study sites (mean, min and max during 2002–2014) in 11
 185 mountain areas distributed over four major mountain regions. In the Giant
 186 Mountains and the Apennines, the number of point count locations were
 187 transformed into sites dividing number of point stations by 15 (a typical number in
 188 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)

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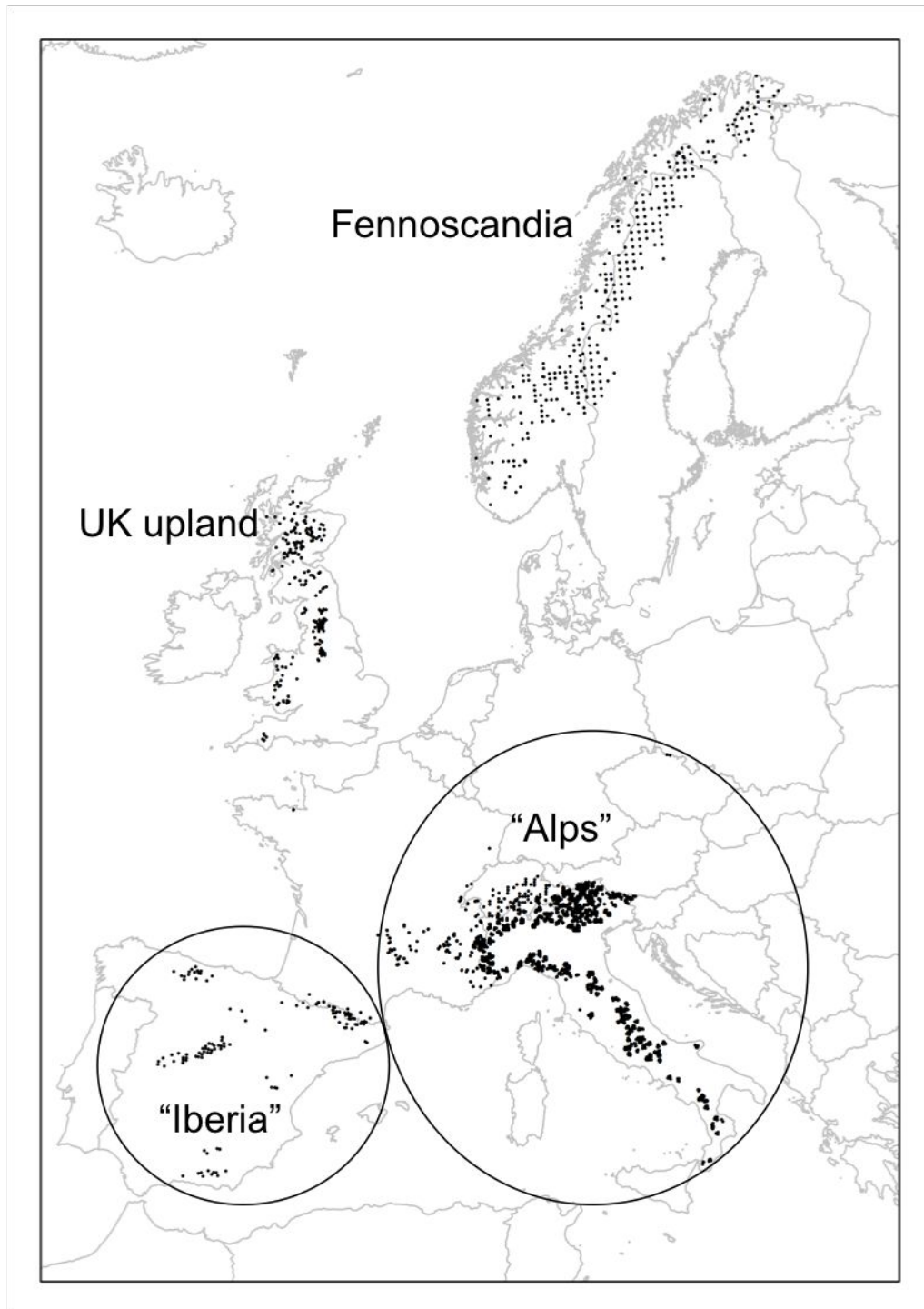
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192 *Site and species selection*

