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

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

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

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

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

Amongst birds, changes in climate have been reported to influence migration timing (Hüppop & Hüppop 2003, Knudsen *et al.* 2011), breeding output (Crick *et al.* 1997, Laaksonen *et al.* 2006), population size (Sæther *et al.* 2000, Townsen *et al.* 2016), and changes in elevational (Reif & Flousek 2012) and latitudinal (Hickling *et al.* 2006, Zuckerberg *et al.* 2009) distributions. Because the severity of climatic change varies over the Earth's surface (e.g. Meehl *et al.* 2007), avian responses may also vary in intensity depending on their geographic distribution. Birds may exhibit rapid distributional responses to climatic fluctuations, for example tracking changes in surface temperature latitudinally (Hickling *et al.* 2006, Zuckerberg *et al.* 2009). However, there is also evidence that range shifts in birds are lagging behind climate change (Devictor *et al.* 2008, Ralston *et al.* 2017), potentially due to asynchronous phenology of birds and their prey (e.g. Mayor *et al.* 2017). Species inhabiting high-elevation mountain systems often exhibit a high degree of habitat specialisation and unique ecological traits within narrow thermal ranges (Reif & Flousek 2012, Reif *et al.* 2015, Mahon *et al.* 2016, Pacifici *et al.* 2017, Scridel *et al.* 2017a). Adapting to rapid climate change may be particularly challenging along the elevational gradients of many mountains where temperatures and area decrease monotonically with elevation (Elsen & Tingley 2015). As a result, species tracking rising temperatures in these systems are predicted to decline according to the species-area relationship (Preston 1962) as populations become isolated, and thus increasingly vulnerable to stochastic events (Lande 1993, Bech *et al.* 2009, Fjeldså *et al.* 2012). A successful shift into a new area by a species is possible only when abiotic as well biotic requirements are fulfilled (Martin 2001a, Heikkinen *et al.* 2007, Wilson & Martin 2012). Given the fast rate of warming, species might have to track temperatures in areas where their associated habitat and resources require longer to establish (e.g. mature trees, alpine and sub-nival plants; Engler *et al.* 2011, Reif & Flousek 2012, Brambilla & Gobbi 2014), or where suitable habitat formation cannot occur due to constraints of other factors such as soil processes or rock substrate (Freppaz *et al.* 2010), or by direct human activities (e.g. deforestation; Nogués-Bravo *et al.* 2008, Patthey *et al.* 2008, Kohler *et al.* 2014; disturbance via outdoor recreation; Arlettaz *et al*. 2007, 2015). Finally, climatic effects coupled with negative synergistic changes in land use might pose even more severe constraints on adaptation of mountain birds to future climatic conditions.

Due to the documented general responses of birds, and the more extreme climatic changes observed in mountains, it seems reasonable to expect that mountain birds may be particularly threatened by climate change. In this review, we assess the existing evidence for direct and indirect effects of climate change on mountain birds in the Holarctic region (Heilprin 1887), and we evaluate their future conservation prospects. We address six specific objectives: (i) to define mountain generalist and high-elevation specialist birds for the Holarctic region; (ii) to review the impacts of climate change on mountain birds through a summary of the literature, and a quantification of general responses throughout the Holarctic, including a meta-analysis; (iii) to review and quantify projected impacts from future climate change scenarios using a meta-analysis; (iv) to assess stressors that are likely to interact with climate change in affecting birds living at high elevations; (v) to review proposed conservation actions; and (vi) to identify current gaps and future priorities for research.

METHODS

Defining mountain birds

Mountain systems and species inhabiting them are difficult to describe geographically and ecologically, and definitions may not apply consistently across the globe (Strahler 1946, Gerrard 1990, Körner 2012, Scridel 2014). In order to assess the status of mountain birds, it was first necessary to define mountain areas and habitats. Using elevational thresholds to define these regions would immediately exclude older and lower mountain systems such as the Urals, Scottish Highlands and Appalachians, and include areas with little topographic relief and few environmental gradients (e.g. large, high-elevation plateaux). Using slope as a criterion on its own or in combination with elevation may resolve the latter problem, but not the former. For these reasons, we adopted the definition of Kapos *et al.* (2000), who classified mountain systems in seven classes on the basis of elevation, slope and local elevation range (Fig. 1). The latter criterion is particularly useful as it identifies lower elevation mountain ranges (300-999m) by defining a radius of interest (5km) around each grid cell (30 arc-second) and measuring the maximum and minimum elevation within a particular neighborhood, and their difference, allowing the identification of areas that occur in regions with significant relief, even though elevations may not be especially high (Kapos *et al.* 2000). This is a broad definition which includes high latitude ‘upland’ habitats at relatively lower elevations, as well as mountain forest, the alpine belt (the treeless region between the natural climatic forest limit and the snow line) and the nival belt (the terrain above the snowline, which is defined as the lowest elevation where snow is commonly present all year round; Kapos *et al.* 2000, Körner & Ohsawa 2006). Hereafter, we refer to 'mountain regions' as those as defined by Kapos *et al.* (2000).

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

Literature survey

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

Current and future elevational shifts in bird populations

Papers that presented estimates for shifts in species distributions over time in relation to elevation were considered for meta-analyses if they focussed, either wholly or mostly, on the defined mountain regions. Given that conditions may change rapidly over small distances in mountains due to the steep topography, smaller-scale studies are more appropriate than larger-scale atlas studies in tracking species distributions (Chamberlain *et al.* 2012), and thus we focused on studies with a maximum sampling unit area of 1-km^2. Additional data were collected for each study on the period considered (in years), the elevational range (in metres), and the estimated mean annual rate of temperature change (°C/year) over the period considered. Similarly, papers that predicted future effects of climate change on mountain birds were considered if they were largely restricted to mountain areas, if they estimated a proportional change in geographic distribution or population size over time, and if the sample size of the underlying data set on which models were based was presented. Additional variables recorded were the period over which projections were made, and the climate change scenarios considered, which were classed as either 'severe' (scenarios A2 and A1F1 or RCP8.5) or 'moderate' (all other scenarios and RCPs; IPCC 2007, 2013).

Statistical analysis

For elevational shifts, papers were included in the meta-analysis only if sample sizes and test statistics were presented, or if parameter estimates (including mean shift) and standard errors, standard deviations or confidence limits, were reported. In cases where only estimates of change in elevation and errors were presented (i.e. without any test statistics), z-scores were derived, testing against a hypothesis of zero change. In common with standard meta-analytical approaches (e.g. Koricheva *et al*. 2013), the goal was to estimate standardized responses of elevational shifts in bird distributions over time from studies that used a diversity of methods for quantifying a potential shift, which in most cases was calculated as the change, in meters, of the distribution of a given species (sometimes a group of species) between two time periods. However, some papers also tested the effect of the interaction between elevation and time period on the probability of species presence, a significant interaction indicating a significant shift over time (e.g. Reif & Flousek 2012, Mizel *et al*. 2016).

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

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

Papers that made future projections of species distributions or abundances did not typically present significance tests, therefore standardized effect sizes could not be estimated. Instead, the mean percentage change in the response variable (either range size or a measure of population size) was analysed. The response variable was approximately normally distributed. The model structure was similar to that for observed elevation shifts in that initially an intercept-only model was specified which included ‘study’ and ‘family’ as random effects, and then further fixed effects (high-elevation specialist or generalist species, period over which projections were made, climate change scenario) were tested. The sample size of the initial input data was specified as a weight in the model statement, the assumption being that models based on a larger sample size are likely to be more reliable than those based on small sample sizes. Confidence intervals of estimates which did not overlap zero were taken as evidence of consistent effects of future projections of elevational shifts.

RESULTS

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

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

Mountain birds of the Holarctic region

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

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

Climate change, physiological constraints and life history strategies

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

A species' life history strategy may be crucial in responding to climatic alterations. Patterns along elevational gradients have highlighted that populations of the same species confined to higher elevations have slower life-history strategies (fewer nesting attempts, lower clutch size) compared to populations at lower elevation (Boyle *et al.* 2016). Higher nest survival has been found for higher elevation populations that may partially compensate for the reduction in potential fecundity. Boyle *et al.* (2016) did not record a pattern of significant differences in body mass, egg or nestling size, or survival between paired populations of bird species breeding at high and low elevation. Tingley *et al.* (2012), however, found that species were more likely to shift their elevational range in the Sierra Nevada (USA) if they had smaller clutches, defended all-purpose territories and were residents or short-distance migrants, although these involved both upslope and downslope shifts. It is therefore possible that higher-elevation species may indeed be more threatened by climate change than lower-elevation species due both to their morphological adaptations to cooler systems (e.g. insulation), and their life history strategies. However, future work is required to elucidate these ideas.

Links between climate and population dynamics

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

There is also evidence for negative effects of climate on demographic parameters. Barnagaud *et al.* (2011) showed that winter and summer NAO (North Atlantic Oscillation) affects several indicators of breeding success of Black Grouse *Tetrao tetrix* in the French Alps, particularly during years of extreme weather. Interestingly, birds showed some acclimatisation, being able to optimise their reproductive output in relation to the NAO index, but they performed particularly badly when extreme weather events occurred. Twenty-five years of prolonged spring warming caused low breeding success in a Scottish population of Capercaillie (Moss *et al.* 2001).

