

Original article

Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps

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Running header: *Climate change, skiing and birds in the Alps*

word count: 7359

estimate of the number of journal pages required by your figures and tables: 2

22 ABSTRACT

23 **Aim** To assess the extent of the possible future conflict between skiing and biodiversity driven by
24 climate change, human adaptation and species' distribution shifts.

25 **Location** Italian Alps.

26 **Methods** We assessed the extent of the possible future conflict between skiing and biodiversity by
27 predicting locations likely to be suitable for both skiing and for high-elevation birds in the Italian
28 Alps by modelling ski-piste and species presence in relation to climate, topography and habitat.
29 Potential conflict was assessed by comparing the overlap of areas projected as suitable for skiing
30 and those suitable for five high-elevation bird species under different scenarios of climate change
31 for the year 2050.

32 **Results** Areas suitable for both ski-pistes and birds were projected to contract towards upper
33 elevations, which for birds resulted in an average decrease of 58% - 67% of suitable area. The
34 degree of overlap between species and skiing was projected to increase, especially for the most
35 valuable sites, i.e. those hosting the most species, or the most threatened species.

36 **Main conclusions** Given the alarming range contractions forecast for high elevation species, and
37 the potential impact of ski-pistes on those species, it is essential to safeguard high mountain
38 grasslands against negative effects of ski development. An effective conservation strategy at a
39 landscape scale needs to consider prevention of ski-piste construction in sites of high conservation
40 value. The approach developed here provides a means by which such a strategy could be
41 formulated, and which could be potentially applied elsewhere to investigate the effect of human
42 adaptation on biodiversity.

43

44 **Keywords:** alpine grassland; bird conservation; global warming; human adaptation; mountain; ski-
45 piste

46 INTRODUCTION

47

48 Climate change induced by anthropogenic emissions of greenhouse gases is among the most severe
 49 threats to ecosystems and species at a global level (IPCC, 2013). Indirect impacts arising from
 50 human adaptation to new climates (i.e. taking appropriate action to prevent or minimize the adverse
 51 effects of climate change) pose imminent and important threats to biodiversity (Bradley *et al.*, 2012;
 52 Chapman *et al.*, 2014), and may impair the ability of species to cope with climate change (Watson,
 53 2014). However, the impacts driven by human adaptation are rarely considered in the conservation
 54 literature (Watson & Segan, 2013; Chapman *et al.*, 2014), although notable exceptions exist (e.g.
 55 Bradley *et al.*, 2012; Wetzel *et al.*, 2012). Humans continue to respond to climate change, and such
 56 a response is to some degree predictable (Watson, 2014). Therefore, researchers need to focus not
 57 only on the direct effect of changing climate, but also on the climate-related variation in human-
 58 mediated threats (Turner *et al.*, 2010; Watson, 2013). The latter can take place rapidly and have
 59 overwhelming impacts, being of equal or greater intensity for species and ecosystems than the
 60 direct impacts of climate change (Turner *et al.*, 2010; Watson & Segan, 2013; Chapman *et al.*,
 61 2014).

62 High-mountain regions harbour a high biodiversity (Dirnböck *et al.*, 2011) and a high
 63 percentage of both endemic (Essl *et al.*, 2009) and vulnerable species (Viterbi *et al.*, 2013). Many
 64 species are restricted to the upper elevations of their former range because of human pressures
 65 (Martin, 2001) and thus careful management of mountains is crucial for conservation (Rolando *et*
 66 *al.*, 2013). Mountain regions are particularly threatened by climate change (Brunetti *et al.*, 2009)
 67 and show a higher rate of warming compared to the global average (Böhm *et al.*, 2001). Species and
 68 habitats are already undergoing elevational range shifts due to climate warming, which is predicted
 69 to have important impacts on biodiversity at high elevation (Sekercioglu *et al.*, 2008; Dirnböck *et*
 70 *al.*, 2011; Chamberlain *et al.*, 2013). However, habitat changes caused by human action may have
 71 more severe consequences than climate change (Jetz *et al.*, 2007), or the two may interact, showing

72 synergistic effects (Mantyka-Pringle *et al.*, 2012).