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

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

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207 Before we could define which species to use in the study, we needed to define
208 "mountain" monitoring sites and species in each region. Our aim was to target
209 species that prefer open or semi-open mountain habitats. These are mainly situated
210 on the highest altitudes of the mountains and are thus in the highest risk in terms of
211 climate change (Gonzalez et al., 2010). Since mountain top populations have limited
212 places to move upwards, the expected population declines should be strongest in
213 high altitude habitats. Thus we selected mountain tundra, meadows, grasslands,
214 bare rock, sparsely vegetated areas, peat bogs and scrubland above certain altitude.
215 We also included the, often spatially adjacent, zones of mountain birch forest and
216 dwarf mountain pine (for simplicity all the mentioned habitats are generally
217 referred to as 'mountain habitat'). For latitudinal reasons (and also exposure on the
218 western seaboard) also the altitudes where open mountain habitat occur varies and
219 this needs to be defined separately for each mountain range. Since some of the
220 species occur also outside the mountains - though we were only interested in the
221 populations living in the mountain areas - we needed to use habitat information to
222 define mountain sites from each area. For instance, due to the long northeast-
223 southwest gradient (1600 km) of the Fennoscandian mountain area, mountain
224 habitats vary in altitude. E.g. tundra is first found above 1300 m altitude in the
225 south, but at sea level in the very north (Lehikoinen et al., 2014). It should be noted
226 though, that only 4 out of 289 Fennoscandian sites were situated below 100 metres
227 of altitude. In the rest of the mountain regions, "mountain sites" were set to include
228 at least one-third open mountain habitat and to be above a certain altitude,

229 depending on local conditions such as climate, latitude and historical land use. These
230 altitude thresholds for mountain sites were set to 400 m for UK upland (and where
231 the surveyed habitats were generally open), 1100 m for the Giant Mountains, and
232 1200 m for all the remaining southern mountains, respectively. The UK uplands
233 have a particularly long history of anthropogenic deforestation and in combination
234 with high levels of extensive grazing and climatic exposure. Therefore, open habitats
235 resembling those of montane and alpine areas exist at lower altitudes than would
236 naturally occur (Smout, 2005; Thompson, MacDonald, Marsden, & Galbraith, 1995).
237 Also in the southern and central European sites open areas above the altitude limit
238 are not necessarily caused by the natural tree line, but areas also include subalpine
239 meadows that remain open due to grazing. The number of study sites in each area is
240 given in Table 1.

241 To define species which have significant populations in high altitude mountain
242 habitats (so called mountain species), we used altitude information from each larger
243 mountain range area using data from the UK (line transects, UK uplands) and
244 Switzerland (territory mapping, the Alps) and Spain (line transects, Catalanian
245 Pyrenees). First, we calculated relative densities based on mountain site-specific
246 species abundances and sampling effort (birds/km line transect) in 100m altitude
247 zones starting from the above mentioned mountain thresholds of the regions.
248 Second, based on altitude zone densities, we calculated the mean altitudes of species
249 for each mountain region. In the UK, species whose mean altitude were above 550
250 meters (a.s.l.; more than half of the population should be breeding above this
251 altitude in mountain routes) and preferred open mountain habitats were included

252 (Table S2). We calculated mean altitudes separately for the Swiss Alps and the
253 Catalanian Pyrenees and used the mean of these two values for both “Iberia” and
254 “Alps”. The altitude threshold for the species in these areas was above 1800 meters
255 (Table S3). In Fennoscandia, a set of 14 common mountain species were already
256 defined by Lehtikoinen et al. (2014). However, due to an increased monitoring effort
257 in recent years, we could include nine additional, less common, mountain species for
258 this region (Table 2).

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262 Table 2. The average annual population growth rates (trends) and traits of 44
 263 mountain bird species in 11 European mountain areas, as well as separate species
 264 trends for the “Alps”, Fennoscandia, “Iberia” and UK upland during 2002–2014.
 265 Traits include specialisation (Sp = mountain specialists, G = generalists;
 266 classification based on distribution areas of Hagemeyer & Blair (1997)) and
 267 migratory behaviour (Ld = long-distance migrant, Ot = other). Significant population
 268 change rates are in bold. ‘-’ means that the species is not a typical mountain bird in
 269 the particular mountain region and NE means that species is a typical mountain
 270 species in the area, but there were too little data available to calculate trends (see
 271 also Table S4).

