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The Effects of Climate Change on Holarctic Mountain and Upland Bird Populations: A Review and Meta-Analysis

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Running head: Climate change and mountain birds

Keywords: Avian physiology, biotic interactions, conservation, elevational shift, global warming, high-elevation species, interspecific competition, phenology, population dynamics, projections, snow, trophic mismatch.

63 Mountain regions are globally important areas for biodiversity, but are subject to multiple human-induced
64 threats, including climate change, which has been more severe at higher elevations. We reviewed evidence
65 for impacts of climate change on Holarctic mountain bird populations in terms of physiology, phenology,
66 trophic interactions, demography, and observed and projected distribution shifts, including effects of other
67 factors that interact with climate change. We developed an objective classification of high-elevation,
68 mountain specialist and generalist species, based on the proportion of their breeding range occurring in
69 mountain regions. Our review found evidence of responses of mountain bird populations to climatic
70 (extreme weather events, temperature, rainfall and snow) and environmental (i.e. land use) change, but we
71 know little about either the underlying mechanisms or about the synergistic effects of climate and land use.
72 Long-term studies assessing reproductive success or survival of mountain birds in relation to climate
73 change were rare. Few studies have considered shifts in elevational distribution over time and a meta-
74 analysis did not find a consistent direction in elevational change. A meta-analysis carried out on future
75 projections of distribution shifts suggested that birds whose breeding distributions are largely restricted to
76 mountains are likely to be more negatively impacted than other species. Adaptation responses to climate
77 change rely mostly on managing and extending current protected areas for both species already present,
78 and for expected colonising species that are losing habitat and climatic space at lower elevation. However,
79 developing effective management actions requires an improvement in the current knowledge of mountain
80 species ecology, in the quality of climatic data, and in understanding the role of interacting factors.
81 Furthermore, the evidence was mostly based on widespread species rather than mountain specialists.
82 Scientists should provide valuable tools to assess the status of mountain birds, for example through the
83 development of a mountain bird population index, while policy-makers should influence legislation to
84 develop efficient agri-environment schemes and forestry practices for mountain birds, as well as to
85 regulate leisure activities at higher elevations.

86

87 Climate change has been recognised, alongside modifications in land-use, as a key driver of global change in
88 biological diversity (e.g. IPCC 2007, Ameztegui *et al.* 2016), and there is now a large body of evidence that
89 animals and plants are responding to climate change through shifts in distribution (e.g. Chen *et al.* 2011),
90 changes in population size (e.g. Stephens *et al.* 2016), and changes in phenology leading to inter-linked
91 effects at different trophic levels (e.g. Both *et al.* 2006, Thackeray *et al.* 2016). Such effects vary
92 geographically, and biodiversity in temperate, boreal and arctic regions is considered particularly vulnerable,
93 with greater warming at higher latitudes (e.g. Meehl *et al.* 2007). Furthermore, rates of warming and
94 frequency of extreme cold events are more pronounced at higher elevations (Beniston & Rebetez 1996, Liu
95 & Chen 2010, Pepin *et al.* 2015). As a result, high-elevation areas are particularly threatened as they are
96 more susceptible to changes in climate (Diaz *et al.* 2003, Böhning-Gaese & Lemoine 2004, La Sorte & Jetz
97 2010).

98 Mountain and high latitude upland regions (henceforth 'mountains') cover around 25% of the Earth's
99 surface (Kapos *et al.* 2000). They support one quarter of terrestrial biodiversity (Körner & Ohsawa 2006) and
100 contain nearly half the world's biodiversity hotspots (Myers *et al.* 2000). These are complex ecosystems of
101 high conservation value as they encapsulate a high diversity of small-scale habitats dictated by different
102 topoclimates within narrow elevational gradients (Körner & Ohsawa 2006). As a result, mountains
103 accommodate high levels of species diversity with heterogeneous communities adapted to specific
104 environmental conditions that change along the elevational gradient, including climate and other abiotic
105 factors such as slope, exposure, solar radiation, wind direction and substrate (Körner & Spehn 2002, Nagy &
106 Grabherr 2009, Viterbi *et al.* 2013, Boyle & Martin 2015). For example, marked changes occur over short
107 distances, with temperature varying in temperate regions on average by 0.6°C every 100m in elevation
108 (Dillon *et al.* 2006). Aspect can also influence temperature, with greater solar radiation on southern than
109 northern slopes in the Northern Hemisphere (Nagy & Grabherr 2009). Global warming is causing changes to
110 these environments, with documented responses including the elevational advance of the tree-line and a
111 general increase in dominance of woody deciduous shrubs at high elevations (Gehrig-Fasel *et al.* 2007,
112 Myers-Smith *et al.* 2011).

113 Many unique ecological features of temperate mountain systems also arise from the strong
114 seasonality in temperatures which result in a very short growing and reproductive season, typically less than
115 three months in alpine-arctic and boreal habitats (Nagy & Grabherr 2009). Strong inter-annual variations in
116 temperature, precipitation, and snow cover regimes are also observed in these systems (IPCC 2013, Klien *et al.*
117 *et al.* 2016) with changes in the timing, quantity and duration of precipitation likely to influence mountain
118 habitats and biodiversity (Beniston *et al.* 2003, IPCC 2013, Martin *et al.* 2017). Snow cover has been shown
119 to have insulating properties, protecting plants and invertebrates from frost during the coldest months of
120 the year and thereby influencing survival rates of many slow-growing high-elevation plants, insects and
121 mammals (Hågvar 2010, Wipf & Rixen 2010, Berteaux *et al.* 2016). Snow cover in the Northern Hemisphere
122 has declined since the 1920s, particularly in spring and summer (IPCC 2007).

123 Although often perceived as true wildlands, mountain ecosystems typically have a long history of
124 human activity, especially in Europe and Asia (FAO 2015). Twenty percent of the global human population
125 inhabits mountain regions, with about 8% living above 2500m (Körner & Ohsawa 2006). However, mountains
126 provide essential ecosystem services, including nearly half of the human population's water supply, carbon
127 storage and sequestration (forests and peatlands), and natural resources (timber, productive soils and
128 medicinal plants; Körner & Ohsawa 2006). Mountains are also very important in terms of leisure and tourism
129 activities (skiing, snowboarding, hiking, biking, wildlife watching and hunting). Mountain systems are thus
130 continuously subject to landscape changes due to human activities, which might have more severe
131 consequences than climate change itself (Jetz *et al.* 2007), or which could potentially exacerbate climatic
132 effects (Mantyka-Pringle & Rhodes 2012).

133 Amongst birds, changes in climate have been reported to influence migration timing (Hüppop &
134 Hüppop 2003, Knudsen *et al.* 2011), breeding output (Crick *et al.* 1997, Laaksonen *et al.* 2006), population
135 size (Sæther *et al.* 2000, Townsen *et al.* 2016), and changes in elevational (Reif & Flousek 2012) and
136 latitudinal (Hickling *et al.* 2006, Zuckerberg *et al.* 2009) distributions. Because the severity of climatic change
137 varies over the Earth's surface (e.g. Meehl *et al.* 2007), avian responses may also vary in intensity depending
138 on their geographic distribution. Birds may exhibit rapid distributional responses to climatic fluctuations, for

139 example tracking changes in surface temperature latitudinally (Hickling *et al.* 2006, Zuckerberg *et al.* 2009).
140 However, there is also evidence that range shifts in birds are lagging behind climate change (Devictor *et al.*
141 2008, Ralston *et al.* 2017), potentially due to asynchronous phenology of birds and their prey (e.g. Mayor *et*
142 *al.* 2017). Species inhabiting high-elevation mountain systems often exhibit a high degree of habitat
143 specialisation and unique ecological traits within narrow thermal ranges (Reif & Flousek 2012, Reif *et al.*
144 2015, Mahon *et al.* 2016, Pacifici *et al.* 2017, Scridel *et al.* 2017a). Adapting to rapid climate change may be
145 particularly challenging along the elevational gradients of many mountains where temperatures and area
146 decrease monotonically with elevation (Elsen & Tingley 2015). As a result, species tracking rising
147 temperatures in these systems are predicted to decline according to the species-area relationship (Preston
148 1962) as populations become isolated, and thus increasingly vulnerable to stochastic events (Lande 1993,
149 Bech *et al.* 2009, Fjeldså *et al.* 2012). A successful shift into a new area by a species is possible only when
150 abiotic as well biotic requirements are fulfilled (Martin 2001a, Heikkinen *et al.* 2007, Wilson & Martin 2012).
151 Given the fast rate of warming, species might have to track temperatures in areas where their associated
152 habitat and resources require longer to establish (e.g. mature trees, alpine and sub-nival plants; Engler *et al.*
153 2011, Reif & Flousek 2012, Brambilla & Gobbi 2014), or where suitable habitat formation cannot occur due
154 to constraints of other factors such as soil processes or rock substrate (Freppaz *et al.* 2010), or by direct
155 human activities (e.g. deforestation; Nogués-Bravo *et al.* 2008, Patthey *et al.* 2008, Kohler *et al.* 2014;
156 disturbance via outdoor recreation; Arlettaz *et al.* 2007, 2015). Finally, climatic effects coupled with negative
157 synergistic changes in land use might pose even more severe constraints on adaptation of mountain birds to
158 future climatic conditions.

159 Due to the documented general responses of birds, and the more extreme climatic changes
160 observed in mountains, it seems reasonable to expect that mountain birds may be particularly threatened by
161 climate change. In this review, we assess the existing evidence for direct and indirect effects of climate
162 change on mountain birds in the Holarctic region (Heilprin 1887), and we evaluate their future conservation
163 prospects. We address six specific objectives: (i) to define mountain generalist and high-elevation specialist
164 birds for the Holarctic region; (ii) to review the impacts of climate change on mountain birds through a

165 summary of the literature, and a quantification of general responses throughout the Holarctic, including a
166 meta-analysis; (iii) to review and quantify projected impacts from future climate change scenarios using a
167 meta-analysis; (iv) to assess stressors that are likely to interact with climate change in affecting birds living at
168 high elevations; (v) to review proposed conservation actions; and (vi) to identify current gaps and future
169 priorities for research.