73 Recreational activities, and in particular winter sports, represent one of the main threats to
 74 wild species in many mountain regions (e.g. Buckley *et al.*, 2000; Arlettaz *et al.*, 2013). There is
 75 increasing evidence of negative effects of skiing activities from a range of taxa (Rixen & Rolando,
 76 2013) via habitat destruction/alteration/fragmentation, soil degradation, and ski-related urban
 77 development (Rolando *et al.*, 2013). Ski-pistes for downhill skiing in the Alps are associated with
 78 both lower bird species richness and bird abundance (Rolando *et al.*, 2007; Caprio *et al.*, 2011;
 79 Rolando *et al.*, 2013). The negative effect of ski-pistes is mostly tied to the removal of vegetation
 80 and soil (Fig. S1 in Appendix S1); this is not invariably performed on all ski-pistes, but has become
 81 the standard practice for modern ski-piste construction (Negro *et al.*, 2013). Altered soil structure,
 82 harsh climate and plant species traits together prevent the re-establishment of vegetation, and grass
 83 cover for wild species remains extremely low for long periods even with modern restoration
 84 techniques such as hydro-seeding (Negro *et al.*, 2013).

85 Skiing activities are likely to be affected by climate change, and in particular by temperature
 86 rise and variation in precipitation regimes (Behringer *et al.*, 2000; Uhlmann *et al.*, 2009), and as
 87 such they have the potential to cause indirect impacts on biodiversity deriving from human
 88 adaptation. Due to decreasing snowfall and/or less reliable snow cover at lower altitudes, the area
 89 suitable for skiing is likely to show a range contraction and an upwards altitudinal shift (Elasser &
 90 Messerli, 2001; Disch *et al.*, 2007; Scott *et al.*, 2008), as already evident in some alpine areas
 91 (Pozzi, 2009; Marty, 2013). Given that a similar pattern of range contraction is likely to occur in the
 92 distribution of many mountain species (e.g. Sekercioglu *et al.*, 2008; Chamberlain *et al.*, 2013), this
 93 could lead to an increase in the potential conflict between winter sports and wildlife. However, the
 94 potential consequences for mountain wildlife of changes in ski developments as a response to
 95 climate change have not been fully assessed.

96 We aim to describe the increase in the potential impact of ski-pistes on alpine biodiversity
 97 by modelling the potential future distributions of both species and ski-pistes in relation to projected

98 climate changes in the European Alps. Our goal is to highlight where conflicts between downhill
99 skiing and nature conservation are most likely to occur over the next decades, by constructing
100 spatially explicit models of conflict zones between ski-pistes for downhill skiing and wildlife
101 (Braunisch *et al.*, 2011), using high-elevation birds as an example group. We first model the current
102 and future distribution of high-altitude bird species potentially vulnerable to ski-piste development
103 in relation to climate, habitat and topography. Then, we model the current and future distribution of
104 ski-pistes in relation to climate and topography; finally, we develop an approach to reduce possible
105 future conflicts by evaluating where they may arise. Among the areas that should be considered as
106 high-priority for the conservation of high-elevation species in a warmer climate, we identify those
107 which are likely to be suitable for ski-pistes in the future, and hence those where ski-developments
108 should be restricted or regulated.

109 The approach that we have adopted for Alpine birds and ski-pistes provides a potential
110 framework by which conservation strategies to cope with the effects of other types of human
111 adaptation to climate change on biodiversity could be formulated.

112 MATERIALS AND METHODS

113

114 Study area, fieldwork and model species

115 The study area comprised a large area of the southern Alps in northern Italy included within the
 116 borders defined by the Alpine Convention (Fig. 1). As model species, we selected passerine birds
 117 that in the Alps are mostly or exclusively tied to grassland and other open habitats at high elevation,
 118 and that could be potentially affected by climate change and by the occurrence of ski-pistes (Tables
 119 S1 and S2 in Appendix S1): water pipit *Anthus spinoletta*, alpine accentor *Prunella collaris*,
 120 northern wheatear *Oenanthe oenanthe*, black redstart *Phoenicurus ochruros*, and snowfinch
 121 *Montifringilla nivalis*. Bird data were collated from different studies that were carried out between
 122 2000 and 2015 in all the main sectors of the study region (see Appendix S1). The number of
 123 occurrences for each species was: water pipit 658; alpine accentor 235; northern wheatear 443;
 124 black redstart 1428; snowfinch 74.