Species (specialisation)	Traits	All areas	“Alps”	Fennoscandia	“Iberia”	UK
		Slope ± SE	Slope ± SE	Slope ± SE	Slope ± SE	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>Pyrhhorax graculus</i>	Sp, Ot	-0.015 ± 0.011	-0.002 ± 0.012	-	-0.044 ± 0.025	-
<i>Pyrhhorax pyrrhonorax</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	-

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

283 Species were classified into mountain specialists or generalists, based on their
284 distribution areas in Europe. Species mainly restricted to mountain areas and
285 uncommon in the lowlands were classified as mountain specialists whereas species
286 which have substantial populations in the mountains but also commonly breed in
287 lowlands were classified as mountain generalists (Hagemeijer & Blair, 1997, see also
288 Schridel et al., 2018; Thompson, Kålås, & Byrkjedal, 2012; Table 2). Furthermore,
289 species were grouped into long-distance (wintering in tropical areas) and others
290 (including both species wintering in the Western Palearctic and residents) based on
291 their distribution ranges in winter (Cramp, Simmons, & Perrins, 1977–1994;
292 Lehtikoinen et al., 2014).

293

294 *Weather data*

295

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

304

305 *Statistical analyses*

306

307 Log-linear population trends and annual indices were calculated for each species
308 separately using the software TRIM (Pannekoek & Van Strien, 2005). TRIM is a
309 commonly used tool in bird monitoring in Europe that accounts for overdispersion
310 and serial correlation and interpolates missing observations using a Poisson general
311 log-linear model (European Bird Census Council, 2018). TRIM produces annual
312 growth rate as well as annual abundance indices, including their standard errors.

313 Long-term annual growth rates and annual abundance indices were calculated for
314 Europe using aggregated data from all regions and separately for each of the four
315 major mountain regions. We compared the change in the overall mountain bird
316 indicator to the corresponding magnitude of change in European i) common bird, ii)
317 farmland and iii) forest bird indicators during 2002–2014 provided by European
318 Bird Census Council (2018).

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

328 Spatial differences in sampling network could lead into a situation where
329 trends are more driven by areas where number of census sites is dense compared to
330 areas where the network is sparse. We therefore, per each contributing country,
331 weighted the trend analyses by the spatial coverage of the national network. As
332 weight we used the country-specific mountain region area divided by the number of
333 census sites (average area per census sites: larger value mean lower density of
334 census sites). Thus, census sites in countries with proportionally fewer routes in
335 mountain areas weighed more in the analyses. France contributed to data of two
336 regions ("Iberia" and "Alps") and thus the weights were calculated separately for
337 these regions. The mountain area was measured using Corine land cover data
338 (Copernicus Land Monitoring Service 2016), where mountain habitats were i)
339 natural grasslands, ii) moors and heathlands, iii) transitional woodland shrubs, iv)
340 bare rock, v) sparsely vegetated areas, vi) glaciers and perpetual snow and vii) peat
341 bogs, which were above certain region-specific altitude (see Table S5). Here we have

342 used the data of the year 2012 only. We believe that this represents the general
343 situation in each country, because these habitat types unlikely show large scale
344 changes during the relatively short study period.

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

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

373

374 Results

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

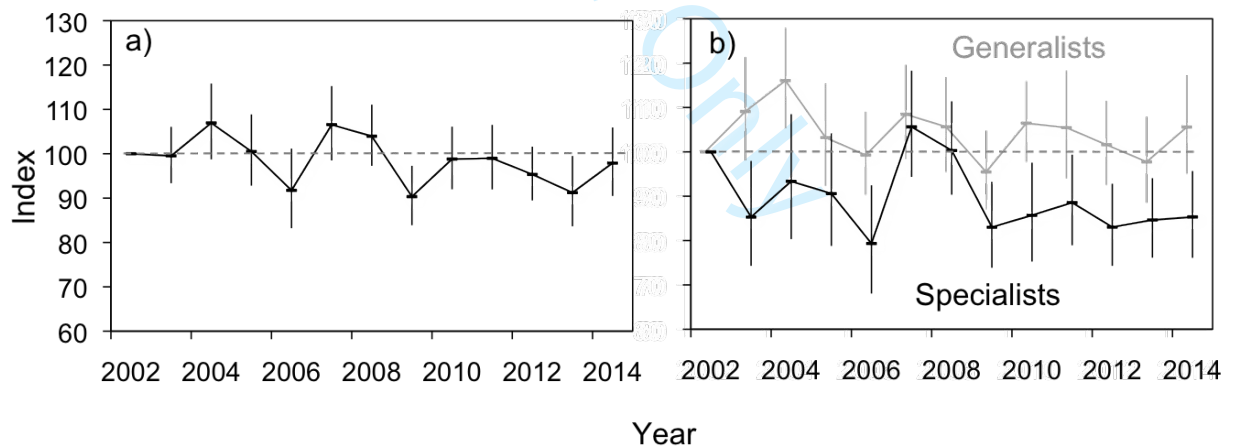
379 The European mountain bird indicator showed a significant negative decline
380 during 2002–2014 (44 species; -0.61% / year, 95% CI -1.14 to -0.08, overall decline
381 c. -7%; Fig. 2a). The European mountain specialist indicator also declined
382 significantly (n = 16 species, -0.88 % / year, 95% CI -1.66 to -0.10, overall decline c. -
383 10%). The mountain generalist slope was also negative (n = 28 species, -0.46% /
384 year), but not significantly so (95% CI -1.06 to 0.17; Fig. 2b). The slopes of
385 specialists and the generalists did not differ from each other (trend difference =
386 0.0040, se = 0.0051, $P > 0.05$, see also Table 3). Among the specialists, five out of 16
387 species showed negative and one showed positive trends. Among the generalists,