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

Changes in phenology

Amongst birds, climate change has affected the phenology of many species, leading to changed timing of breeding and migration (e.g. Crick *et al.* 1997, Rubolini *et al.* 2007), which in some cases has led to population declines when phenological trends are mismatched with those of their key food resources (e.g. Both *et al.* 2006). Such phenological mismatches are hypothesised to underpin the declines in many long-distance migrant species in the western Palearctic (e.g. Møller *et al.* 2008). However, in the Fennoscandian mountains, Lehikoinen *et al.* (2014) found that long-distance migrants declined less on average than residents and short-distance migrants, suggesting the latter were more sensitive to climate change impacts.

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

Trophic linkages

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

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

Snow patches can represent an important foraging habitat, providing both arthropod fallout and suitable sites at their margins for the collection of soil invertebrates, particularly during the nesting and rearing period of many mountain birds such as White-winged Snowfinch, Snow Bunting *Plectrophenax nivalis,* Horned Lark *Eremophila alpestris* and Alpine Accentor *Prunella collaris* (Antor 1995, Camfield *et al.* 2010, Brambilla *et al.* 2016a,b, Rosvold 2016). In some extreme cases, birds may even choose to nest directly in glaciers (White-winged Diuca Finch *Diuca speculifera;* Hardy & Hardy 2008) or in very close proximity (Grey-crowned Rosy Finch *Leucosticte tephrocotis,* Johnson 1965, Rosvold 2016; Brandt's Rosefinch *Leucosticte brandt,* Potatov 2004) to capitalize on abundant supplies of insects. Changes in amount and duration of snow may therefore affect these species via food resources.

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

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

Observed evidence of elevational shifts

Evidence exists, typically from broad-scale atlases of species distributions, that some species are shifting their geographic distributions to higher elevations in response to climate change, the distributions presumably tracking more suitable climatic conditions (e.g. Auer & King 2014, Roth *et al.* 2014), although such effects are not universal (e.g. Zuckerberg *et al.* 2009, Tingley *et al.* 2012, Massimino *et al.* 2015). Furthermore, apparent elevational shifts may occur due to habitat deterioration or destruction at lower elevations (Archaux 2004, Bodin *et al.* 2013).

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

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

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

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

Projected elevational shifts

Extinction risks are expected to increase as a result of climate-induced elevational range shifts in the future (Sekercioglu *et al.* 2008, La Sorte & Jetz 2010). Shifting vegetation zones in mountains, and in particular an 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 ± se = -28.9± 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 ± 27.1%, 95% CLs = -129.2, -23.0; other = 29.8 ± 25.7%, 95% CLs = -20.6, 80.2). There was a tendency for greater negative impacts in severe than moderate scenarios (moderate= -26.6 ± 17.1%, 95% CLs = -60.1, 6.9; severe = -33.6 ± 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).

Interactions of climate change effects with other drivers of change

Land use

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

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

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

Agro-forestry and pastoral practices have shaped the landscape of Holarctic mountains in Europe and Asia, influencing the species composition and abundance of mountain birds (e.g. Gehrig-Fasel *et al.* 2007, Caprio *et al.* 2011, Douglas *et al.* 2014, Wilson *et al.* 2014, Mollet *et al.* in press). Over time, forest management has changed in intensity (e.g. clear-felling vs single-tree selection), composition (planting of exotic conifers) and age dynamics (establishment of even-aged monocultures; Kirby & Watkins 2015). At the same time, climate change may be affecting forest bird assemblages either directly or indirectly by influencing cover, productivity, and composition of forest systems. However, it is generally unclear which of these two pressures (climate change or forestry practices) is the most important driver in changes in bird distribution. Changes in forest composition could cause opposite shifts (i.e. downhill) to those forecast due to effects of climate warming (uphill). For example, Archaux (2004) suggested that changes in forest management that favoured coniferous at the expense of broadleaved trees might have caused forest birds to have shifted their mean elevation downwards. In other cases, there is evidence from boreal forests (including some mountain areas) that climate, in addition to vegetation type and management, is a crucial driver for determining passerine species distribution (Cumming *et al.* 2014, Frey *et al.* 2016). Virkkala (2016) found that forest management favoured passerine species benefitting from climate change, so that direct habitat alteration was connected to the indirect effects of climate change.

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

Historically, agricultural expansion and changes in livestock management have had major impacts on mountain birds (Lundmark 2007, Elmhagen *et al.* 2015). In many mountain areas, traditional grazing practices are characterised by low stocking densities or transhumant pastoralism, i.e. the seasonal movement of livestock between high-elevation summer pastures and lowland winter pastures (Arnold & Greenfield 2006). These traditional grazing practices have been largely abandoned in some areas due to social and economic factors, especially in the European Alps. For example, in Italy, the number of farms has decreased drastically and many have changed to indoor production systems (Battaglini *et al.* 2014), which has led to substantial changes within mountain vegetation zones through encroachment of formerly open grasslands by trees and shrubs and a loss of structural heterogeneity (Braunisch *et al.* 2016). Elevational shifts in vegetation may be therefore due both to climate change and land abandonment (Gehrig-Fasel *et al.* 2007).

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

Climate change can also have direct impacts on grazing management, although this seems to be less well studied. In Nepal, where transhumance is a common practice, herders perceived the impact of climate change through personal experience. In several studies, where herders have been interviewed, they described a rise in temperature, a decline of rain- and snowfall, a scarcity of water resources (Aryal *et al.* 2014, Wu *et al.* 2015) and the presence of invasive weeds, which are replacing the valuable grasses on farmlands (Gentle & Thwaites 2016). These perceptions were also in line with temperature and rainfall trends in the studied region. As a result, herders tried to adjust their transhumance patterns to the changed conditions by altering the timing of seasonal livestock movements. The consequences of such management responses for mountain bird populations, however, remain unknown. Given the varieties of different effects of grazing on mountain birds, and the lack of research on likely responses of grazing management practices to future climate change, further investigations are needed to examine potential effects of grazing regimes on mountain bird populations before we can apply them as potential conservation tools.

Leisure and other potential threats

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

There are several lines of evidence showing that ski-pistes have deleterious effects on both grassland and forest birds via loss and degradation of habitat, and a decrease in food availability (Laiolo & Rolando 2005, Rolando *et al.* 2007, Caprio *et al.* 2011, Rixen & Rolando 2013). In addition, there is evidence that hormonal stress in birds generated by intensive human activities can negatively impact already vulnerable populations of Capercaillie (Thiel *et al.* 2011) and Black Grouse (Arlettaz *et al.* 2007, 2013). Anthropogenic disturbance has furthermore been shown to entail extra energetic costs that may negatively affect population dynamics (Arlettaz *et al.* 2015). Effects may also operate through infrastructure associated with skiing, for example increased mortality due to collision with ski cables (Baines & Andrew 2003, Watson & Moss 2004), and reduced reproductive success of ground nesting birds associated with development of tourist resorts (Watson & Moss 2004, Patthey *et al.* 2008, Tolvanen & Kangas 2016), although negative effects are not universal (Rimmer *et al.* 2004).

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

Novel interspecific interactions

Species may respond to climate change by shifting their distribution to track local climates (Tingley *et al.* 2009, Jackson *et al.* 2015), which may result in novel interactions as species colonize new areas. Including such interactions has improved model predictions at different scales (Araújo & Luoto 2007). Heikkinen *et al.* (2007) and Brambilla *et al.* (2013) suggested that including the presence of woodpeckers that produce the cavities used by secondary cavity nesting raptors improved model performance in predicting cavity-nesting forest owl distributions. We found only one relevant example that tested the importance of biotic interactions among birds along elevational gradients. Freeman & Montgomery (2015) assessed potential competition between Swainson's Thrush *Catharus ustulatus,* which generally inhabits lower elevations but which has shifted its distributions towards higher elevations, and the conspecific Bicknell's Thrush *Catharus ustulatus,* which is largely confined to mountaintops. Using playback techniques, the authors found that, where the species co-occurred, Swainson's Thrush responded aggressively to Bicknell's Thrush, but not *vice-versa*.

Conservation and policy

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

Some habitats may also be more prone to climate change than others. Montane forest species are predicted to be less impacted by climate change due to the stronger self-regulation of the forest microclimate compared to open habitats (Reif & Flousek 2012), and to native forest expansion that has already occurred, and which is predicted to continue in many areas (European Alps; British uplands; Chamberlain *et al.* 2013, Scridel *et al.* 2017b), but they could be prone to other climate change related threats such as pests, disease and wild fires (Dale *et al.* 2001, Sturrock *et al.* 2011, Lesk *et al.* 2017). Furthermore, natural grasslands in the Alpine region may face serious challenges to shift their distributions, as they are being progressively colonised due to both forest encroachment following land abandonment or release of grazing pressure and advancing treelines at lower elevations, while facing constraints on colonizing higher elevations, for example due to slow rates of soil formation (Freppaz *et al.* 2010, Chamberlain *et al.* 2013, Jackson *et al.* 2015).