125

126 Modelling species distributions

127 Species distributions were modelled using MAXENT 3.3.3k (Phillips *et al.*, 2006), which can deal
 128 appropriately with the climate variables potentially relevant for species distribution (Braunisch *et*
 129 *al.*, 2013) and is routinely adopted to analyse species distribution using data collected with different
 130 survey methodologies (e.g. Bose *et al.*, 2015; Latinne *et al.*, 2015), as here (Appendix S1) or
 131 collected by means of unknown field methods (e.g. Engler *et al.*, 2014). All bird data were collected
 132 at a spatial resolution ≤ 100 -m.

133 To make distribution models as general and robust as possible, we applied the approach
 134 proposed by Radosavljevic & Anderson (2014), adopting a masked geographically structured
 135 evaluation of models. We divided our study area into four longitudinal belts (see Fig. S9 in
 136 Appendix S2), and used records and background points (10 000) from eastern and central-western
 137 portions to build models (training data), and records from western and central-eastern portions to

138 evaluate models (test data).

139 Environmental variables included land cover, bioclimatic and topographical variables (Table
 140 S3). Ten land cover types were selected from the CORINE Land Cover (CLC2006; EEA, 2007)
 141 database in order to describe the habitat composition of each cell, assuming constant land cover
 142 over the time period (up to 2050). Bioclimatic variables (BIO1: average annual temperature, BIO5:
 143 maximum temperature of the warmest month, BIO10: mean temperature of warmest quarter,
 144 BIO12: annual precipitation, BIO18: precipitation of the warmest quarter) were calculated for each
 145 grid cell from the values downloaded from WorldClim v.1.4 (Hijmans *et al.*, 2005;
 146 <http://www.worldclim.org>; resolution 30 arc-seconds, corresponding to less than 1-km at this
 147 latitude). Annual and warmest period values were selected because the target species occur in the
 148 study area around their thermal maximum and are largely resident (alpine accentor, snowfinch) or
 149 short-range migrants (water pipit, black redstart), and breed in late spring-summer, thus are most
 150 likely to be affected by average and maximum temperatures (see also Brambilla *et al.*, 2015). Slope
 151 and solar radiation (calculated taking 21st June as the reference day), were extracted from a digital
 152 terrain model (resolution 20 m) of the study area.

153 Before distribution modelling, we checked for multicollinearity among all environmental
 154 predictors in order to minimize the risk of overfitting species' responses to climate. Variance
 155 inflation factors (VIFs) were evaluated, and highly collinear variables ($VIF > 5$) were omitted,
 156 following Zuur *et al.* (2009). Seasonal bioclimatic variables showed high levels of collinearity,
 157 therefore only annual temperature and rainfall were used in distribution modelling (see below).

158 All environmental variables were calculated for 40 x 40 m cells; for each cell, values
 159 represented i) the sum of cover (total area) per each type of land cover, ii) the average slope, and iii)
 160 the mean solar radiation, all referring to a radius of c. 100 m from each cell. For bioclimatic
 161 variables, we assigned to each 40 x 40 m cell the value of the 30 arc-seconds cell with which it
 162 overlapped. Given the raster structure, this resulted in variables measured over an area of slightly
 163 more than 2 ha, a grain that matches fairly well with the supposed territory sizes, and hence the

164 main areas of activity, of the species considered (Cramp, 1998; Gustin *et al.*, 2010). To reduce the
 165 risk of overfitting, we fitted models considering only linear and quadratic terms (not including
 166 interaction, threshold and hinge functions), irrespective of sample size.

167

168 **A spatial test of the representativeness of the climatic niche defined by the data**

169 Given that we focussed on a portion of the range of our study species, we could potentially
 170 overestimate the effect of climate change on those species (Barbet-Massin *et al.*, 2010). To avoid
 171 this risk, using our data (all locations per each species) and only climatic factors, we modelled
 172 species distribution across a large part of Europe (using tile no. 16 of the Worldclim database as a
 173 study area, from southern Scandinavia to North Africa) and compared it with independent estimates
 174 of species distributions at larger scales (e.g. Cramp, 1998). Moreover, we compared the distribution
 175 predicted for Italy with the distribution data derived from reporting to the European Union under
 176 the Birds Directive (Nardelli *et al.*, 2015; data downloaded from
 177 <http://cdr.eionet.europa.eu/it/eu/art12/envuzmuow/>).