388 nine out of 28 species declined and seven increased (Table 2). Despite the fact that
 389 many mountain bird species have a wide distribution in Europe, it is important to
 390 note that only for two out of 44 species (northern wheatear and ring ouzel) were
 391 there enough data to calculate trends in all four mountain areas. In addition, for
 392 about half of the species, population trends were only calculated for one of the four
 393 regions, because the species were too rare in other regions (Table 2).

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399 Fig. 2. (a) The mountain bird indicator for Europe and (b) the separate indicators for
 400 specialists and generalists, during 2002–2014. Calculated mean of the indices and
 401 their 95% CIs are given.

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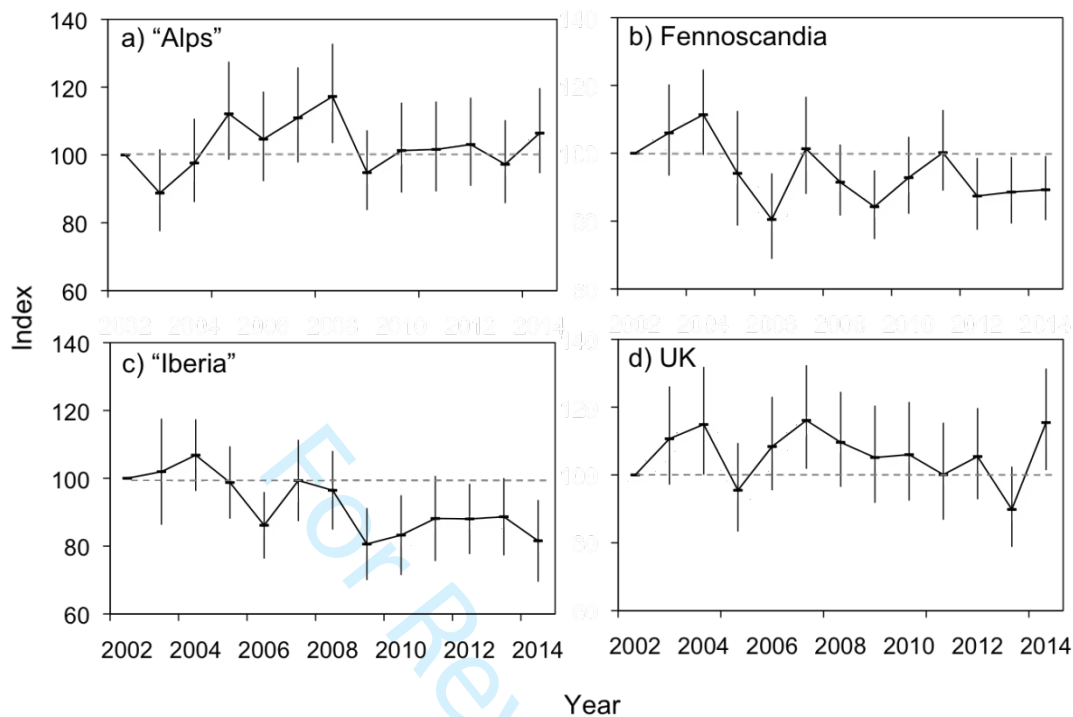
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The indicator of “Alps” showed no significant trends during 2002–2014 ($n = 20$ species, $+0.29\%$ / year, 95% CI -0.59 to 1.17 , Fig. 3a). Four species showed positive and three species showed negative trends during 2002–2014 (Table 2). The Fennoscandian 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 0.022 ± 0.010 se, $P < 0.05$). Slopes of the other regions did not differ from each other (all $P > 0.05$).