170

171 **METHODS**

172

173 **Defining mountain birds**

174 Mountain systems and species inhabiting them are difficult to describe geographically and ecologically, and
175 definitions may not apply consistently across the globe (Strahler 1946, Gerrard 1990, Körner 2012, Scridel
176 2014). In order to assess the status of mountain birds, it was first necessary to define mountain areas and
177 habitats. Using elevational thresholds to define these regions would immediately exclude older and lower
178 mountain systems such as the Urals, Scottish Highlands and Appalachians, and include areas with little
179 topographic relief and few environmental gradients (e.g. large, high-elevation plateaux). Using slope as a
180 criterion on its own or in combination with elevation may resolve the latter problem, but not the former. For
181 these reasons, we adopted the definition of Kapos *et al.* (2000), who classified mountain systems in seven
182 classes on the basis of elevation, slope and local elevation range (Fig. 1). The latter criterion is particularly
183 useful as it identifies lower elevation mountain ranges (300-999m) by defining a radius of interest (5km)
184 around each grid cell (30 arc-second) and measuring the maximum and minimum elevation within a
185 particular neighborhood, and their difference, allowing the identification of areas that occur in regions with
186 significant relief, even though elevations may not be especially high (Kapos *et al.* 2000). This is a broad
187 definition which includes high latitude 'upland' habitats at relatively lower elevations, as well as mountain
188 forest, the alpine belt (the treeless region between the natural climatic forest limit and the snow line) and
189 the nival belt (the terrain above the snowline, which is defined as the lowest elevation where snow is

190 commonly present all year round; Kapos *et al.* 2000, Körner & Ohsawa 2006). Hereafter, we refer to
191 ‘mountain regions’ as those as defined by Kapos *et al.* (2000).

192 We developed a broad definition of Holarctic mountain birds based on the proportion of their
193 Holarctic breeding range that was within the defined mountain regions in order to assess the evidence base
194 for impacts of climate change on birds largely restricted to mountains as a breeding habitat. We stress that
195 we are interested in all bird species occurring in Holarctic mountain regions, including species that also occur
196 in a range of habitats, rather than only focusing on high-elevation specialist species. We used a geographic
197 information system (GIS) software (QGIS, Quantum GIS Development Team 2016; GRASS, GRASS
198 Development Team 2015) to restrict the map of Kapos *et al.* (2000) to the Holarctic realm, and imposed over
199 it the breeding range of global bird species ($n = 10280$ species; BirdLife International & NatureServe 2015).
200 We defined as ‘high-elevation mountain specialist’ a species for which at least 50% of its range was in the
201 higher elevation classes 1-4 of Kapos *et al.* (2000). We further defined a ‘mountain generalist’ as a species
202 for which at least 50% of its entire breeding range was within the defined Holarctic mountain region (i.e.
203 classes 1-7 of Kapos *et al.* 2000) and which was not classed as a high-elevation mountain specialist. These
204 definitions therefore identify broadly which species are particularly associated with mountains over the
205 whole Holarctic region. There are many species (e.g. Capercaillie *Tetrao urogallus*, Pygmy Owl *Glaucidium*
206 *passerinum*, Rock Ptarmigan *Lagopus muta*), termed boreo-alpine taxa, that occur in mountains at low
207 latitudes (e.g. European Alps) which are also present at higher latitudes, but at lower elevations (e.g.
208 northern Europe). The definition adopted here seeks to identify species that are linked more closely with
209 mountains *per se* (for example due to topography or particular habitat types) across a broad region. We use
210 the terms ‘high-elevation mountain specialist’ and ‘mountain generalist’ when specifically referring to our
211 classification. We use the term ‘mountain bird’ to refer to any species occurring in our defined Holarctic
212 mountain region, which also includes species which potentially breed in a range of habitats and at a range of
213 elevations across their geographic range.

214

215 **Literature survey**

216 The literature search was generated through ISI Web of Knowledge (www.webofknowledge.com). In order to
217 obtain relevant studies we used the following keywords: (bird* OR avian*) AND (mountain* OR montane*
218 OR upland* OR alpine* OR moorland* OR arctic* OR polar* OR altitude* OR elevation*) AND (climate
219 change* OR global warming*) NOT tropic*. The search period was from 1950 until the 31st December 2016.
220 Papers identified from this search were subsequently included if they concerned research wholly or partly
221 carried out within the defined mountain regions, or if the study species was/were defined as a high-elevation
222 mountain specialist or mountain generalist (see Supporting Information, Table S1 & S4). The latter group of
223 studies included some broad-scale analyses that were not specifically focused on mountains, but which
224 considered some high-elevation mountain specialists (typically analyses covering large regions, for example
225 based on national atlases). A total of 764 studies was initially identified. The abstract of each of these papers
226 was read to determine whether they were relevant for the purposes of this review, and 591 studies were
227 eliminated at this stage. The remaining 173 papers were also checked for other relevant references missed
228 in the previous search. This resulted in a further 61 relevant papers, giving a total of 234 which were
229 subsequently assigned to eight broad topics: i) climate change, physiological constraints and life history
230 strategies; ii) links between climate and population dynamics; iii) changes in phenology; iv) trophic linkages;
231 v) observed evidence of elevational shift; vi) projected elevational shifts; vii) interactions between climate
232 change and other drivers (agriculture, grazing and forestry, leisure and other threats, interspecific
233 interactions); and, viii) conservation and policy papers. We used the standardized literature search to
234 summarise the main trends in the resulting database in terms of location and topic, and also in terms of
235 analysing elevational shifts and future projections of species' geographic range and population size. In detail,
236 we conducted two meta-analyses: one testing whether mountain birds have shifted in elevation to track
237 suitable climate, and a second one to test whether mountain birds will be more negatively impacted by
238 climate change than non-mountain species according to projected distribution range and population size.
239 We also used the selected papers, in conjunction with the wider literature, as the basis of a qualitative
240 review to highlight the key issues and findings.

241

242 **Current and future elevational shifts in bird populations**

243 Papers that presented estimates for shifts in species distributions over time in relation to elevation were
244 considered for meta-analyses if they focussed, either wholly or mostly, on the defined mountain regions.
245 Given that conditions may change rapidly over small distances in mountains due to the steep topography,
246 smaller-scale studies are more appropriate than larger-scale atlas studies in tracking species distributions
247 (Chamberlain *et al.* 2012), and thus we focused on studies with a maximum sampling unit area of 1-km².
248 Additional data were collected for each study on the period considered (in years), the elevational range (in
249 metres), and the estimated mean annual rate of temperature change (°C/year) over the period considered.
250 Similarly, papers that predicted future effects of climate change on mountain birds were considered if they
251 were largely restricted to mountain areas, if they estimated a proportional change in geographic distribution
252 or population size over time, and if the sample size of the underlying data set on which models were based
253 was presented. Additional variables recorded were the period over which projections were made, and the
254 climate change scenarios considered, which were classed as either 'severe' (scenarios A2 and A1F1 or
255 RCP8.5) or 'moderate' (all other scenarios and RCPs; IPCC 2007, 2013).

256

257 **Statistical analysis**

258 For elevational shifts, papers were included in the meta-analysis only if sample sizes and test statistics were
259 presented, or if parameter estimates (including mean shift) and standard errors, standard deviations or
260 confidence limits, were reported. In cases where only estimates of change in elevation and errors were
261 presented (i.e. without any test statistics), z-scores were derived, testing against a hypothesis of zero
262 change. In common with standard meta-analytical approaches (e.g. Koricheva *et al.* 2013), the goal was to
263 estimate standardized responses of elevational shifts in bird distributions over time from studies that used a
264 diversity of methods for quantifying a potential shift, which in most cases was calculated as the change, in
265 meters, of the distribution of a given species (sometimes a group of species) between two time periods.
266 However, some papers also tested the effect of the interaction between elevation and time period on the

267 probability of species presence, a significant interaction indicating a significant shift over time (e.g. Reif &
268 Flousek 2012, Mizel *et al.* 2016).

269 Shifts in species distributions were tested using a variety of methods in the above papers. Different
270 test statistics (e.g. F , t , χ^2) presented in these papers were converted to Pearson's r using standard
271 conversion formulas (Lajeunesse 2013) so that effect sizes (i.e. change in elevational distribution over time)
272 could be compared across studies (further details are given in the Supplementary material, S2. Meta-analysis
273 methods). Pearson's r varied between 1 and -1, a positive value indicating an upslope shift in elevation over
274 time. Pearson's r values were not normally distributed, so prior to analysis, standardized Pearson's r values
275 from each study were transformed using Fisher's Z transformation to derive both normalized estimates and
276 their variance (as per Musitelli *et al.* 2016).

277 Parameter estimates of standardized elevational shifts were derived by analysing Z -transformed
278 Pearson's r values (henceforth 'standardized effects') and 95% confidence intervals based on linear mixed
279 effects models using the nlme package in R (Pinheiro *et al.* 2017). The analytical unit was the estimate for a
280 given species or group of species (some papers estimated shifts for the whole community), hence 'study'
281 was included as a random effect to account for multiple estimates derived from the same paper, and 'family'
282 was included as a random effect to account for the potential phylogenetic dependence of closely related
283 species (or multiple observations from the same species). Models were weighted according to the inverse of
284 the variance of standardized effects. An effect was considered as significant if confidence intervals on the
285 parameter estimate did not overlap zero. To derive a single overall estimate of shift, no fixed effect was
286 included (i.e. an intercept-only model). A significant effect of the intercept in this case would indicate a
287 consistent standardized effect in terms of elevational shift across studies and species. Study duration and
288 rate of temperature change were then tested by including each as a fixed effect in the model.

289 Papers that made future projections of species distributions or abundances did not typically present
290 significance tests, therefore standardized effect sizes could not be estimated. Instead, the mean percentage
291 change in the response variable (either range size or a measure of population size) was analysed. The
292 response variable was approximately normally distributed. The model structure was similar to that for

293 observed elevation shifts in that initially an intercept-only model was specified which included 'study' and
294 'family' as random effects, and then further fixed effects (high-elevation specialist or generalist species,
295 period over which projections were made, climate change scenario) were tested. The sample size of the
296 initial input data was specified as a weight in the model statement, the assumption being that models based
297 on a larger sample size are likely to be more reliable than those based on small sample sizes. Confidence
298 intervals of estimates which did not overlap zero were taken as evidence of consistent effects of future
299 projections of elevational shifts.

300

301 RESULTS

302

303 The literature review considered a total of 234 articles relevant to climate change across various mountain
304 regions of the Holarctic (Table 1). In Europe, most studies occurred in the Alps and Pyrenees ($n = 45$),
305 followed by Fennoscandia ($n = 25$) and the uplands of Britain and Ireland ($n = 24$). Many studies were also
306 carried out in North America ($n = 75$), particularly in the Rocky ($n = 14$), and Appalachian ($n = 10$) Mountains,
307 while only seven studies were carried out in Holarctic Asia. There were 26 papers included that investigated
308 climate change impacts on bird communities at a global scale. The number of published studies according to
309 our research criteria increased considerably over time from one study in 1991 to 48 studies published in
310 2016 (Fig. 2).

311 The most commonly investigated climate change-related topic was the general ecology/physiology
312 and ecology of mountain bird species ($n = 61$; Fig. 3), followed by papers that tested for effects of climate
313 change on changes in population trends, elevational/latitudinal shifts or changes in community composition
314 ($n = 57$). Papers investigating future prospects of species according to various climatic scenarios were also
315 frequent ($n = 47$). The least studied category involved studies that investigated interspecific and/or
316 synergistic interactions between climatic changes and other environmental or ecological factors ($n = 4$).