178 We compared models obtained using only either annual temperature, or temperature and
 179 rainfall, and selected the model better describing the European and Italian distribution for each
 180 species (Appendix S1) using visual assessment (in accord with the general approach of Zuur *et al.*
 181 2009). We obtained reliable climate models for all species except northern wheatear, which was
 182 excluded from subsequent analyses.

183

184 **Future distribution models**

185 To simulate future conditions under climate warming, we chose two scenarios with different values
 186 of representative concentration pathways (RCPs; van Vuuren *et al.*, 2011), with respectively low
 187 and high rates of climate change. We selected the RCP values of +4.5 and +8.5 W/m² (Brambilla *et al.*
 188 2015), corresponding to an average increase in global temperature of 1.4 and 2.0°C respectively
 189 (IPCC 2013), and of 3.3 and 4°C in our study area, consistent with previously recorded rates of

warming in the Alps that are approximately double the global average (Brunetti *et al.*, 2009). We downloaded relative bioclimatic variables for 2050, according to the Hadley Global Environment Model 2 (HadGEM2-ES), at a resolution of 30" from www.worldclim.org. Our choice of using 2050 as a future reference was due to the need to measure impacts on a rather short-term timescale, given that human decisions are rarely established on the basis of long-term predictions and assessments, and that the life-cycle of species is usually much shorter than the timescale often considered in studies on the effect of climate change (Chapman *et al.*, 2014). To check for consistency not only across scenarios but also across general climate models, future species distribution was modelled also according to the scenarios derived from an alternative global model (MIROC-ESM-CHEM; Watanabe *et al.*, 2011).

We selected logistic model output to allow for a binary reclassification (into suitable and unsuitable sites) of the continuous estimate of habitat suitability from MAXENT using recommended thresholds for presence-only models (e.g. Liu *et al.*, 2013; Appendix S2), selected by mapping the predicted occurrences on the basis of the individual thresholds, and comparing them with the current species range (Nardelli *et al.*, 2015). To assess model validity, we considered the respective performance over the test data set. We expected good models to show a substantial stability of the area under the curve (AUC) of the receiver-operator plot between training and test data sets (see above and Appendix S2). In general, very small differences in AUC values suggested model stability, with the partial exception of black redstart (Table S5 in Appendix S2).

A model for ski-piste distribution

We used all available information on the location of ski-pistes to identify their current distribution. Then, we manually placed in a GIS environment (by looking at detailed and updated aerial photographs) points over ski-pistes known to be currently in use, each separated by a minimum of 500m and a maximum of 1000m from the next nearest point; this procedure resulted in 610 points placed along ski-pistes throughout the entire study area. As we knew both occurrence and true

absence sites, we adopted a presence-absence modelling approach. We used multivariate adaptive regression splines (MARS, package EARTH 3.2-1, Milborrow, 2011) in R (R Development Core Team, 2013) to develop a model for ski-piste occurrence (Appendix 2). We compared the 610 points representing ski-pistes with 610 randomly placed points representing areas free from ski-pistes. The latter were placed at 5-10 kilometers from ski-piste points, to simultaneously avoid overlap with ski-areas and ensure that absence points were in mountain areas potentially suitable for ski-pistes, and were outside protected areas to avoid biases due to regulatory instead of morphological/climatic factors. We tested the potential effect of mean slope, mean radiation, annual temperature, annual rainfall, and the relative interactions. Minimum temperature and precipitation of the coldest quarter were also tested, but they were removed because of high VIF values. Variables were calculated using the same environmental layers and resolution adopted for species distribution modelling. The evimp command in EARTH 3.2-1 was used to evaluate relative variable importance in the MARS model (Milborrow, 2011; Jedlikowski *et al.*, 2014) and to confirm model validity (Appendix S2). Minimum and maximum suitable areas actually used for ski-pistes varied between 2.7 to almost 30 000 ha (average $2\,231\text{ ha} \pm 3\,877\text{ SD}$). Then, we projected the model over the whole study area both for current and future climatic conditions.