421

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

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The species only was the best random structure compared to more complicated phylogenetic structures (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 2 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, specialisation or migratory behaviour were linked with

434 the regional population trends (Table 3). The intercept of the null model was
 435 significantly below zero (-0.0072 ± 0.0035 , $t = 2.0$, $P < 0.05$), suggesting in general
 436 negative regional population trends during this particular period.

437

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

442

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

443

444

445 Annual temperatures during the breeding season (April–August) increased
 446 significantly in all four regions in the long-term (rate of increase 0.81–1.55°C during
 447 1980–2014; Table 4). During the last 20 years (1995–2014) the temperature
 448 increase was only significant in Fennoscandia (Table 4).

449

450 Table 4. Annual changes in temperature (in °C from April to August) in four
 451 mountain regions in Europe during 1980–2014 and 1995–2014. Significant
 452 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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456 Discussion

457

458 We set out to test three hypotheses regarding the recent population trends in
 459 European mountain birds. We got unequivocal support for the first hypothesis
 460 regarding a negative trend of European mountain bird populations since we found
 461 that the indicator has an overall decline of -7% during 2002 – 2014 (-0.61 %/year).

462 Fennoscandian and “Iberian” mountain bird indicators declined significantly and
463 differed from the slope of the corresponding indicator in the “Alps”. Based on
464 European common bird monitoring the magnitude of the decline is the same as all
465 common birds in Europe during the same study period. More specifically the trends
466 of bird indicators in two important habitats, farmland and forests, were -13% and -
467 1%, respectively (European Bird Census Council, 2018). Thus, in general mountain
468 birds are doing less bad than for farmland birds, but clearly worse than for forest
469 birds in Europe. The severe declines of farmland birds are mainly driven by
470 intensification of agriculture rather than climate change (Butler, Boccacio, Gregory,
471 Voříšek, & Norris 2010; Eglinton & Pearce-Higgins, 2012; Jørgensen et al., 2016).
472 However, in case of mountain birds, climate change can have a larger impact as the
473 climatic niche of especially mountain specialists is shrinking, highlighted by the
474 relatively fast declines of mountain species.

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

484 more worried about mountain specialists, since this group of species showed
485 already significant population declines.

486 We got no support for our third main hypothesis, that long-distance migrant
487 mountain birds have fared worse than resident and short-distance migrant
488 mountain birds, finding no significant differences between migratory groups on the
489 regional level. Therefore the diminishing mountain bird populations are not only
490 driven by general declines of long-distance migrants (e.g. Sanderson et al., 2006;
491 Vickery et al., 2014), but also species wintering in Europe are contributing to the
492 decline in mountain birds. This could indicate that mountain species have also
493 problems in their breeding areas (Lehikoinen et al., 2014). More work need to be
494 done to understand, what are the valid traits to evaluate the vulnerability of
495 mountain species in the face of climate change (see also MacLean & Beissinger,
496 2017).

497 The reason why there seem to be no universal patterns explaining species-
498 specific variation in responses to climate change could be that regional
499 circumstances, such as land use practices, differ between areas. In one area, impacts
500 of climate change may be more important than changes in land use and *vice versa*.
501 Agro-pastoral land use practices have become less intense or have been abandoned
502 completely allowing forest cover to increase again, especially in the low altitude
503 mountains of the southern mountain regions (“Alps” and “Iberia”; Brambilla et al.,
504 2010; Herrando et al., 2016; Maggini et al., 2014). Interactions with agricultural
505 abandonment and forest expansion can be complex and offer both threats and
506 opportunities depending on the ecological requirements of species and assemblages

507 involved (Calladine, Bielinski, & Shaw, 2013; Gillings, Fuller, & Henderson, 1998;
508 Herrando et al., 2016).