317

318 Mountain birds of the Holarctic region

319 We identified 2316 bird species breeding in the Holarctic realm, 818 (35.3 %) of which were defined as either
320 high-elevation mountain specialists ($n = 324$ species) or mountain generalists ($n = 494$ species). The most
321 frequent Order of birds in both groups was Passeriformes (generalist $n = 333$ species; high-elevation
322 specialist $n = 256$ species), followed by Piciformes for generalists ($n = 29$) and Galliformes for high-elevation
323 specialists ($n = 27$; a complete list of the 2316 species is provided in the Supporting information, Table S4). A
324 great proportion of the high-elevation specialists breed almost exclusively on the Tibetan plateaux (i.e.
325 Tibetan Babax *Garrulax koslowi*, Tibetan Rosefinch *Carpodacus roborowskii*) or have a large proportion of
326 their breeding range confined to this region (i.e. Bearded Vulture *Gypaetus barbatus*, Wallcreeper
327 *Tichodroma muraria*, Twite *Carduelis flavirostris*). Examples of non-Tibetan high-elevation specialists were
328 few and generally displayed a restricted breeding distribution confined to the lowest class that defines high-
329 elevation specialists (class 4; Fig.1) and at the southern-most range of the Holarctic realm (i.e. Maroon-
330 fronted Parrot *Rhynchopsitta terrisi*, White-naped Swift *Streptoprocne semicollaris*, Black Rose Finch
331 *Leucosticte atrata*). Generalist mountain birds occur across various Holarctic mountains, ranging from the
332 Tibetan Plateau and European Alps to the Pacific Mountain System in North America.

333 Comparing the list of mountain birds across 232 relevant articles from the literature search (no
334 information was available for two articles) revealed that almost all generalist (97%; $n = 453/464$) and high-
335 elevation specialist species (96%; $n = 311/324$) have been investigated in the literature, with the three most
336 frequent generalist species studied being Black Restart *Phoenicurus ochruros* ($n = 32$ studies), Water Pipit
337 *Anthus spinoletta* and Ring Ouzel *Turdus torquatus* ($n = 31$ each), whilst for high-elevation specialists, the
338 most frequent species were White-winged Snowfinch *Montifringilla nivalis* ($n = 22$), Yellow-billed Chough
339 *Pyrrhocorax graculus* ($n = 20$) and Wallcreeper *Tichodroma muraria* ($n = 13$). However, when excluding
340 studies based on solely distributional data (e.g. species distribution models), meta-analysis and reviews, only
341 2% ($n = 7/324$) of high-elevation mountain specialists and only 14% ($n = 67/494$) of mountain generalist

342 species were investigated. This suggests that fine-scale studies on species ecology are scarce for these
343 species.

344

345 **Climate change, physiological constraints and life history strategies**

346 Birds breeding in mountain systems have evolved complex physiological, behavioural and morphological
347 adaptations (Dragon *et al.* 1999, Cheviron & Brumfield 2012). Adaptations to prevent heat loss rely
348 particularly on insulation, for example by producing a denser coat of feathers (Broggi *et al.* 2011) and by
349 exhibiting a greater body mass than lower-elevation conspecifics (Bergmann's rule; Ashton 2002).
350 Physiological constraints are likely to be major determinants of how species respond to climate change. For
351 example, Root *et al.* (2003) found that more than 80% of the species from various taxa and habitats that
352 showed changes linked to global warming shifted geographically in the direction expected on the basis of
353 known physiological constraints. Birds with physiological responses that are tightly coupled to specific
354 environmental conditions (such as mountain species) are believed to be particularly sensitive to changes in
355 climate, but little has been done to test whether these adaptations (especially morphological) are
356 counterproductive in a warming climate. Anecdotal evidence and the limited literature available suggest
357 there may be costs to higher temperatures for species like Rock Ptarmigan, Ring Ouzel and White-winged
358 Snowfinch which have been observed panting and bathing in water or snow during hot sunny days in the
359 Swiss Alps and Scottish Highlands (Glutz von Blotzheim *et al.* 1973; DS pers. obs.), whilst Johnson (1986)
360 found that White-tailed Ptarmigan *Lagopus leucurus* started panting at 21° C. The above studies did not
361 establish whether these behavioural changes were sufficient to prevent reduced survival or reproduction in
362 warming conditions.

363 A species' life history strategy may be crucial in responding to climatic alterations. Patterns along
364 elevational gradients have highlighted that populations of the same species confined to higher elevations
365 have slower life-history strategies (fewer nesting attempts, lower clutch size) compared to populations at
366 lower elevation (Boyle *et al.* 2016). Higher nest survival has been found for higher elevation populations that

367 may partially compensate for the reduction in potential fecundity. Boyle *et al.* (2016) did not record a
368 pattern of significant differences in body mass, egg or nestling size, or survival between paired populations
369 of bird species breeding at high and low elevation. Tingley *et al.* (2012), however, found that species were
370 more likely to shift their elevational range in the Sierra Nevada (USA) if they had smaller clutches, defended
371 all-purpose territories and were residents or short-distance migrants, although these involved both upslope
372 and downslope shifts. It is therefore possible that higher-elevation species may indeed be more threatened
373 by climate change than lower-elevation species due both to their morphological adaptations to cooler
374 systems (e.g. insulation), and their life history strategies. However, future work is required to elucidate these
375 ideas.

376

377 **Links between climate and population dynamics**

378 Although not addressing climate change *per se*, several studies have indicated that fluctuations in climate do
379 influence demographic rates in mountain birds, and hence that potential climate change effects can be
380 inferred. In several cases, increasing temperatures may increase reproductive output. Sæther *et al.* (2000)
381 demonstrated that increases in winter temperature (together with population density) positively affected
382 White-throated Dipper *Cinclus cinclus* dynamics in the upland regions of southern Norway. Cold winters
383 caused low recruitment and a decrease in population size associated with the amount of ice cover, which
384 impaired foraging opportunities. Novoa *et al.* (2008) demonstrated that weather variables during both pre-
385 laying and post-laying influenced reproductive success in Rock Ptarmigan in the French Pyrenees.
386 Reproductive success was positively associated with early snow free patches, but rainfall had negative
387 effects, particularly after hatching. Positive effects of snowmelt on Rock Ptarmigan were also confirmed in a
388 later study by Novoa *et al.* (2016), but the intensity of the effect varied with respect to the geographical
389 region considered (i.e. Alps vs Pyrenees). In Mountain Plover *Charadrius montanus*, nest survival was
390 favoured by drier and cooler weather over a seven-year period (Dreitz *et al.* 2012).

391 There is also evidence for negative effects of climate on demographic parameters. Barnagaud *et al.*
392 (2011) showed that winter and summer NAO (North Atlantic Oscillation) affects several indicators of

393 breeding success of Black Grouse *Tetrao tetrix* in the French Alps, particularly during years of extreme
394 weather. Interestingly, birds showed some acclimatisation, being able to optimise their reproductive output
395 in relation to the NAO index, but they performed particularly badly when extreme weather events occurred.
396 Twenty-five years of prolonged spring warming caused low breeding success in a Scottish population of
397 Capercaillie (Moss *et al.* 2001).

398 In mountain systems, bird response to temperature may vary at both small and large scales. For
399 example, nest-site characteristics of Water Pipits are selected based on their accessibility to predators,
400 snowfall and microclimate, with the latter two influencing nestling rearing periods and survival (Rauter *et al.*
401 2002). Because snowfall and predation pressure vary over time and space, it is possible that large-scale
402 factors also influence species choices. The relative importance of small and large scale weather effects is still
403 unclear as these seem to vary depending between species, populations, seasons and time periods
404 considered. Ptarmigan exemplify such complex responses: even though they have been considered as
405 indicators of temperature-induced effects on mountain biodiversity (Novoa *et al.* 2008, Wilson & Martin
406 2010, Imperio *et al.* 2013), some studies have shown little effect of climate change on their demography
407 (Sandercock *et al.* 2005, Novoa *et al.* 2016). In one study by Wang *et al.* (2002), local minimum winter
408 temperatures had a stronger effect on White-tailed Ptarmigan population dynamics than large-scale indices
409 like NAO. On the other hand, Wann *et al.* (2014) found that the same species in the same study area
410 responded to climatic effects over a longer period when a two-year lag time was considered. This nuanced
411 evidence highlights the importance of testing both small and large-scale weather predictors, and in particular
412 in focussing more studies on lagged effects of NAO on demographic parameters of mountain species.

413

414 **Changes in phenology**

415 Amongst birds, climate change has affected the phenology of many species, leading to changed timing of
416 breeding and migration (e.g. Crick *et al.* 1997, Rubolini *et al.* 2007), which in some cases has led to
417 population declines when phenological trends are mismatched with those of their key food resources (e.g.
418 Both *et al.* 2006). Such phenological mismatches are hypothesised to underpin the declines in many long-

419 distance migrant species in the western Palearctic (e.g. Møller *et al.* 2008). However, in the Fennoscandian
420 mountains, Lehtikoinen *et al.* (2014) found that long-distance migrants declined less on average than
421 residents and short-distance migrants, suggesting the latter were more sensitive to climate change impacts.

422 There are few studies that have shown changes in mountain bird phenology explicitly linked to
423 climate change. Timing of breeding in Mexican Jays *Aphelocoma wollweberi* has advanced in line with
424 climate changes in the Chiricahua Mountains of Arizona (Brown *et al.* 1999). Inouye *et al.* (2000) found that
425 American Robins *Turdus migratorius* in the Colorado Rocky Mountains arrived 14 days earlier over a 19 year
426 period. However, local conditions (e.g. the average date of snowmelt) did not change on the study site
427 resulting in a 65 day gap between date of the first robin sighting and date of snowmelt, suggesting that
428 American Robins may have to cope with an extended pre-breeding period at higher elevation. Indeed, the
429 extent, duration and timing of snow cover is likely to be an important factor acting on the phenology of
430 mountain birds in general. For birds in the European Alps and North American mountains, patterns in
431 breeding season phenology are typically tied to the snow melt (e.g. Novoa *et al.* 2008, Imperio *et al.* 2013,
432 García-González *et al.* 2016). There is evidence that responses to changes in snowmelt phenology vary
433 between species and populations. Martin & Wiebe (2004) compared White-tailed Ptarmigan and Willow
434 Ptarmigan *Lagopus lagopus* breeding in alpine and arctic environments respectively, and found that extreme
435 weather events greatly reduced breeding success in both species. In average years, breeding parameters of
436 White-tailed Ptarmigan were not correlated with snowmelt phenology, therefore suggesting a constraint in
437 adjusting their reproductive phenology to a changing environment. Willow Ptarmigan, however, tracked
438 local conditions, breeding earlier in years of early snowmelt (Hannon *et al.* 1988, Martin & Wiebe 2004).
439 Similarly Novoa *et al.* (2016) found that the median hatching date for Rock Ptarmigan was significantly
440 correlated with the date of snowmelt in the French Alps, but not in the Pyrenees. None of the above studies
441 found trends over time linked to climate change, but it can be inferred that climate change acting on snow
442 melt phenology could affect these species in the future, especially given that snow melt has become
443 progressively earlier, and snow cover has declined in extent in the northern hemisphere (IPCC 2007).