Evaluating the risk of potential overlap between birds and ski-pistes

We evaluated the overlap between the area potentially suitable for ski-pistes and i) the area potentially suitable for each target species, ii) the area suitable for different numbers of target species (from one to four), iii) the areas suitable for all the species except for snowfinch (the species displaying the most extreme variation), iv) the conservation priority areas for high-elevation passerine birds. For the latter, we identified those areas which would harbour the largest number of species, or the most affected species (snowfinch; see Results), both now and in a warmer future, whatever the scenario considered.

Ski-piste expansion is more likely to occur in the proximity of already existing ski-resorts,

242 because of accessibility and other practical reasons. Therefore, we re-ran the above analyses
243 limiting areas potentially suitable for ski-pistes to within 5 km of existing ski-pistes (i.e.
244 considering the 610 points mapped to define the current occurrence of ski-pistes; see above). We
245 selected the 5 km buffer as this figure matched the average linear extent of existing ski-resorts
246 (mean 4.75 km \pm 3.00 SD, N = 48). In summary, four scenarios were considered, low and high rates
247 of warming where any climatically and topographically suitable area could be considered for future
248 ski-piste development, and low and high rates of warming where only climatically and
249 topographically suitable areas within close proximity of an existing ski-piste could be considered
250 for future ski development.

251 **RESULTS**

252

253 Average temperature had consistently high contributions to predicting distributions across species
 254 (Appendix S2). Consequently, all species were projected to undergo a more or less marked
 255 reduction in potentially suitable areas in the future, ranging from 24% (black redstart, RCP +4.5) to
 256 97% (snowfinch, RCP +8.5) of the current range, with an average decrease across species of 58%-
 257 67% according to the two scenarios, with the scenario of higher rates of warming having the highest
 258 impact (Table 1). The future species distribution models based on scenarios derived from another
 259 global model (MIROC-ESM-CHEM) led to similar, although less severe, predictions (Appendix
 260 S2). As expected for species tied to grassland and rocky habitats, a negative effect of forest habitats
 261 and/or a positive effect of natural grassland and other open habitats was found in all species (Table
 262 S5).

263 Ski-piste occurrence was associated with annual temperatures below 6-7° (with a peak in
 264 occurrence probability at 3.1°), slopes lower than 27-28°, and was affected by the interactions
 265 between annual temperature and both slope and mean radiation: ski-piste occurrence probability
 266 was particularly low in areas less favourable to snow accumulation (Appendix S2). The area
 267 potentially suitable for ski-pistes was also projected to decrease from 529 000 to 254 000 (RCP
 268 +4.5) or 196 000 ha (RCP +8.5), thus being more than halved in 2050 compared to current
 269 conditions. The potential location of ski-pistes and the distribution of the target species were
 270 projected to show a contraction towards upper elevations (Appendix S2).

271 In addition to the overall contractions in species range, for some species the models also
 272 predicted that the overlap between areas potentially suitable for alpine birds and areas potentially
 273 suitable for ski-pistes will increase. This was the case for water pipit, alpine accentor and snowfinch
 274 (under the RCP +4.5 scenario), whereas the potential overlap for black redstart was predicted to
 275 decrease (Table 1). The area potentially suitable for all the target species was projected to undergo a
 276 large decline (91-97% according to scenario), and the potential conflict with ski-pistes marginally

277 increased, from 66% to 68-70%. Similar results were found for the areas potentially suitable for
278 three out of four species, with a less dramatic overall decrease (44-60%) coupled with a greater
279 increase in potential conflict with ski-pistes, from 44% to 61-64% (Table 2). The pattern of
280 variation in area suitable for all species combined except snowfinch was similar, although of lower
281 magnitude: a decrease in potentially suitable area of 56-70% and an increase in potential overlap
282 with ski-pistes from 60% to 63-65% were predicted.

283 The procedure for priority area definition identified c. 118000 hectares. Of those priority
284 sites, 50% are currently potentially suitable for ski-pistes; in 2050, the proportion of these areas also
285 suitable for ski-pistes will increase to 63-65% (RCP +4.5 and RCP +8.5 respectively).