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

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

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

DISCUSSION

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

Defining a 'mountain bird' across a large region like the Holarctic is difficult because many species that are mountain birds in warmer climates are lowland species in colder climates. Our goal was to derive an objective definition that could be applicable over a large geographic area and which identified species associated with mountains *per se*, rather than occurring in mountains due to interactive effects of climate, elevation, latitude and land use. This is important when considering species distributions over large scales, and in particular when projecting future distributions. For example, the Water Pipit was identified as a generalist mountain breeding bird across various mountain slopes, even in the northern, colder, parts of its geographic range. Predictions based on climate alone may therefore be inaccurate for such species (e.g. Huntley *et al.* 2008). In general, the species identified as high-elevation specialists or mountain birds (see Supporting Information; Table S4) were in-line with the authors' expectations, although there were some surprising results. For example, Rock Ptarmigan is considered an archetypal mountain bird in many parts of its range (the European Alps, the Pyrenees, British Columbia and Alberta), but not according to our definition. This to some extent may have been due to the coarse scale of the defined breeding range used in the method, but it is also reflective of the widespread populations of this species inhabiting lowland arctic tundra. As conservation policy is typically applied at national or regional level, a regional-based definition of mountain birds would also be useful, which would be readily achievable under the current methodology. Although this first classification of Holarctic high-elevation mountain specialist and generalist birds was not the primary aim of this review, we regard this exercise of considerable value for future work on this group of poorly studied species (e.g. baseline monitoring, development of a joint mountain bird index, and ecological and conservation research).

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

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

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

Research gaps and conclusions

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

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

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

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

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REFERENCES

Ameztegui, A., Coll, L., Brotons, L. & Ninot, J.M. 2016. Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. *Glob. Ecol. Biogeogr.* **25**: 263–273.

Antor, R.J. 1995. The importance of arthropod fallout on snow patches for the foraging of high-alpine birds. *J. Avian Biol.* **26**: 81–85.

Araújo, M.B. & Luoto, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol. Biogeogr.* **16**: 743–753.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. 2011. Climate change threatens European conservation areas. *Ecol. Lett.* **14**: 484–492.

Archaux, F. 2004. Breeding upwards when climate is becoming warmer: no bird response in the French Alps. *Ibis* **146**: 138-144.

Archaux, F. 2007. Are mountains refuges for farmland bird species? A case study in the northern French Alps. *Bird Study* **54**: 73–79.

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R. & Jenni-Eiermann, S. 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proc. R. Soc. B* **274**: 1219–1224.

Arlettaz, R., P. Patthey & Braunisch, V. 2013. Impacts of Outdoor Winter Recreation on Alpine Wildlife and Mitigation Approaches: A Case Study of the Black Grouse. In: The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments (eds C. Rixen & A. Rolando), pp. 137-154. Bentham eBooks, Bussum.

Arlettaz, R., Nusslé, S., Baltic, M., Vogel, P., Palme, R., Jenni-Eiermann, S., Patthey, P. & Genoud, M. 2015. Disturbance of wildlife by outdoor winter recreation: allostatic stress response and altered activity-energy budgets. *Ecol. App.* **25**: 1197-1212.

Arnold, E.R. & Greenfield, H.J. 2006. *The Origins of Transhumant Pastorialism in Temperate South Eastern Europe. A zooarchaeological perspective from the Central Balkans.* Oxford: BAR International Series 1538.

Aryal, S., Maraseni, T. N. & Cockfield, G. 2014. Sustainability of transhumance grazing systems under socio-economic threats in Langtang, Nepal. *J. Mt. Sci.* **11**: 1023-1034.

Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecol. Biogeogr*. **11**: 505-523.

Auer, S. & King, D. 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Glob. Ecol. Biogeogr.* **23**: 867–875.

Baines, D. & Andrew, M. 2003. Marking of deer fences to reduce frequency of collisions by woodland grouse. *Biol. Conserv.* **110**: 169-176.

Barnagaud, J.Y., Crochet, P.A., Magnani, Y., Bernard Laurent, A., Menoni, E., Novoa, C. & Gimenez, O. 2011. Short-term response to the North Atlantic Oscillation but no long-term effects of climate change on the reproductive success of an alpine bird. *J. Ornithol.* **152**: 631–641.

Battaglini, L., Bovolenta, S., Gusmeroli, F., Salvador, S. & Sturaro, E. 2014. Environmental sustainability of Alpine livestock farms. *Ital. J. Anim. Sci.* **13**: 431-443.

Bazzi, G., Foglini, C., Brambilla, M., Saino, N. & Rubolini, D. 2015. Habitat management effects on Prealpine grassland bird communities. *Ital. J. Zool.* **82**: 251-261.

Bech, N., Boissier, J., Drovetski, S. & Novoa, C. 2009. Population genetic structure of rock ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation. *Anim. Conserv.* **12**: 138–146.

Beniston, M. & Rebetez, M. 1996. Regional behavior of minimum temperatures in Switzerland for the period 1979 - 1993. *Theor. Appl. Climatol.* **53**: 231 – 243.

Beniston, M., Keller, F. & Goyette S. 2003. Snow pack in the Swiss Alps under changing climatic conditions: an empirical approach for climate impact studies. *Theor. Appl. Climatol.* **74**: 19–31.

Berteaux, D., Gauthier, G., Dominé, F., Ims, R.A., Lamoureux, S.F., Lévesque, E. & Yoccoz, N. 2016. Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times. *Arctic Science*, 10.1139/as-2016-0023.

BirdLife International & NatureServe. 2015. *Bird species distribution maps of the world.* BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.

Bodin, J., Badeau, V., Bruno, E., Cluzeau, C., Moisselin, J.M., Walther, G.R. & Dupouey, J.L. 2013. Shifts of forest species along an elevational gradient in Southeast France: climate change or stand maturation. *J. Veg. Sci.* **24**: 269–283.

Boelman, N.T., Gough, L., Wingfield, J., Goetz, S., Asmus, A., Chmura, H. E., Krause, J. S., Perez, J. H., Sweet, S. K. & Guay, K. C. 2015. Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Glob. Change Biol.* **21**: 1508–1520.

Böhning-Gaese, K., & Lemoine, N. 2004. Importance of climate change for the ranges, communities and conservation of birds. *Adv. Ecol. Res.* **35:** 211-236.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81–83.

Boyle, A.W. & Martin, K. 2015. The conservation value of high elevation habitats to North American migrant birds. *Biol. Conserv.* **192:** 461-476.

Boyle, A.W., Sandercock, B.K. & Martin, K. 2016. Patterns and drivers of intraspecific variation in avian life history along elevational gradients: a meta-analysis. *Biol. Rev.* **91**: 469-482.

Brambilla, M., Bassi, E., Bergero, V., Casale, F., Chemollo, M., Falco, R., Longoni, V., Saporetti, F., Viganò, E. & Vitulano, S. 2013. Modelling distribution and potential overlap between Boreal Owl *Aegolius funereus* and Black Woodpecker *Dryocopus martius*: implications for management and monitoring plans. *Bird Conserv. Int.* **23**: 502-511.

Brambilla, M. & Gobbi, M. 2014. A century of chasing the ice: delayed colonisation of ice-free sites by ground beetles along glacier forelands in the Alps. *Ecography* **37**: 33–42.

Brambilla, M., Bergero, V., Bassi, E. & Falco, R. 2015. Current and future effectiveness of Natura 2000 network in the central Alps for the conservation of mountain forest owl species in a warming climate. *Eur. J. Wildl. Res.* **61**: 35–44.

Brambilla, M., Pedrini, P., Rolando, A. & Chamberlain, D. 2016a. Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. *J. Biogeogr.* **43**: 2299–2309.

Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P., Rubolini, D. 2016b. Foraging habitat selection by Alpine White-winged Snowfinches *Montifringilla nivalis* during the nestling rearing period. *J. Ornithol.* **158**: 277-286.

Braunisch, V., P. Patthey & Arlettaz, R. 2011. Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. *Ecol. App.* **21**: 955-967.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H. & Bollmann, K. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. Ecography **36**: 971–983.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F. & Bollmann, K. 2014. Temperate mountain forest biodiversity under climate change: compensating negative effects by increasing structural complexity. *PLoS ONE* **9**: e97718.

Braunisch, V., P. Patthey & Arlettaz, R. 2016. Where to Combat Shrub Encroachment in Alpine Timberline Ecosystems: Combining Remotely-Sensed Vegetation Information with Species Habitat Modelling. *PLoS ONE* **11**: e0164318.

Broggi, J., Gamero, A., Hohtola, E., Orell, M., Nilsson, J.Å. 2011. Interpopulation Variation in Contour Feather Structure Is Environmentally Determined in Great Tits. *PLoS ONE* **6**: e24942.

Brown, J.L., Li, S.H. & Bhagabati, N. 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc. Natl. Acad. Sci. U.S.A.* **96**: 5565–5569.

Camfield, A.F., Pearson, S. & Martin, K. 2010. Life history variation between high and low elevation subspecies of horned larks *Eremophila spp*. *J. Avian Biol.* **41**: 273-281.

Caprio, E., Chamberlain, D., Isaia, M. & Rolando, A. 2011. Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. *Conserv. Biol.* **144**: 2958–2967.

Caprio, E., Chamberlain, D. & Rolando, A. 2016. Ski-piste revegetation promotes partial bird community recovery in the European Alps. *Bird study* **63**: 470-478.

Carroll, M., Dennis, P., Pearce-Higgins, J.W. & Thomas, C.D. 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on Craneflies. *Glob. Chang. Biol.* **17**: 2991–3001.

Carroll, M., Heinemeyer, A., Pearce-Higgins, J., Dennis, P., West, C., Holden, J., Wallage, Z. & Thomas, C. 2015. Hydrologically-driven ecosystem processes determine the distribution and persistence of ecosystem-specialist predators under climate change. *Nat. Commun.* doi: 10.1038/ncomms8851.