444

445 Trophic linkages

446 Global warming may influence the distribution and abundance of invertebrate communities directly
447 (Grigaltchik *et al.* 2012) or indirectly via the modification of suitable habitat conditions (i.e. soil desiccation,
448 changes in vegetation communities; Carroll *et al.* 2011). However, the links between such changes and bird
449 populations have received little investigation. Most of the evidence comes from the British uplands. Pearce-
450 Higgins *et al.* (2010) demonstrated how abundance of adult craneflies (Diptera: Tipulidae), a keystone group
451 in many mountain systems, was negatively correlated with August temperatures in the previous year, and in
452 turn how changes in the Golden Plover *Pluvialis apricaria* populations were negatively correlated with August
453 temperatures two years earlier. Furthermore, Fletcher *et al.* (2013) also concluded that low temperatures in
454 May (a surrogate for late cranefly emergence; Pearce-Higgins *et al.* 2005) positively influenced Red Grouse
455 *Lagopus lagopus scoticus* chick survival. These findings suggest that continued warming would have negative
456 effects on these species.

457 We found only one study considering the role of climate change on plant food sources for mountain
458 birds. Santisteban *et al.* (2012) correlated declines in adult survival of Cassia Crossbill *Loxia sinesciuris* with
459 increasing temperatures in South Hills and Albion Mountains (USA). The most supported explanation was
460 that Lodgepole Pine *Pinus contorta* seed availability varied with temperature, where with increasing
461 temperatures, trees prematurely shed their seeds, reducing the carrying capacity for Cassia Crossbill
462 breeding later in the year. The warmer springs and increased precipitation in Europe will also influence food
463 availability and the future geographical distribution for European Crossbills (Common Crossbill *L. curvirostra*,
464 Parrot Crossbill *L. pytyopsittacus*, Scottish Crossbill *L. scotica*) (Mezquida *et al.* 2017)

465 Snow patches can represent an important foraging habitat, providing both arthropod fallout and
466 suitable sites at their margins for the collection of soil invertebrates, particularly during the nesting and
467 rearing period of many mountain birds such as White-winged Snowfinch, Snow Bunting *Plectrophenax*
468 *nivalis*, Horned Lark *Eremophila alpestris* and Alpine Accentor *Prunella collaris* (Antor 1995, Camfield *et al.*
469 2010, Brambilla *et al.* 2016a,b, Rosvold 2016). In some extreme cases, birds may even choose to nest directly

470 in glaciers (White-winged Diuca Finch *Diuca speculifera*; Hardy & Hardy 2008) or in very close proximity
471 (Grey-crowned Rosy Finch *Leucosticte tephrocotis*, Johnson 1965, Rosvold 2016; Brandt's Rosefinch
472 *Leucosticte brandt*, Potatov 2004) to capitalize on abundant supplies of insects. Changes in amount and
473 duration of snow may therefore affect these species via food resources.

474 Where trees and shrubs have expanded their distribution upslope in response to increasing
475 temperatures (Harsch *et al.* 2009, Myers-Smith *et al.* 2011), changes in invertebrate communities are
476 expected. Ground and canopy-dwelling arthropod communities have been assessed in the arctic foothills of
477 Alaska in relation to the presence of two passerine predators, Gambel's White-Crowned Sparrow *Zonotrichia*
478 *leucophrys gambelii* and Lapland Longspur *Calcarius lapponicus*. Predicted changes in shrub dominance are
479 likely to favour White-crowned Sparrow nesting habitat and food (canopy-dwelling arthropods), whilst
480 declines of Lapland Longspurs have been projected as a consequence of shrub encroachment and
481 consequent reduced availability of ground-dwelling arthropods (Boelman *et al.* 2015).

482 Climate change may also have effects by affecting more complex linkages across different trophic
483 levels. Martin & Maron (2012) conducted an experiment showing that climate change in the form of reduced
484 snowfall in mountains, and leading to increased ungulate herbivory in winter, can negatively affect diverse
485 species interactions. They experimentally tested the hypothesis that declining snowfall, which enables
486 greater over-winter herbivory by Elk *Cervus canadensis*, indirectly influences plants and associated bird
487 populations in montane forests. When they excluded Elk from one of two paired snowmelt drainages, and
488 replicated this paired experiment across three distant canyons over a six year period, there was a reversal in
489 the multi-decadal declines in plant and bird populations. These experimental results suggest that climate
490 impacts can interact with other drivers of habitat change and strongly influence plant–animal and other
491 ecological interactions.

492

493 **Observed evidence of elevational shifts**

494 Evidence exists, typically from broad-scale atlases of species distributions, that some species are shifting
495 their geographic distributions to higher elevations in response to climate change, the distributions

496 presumably tracking more suitable climatic conditions (e.g. Auer & King 2014, Roth *et al.* 2014), although
497 such effects are not universal (e.g. Zuckerberg *et al.* 2009, Tingley *et al.* 2012, Massimino *et al.* 2015).
498 Furthermore, apparent elevational shifts may occur due to habitat deterioration or destruction at lower
499 elevations (Archaux 2004, Bodin *et al.* 2013).

500 Few studies have considered elevational shifts in the distributions of Holarctic mountain birds. We
501 found 10 relevant studies in our literature search that considered specifically elevational shifts in bird species
502 distributions along elevational gradients, partly or wholly in mountains, over time (Table 2). Including papers
503 that considered more than one study site ($n = 13$ sites from 10 papers), the mean period considered was 38
504 ± 2.5 SE years (range 9 – 102) and the mean length of elevation gradients was 1970 ± 76 SE m (range = 500 –
505 3400m). There was little evidence of consistent patterns in elevational shifts across the studies, and there
506 was a wide variation among species. In some cases, there were fairly consistent upward shifts in most
507 species (e.g. Reif & Flousek 2012, Rocchia 2016), but other studies found that different species exhibited
508 upward and downward shifts (Tingley *et al.* 2012, DeLuca & King 2017), or found shifts in only a small
509 proportion of the species considered (Archaux 2004). Additionally, there was sometimes marked variation in
510 species' responses between geographic locations within the same study (Tingley *et al.* 2012, Pernellet *et al.*
511 2015).

512 The lack of consistent trends apparent in Table 2 was supported by the meta-analysis. There were
513 203 estimates of elevational shift from seven published studies analysed, five from Europe and two from
514 North America. Pooling all estimates across the studies, there was no strong support for a general shift
515 towards higher elevations (parameter estimate \pm SE = 0.083 ± 0.052 , 95% CLs = -0.018, 0.184). Shifts towards
516 higher elevations were more positive when rates of temperature change were higher (estimate \pm se = $0.543 \pm$
517 0.152 , 95% CLs = 0.245, 0.841). Duration of study had an unexpected negative effect on shifts, studies over
518 longer time spans resulting in more downward shifts (estimate \pm se = -0.026 ± 0.004 , 95% CLs = -0.034, -
519 0.018). The above findings were robust to different model structures and different subgroups of species
520 (Supplementary Material, Table S3).

521 Most studies in Table 2 also considered temperature variations over the same period, either
522 modelling them in relation to bird distributions (Archaux 2004, Popy *et al.* 2010, Reif & Flousek 2012, Tingley
523 *et al.* 2012, Pernollet *et al.* 2015, Rocchia 2016), or considering climate trends over the same periods
524 (Maggini *et al.* 2011, Mizel *et al.* 2016). In most cases, trends in elevational shifts were temporally matched
525 with temperature trends over the same period, with a few exceptions (Pernollet *et al.* 2015, Mizel *et al.*
526 2016). Tingley *et al.* (2012) found a broad range of responses of bird species along elevation gradients in the
527 Sierra Nevada, due in part to differential responses to increasing temperature (exerting a general positive
528 upwards shift) and increasing precipitation (exerting a general downslope shift), although few other studies
529 considered potential effects of precipitation (only Archaux 2004, Popy *et al.* 2010 and Pernollet *et al.* 2015).

530 Changes in bird population trends along elevation gradients over time are similarly inconsistent
531 across studies. Some find positive changes in lower-elevation species and negative changes in higher-
532 elevation species that are consistent with elevational shifts as lower-elevation species colonise mountains
533 and higher- elevation species lose suitable habitat (Flousek *et al.* 2015). However, others have reported
534 opposite (Archaux 2007) or inconsistent (Zamora & Barea-Azcón 2015, Furrer *et al.* 2016) patterns. Tingley
535 and Beissinger (2013) found a decrease in total species richness, and in species richness of high elevation
536 species, over time in the Sierra Nevada, despite heterogeneous shifts in individual species in the same area
537 (Tingley *et al.* 2012). At wider scales, there is evidence that bird communities are shifting towards warm-
538 dwelling species (Switzerland; Roth *et al.* 2014), but also that communities at higher elevations have lower
539 'climate debt' (the spatio-temporal divergence between temperature changes and community changes) as
540 elevation increases (France; Gaüzère *et al.* 2016).

541

542 **Projected elevational shifts**

543 Extinction risks are expected to increase as a result of climate-induced elevational range shifts in the future
544 (Sekercioglu *et al.* 2008, La Sorte & Jetz 2010). Shifting vegetation zones in mountains, and in particular an
545 advance of the tree-line towards higher elevations, has been observed in many studies (e.g. Lenoir *et al.*

2008, Harsch *et al.* 2009). As a consequence, high-elevation specialists, and in particular those of open, treeless habitats, are expected to be most threatened due to habitat loss or fragmentation (e.g. Chamberlain *et al.* 2013, Goodenough & Hart 2013, Siegel *et al.* 2014, Brambilla *et al.* 2016a). Nevertheless, some studies have also projected overall range loss in higher-elevation forest specialists (Braunisch *et al.* 2014, Brambilla *et al.* 2015). There were 95 estimates derived from 12 studies that satisfied the criteria to be included in the analysis (see Supporting Information; Table S2). There was a net prediction of negative impacts on species populations or distributions, although there was a degree of variability and confidence limits overlapped zero (estimate \pm se = $-28.9 \pm 17.0\%$, 95% CLs = -62.4, 4.6). High-elevation mountain specialists and generalists were projected to be more negatively impacted than other species (mountain specialists and generalists = $-76.1 \pm 27.1\%$, 95% CLs = -129.2, -23.0; other = $29.8 \pm 25.7\%$, 95% CLs = -20.6, 80.2). There was a tendency for greater negative impacts in severe than moderate scenarios (moderate = $-26.6 \pm 17.1\%$, 95% CLs = -60.1, 6.9; severe = $-33.6 \pm 17.5\%$, 95% confidence limits = -67.9, 0.7). There was no evidence of an effect of the number of years over which projections were made (0.01 ± 0.79 , 95% CLs = -1.53, 1.55). Re-running the models without weighting for sample size showed the same patterns, although results were less conservative (i.e. it was less likely that confidence intervals overlapped zero).