509 The April–August temperatures have increased substantially in recent decades
510 in all four mountain areas. Although the temperature increase has been significant
511 only in Fennoscandia over the last two decades, the temperatures are nowadays
512 above the long-term mean in all regions (Lehikoinen et al., 2014). Climate change
513 may affect bird populations in a different manner depending on the region (Sæther
514 & Engen, 2010). Furthermore, temperatures are expected to rise faster in higher
515 northern latitude mountains than in mountains located in temperate and tropical
516 zones, and the rate of warming in mountain systems can be two to three times
517 higher than that recorded during the 20th century (Nogués-Bravo, Araújo, Errea, &
518 Martínez-Rica, 2007). These can cause considerable effects on biodiversity even
519 though the direct impacts can be difficult to measure (Araújo, Errea, & Martínez-
520 Rica, 2007). Although we could not link the population dynamics with the observed
521 climate change, the observed declines are in line with the population predictions in
522 relation to climate change (Huntley et al., 2007). Human induced land use changes
523 are not as extensive in Fennoscandian mountains (Lehikoinen et al., 2014)
524 compared to “Iberia” (Herrando et al., 2016), and several Fennoscandian studies
525 have revealed changes in plant community due to climate change (Kullman & Öberg,
526 2009; Michelsen, Syverhuset, Pedersen, & Holten, 2011; Vuorinen et al., 2017). One
527 should also keep in mind that especially in Fennoscandia some mountain species are
528 nomadic to some extent (Lindström, 1987) and both plant and animal communities
529 are strongly influenced by multi-annual cyclic fluctuation of small rodents (Hanski,

530 Hansson, & Henttonen, 1991; Turchin, Oksanen, Ekerholm, Oksanen & Henttonen,
531 2000). Even animal species, which are not using rodents in their diet, are influenced
532 by the cycles due to predator-prey interactions (Lehikoinen et al., 2016). Despite
533 these kinds of fluctuations, we were able to detect a negative long-term trend in
534 Fennoscandia.

535 We must stress that the methods of the monitoring schemes and their
536 intensity showed spatial variation within the overall study area. However, we do not
537 believe that this has biased the analysis. First, the magnitude of the trend should be
538 comparable independently of whether it is based on point count, line transect or
539 territory mapping (Gregory et al., 2005). Second, we tried to compensate for the
540 potential biases in the sampling by using country-specific weights. The use of
541 weights did not influence the main results. We believe that there are two reasons
542 why our weighting did not influence the population trends: (1) Many of the species
543 data is only available from one of the study regions and thus weighting between
544 regions have no importance; and (2) population trends of nearby countries are
545 similar. As the monitoring schemes have improved in many countries in recent
546 years including systematic sampling, future analyses of monitoring data will be even
547 more reliable due to increased sample sizes.

548 Modelling work on the future effects of climate and land use change have
549 suggested that species-specific conservation measures aiming at improving habitat
550 to counteract the negative influence of climate change can only deliver minor
551 improvements of the future fate of mountain birds (Braunisch et al., 2014). Even if
552 high mountains may provide refuges for threatened mountain species currently

553 populating lower altitudes, in the long term, climate change can be expected to have
554 a strong impact on alpine species. Alpine habitats are expected to be reduced and
555 become more fragmented and isolated due to rise of the tree line where species
556 have increasing limited dispersal possibilities. Our findings also emphasize that
557 local studies are needed to understand the mechanisms and drivers of the
558 population changes of individual species and species communities in mountains
559 including information about species habitat selection and changes in the amount of
560 preferred habitat. Despite international actions to halt climate change, climate will
561 change in the near future (EEA, 2012). To mitigate the potential impacts of climate
562 change, it is important to take measures that can improve connectivity between
563 suitable mountain habitats and to minimize the effects of other threats such as non-
564 sustainable tourism and afforestation of grasslands (Lloret, 2017).

565 Last, to understand the big picture on the continental and global scale we also
566 need to continue existing monitoring work in the mountain areas and expand both
567 the taxonomic and spatial coverage of monitoring schemes. Monitoring should
568 preferably be based on systematic sampling design with a reasonable number of
569 study sites covered on annual basis. One reason why we did not observe significant
570 differences in trends between specialization groups could be the still relatively small
571 sample sizes and thus larger uncertainties in our trend estimates. Nevertheless, our
572 European mountain bird indicator and regional indicators provide an important tool
573 to measure and monitor the changes in mountain biodiversity with regular updates
574 in the future and the spatial coverage of the indicator can easily be expanded when
575 suitable monitoring data become available. Given that climate and land use changes

576 in the uplands are likely to manifest themselves into the loss of open mountain
577 habitats and expansion of shrubland/forest, we suggest that future work should also
578 look at mechanistic reasons behind the declines. More and important information
579 may come from comparing potential differences in trends between mountain and
580 lowland population of the mountain generalists, where the land use pressures can
581 differ between the areas.

582

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584

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