Chamberlain, D., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A. & Zbinden, N. 2012. The altitudinal frontier in avian climate impact research. *Ibis* **154**: 205–209.

Chamberlain, D., Negro, M., Caprio, E. & Rolando, A. 2013. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biol. Conserv.* **167**: 127–135.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**: 1024 – 1026.

Cheviron Z.A. & Brumfield, R.T. 2012. Genomic insights into adaptation to high-altitude environments. *Heredity* **108**: 354–361.

Clavero, M. & Brontons, L. 2010. Functional homogenization of bird communities along habitat gradients: accounting for niche multidimensionality. *Glob. Ecol. Biogeogr.* **19**: 684-696.

Conroy, M.J., Runge, M.C., Nichols, J.D., Stodola, K.W. & Cooper, R.J. 2011. Conservation in the face of climate change: the roles of alternative models, monitoring, and adaptation in confronting and reducing uncertainty. *Biol. Conserv.* **144**: 1204–1213.

Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. 1997. UK birds are laying eggs earlier. *Nature* **388**: 526.

Cumming, S.G., Stralberg, D., Lefevre, K.L., Solymos, P.,Bayne, E.M., Fang, S., Fontaine, T., Mazerolle, D., Schmiegelow, F.K.A. & Song, S.J. 2014. Climate and vegetation hierarchically structure patterns of songbird distribution in the Canadian boreal region. *Ecography* **37**: 137–151.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Wotton, B.M. 2001. Climate change and forest disturbances. *Bioscience* **51**: 723-734

DeLuca, W.V. & King, D. I. 2014. Influence of hiking trails on montane birds. *Jour. Wild. Mgmt.* **78**: 494–502.

DeLuca, W.V. & King, D.I. 2017. Montane birds shift downslope despite recent warming in the northern Appalachian Mountains. *J. Ornithol.* **158:** 493.

Debarbieux, B., Oiry Varacca, M., Rudaz, G, Maselli, D., Kohler, T. & Jurek, M. 2014. Tourism in Mountain Regions: Hopes, Fears and Realities. Sustainable Mountain Development Series. Geneva, Switzerland: UNIGE, CDE, SDC, pp. 108.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. 2008. Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B* **275**: 2743–2748.

Diaz, H.R., Grosjean, M. & Graumlich, L. 2003. Climate variability and change in high elevation regions: past, present and future. *Clim. Chang.* **59:** 1-4.

Dillon, M., Frazier, M. & Dudley, R. 2006. Into thin air: Physiology and evolution of alpine insects. *Integr. Comp. Biol.* **46**: 49–61.

Douglas, D.J.T. & Pearce-Higgins, J. W. 2014. Relative importance of prey abundance and habitat structure as drivers of shorebird breeding success and abundance. *Anim. Conserv.* **17**: 535–543.

Douglas, D.J.T., Buchanan, G.M., Thompson, P., Amar, A., Fielding, D.A., Redpath, S.M. & Wilson, J.D. 2015. Vegetation burning for game management in the UK uplands is increasing and overlaps spatially with soil carbon and protected areas. *Biol. Conserv.* **191**: 243–250.

Dragon, S., Carey, C., Martin, K. & Baumann, R. 1999. Effect of high altitude and in vivo adenosine/b-adrenergic receptor blockade on ATP and 2,3BPG concentrations in red blood cells of avian embryos. J. Exp. Biol. 202: 2787– 2795.

Dreitz, V. J., Yale Conrey, R. & Skagen, S. K. 2012. Drought and cooler temperatures are associated with higher nest survival in Mountain Plovers. *Aian Conserv. Ecol.* **7**: 6.

Eglington, S.M. & Pearce-Higgins, J.W. 2012. Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. *PLoS ONE* **7**: e30407.

Elmhagen, B., Kindberg, J., Hellström, P. & Angerbjörn, A. 2015. A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *AMBIO* **44**: 39–50.

Elsen, P.R., Tingley, M.W. 2015 Global mountain topography and the fate of montane species under climate change. *Nat. Clim. Change* **5**: 772–776.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araújo, M.B., Pearman, P.B., Gwenaëlle, l.l., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De lamo, X., Dirnböck, T., Gégout, J.C., Gómez-García, D., Grytnes, J.A., Heegaard, E., Høistad, F., Nogués-Bravo, D., Normand, S., Puşcaş, M., Sebastià, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P. &, Guisan, A. 2011. 21st century climate change threatens mountain flora unequally across Europe. *Glob. Chang. Biol.* **17**: 2330–2341.

Evans, D. M., Redpath, S. M., Evans, S. A., Elston, D. A., Gardner, C. J., Dennis, P. & Pakeman, R. J. 2006. Low intensity, mixed livestock grazing improves the breeding abundance of a common insectivorous passerine. *Biology Letters* **2**: 636-638.

FAO 2015. Mapping the vulnerability of mountain peoples to food insecurity. Romeo, R., Vita, A., Testolin, R. & Hofer, T. Rome.

Fjeldså, J., Bowie, R.C.K. & Rahbek, C. 2012. The role of mountain ranges in the diversification of birds. *Annu. Rev. Ecol. Evol. Syst.* **43**: 249–265.

Fletcher, K., Howarth, D., Kirby, A., Dunn, R. & Smith, A. 2013. Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis* **155**: 456-463.

Flousek, J., Telensky, T., Hanzelka, J. & Reif, J. 2015. Population trends of central European montane birds provide evidence for adverse impacts of climate change on high-altitude species. *PLoS ONE* **10**: e0139465.

Freeman, B. & Montgomery, G. 2015. Interspecific aggression by Swainson's Thrush (*Catharus ustulatus*) may limit the distribution of the threatened Bicknell's Thrush (*Catharus bicknelli*) in the Adirondack Mountains. *Condor* **118**: 169-178.

Freppaz, M., Filippa, G., Caimi, A., Buffa, G. & Zanini, E. 2010. Soil and plant characteristics in the alpine tundra (NW Italy). In: Gutierrez, B., Pena, C. (Eds.). *Tundras: Vegetation, Wildlife and Climate Trends.* Nova Science Publishers, New York: 81–110.

Frey, S. J. K., Hadley, A. S. & Betts, M. G. 2016. Microclimate predicts within-season distribution dynamics of montane forest birds. *Divers. Distrib.* **22**: 944–959.

Furrer, R., Schaub, M., Bossert, A., Isler, R., Jenny, H., Jonas, T., Marti, C. & Jenni, L. 2016. Variable decline of alpine Rock Ptarmigan (*Lagopus muta helvetica*) in Switzerland between regions and sites. *J. Ornithol.* **157**: 787 –796.

García-González, R., Aldezabal, A., Laskurain, N.A., Margalida, A. & Novoa, C. 2016. Influence of snowmelt timing on the diet quality of Pyrenean Rock Ptarmigan (*Lagopus muta pyrenaica*): implications for reproductive success. *PLoS ONE* **11**: doi:10.1371/journal.pone.0148632.

Gaüzère, P., Jiguet, F. & Devictor, V. 2016. Can protected areas mitigate the impacts of climate change on bird's species and communities? *Divers. Distrib.* **22**: 625–637.

Gehrig-Fasel, J., Guisan, A. & Zimmermann, N. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *J. Veg. Sci.* **18**: 571–582.

Gellrich, M. & Zimmermann, N.E. 2007. Land abandonment in the Swiss mountains: A spatial statistical analysis at the regional scale. *Landsc. Urban Plan.* **79**: 65-76.

Gentle, P. & Thwaites, R. 2016. Transhumant pastoralism in the context of socioeconomic and climate change in the mountains of Nepal. *Mt. Res. Dev.* **36**: 173-182.

Gerrard, A.J. 1990. *Mountain environments: an examination of the physical geography of mountains*. MIT Press.

Gienapp, P., Leimu, R. & Merila, J. 2007. Responses to climate change in avian migration time – micro-evolution versus phenotypic plasticity. *Clim. Res.* **35**: 25–35.

Giuliano, W. 1994. The impact of hiking and rock climbing in mountain areas. *Environ. Conserv.* **21**: 287-279.

Glutz von Blotzheim, U.N., Bauer, K.M., Bezzel, E. 1973. Handuch der Vögel Mitteleuropas, **5**: Galliformes und Gruiformes. Akademische Verlagsgesellschaft, Frankfurt.

Goodenough A.E. & Hart A.G. 2013. Correlates of vulnerability to climate-induced distribution changes in European avifauna: habitat, migration and endemism. *Clim. Change* **118**: 659–669.

Grigaltchik, V.S., Ward, A.J.W. & Seebacher, F. 2012. Thermal acclimation of interactions: differential responses to temperature change alter predator-prey relationship. *Proc. R. Soc. A* **279***:* 4058–4064.

Hågvar, S. 2010. A review of Fennoscandian arthropods living on and in snow*. Eur. J. Entomol.* **107**: 281–298.

Hannon, S. J., Martin, K. & Schieck, J.A. 1988. Timing of reproduction in two populations of Willow Ptarmigan in northern Canada. *Auk* **105**: 330–338.

Hardy, D.R. & Hardy, S.P. 2008. White-winged Diuca Finch (*Diuca speculifera*) nesting on Quelccaya Ice Cap, Perù. *Wilson J. Ornithol.* **120:** 613–617.

Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.* **12**: 1040–1049.