561

562 **Interactions of climate change effects with other drivers of change**

563 *Land use*

564 Disentangling the relative importance of climatic effects and other drivers of environmental change that
565 influence the persistence and maintenance of biodiversity has been a key issue across mountain regions
566 (Mantyka-Pringle & Rhodes 2012, Cumming *et al.* 2014, Maggini *et al.* 2014, Elmhagen *et al.* 2015), and is
567 central to produce efficient, adaptive conservation frameworks for threatened species (Gehrig-Fasel *et al.*
568 2007, Gienapp *et al.* 2007, Eglinton & Pearce-Higgins 2012, Titeux *et al.* 2016). For example, climate change
569 and land-use often interact in ways that influence biodiversity (Parmesan & Yohe 2003), and these
570 interactions may amplify or reduce the magnitude of potential effects (Clavero & Brotons 2010, Dreitz *et al.*

571 2012, Chamberlain *et al.* 2013, Oliver *et al.* 2017). Lehtikoinen & Virkkala (2016) acknowledged a land-use and
572 species trait effect due to the high level of unexplained variation in models predicting the change in density
573 of birds in relation to temperature change. Jetz *et al.* (2007) attempted to assess the relative importance of
574 climate and land use changes using future scenarios. We identified 617 birds defined as either high-elevation
575 mountain specialists or mountain generalists present in the study of Jetz *et al.* (2007). For these species, the
576 average percentage loss in geographic range due to land use change was estimated at 24.8% and 28.6% by
577 the years 2050 and 2100 respectively. In comparison, loss due to climate change alone was predicted to be
578 7.3% and 11.5% respectively.

579 The interaction between climate and land use is particularly relevant to mountain habitats that are
580 experiencing a faster rate of climate change than the global average (Diaz *et al.* 2003, Nogués-Bravo *et al.*
581 2007) and are subjected to various anthropogenic changes at a landscape level (Arlettaz *et al.* 2007, 2015,
582 Gellrich & Zimmermann 2007, Nogués-Bravo *et al.* 2008, Patthey *et al.* 2008, Braunisch *et al.* 2011, 2013,
583 2016, Douglas *et al.* 2015). However, land use change has only been rarely incorporated into analyses of
584 distribution shifts: Reif & Flousek (2012) and Rocchia (2016) found that elevation shifts more closely
585 matched temperature than habitat changes, Tryjanowski *et al.* (2005) found significant effects of both,
586 whereas Popy *et al.* (2010) could not separate the effects of the two.

587 Agro-forestry and pastoral practices have shaped the landscape of Holarctic mountains in Europe
588 and Asia, influencing the species composition and abundance of mountain birds (e.g. Gehrig-Fasel *et al.*
589 2007, Caprio *et al.* 2011, Douglas *et al.* 2014, Wilson *et al.* 2014, Mollet *et al.* in press). Over time, forest
590 management has changed in intensity (e.g. clear-felling vs single-tree selection), composition (planting of
591 exotic conifers) and age dynamics (establishment of even-aged monocultures; Kirby & Watkins 2015). At the
592 same time, climate change may be affecting forest bird assemblages either directly or indirectly by
593 influencing cover, productivity, and composition of forest systems. However, it is generally unclear which of
594 these two pressures (climate change or forestry practices) is the most important driver in changes in bird
595 distribution. Changes in forest composition could cause opposite shifts (i.e. downhill) to those forecast due
596 to effects of climate warming (uphill). For example, Archaux (2004) suggested that changes in forest

597 management that favoured coniferous at the expense of broadleaved trees might have caused forest birds
598 to have shifted their mean elevation downwards. In other cases, there is evidence from boreal forests
599 (including some mountain areas) that climate, in addition to vegetation type and management, is a crucial
600 driver for determining passerine species distribution (Cumming *et al.* 2014, Frey *et al.* 2016). Virkkala (2016)
601 found that forest management favoured passerine species benefitting from climate change, so that direct
602 habitat alteration was connected to the indirect effects of climate change.

603 Climatic variables can also be important factors for non-passerine species. Brambilla *et al.* (2015)
604 found in the Italian Alps an important effect of climate in addition to habitat composition at the landscape
605 scale in dictating the distribution of the cold-adapted Pygmy Owl and Boreal Owl *Aegolius funereus*. Both of
606 these forest species were predicted to undergo range contraction in the Alps as a consequence of climate
607 change. Braunisch *et al.* (2014) evaluated the importance of climate, landscape and vegetation variables on
608 the occurrence of indicator species (i.e. Capercaillie, Hazel Grouse *Tetrastes bonasia*, Three-toed
609 Woodpecker *Picoides tridactylus* and Pygmy Owl) in central European mountain forests, and assessed future
610 changes in habitat suitability of these species according to future climatic projections. Although climate
611 variables were the most important factors for most species, the models predicted that *in situ* management
612 actions, such as increasing the number of forest gaps (for Capercaillie), increasing bilberry *Vaccinium* spp.
613 cover (for Hazel Grouse) and increasing the number of snags and/or the proportion of high (>15m) canopy
614 forest (for Three-toed Woodpecker), could to some extent mitigate the detrimental impact of climatic events
615 and sustain bird populations. However, such interventions may have to work against the natural forest
616 dynamics and could be expensive.

617 Historically, agricultural expansion and changes in livestock management have had major impacts on
618 mountain birds (Lundmark 2007, Elmhagen *et al.* 2015). In many mountain areas, traditional grazing
619 practices are characterised by low stocking densities or transhumant pastoralism, i.e. the seasonal
620 movement of livestock between high-elevation summer pastures and lowland winter pastures (Arnold &
621 Greenfield 2006). These traditional grazing practices have been largely abandoned in some areas due to
622 social and economic factors, especially in the European Alps. For example, in Italy, the number of farms has

623 decreased drastically and many have changed to indoor production systems (Battaglini *et al.* 2014), which
624 has led to substantial changes within mountain vegetation zones through encroachment of formerly open
625 grasslands by trees and shrubs and a loss of structural heterogeneity (Braunisch *et al.* 2016). Elevational
626 shifts in vegetation may be therefore due both to climate change and land abandonment (Gehrig-Fasel *et al.*
627 2007).

628 The reintroduction of grazing is an often recommended management solution to counteract tree
629 and shrub encroachment in open areas (Gehrig-Fasel *et al.* 2007), and it has the potential to increase plant
630 structural diversity and composition (Hoiss *et al.* 2013, Peringer *et al.* 2013) which is key to preserve
631 emblematic birds of semi-open habitat (Patthey *et al.* 2012). However, the effects of grazing on mountain
632 bird populations are still not well understood. Long-term grazing at high stocking densities is known to have
633 negative impacts on soil fertility and consequently on the productivity of the whole system (McVean &
634 Lockie 1969), although effects on mountain birds are not consistent and vary substantially among
635 geographical regions, livestock types and stocking levels. Several studies have reported that grazing increases
636 richness or densities of mountain grassland birds (Laiolo *et al.* 2004, Evans *et al.* 2006, Bazzi *et al.* 2015).
637 Evans *et al.* (2006) found that mixed sheep and cattle grazing, at low intensity, improved the breeding
638 abundance of Meadow Pipit *Anthus pratensis* compared to sites stocked with sheep only (at high or low
639 density) or unstocked sites in the Scottish uplands, while Loe *et al.* (2007) reported the highest bird density
640 on pastures with high sheep density in Norway. Other studies have shown no differences in bird abundance
641 or species richness between grazed and ungrazed sites (Moser & Witmer 2000) or a negative influence of
642 grazing animals on nesting success (Pavel 2004, Warren *et al.* 2008).

643 Climate change can also have direct impacts on grazing management, although this seems to be less
644 well studied. In Nepal, where transhumance is a common practice, herders perceived the impact of climate
645 change through personal experience. In several studies, where herders have been interviewed, they
646 described a rise in temperature, a decline of rain- and snowfall, a scarcity of water resources (Aryal *et al.*
647 2014, Wu *et al.* 2015) and the presence of invasive weeds, which are replacing the valuable grasses on
648 farmlands (Gentle & Thwaites 2016). These perceptions were also in line with temperature and rainfall

649 trends in the studied region. As a result, herders tried to adjust their transhumance patterns to the changed
650 conditions by altering the timing of seasonal livestock movements. The consequences of such management
651 responses for mountain bird populations, however, remain unknown. Given the varieties of different effects
652 of grazing on mountain birds, and the lack of research on likely responses of grazing management practices
653 to future climate change, further investigations are needed to examine potential effects of grazing regimes
654 on mountain bird populations before we can apply them as potential conservation tools.

655

656 *Leisure and other potential threats*

657 Mountains are important ecosystems for biodiversity, but are also multi-functional sites for various human
658 activities, including leisure. People seek mountain landscapes to practice a range of different sports and
659 hobbies such as skiing, snowboarding, hiking, biking, birdwatching, rock-climbing, paragliding and hunting.
660 Local communities benefit economically from tourism. The leisure industry in mountain areas is growing
661 (Debarbieux *et al.* 2014), and the potential effects of these activities on avian communities have received
662 increasing attention from conservationists (e.g. Patthey *et al.* 2008, Arlettaz *et al.* 2013, DeLuca & King
663 2014). The impact of snowsports on biodiversity is a major topic studied in the European Alps, where there
664 are c. 40,000 kilometres of ski-runs served by c. 14,000 ski-lifts that are capable of transporting c. 1.5 million
665 skiers per hour (Weed & Bull 2004). As a consequence of this and other activities, the Alps receive nearly 100
666 million visitors per year, spending \$60 billion annually (Giuliano 1994). In contrast, snowsport activities,
667 including skiing operations in North America and the Eastern Holarctic remain at relatively low density, with
668 most likely local effects on biodiversity (Martin 2001b).

669 There are several lines of evidence showing that ski-pistes have deleterious effects on both grassland
670 and forest birds via loss and degradation of habitat, and a decrease in food availability (Laiolo & Rolando
671 2005, Rolando *et al.* 2007, Caprio *et al.* 2011, Rixen & Rolando 2013). In addition, there is evidence that
672 hormonal stress in birds generated by intensive human activities can negatively impact already vulnerable
673 populations of Capercaillie (Thiel *et al.* 2011) and Black Grouse (Arlettaz *et al.* 2007, 2013). Anthropogenic
674 disturbance has furthermore been shown to entail extra energetic costs that may negatively affect

675 population dynamics (Arlettaz *et al.* 2015). Effects may also operate through infrastructure associated with
676 skiing, for example increased mortality due to collision with ski cables (Baines & Andrew 2003, Watson &
677 Moss 2004), and reduced reproductive success of ground nesting birds associated with development of
678 tourist resorts (Watson & Moss 2004, Patthey *et al.* 2008, Tolvanen & Kangas 2016), although negative
679 effects are not universal (Rimmer *et al.* 2004).

680 Interactive effects of climate change and outdoor sports could increase the above negative impacts
681 on bird populations in the future. Global warming is having important economic consequences for the skiing
682 industry due to reduced snow cover and persistence. Compensatory mechanisms are targeted at prolonging
683 the ski season by direct spraying of artificial snow, or by creating new ski pistes at higher elevations where
684 snow conditions are more reliable. Brambilla *et al.* (2016a) modelled ski-pistes and mountain bird presence
685 according to future climatic scenarios. Strong overlaps between areas climatically and topographically
686 suitable for the development of ski-pistes and areas suitable for breeding alpine birds were predicted to
687 occur, suggesting that the conservation of mountain bird communities will require careful planning in order
688 to reduce potential increased future conflicts between outdoor winter sports and birds. Global warming is
689 also causing the abandonment of ski-runs at lower elevations. Natural grassland revegetation at some
690 abandoned sites resulted in a partial recovery of important alpine birds, but never back to the state of the
691 'original' alpine grasslands (Caprio *et al.* 2016).

692

693 *Novel interspecific interactions*

694 Species may respond to climate change by shifting their distribution to track local climates (Tingley *et al.*
695 2009, Jackson *et al.* 2015), which may result in novel interactions as species colonize new areas.

696 Including such interactions has improved model predictions at different scales (Araújo & Luoto 2007).

697 Heikkinen *et al.* (2007) and Brambilla *et al.* (2013) suggested that including the presence of woodpeckers
698 that produce the cavities used by secondary cavity nesting raptors improved model performance in
699 predicting cavity-nesting forest owl distributions. We found only one relevant example that tested the
700 importance of biotic interactions among birds along elevational gradients. Freeman & Montgomery (2015)

701 assessed potential competition between Swainson's Thrush *Catharus ustulatus*, which generally inhabits
702 lower elevations but which has shifted its distributions towards higher elevations, and the conspecific
703 Bicknell's Thrush *Catharus ustulatus*, which is largely confined to mountaintops. Using playback techniques,
704 the authors found that, where the species co-occurred, Swainson's Thrush responded aggressively to
705 Bicknell's Thrush, but not *vice-versa*.

706

707 **Conservation and policy**

708 Our literature review has clearly highlighted the need for more detailed studies of mountain birds, with
709 several papers stating that a valuable conservation framework can be achieved only if such knowledge gaps
710 are bridged (see Research gaps and Conclusion; Fig. 4). Despite this, we found that most studies on this topic
711 identified adaptation strategies for mountain and upland species threatened by climate change. Most of
712 these studies ($n = 21$; Fig. 4) focussed on the quality, quantity and geographical location of protected areas.
713 Existing protected areas may have already functioned as important compensatory systems, increasing
714 species resilience to climate change (Virkkala *et al.* 2014, Gaüzère *et al.* 2016, Santangeli *et al.* 2016), and in
715 future scenarios of greenhouse gas emission, greater biodiversity losses have been predicted in unprotected
716 than in protected areas (Virkkala *et al.* 2013). In Europe, nationally designed protected areas are likely to
717 retain climatic suitability better than unprotected areas in the future, as they tend to occur at high elevations
718 and hence act as climatic *refugia* for species, although this was not found to be the case for the European
719 Union-wide Natura 2000 network (Araújo *et al.* 2011). The same authors also highlighted that nearly all (i.e.
720 97.2%) alpine species and sub-species of vertebrates and plants of European concern are projected to lose
721 suitable habitat due to their small ranges. However, it must be highlighted that the study did not consider
722 species dispersal.

723 Some habitats may also be more prone to climate change than others. Montane forest species are
724 predicted to be less impacted by climate change due to the stronger self-regulation of the forest
725 microclimate compared to open habitats (Reif & Flousek 2012), and to native forest expansion that has

726 already occurred, and which is predicted to continue in many areas (European Alps; British uplands;
727 Chamberlain *et al.* 2013, Scridel *et al.* 2017b), but they could be prone to other climate change related
728 threats such as pests, disease and wild fires (Dale *et al.* 2001, Sturrock *et al.* 2011, Lesk *et al.* 2017).
729 Furthermore, natural grasslands in the Alpine region may face serious challenges to shift their distributions,
730 as they are being progressively colonised due to both forest encroachment following land abandonment or
731 release of grazing pressure and advancing treelines at lower elevations, while facing constraints on
732 colonizing higher elevations, for example due to slow rates of soil formation (Freppaz *et al.* 2010,
733 Chamberlain *et al.* 2013, Jackson *et al.* 2015).

734 Targeted habitat management should be considered as an adaptive conservation tool for various
735 species threatened by climate change (Fig. 4). Improving habitat structure and offering greater prey
736 availability has been reported to increase mountain species' resilience and resistance for forest, semi-open
737 and open-habitat species (Caroll *et al.* 2011, Braunisch *et al.* 2014, Scridel *et al.* 2017b). This might be
738 achieved by targeted grazing to maintain open habitats and enhance invertebrate populations (Signorell *et*
739 *al.* 2010, Patthey *et al.* 2012, Braunisch *et al.* 2016). Such intensive actions can be very costly and in conflict
740 with many economic goals, hence management should be targeted in large areas projected to support viable
741 wildlife populations. Increasing the quantity and quality of protected areas is not just important for mountain
742 species *per se*, but also because these areas are likely to become stopover *refugia* for many migrant species
743 tracking climate change (Loarie *et al.* 2009, Boyle & Martin 2015), and management action should also
744 accommodate these species' requirements. When intensive management *in situ* does not compensate for
745 climatic effects, potential captive programs ($n = 2$; Fig. 4), translocation of species to new suitable areas ($n =$
746 2 ; Bech *et al.* 2009), or the creation of corridors to favour dispersal and colonization of new areas (Huntley *et*
747 *al.* 2008, Conroy *et al.* 2011, Lu *et al.* 2012, Virkkala *et al.* 2013) have been proposed.

748 All of these adaptation responses for mountain species threatened by climate change can work only
749 if scientists and policy makers collaborate to influence current legislation. Our classification of high-elevation
750 mountain specialists and mountain generalists indicates initial steps for a joint common Holarctic mountain
751 bird index, which so far has been developed for some regions in the world (Fennoscandia; Lehikoinen *et al.*

752 2014; North America and British Columbia, Canada; Boyle & Martin 2015) and which could be essential for
753 scientists and policy-makers to measure progress in the conservation of mountain birds, especially if this
754 index includes full life cycle avian use of mountain habitats. While in the long-term, global measures to
755 contain and reverse anthropogenic emissions are important ($n = 3$; Fig. 4), most authors admit that the
756 persistence of mountain species also depends on immediate short-term national and local conservation
757 actions and legislation ($n = 9$; Fig. 4).

758

759 DISCUSSION

760

761 Our literature review has shown that there is a growing body of evidence that climate change is impacting
762 mountain birds in terms of distribution and population trends, reproduction and survival. These changes may
763 have been mediated through direct effects of climate on physiology, indirect effects of changes in habitat, or
764 via interactions with other biotic and abiotic changes. However, patterns were often highly variable (e.g.
765 both increases and decreases in population size, range changes towards both higher and lower elevations),
766 between species, and between different study areas for the same species.

767 Defining a 'mountain bird' across a large region like the Holarctic is difficult because many species
768 that are mountain birds in warmer climates are lowland species in colder climates. Our goal was to derive an
769 objective definition that could be applicable over a large geographic area and which identified species
770 associated with mountains *per se*, rather than occurring in mountains due to interactive effects of climate,
771 elevation, latitude and land use. This is important when considering species distributions over large scales,
772 and in particular when projecting future distributions. For example, the Water Pipit was identified as a
773 generalist mountain breeding bird across various mountain slopes, even in the northern, colder, parts of its
774 geographic range. Predictions based on climate alone may therefore be inaccurate for such species (e.g.
775 Huntley *et al.* 2008). In general, the species identified as high-elevation specialists or mountain birds (see
776 Supporting Information; Table S4) were in-line with the authors' expectations, although there were some
777 surprising results. For example, Rock Ptarmigan is considered an archetypal mountain bird in many parts of

778 its range (the European Alps, the Pyrenees, British Columbia and Alberta), but not according to our
779 definition. This to some extent may have been due to the coarse scale of the defined breeding range used in
780 the method, but it is also reflective of the widespread populations of this species inhabiting lowland arctic
781 tundra. As conservation policy is typically applied at national or regional level, a regional-based definition of
782 mountain birds would also be useful, which would be readily achievable under the current methodology.
783 Although this first classification of Holarctic high-elevation mountain specialist and generalist birds was not
784 the primary aim of this review, we regard this exercise of considerable value for future work on this group of
785 poorly studied species (e.g. baseline monitoring, development of a joint mountain bird index, and ecological
786 and conservation research).

787 According to our meta-analysis, there was no evidence for consistent elevational shifts in mountain
788 bird species. Although we failed to detect any direct and conclusive effects that climate change has caused
789 widespread distribution shifts in Holarctic mountain birds, it is likely that we lack sufficient data to generate
790 robust conclusions. The meta-analysis included a range of species encompassing a great variation in life
791 history strategies, demographic parameters and geographical regions. All of these factors are likely to
792 influence potential responses to climate change and hence cause a wide variation in patterns of elevational
793 shift among mountain birds across the mountain ecosystems and avian taxa considered (Martin & Wiebe
794 2004, Wilson & Martin 2010, Tingley *et al.* 2012, Novoa *et al.* 2016).

795 There was consistency in climate projections across studies that was somewhat at odds with the
796 heterogeneity in responses of observed elevational shifts. This may in part have been due to more mountain
797 high-elevation specialists being included in the projection papers. However, in many cases, there was a focus
798 on climate (usually temperature and precipitation) as a driving factor, and only half of the studies considered
799 alternative scenarios of climate change in tandem with land use change or other anthropogenic pressures. In
800 general, species distribution models only rarely include scenarios of changes in land use and human
801 disturbance alongside those of climate change (Sirami *et al.* 2016). It is clear that range shifts in mountains
802 may be influenced by many factors, including temperature, but also precipitation, habitat and topography,

803 and that species may vary widely in their response. All of these factors should be considered when assessing
804 elevational range shifts, and predicting future shifts, in mountain birds.