Heikkinen, R. K., Luoto, M., Virkkala, R., & Pearson,R.G. & Körber, J.H. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Glob. Ecol. Biogeogr.* **16**: 754 – 763.

Heilprin, A. 1887. *The Geographical and Geological Distribution of Animals*. International Scientific Series: London.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Chang. Biol.* **12**: 450– 455.

Hoiss, B., Gaviria, J., Leingartner, A., Krauss, J. & Steffan-Dewenter, I. 2013. Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. *Divers. Distrib.* **19**: 386-395.

Huntley, B., Collingham, Y.C., Willis, S.G. & Green, R.E. 2008. Potential impacts of climate change on European breeding birds. *PLoS ONE* **3**: e1439.

Hüppop, O. & Hüppop, K. 2003. North Atlantic Oscillation and timing of spring migration in birds. *Proc. R. Soc. A* **270**: 233–240.

Imperio, S., Bionda, R., Viterbi, R. & Provenzale, A. 2013. Climate change and human disturbance can lead to local extinction of Alpine rock ptarmigan: new insight from the western Italian Alps. *PLoS ONE* **8**: e81598.

Inouye, D.W., Barr, B., Armitage, K.B. & Inouye, B.D. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 1630–1633.

IPCC 2007. *Climate change 2007: Synthesis report*. Intergovernmental Panel on Climate Change, Paris.

IPCC 2013 *Climate change 2013: the physical science basis*. In: Stocker TF *et al.* (eds) Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 1–14.

Jackson, M.M., Gergel, S.E. & Martin, K. 2015. Effects of climate change on habitat availability and configuration for an endemic coastal alpine bird. *PLoS ONE* **10**: e0142110.

Jetz, W., Wilcove, D.S. & Dobson, A.P. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* **5**: 1211–1219.

Johnson, R. 1965. Reproductive activities of rosy finches, with special reference to Montana. *The Auk* **82**: 190 –205.

Johnson, R. 1968. Temperature regulation in the white-tailed ptarmigan, *Lagopus leucurus*. *Comp. Biochem. Physiol.* **24**:1003–1014.

Kapos, V., J. Rhind, J., Edwards, M., Price, M.F. & Ravilious, C. 2000. *Developing a map of the world's mountain forests.* In: Forests in Sustainable Mountain Development: A State-of-Knowledge Report for 2000, M.F. Price and N. Butt (eds.), CAB International, Wallingford: 4–9.

Kearney, M. & Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**: 334 – 350.

Kirby, K.J. & Watkins, C. 2015. *Europe's changing woods and forests: from wildwood to managed landscapes*. CABI, Wallingford, UK.

Klein, G., Vitasse, Y., Rixen, C., Marty, C., & M. Rebetez, M. 2016. Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. *Clim. Chang*, **139**: 637, doi: 10.1007/s10584-016-1806-y.

Kohler, T., Wehrli, A. & Jurek, M. 2014. *Mountains and climate change: a global concern. Sustainable mountain development series.* Bern, Switzerland, Centre for Development and Environment (CDE), Swiss Agency for Development and Cooperation (SDC) and Geographica Bernensia: 136.

Koricheva, J., Gurevitch, J. & Mengersen, K. 2013. *Handbook of Meta-analysis in Ecology and Evolution*. Oxford: Princeton University Press.

Körner, C. & Spehn, E. M. 2002. *Mountain biodiversity: a global assessment.* Boca Raton, FL: Parthenon Publication Group.

Körner, C. & Ohsawa, M. 2006. *Mountain systems.* In: Hassan R, Scholes R, Ash N (eds) Ecosystem and human well-being: current state and trends. Millennium Ecosystem Assessment, Island Press, Washington **1**: 681-716.

Körner, C. 2012*. Alpine treelines: Funct. Ecol. of the global high elevation tree limits.* Basel, Switzerland: Springer.

Knudsen, E., Linden, A., Both, C., Jonzen, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P.P., Møller, A.P., Nilsson, A.L.K., Péron, G., Ranta, E., Rubolini, D., Sparks, T.H., Spina, F., Studds, C.E., Sæther, S.A., Tryjanowski, P. & Stenseth, N.C. 2011. Challenging claims in the study of migratory birds and climate change. *Biol. Rev.* **86**: 928–946.

Laaksonen, T., Ahola, M., Eeva, T., Väisänen, R.A. & Lehikoinen, E. 2006. Climate change, migratory connectivity and changes in laying date and clutch size of the Pied Flycatcher. *Oikos* **114**: 277–290.

Laiolo, P., Rolando, A. & Valsania, V. 2004. Responses of birds to the natural re-establishment of wilderness in montane beechwoods of North-western Italy. *Acta Oecol.* **25**: 129–136.

Laiolo, P. & Rolando, A. 2005. Forest bird diversity and ski-runs: a case of negative edge effect. *Anim. Conserv.* **7**: 9–16.

Lajeunesse, M.J. 2013. Recovering missing or partial data from studies: A survey of conversions and imputations for meta-analysis. In Koricheva, J., Gurevitch, J. & Mengersen, K (eds) Handbook of Meta-Analysis in Ecology and Evolution. Princeton: Princeton University Press.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**: 911–927.

La Sorte, F.A. & Jetz, W. 2010. Projected range contractions of montane biodiversity under global warming. *Proc. R. Soc. A* **277**: 3401–3410.

Lehikoinen, A., Green, M., Husby, M., Kålås, J.E. & Lindström, Å. 2014. Common montane birds are declining in Northern Europe. *J. Avian Biol.* **45**: 3–14.

Lehikoinen, A. & Virkkala, R. 2016. North by north-west: climate change and directions of density shifts in birds. *Glob. Chang. Biol.* **22**: 1121–1129.

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. 2008 A significant upward shift in plant spfecies optimum elevation during the 20th century. *Science* **320**: 1768–1771.

Lesk, C., Coffel, E., D'Amato, A.W., Dodds, K., Horton, R. 2017. Threats to North American forests from southern pine beetle with warming winters. *Nat. Clim. Change* **7**: 713–717.

Liu, X.D. & Chen, B.D. 2000. Climatic warming in the Tibetan Plateau during recent decades. *Int. J. Clim.* **20**: 1729–1742.

Loarie, S., Duffy, P., Hamilton, H. & Asner, G. 2009. The velocity of climate change. *Nature* **462**: 1052–5.

Loe, L. E., Mysterud, A., Stien, A., Steen, H., Evans, D. M. & Austrheim, G. 2007. Positive short-term effects of sheep grazing on the alpine avifauna. *Biology Letters* **3**: 109-111.

Lu, N., Jing, Y., Lloyd, H., Sun, Y. 2012. Assessing the distributions and potential risks from climate change for the Sichuan Jay (*Perisoreus internigrans*). The Condor **114**: 365–376.

Lundmark, L. 2007. Reindeer pastoralism in Sweden 1550-1950. *Rangifer* **12**: 9–16.

Maggini, R., Lehmann, A., Kery, M., Schmid, H., Beniston, M., Jenni, L. & Zbinden, N. 2011. Are Swiss birds tracking climate change? Detecting elevational shifts using response curve shapes. *Ecol. Model.* **222**: 21–32.

Maggini, R., Lehman, A., Zbinden, N., Zimmerman, N.E., Bollinger, J., Schröder, B., Foppen, R., Schmid, H., Beniston, M. & Jenni, L. 2014. Assessing species vulnerability to climate and land use change: the case of the Swiss breeding birds. *Divers. Distrib.* **20**: 708–719.

Mahon, C.L., Holloway, G., Sólymos, P., Cumming, S.G., Bayne, E.M. Schmiegelow F.K.A. & Song, S.J. 2016. Community structure and niche characteristics of upland and lowland western boreal birds at multiple spatial scales. *For. Ecol. Manage.* **361**: 99–116.

Mantyka-Pringle, C. S. & Rhodes, J.R. 2012. Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Glob. Chang. Biol.* **18**: 1239– 1252.

Martin, T.E. 2001a. Abiotic vs biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology* **82**: 175–188.

Martin, K. 2001b. *Wildlife communities in alpine and sub-alpine habitats.* In D. H. Johnson and T. A. O'Neil (Managing Directors), Wildlife-habitat relationships in Oregon and Washington. Oregon State Univ. Press, Corvallis, Oregon: 285–310.

Martin, T.E. & Maron, J.L. 2012. Climate impacts on bird and plant communities from altered animal-plant interactions. *Nat. Clim. Chang.* **2**: 195-200.

Martin, K., & Wiebe, K. L. 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. *Integr. Comp. Biol.* **44**: 177-185.

Martin, K., Wilson, S. D., MacDonald, E.C., Camfield, A. F., Martin, M. & Trefrey, S. A. 2017. Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: interactions of climate extremes influence nesting success. *The Auk* 134: 696-709.

Massimino, D., Johnston, A. & Pearce-Higgins, J.W. 2015. The geographical range of British birds expands during 15 years of warming. *Bird Study* **62**: 523–534.

Mayor, S.J., Guralnick, R.P., Tingley, M. W., Outegui, J., Withey, J.C., Elmendorf, S. C., Andrew, M.E., Leyk, S., Pearse, I.S. & Schneider, D.C. 2017 Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Sci. Rep.* **7**: 1902 doi:10.1038/s41598-017-02045-z

McVean, D.; & Lockie, J.D. 1969. Ecology and Land Use in Upland Scotland. Edinburgh: University Press.