805 Adaptation responses for mountain species threatened by climate change rely on enhancing the
806 quality and quantity of suitable habitat in particular via protected areas, but also the conservation of suitable
807 ecological conditions at regional and wider levels, including improving landscape connectivity. We have
808 shown that human activities can be beneficial for climate-sensitive species (i.e. some pastoral activities), and
809 yet mechanisation, leisure and urbanisation may impede potential benefits. Major changes can occur if
810 scientists and legislators work closely together, for example through the development of efficient agri-
811 environmental schemes, forestry practices, regulation of leisure activities and sustainable urban planning in
812 mountain areas, and explicit recognition of the general ecological requisites for wildlife persistence such as
813 connectivity across their full life cycle.

814

815 **Research gaps and conclusions**

816 From our literature review, it was evident that mountain species are little studied relative to species in
817 lowland habitats of the Holarctic, such as farmland, forest and wetlands. Many common species in
818 mountains are lacking even basic biological and ecological knowledge (e.g. Alpine Accentor, White-winged
819 Snowfinch, Twite, Wallcreeper, North American rosy finches *Leucosticte* spp). Whilst both high-elevation
820 mountain specialists and mountain generalist are well-represented in the literature in terms of large-scale
821 distribution studies (e.g. species distribution models based on atlas data), they are very poorly represented
822 when considering finer-scale, usually more intensive, studies which address ecological mechanisms. In
823 particular, there were very few studies that investigated the ecology of high-elevation mountain specialists,
824 yet these are the species that may be most likely to be impacted by climate change. Aside from broad-scale
825 species distribution, the evidence base therefore largely concerns species that occur across a range of
826 habitats and elevations, rather than species whose geographical range, at least in the Holarctic, is largely
827 restricted to mountain areas.

828 Our understanding of physiological mechanisms underpinning avian responses to climate change is
829 still limited, even if recent studies have emphasized the importance of specifying ecological traits, notably
830 physiological tolerance, when predicting responses to climate change (Kearney & Porter 2009, Reif & Flousek
831 2012, Auer & King 2014, Pacifici *et al.* 2017). This is particularly important in terms of developing
832 conservation strategies. If a species responds directly to climate through a physiological effect, then there
833 might be limited conservation action that could be implemented beyond the need to reduce our dependence
834 on non-renewable fossil energy sources. There is more potential for developing conservation actions for
835 species that are affected indirectly by climate change, although for mountain birds, we still lack information
836 about species' basic ecological requirements, such as key trophic resources for reproduction, that are
837 required to develop management strategies. We therefore emphasize the need for more basic studies of
838 both physiological tolerance and ecological requirements of mountain birds, and in particular high-elevation
839 mountain specialists, as well as for all those lower-elevation species that are predicted to colonize mountain
840 regions in the near future (Loarie *et al.* 2009).

841 The importance of considering cross-ecosystem linkages such as trophic structure when identifying
842 climate change effects has been shown to be crucial for a clear understanding of the underlying mechanisms
843 affecting species and populations (Pearce-Higgins *et al.* 2010, Santisteban *et al.* 2012, Fletcher *et al.* 2013).
844 Furthermore, a better understanding of energetic values in food sources (prey) and how these influence
845 demographic rates in species is particularly important for future climate-related adaptation responses. There
846 were relatively few studies that considered long-term trends over several years that could encompass a full
847 range of climate variation, and hence assess climate trends (rather than year-to-year changes in weather
848 over shorter periods). The low number of studies assessing elevational distribution shifts in particular
849 suggests that monitoring in high mountains is inadequate, probably due to a combination of complex terrain
850 and lack of field surveyors available in these sparsely populated areas. Targeted monitoring in mountain
851 areas, with a focus on high-elevation mountain specialists, is therefore essential if we are to improve our
852 assessments of current and future climatic effects on bird distributions.

853 Monitoring reproductive success and survival of mountain birds would be similarly useful. The
854 demographic mechanisms that underpin species distributions and population changes are not well
855 understood for mountain birds. There have been some short-term effects of climate demonstrated in several
856 species, but longer-term studies are rare. More intensive long-term studies would enhance understanding of
857 the key factors that determine population trends and distributions, and therefore would facilitate the
858 predictions of future climate change impacts by elucidating more complex mechanisms, such as phenological
859 effects. Many studies acknowledge that a valuable understanding of climatic impacts can only be achieved if
860 key interacting factors are considered, such as land-use changes and biotic interactions, including
861 interspecific competition. Given that projections of future mountain bird species distributions may be quite
862 sensitive to assumptions about how land use will change in the future (e.g. Chamberlain *et al.* 2013), we urge
863 a greater consideration of land use change in species distribution modelling in mountain environments.
864 Finally, we invite scientists and policy-makers to further develop studies and related frameworks to
865 efficiently develop habitat restoration plans in mountain areas, particularly where climate change and
866 changes in land-use are likely to offer such opportunities in the near future (i.e. encroaching pastures after
867 grazing/ski-pistes abandonment, afforestation of native woodland on moorlands). Indeed, conservation and
868 restoration frameworks have already been developed for various birds species inhabiting mountain regions
869 considered susceptible to changes in climate and land use (e.g. Carroll *et al.* 2011, Patthey *et al.* 2012,
870 Signorell *et al.* 2010, Braunisch *et al.* 2016, Caprio *et al.* 2016, Scridel *et al.* 2017b).

871
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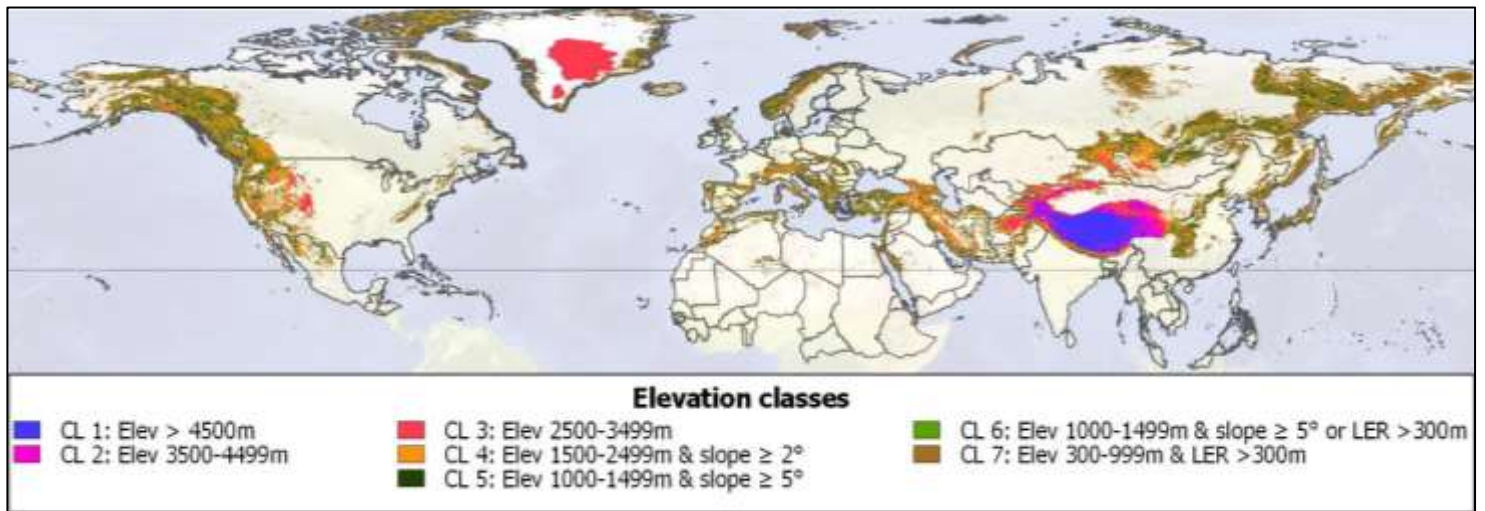
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1399 **Figure 1.** Mountains systems classified by Kapos *et al.* (2000) and adapted to the Holarctic region (above the Tropic of
 1400 Cancer – grey line). The upper three classes ('CL ') are delimited purely by elevation ($\geq 2500\text{m}$). Areas below 2500m
 1401 were classified additionally in terms of slope, terrain roughness and local elevation range (LER).

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Table 1. Frequency of studies of Holarctic mountain birds and climate change resulting from the systematic literature search across various regions and countries of the world. Reviews/commentaries and meta-analyses ($n = 25$) were excluded.

Geographical region	Frequency
Eastern European countries (Poland, Czech Rep., Russia)	6
Western European countries (France, Germany)	6
Spain	8
UK/Ireland uplands	24
Nordic countries (Denmark, Finland, Iceland, Norway, Sweden & Iceland)	27
Alps & Pyrenees (Switzerland, France, Italy, Spain, Germany, Austria, Slovenia)	44
Pan-European	12
Total European studies	127
Greenland	4
Pacific North West Coastal Mtns (Alaska, Yukon, British Columbia Coast Mtns, Hudson Bay Mnts, Cascades)	18
South West Coastal ranges (California, Sierra Nevada, New Mexico)	7
Continental Ranges (Rocky Mnts, Colorado, Arizona, Montana, Dakota, Wyoming)	23
Appalachian Mtns (incl. NY State)	11
N. America wide region (Canada, USA also in combination)	12
Total N. America studies	75
China	5
Asia	2
Total Asian studies	7
Global or nearly global	26
All studies	209

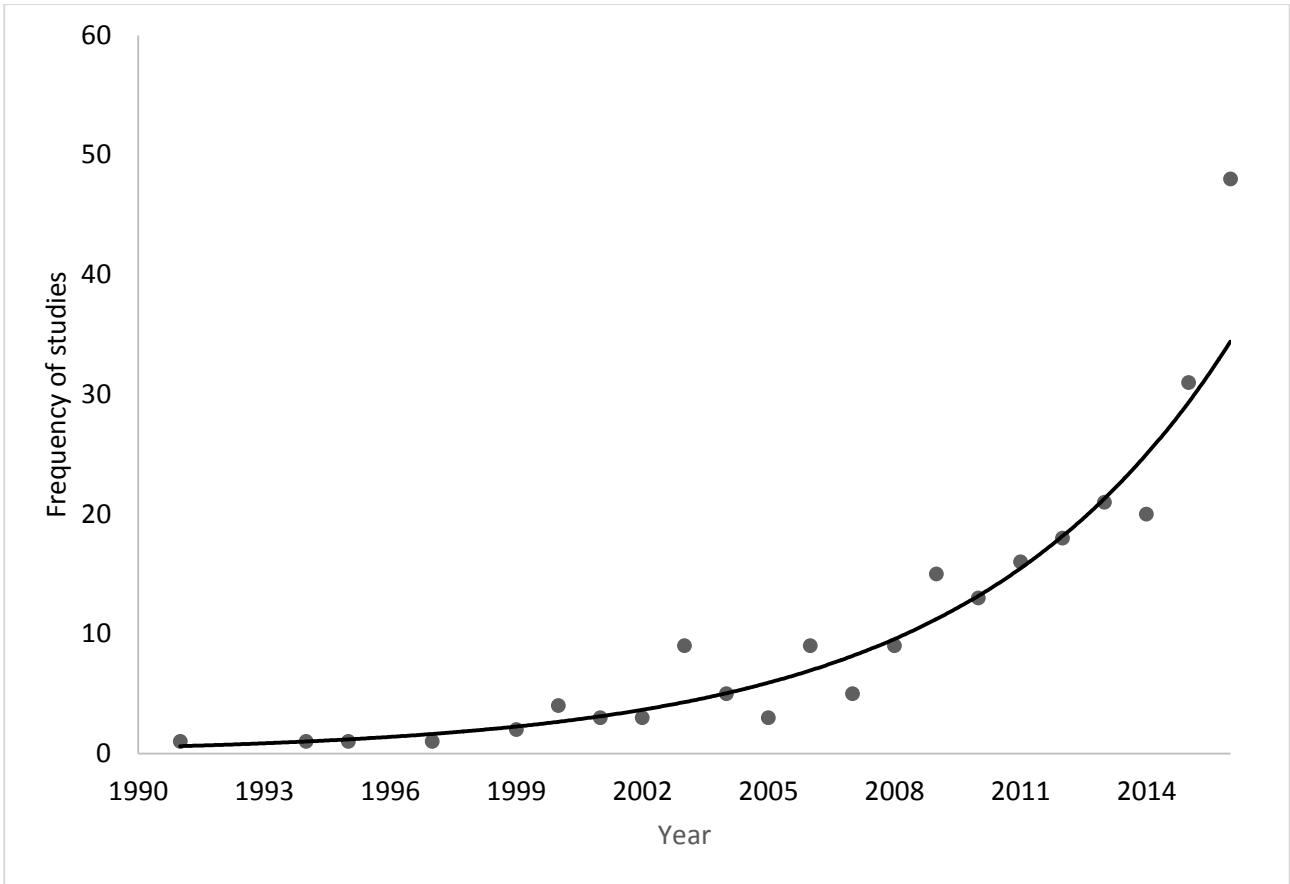


Figure 2. Frequency of relevant published papers and reviews over time resulting from the systematic literature search.

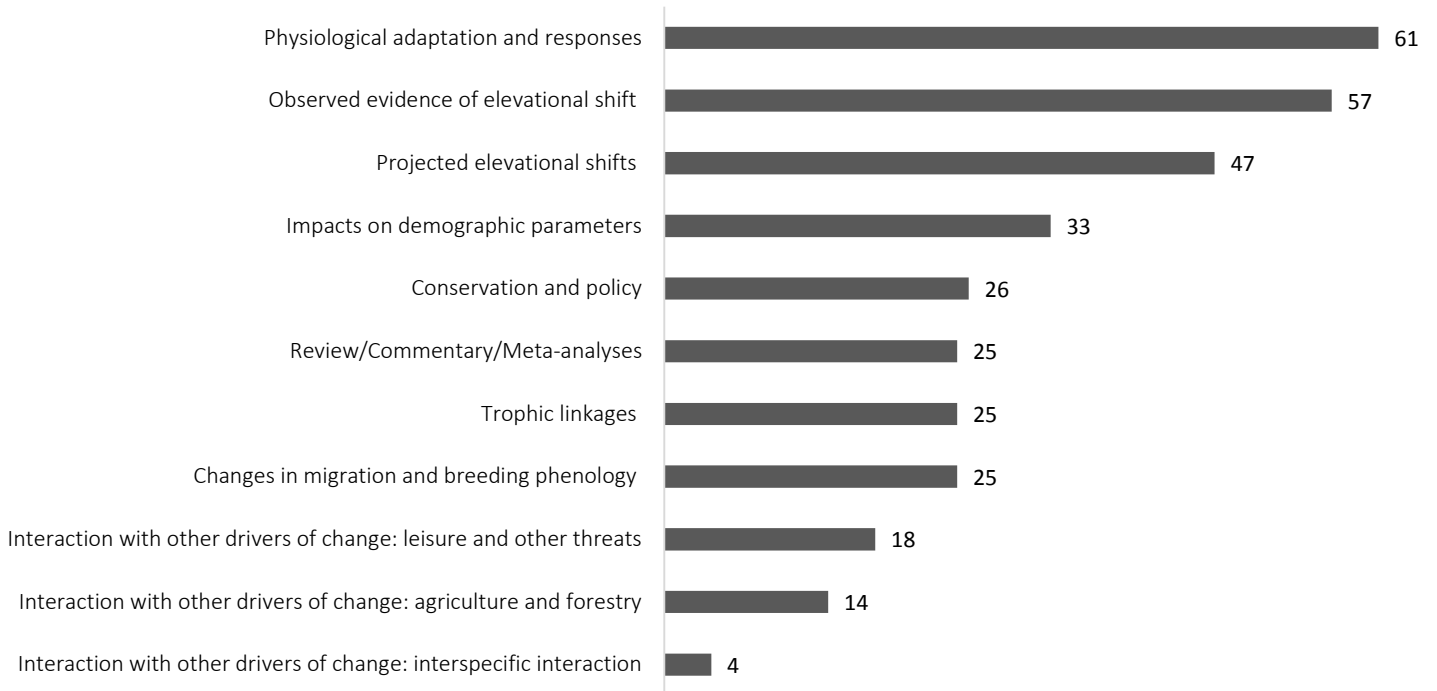


Figure 3. Frequency of climate-change related studies on Holarctic mountain birds (mutually inclusive) resulting from the systematic literature search, classified according to general subjects addressed.

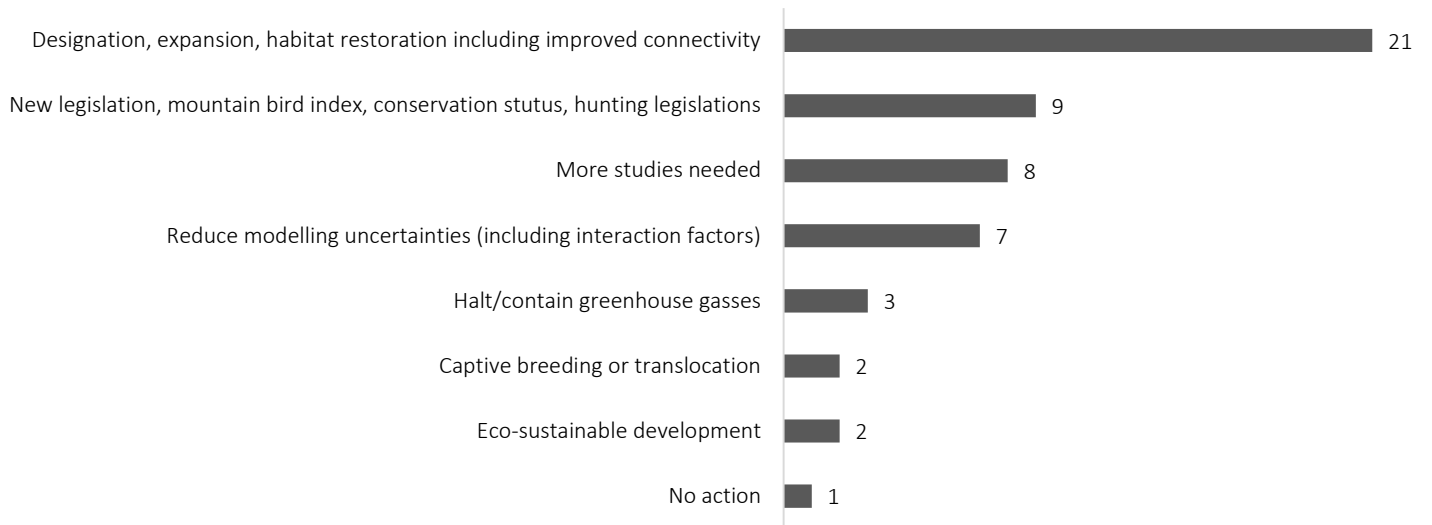


Figure 4. Number of conservation (mutually inclusive) actions suggested across all papers classified as ‘conservation & policy’ ($n = 26$) in the systematic literature search.

Table 2. A summary of papers considering shifts in the elevation of bird species distributions in mountains over time. Papers were included if they were based on data carried out at relatively small scales (maximum 1-km²) and which were wholly or partly in mountainous regions (as per Kapos *et al.* 2000). MA indicates whether a given study was included in the meta-analysis (Y) or not (N).

Author	Location	Species	Sampling unit	Period	Temperature change (°C/year)	Elevation range (m)	MA	Key findings
Archaux 2004	French Alps	All	Point count	1973-2002	0.05	350-3099	Y	41 site/species comparisons: 6 showed significant downwards shifts, 4 significant upwards shifts
DeLuca & King 2017	Appalachian Mountains, USA	All	Point count	1993-2009	0.01 ²	740-1470	Y	9 of 16 low-elevation species shifted upwards; 9 of 11 high-elevation species shifted downwards
Maggini <i>et al.</i> 2011	Switzerland ¹	All	1-km ²	1999/2002 - 2004/07	0.09 ²	210-2710	N	95 species: 33 species shifted upwards, 28 shifted downwards
Mizel <i>et al.</i> 2016	Denali National Park, Alaska	Passerines	Point count	1995-2013	0.04	500-1200	Y	Upwards shifts associated with shrub/tundra-nesting species; weaker evidence of upward shifts in forest species
Pernollet <i>et al.</i> 2015	Swiss Alps	Ptarmigan	1-km ²	1984 - 2012	0.1	1700-3100	Y	Mean elevation of Ptarmigan presence shifted upwards in 3 of 4 regions
Popy <i>et al.</i> 2010	Italian Alps	All	1-km ²	1992/94 - 2003/05	0.08	550-2556	Y	Weak overall upwards community shift; wide variation in the response of individual species
Reif & Flousek 2012	Giant Mountains, Czech Republic	All	Point count	1986/88 - 1996/98	0.12	400-1602	Y	Significant overall mean shifts to higher elevations; open-habitat shifted more than forest species
Rocchia 2016	Italian Alps	All	Point count	1982 - 2012	NA	600-4000	N	Woodland species tended to show range expansion, higher-elevation grassland species range retraction; regional variation
Tingley <i>et al.</i> 2012	Sierra Nevada, USA	All ³	Point count	1911/28 - 2003/09	NA	61-3356	N	Shifts were heterogeneous within species and among regions; both temperature and precipitation likely to be important drivers
Tryjanowski <i>et al.</i> 2005	Tatra Mountains, Poland	White Stork	Nest location	1974 - 2003	0.08	400-900	Y	White Storks nested at progressively higher elevations.

¹ Included as the majority of the area of Switzerland is classed as mountainous by Kapos *et al.* (2000)

² Annual temperature – others are spring temperatures

³ Passerines and five other families (Odontophoridae, Phasianidae, Columbidae, Trochilidae and Picidae)