Meehl, G.A., Covey, C., Delworth, T., Latif, M., McAvaney, B., Mitchell, J.F.B., Stouffer, R.J. & Taylor, K.E. 2007. The WCRP CMIP3 multimodel dataset—a new era in climate change research. *B. Am. Meteorol. Soc.* **88**: 1383–1394.

Mezquida, E.T., Svenning, J.C., Summers, R.W., Benkman, C.W. 2017. Higher spring temperatures increase food scarcity and limit the current and future distributions of crossbills. *Divers. Distrib.* doi.org/10.1111/ddi.12694

Mizel, J. D., Schmidt, J. H., Mcintyre, C. L. & Roland C. A. 2016. Rapidly shifting elevational distributions of passerine species parallel vegetation change in the subarctic. *Ecosphere* **7**: e01264.

Moser, B. W. & Witmer, G. W. 2000. The effects of elk and cattle foraging on the vegetation, birds, and small mammals of the Bridge Creek Wildlife Area, Oregon. *Int. Biodeterior. Biodegradation* **45**: 151-157.

Moss, R., Oswald, J. & Baines, D. 2001. Climate change and breeding success: decline of the Capercaillie in Scotland. *J. Anim. Ecol.* **70**: 47-61.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, t., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.S., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.C., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E. & Hik, D.S. 2011. Shrub expansion in tundra eco- systems: dynamics, impacts and research priorities. *Environ. Res. Lett.* **6**: 045509.

Møller, A.P., Rubolini, D. & Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl. Acad. Sci. U.S.A.* **105**: 16195–16200.

Mollet, P., Bollmann, K., Braunisch, V. & Arlettaz, R. In press. Avian communities in European high altitude woodlands. In: Mikusinski, G., Roberge, J.-M. & Fuller, R.J. (Eds.). *Ecology and Conservation of Forest Birds*. Cambridge University Press. Cambridge, UK, in press.

Musitelli, F., Romano, A., Møller, A.P. & Ambrosini, R. 2016. Effects of livestock farming on birds of rural areas in Europe. *Biodivers. Conserv.* **25**: 615-631.

Nagy, L. & Grabherr, G. 2009. *The biology of alpine habitats*. Oxford University Press, Oxford.

Nogués-Bravo, D., Araújoc, M.B., Erread, M.P. & Martínez-Ricad, J.P. 2007. Exposure of global mountain systems to climate warming during the 21st Century. *Glob. Environ. Chang.* **17**: 420–428.

Nogués-Bravo, D., Araujo, M. B., Romdal, T. S. & Rahbek, C. 2008. Scale effects and human impact on the elevational species richness gradients. *Nature* **453**: 216-220.

Novoa, C., Besnard, A., Brenot, J.F.& Ellison, L.N. 2008. Effect of weather on the reproductive rate of Rock Ptarmigan *Lagopus muta* in the Eastern Pyrenees. *Ibis* **150**: 270–278.

Novoa, C., Astruc, G., Desmet, J.F. & Besnard, A. 2016. No short-term effects of climate change on the breeding of Rock Ptarmigan in the French Alps and Pyrenees. *J. Ornithol.* **157**: 797-810.

Oliver, T. H., Gillings, S., Pearce-Higgins, J. W., Brereton, T., Crick, H. Q. P., Duffield, S. J., Morecroft, M. D. &Roy, D. B. 2017. Large extents of intensive land use limit community reorganization during climate warming. *Glob. Change Biol.* **23**: 2272–2283.

Pacifici, M., Visconti, P., Butchard, S.H.M., Watson, J.E.M., Cassola, F.M. & Rondinini, C. 2017. Species' traits influenced their response to recent climate change. *Nat. Clim. Chang.* doi: 10.1038/NCLIMATE3223.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37 - 42.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669.

Patthey, P., Wirthner, S., Signorell, N. & Arlettaz, R. 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. *J. Appl. Ecol.* **45**: 174–1711.

Patthey, P., N. Signorell, L. Rotelli & Arlettaz, R. 2012. Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. Eur. J. *Wildl. Res.* **58**: 59-70.

Pavel, V. 2004. The impact of grazing animals on nesting success of grassland passerines in farmland and natural habitats: a field experiment. *Folia Zool.* **53**: 171-178.

Pearce-Higgins, J.W., Yalden, D.W. & Whittingham, M.J. 2005. Warmer springs advance the breeding phenology of Golden Plovers *Pluvialis apricaria* and their prey (*Tipulidae*). *Oecologia* **143**: 470–476.

Pearce-Higgins, J.W., Dennis, P., Whittingham, M.J. & Yalden, D.W. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Glob. Chang. Biol.* **16**: 12–23.

Pepin, N., Bradley, R. S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z., Liu, X.D., Miller, J.R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M.B., Williamson, S.N. & Yang, D.Q. 2015. Elevation-dependent warming in mountain regions of the world. *Nat. Clim. Chang.* **5**: 424-430.

Peringer, A., Siehoff, S., Chetelat, J., Spiegelberger, T., Buttler, A. & Gillet, F. 2013. Past and future landscape dynamics in pasture-woodlands of the Swiss Jura Mountains under climate change. Ecol. Soc. **18:** 11.

Pernollet, C.A., Korner-Nievergelt, F. & Jenni, L. 2015. Regional changes in the elevational distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. *Ibis* **157**: 823–836.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team 2017. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-131.

Popy, S., Bordignon, L. & Prodon, R. 2010. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. *J. Biogeogr.* **37**: 57-67.

Potatov, R. 2004. Adaptation of birds to life in high mountains in Eurasia. *Acta Zool. Sinica* **50**: 970-977.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Parts I, II. Ecology* **43**: 185–215, 410–432.

Quantum GIS Development Team. 2015. *Quantum GIS Geographic Information System.* Open source geospatial foundation project.

Ralston, J., DeLuca, W. V., Feldman, R. E. & King, D. I. 2017. Population trends influence species ability to track climate change. *Glob. Change Biol.*, **23**: 1390–1399. doi:10.1111/gcb.13478

Rauter, C.M., Reyer, H.U. & Bollmann, K. 2002. Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit *Anthus spinoletta*. *Ibis* **144**: 433–444.

Reif, J. & Flousek, J. 2012. The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. *Oikos* **121**: 1053–1060.

Reif, J., Hořák, D., Krištín, A., Kopsová, L. & Devictor, V. 2015. Linking habitat specialization with species' traits in European birds. *Oikos* **125**: 405–413.

Rimmer, C.C., McFarland, K.P., Lambert, J.D. & Renfrew, R.B. 2004. *Evaluating the use of Vermont ski areas by Bicknell's thrush: applications for Whiteface mountain*. Vermont Institute of natural Science, Woodstock, VT, New York.

Rixen, C. & Rolando, A. (eds). 2013. *The impacts of skiing and related winter recreational activities on mountain environments.* Bentham doi: 10.2174/97816080548861130101.

Rocchia, E. 2016. *Temporal variation of species distribution and species morphological traits along altitude in the Alps* (Doctoral thesis). University of Milano-Bicocca, Italy.

Rolando, A., Caprio, E., Rinaldi, E. & Ellena, I. 2007. The impact of high-altitude ski-runs on alpine grassland bird communities. *J. Appl. Ecol.* **44**: 210–219.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.

Rosvold, J. 2016. Perennial ice and snow-covered land as important ecosystems for birds and mammals. *J. Biogeogr.* **43:** 3–12.

Roth, T., Plattner, M. & Amrhein, V. 2014. Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. PLoS ONE 9: e82490.

Rubolini, D., Møller, A.P., Rainio, K. & Lehikoinen, E. 2007. Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Clim. Res.* **35**: 135–146.

Sæther, B., Tufto, J., Engen, S. & Jerstad, K. 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* **287**: 854–856.

Sandercock, B.K., Martin, K. & Hannon, S.J. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology* **86**: 2176-2186.

Santangeli, A., Rajasärkkä, A. & Lehikoinen, A. 2016. Effects of high latitude protected areas on bird communities under rapid climate change. *Glob. Chang. Biol.* doi:10.1111/gcb.13518.

Santisteban, L., Benkman, C.W., Fetz, T. & Smith, J.W. 2012. Survival and population size of a resident bird species are declining as temperature increases. *J. Anim. Ecol.* **81:** 352–363.

Scridel, D. 2014. Ecology and conservation of birds in upland and alpine habitats: a report on the BOU's Annual Conference held at the University of Leicester, 1–3 April. *Ibis* **156**: 896–900.

Scridel, D., Bogliani, G., Pedrini, P., Iemma, A., von Hardenberg, A., Brambilla, M. 2017a. Thermal niche predicts recent changes in range size for bird species. *Clim. Res.* **73**:207-216.

Scridel, D., Groom J.D. & Douglas, D.J.T. 2017b. Native woodland creation is associated with increase in a Black Grouse *Lyrurus tetrix* population. *Bird Study* **64**: 70-83.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. 2008. Climate change, elevational range shifts, and bird extinctions. *Conserv. Biol.* **22**: 140–150.

Siegel, R. B., Pyle, P., Thorne, J. H., Holguin, A. J., Howell, C. A., Stock, S. & Tingley, M.W. 2014. Vulnerability of birds to climate change in California's Sierra Nevada. *Avian Conserv. Ecol.* **9**: 7 http://dx.doi.org/10.5751/ACE-00658-090107

Signorell, N., S. Wirthner, P. Patthey, R. Schranz, L. Rotelli & Arlettaz, R. 2010. Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse *Tetrao tetrix* hens: habitat management implications. *Wildlife Biol.* **16**: 249-257.

Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L. & Martin, J.L. (2017), Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. *Global Ecol. Biogeogr.*, **26**: 385–394.

Stephens, P.A., Mason, L.R., Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotons, L., Butchart, S.H., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R.P., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D.G., Paquet, J.Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van, Strien, A.J., van Turnhout, C.A., Vorisek, P. & Willis, S.G. 2016. Consistent response of bird populations to climate change on two continents. *Science* **352**: 84-87.

Strahler, A.N. 1946. Geomorphic terminology and classification of land masses. *J. Geol.* **54**: 32-42.

Sturrock, R. N., Frankel, S. J., Brown, A. V., Hennon, P. E., Kliejunas, J. T., Lewis, K. J., Worrall, J. J. and Woods, A. J. 2011. Climate change and forest diseases. *Plant Pathology*, **60**: 133–149.

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Høye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J. & Wanless, S. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535:** 241–245.

Thiel, D., Jenni-Eierman, S., Palme, R. & Jenni, L. 2011. Winter tourism increases stress hormone levels in the Capercaillie *Tetrao urogallus*. *Ibis* **153**: 122–133.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. 2009. Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. U.S.A.* **106**: 19637–19643.

Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C. & Beissinger, S.R. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Change Biol.* **18**: 3279–3290.

Tingley, M.W. & Beissinger, S.R. 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology* **94**: 598–609.

Titeux, N., Henle, K., Mihoub, J.-B., Regos, A., Geijzendorffer, I. R., Cramer, W., Verburg, P. H. & Brotons, L. 2016. Biodiversity scenarios neglect future land-use changes. *Glob. Chang. Biol.* **22**: 2505–2515.

Tolvanen, A. & Kangas, K. 2016. Tourism, biodiversity and protected areas - Review from northern Fennoscandia. *J. Environ. Manage.* **166**: 58-66.

Townsend, A.K., Cooch, E.G., Sillett, T.S., Rodenhouse, N.L., Holmes, R.T. & Webster, M.S. 2016. The interacting effects of food, spring temperature, and global climate cycles on population dynamics of a migratory songbird. *Glob. Chang. Biol.* **22**: 544–555.

Tryjanowski, P., Sparks, T.H. & Profus, P. 2005. Uphill shifts in the distribution of the white stork *Ciconia ciconia* in southern Poland: the importance of nest quality. *Divers. Distrib.* **11**: 219–223.

Viterbi, R., Cerrato, C., Bassano, B., Bionda, R., von Hardenberg, A., Provenzale, A. & Bogliani, G. 2013. Patterns of biodiversity in the northwestern Italian Alps: a multi-taxa approach. *Community Ecol.* **14**: 18–30.

Virkkala, R., Heikkinen, R.K., Fronzek, S. & Leikola, N. 2013. Climate change, northern birds of conservation concern and matching the hotspots of habitat suitability with the reserve network. *PLoS ONE* **8**: e63376.

Virkkala, R., Pöyry, J., Heikkinen, R.K., Lehikoinen, A. & Valkama, J. 2014. Protected areas alleviate Climate Change effects on northern bird species of conservation concern. *Ecol. Evol.* **15**: 2991–3003.

Virkkala, R. 2016. Long-term decline of southern boreal forest birds: consequence of habitat alteration or climate change? *Biodivers. Conserv.* **25**: 151–167.

Wang, G., Hobbs, T.N., Galbraith, H. & Giesen, K.M. 2002. Signatures of large-scale and local climates on the demography of white-tailed ptarmigan in Rocky Mountain National Park, Colorado, USA. *Int. J. Biometeorol.* **46**: 197–201.

Wann, G.T., Aldridge, C.L. & Braun, **C.E.** 2014. Estimates of annual survival, growth, and recruitment of a white-tailed ptarmigan population in Colorado over 43 years. *Popul. Ecol.* **56**: 555-567.

Warren, J.M., Rotella, J. & Thompson, J.E. 2008. Contrasting Effects of Cattle Grazing Intensity on Upland-Nesting Duck Production at Nest and Field Scales in the Aspen Parkland, Canada. *Avian Conserv. Ecol* **3**: 6.

Watson, A. & Moss, R. 2004. Impacts of ski-development on Ptarmigan (*Lagopus mutus*) at Cairn Gorm, Scotland. *Biol. Conserv.* **116**: 267–275.

Weed, M. & Bull, C. 2004. *Sports tourism: participants, policy and providers*. Elsevier Butterworth-Heinemann, Oxford.

Wilson, J.D., Anderson, R., Bailey, S., Chetcuti, J., Cowie, N.R., Hancock, M.H., Quine, C., Russell, N., Stephen, L. & Thompson, D.B.A. 2014. Modelling edge effects of mature forest plantations on peatland waders informs landscape-scale conservation. *J. Appl. Ecol.* **51**: 204–213.

Wilson S. & K. Martin. 2010. Variable reproductive effort for two ptarmigan species in response to spring weather in a northern alpine ecosystem. *J. Avian. Biol*. **41**: 319-326.

Wilson, S. & Martin, K. 2012. Influence of life history strategies on sensitivity, population growth and response to climate for sympatric alpine birds. *BMC Ecology* **12**:9.

Wipf, S. & Rixen, C. 2010 A review of snow manipulation experiments in Arctic and alpine ecosystems. *Polar Research* **29**: 95–109.

Wu, X.Y., Zhang, X.F., Dong, S.K., Cai, H., Zhao, T.R., Yang, W.J., Jiang, R., Shi, Y.D. & Shao, J.L. 2015. Local perceptions of rangeland degradation and climate change in the pastoral society of Qinghai-Tibetan Plateau. *Rangeland J.* **37**: 11-19.

Zamora, R., & Barea-Azcón, M. 2015. Long-term changes in mountain passerine bird communities in the Sierra Nevada (southern Spain): a 30-year case study. *Ardeola* **62**: 3–18.

Zuckerberg, B., Woods, A.M. & Porter, W.F. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biol.* **15**: 1866–1883.

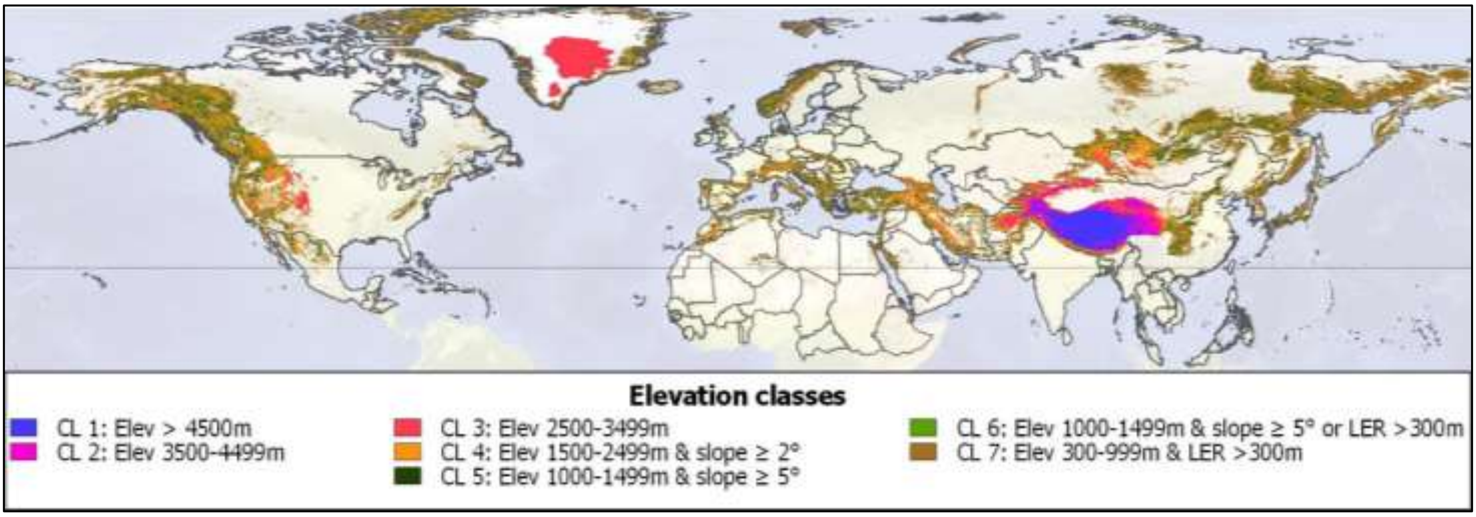

Figure 1. Mountains systems classified by Kapos *et al.* (2000) and adapted to the Holarctic region (above the Tropic of Cancer – grey line). The upper three classes (‘CL ’) are delimited purely by elevation (≥ 2500m). Areas below 2500m were classified additionally in terms of slope, terrain roughness and local elevation range (LER).

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

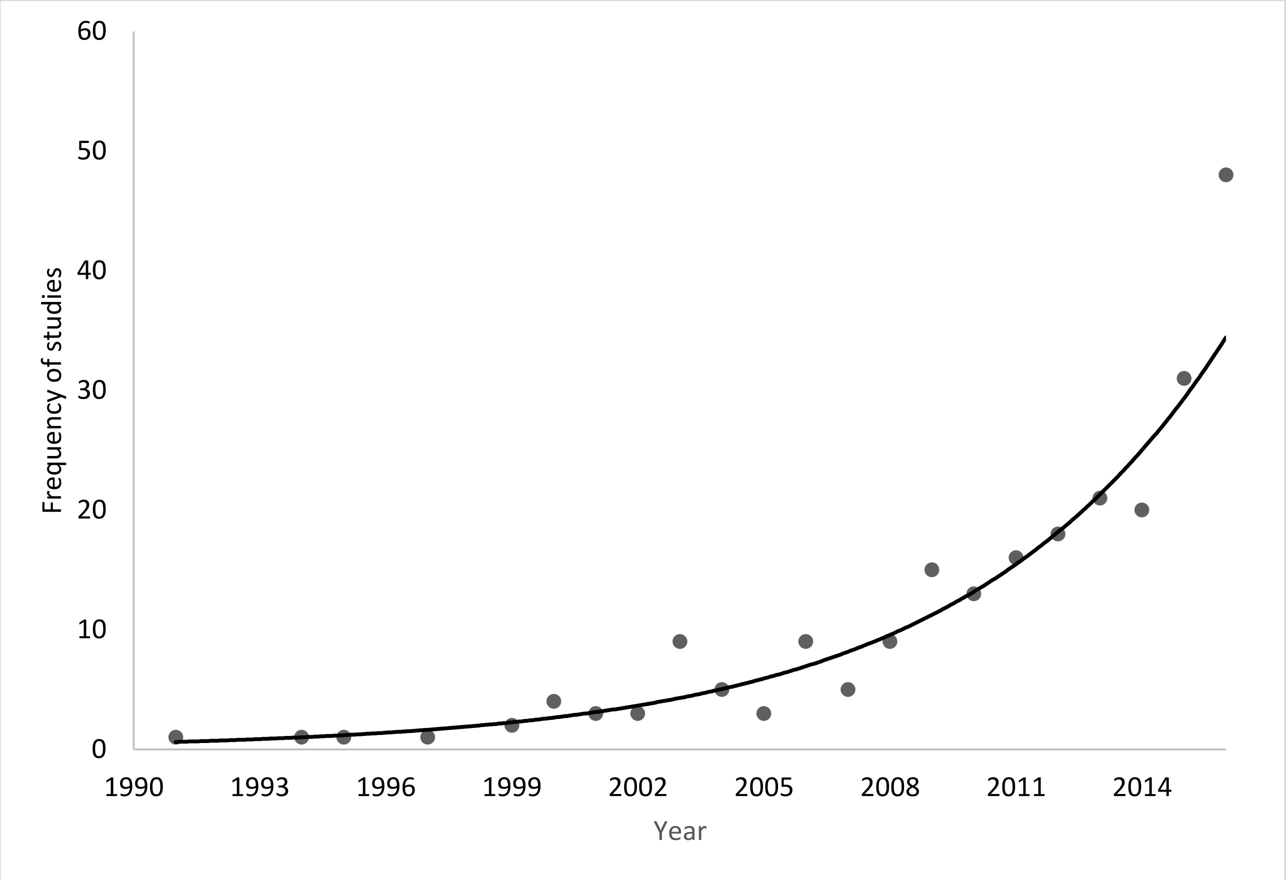

Figure 2. Frequency of relevant published papers and reviews over time resulting from the systematic literature search.

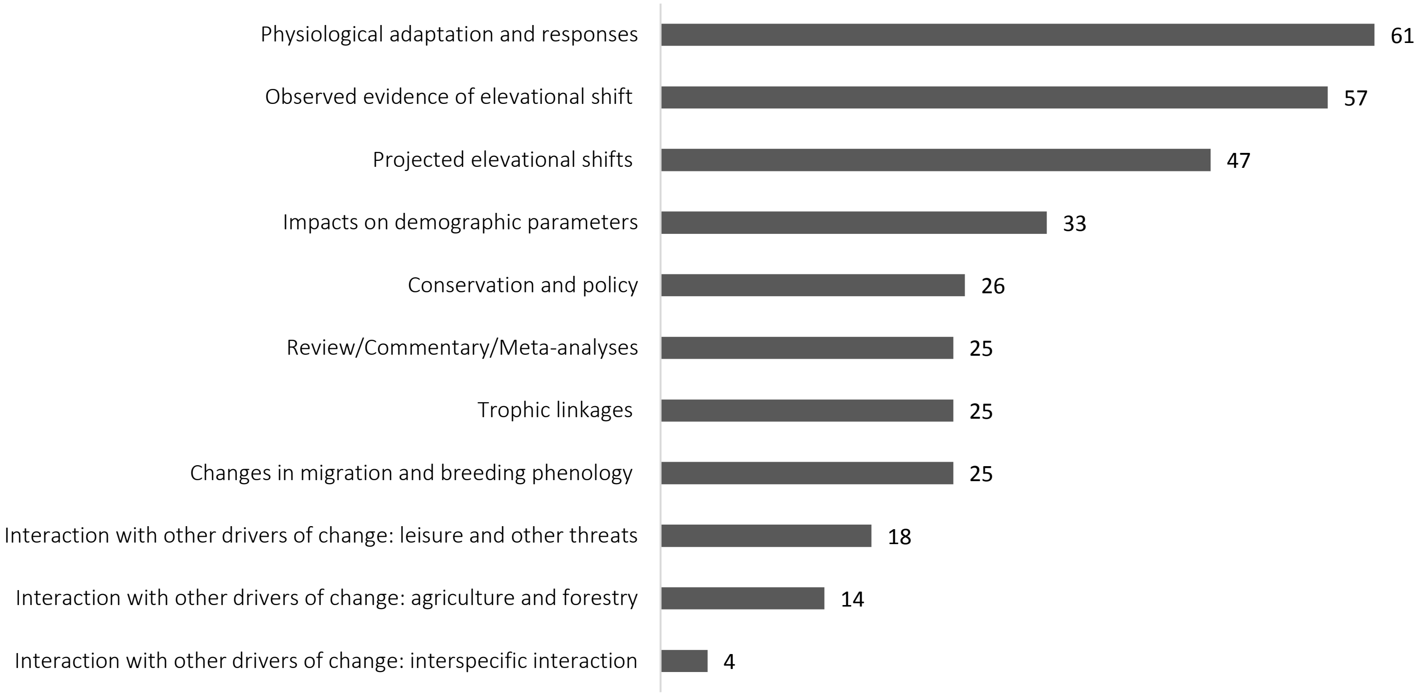

Figure 3. Frequency of climate-change related studies on Holarctic mountain birds (mutually inclusive) resulting from the systematic literature search, classified according to general subjects addressed.

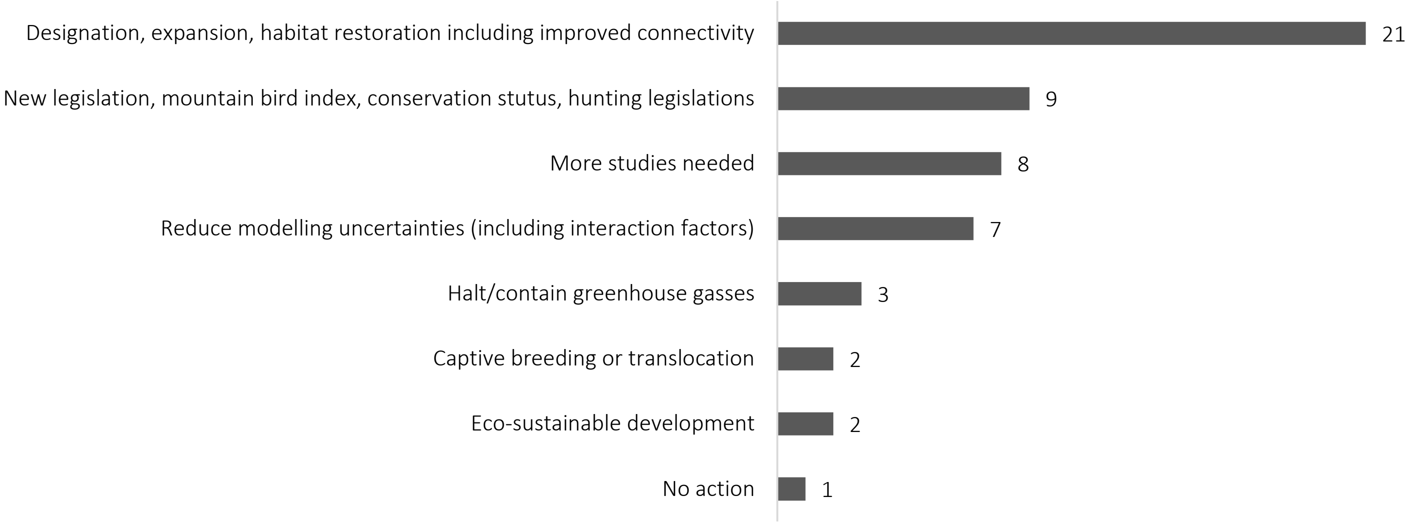

Figure 4. Number of conservation (mutually inclusive) actions suggested across all papers classified as 'conservation & policy' (*n* = 26) in the systematic literature search.

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-km^2) 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 *et al.* 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 *et al.* 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 *et al.* 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 *et al.* 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 *et al.* 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 *et al.* 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 (Odontrophoridae, Phasianidae, Columbidae, Trochilidae and Picidae)