286 Repeating the analyses for areas within 5 km of existing ski-pistes, the pattern of variation in
287 overlap between areas suitable for a given species (or for a given number of species) and the areas
288 suitable for ski-pistes mirrored the general pattern, although overlap was obviously lower (Tables 1
289 and 2). The potential overlap between priority areas and areas suitable for pistes was projected to
290 increase from 16% to 20-21%. This projected increase in overlap was found despite a 51-63%
291 decrease in the areas suitable for pistes (from 172 448 ha to 83 907-63 656 ha) within the adjacent
292 5-km area, i.e. fewer areas adjacent to ski-pistes will be potentially suitable for ski-piste
293 development, but there will still be an increase in the overlap with areas potentially suitable for bird
294 species.

295 **DISCUSSION**

296

297 Future climate change is likely to increase the potential conflict between high elevation bird species
 298 and skiing activities. Model outcomes suggested a shrinkage towards higher elevations and a
 299 contraction in range for both high-elevation bird distributions and locations suitable for ski-pistes in
 300 the Italian Alps by 2050. Moreover, the overlap between areas potentially suitable for high-
 301 elevation birds and those for skiing is projected to increase to the extent that most of the area above
 302 the treeline could be potentially subject to human-wildlife conflict: 61-70% of the area predicted as
 303 potentially suitable in the future for three or four species and two thirds of conservation priority
 304 areas will also be potentially suitable for ski-pistes. Limiting potentially suitable areas for ski-pistes
 305 to within 5 km of existing ones still suggested an increase in the overlap between areas potentially
 306 suitable for three bird species (not black redstart) and areas potentially suitable for ski-pistes.
 307 Obviously, the absolute overlap over the whole potential range of each species is much weaker, but
 308 importantly, this confirmed that an increase in the potential conflict due to climate change between
 309 ski-pistes and high-elevation bird species should be expected in any case.

310 Unlike the other species considered, the black redstart makes wide use of urban habitats in
 311 addition to open mountain habitats. It is projected to disappear from middle-elevation sites, but to
 312 retain a reasonable extent of potentially suitable areas both at high elevations and in urban habitats.
 313 However, the other three species are projected to lose a large part of their potential distribution.
 314 Some of these species are already declining or contracting their range in Italy (Gustin *et al.*, 2010;
 315 Rete Rurale Nazionale & LIPU, 2014; Nardelli *et al.*, 2015), and as a result of such shifts, the status
 316 of mountain grassland birds is particularly concerning (Chamberlain *et al.*, 2013; Rete Rurale
 317 Nazionale & LIPU, 2014). The pattern of range contraction was projected to be similar across
 318 species (Appendix S2), and it is likely that other high-elevation species of open habitats including
 319 birds (e.g. rock ptarmigan *Lagopus muta helvetica*) and other taxa for which high altitude
 320 grasslands hold a high diversity and/or species of conservation interest (e.g. flowers, butterflies,

321 carabids, dung beetles - Nagy *et al.*, 2003; Tocco *et al.*, 2013) may experience similar distributional
 322 changes. To that extent, our results can be considered to represent threats not just to alpine birds, but
 323 to biodiversity of high altitude open habitats in general.

324 A similar pattern of range contraction is predicted for ski-pistes. The ski industry will be
 325 affected by climate change (Behringer *et al.*, 2000; Disch *et al.*, 2007; Uhlmann *et al.*, 2009), and
 326 our results suggest a potentially marked contraction of the areas suitable for ski-pistes. Notably,
 327 given that climatic variables are representative of the period 1950-2000 (Hijmans *et al.*, 2005) and
 328 that the ski industry is particularly sensitive to climate variations, the potential distribution
 329 modelled on the basis of the 'current' conditions gave a good representation of the distribution of
 330 areas suitable for skiing in the second half of the past century. Some of the ski-pistes located in sites
 331 predicted by the model to be on the edge of the suitable area and to be less suitable for ski-pistes
 332 than those located in the 'core' of the Alpine region (e.g. in pre-Alps in Lombardy), have already
 333 been decommissioned in recent years, because of the prolonged lack of adequate snow cover, in
 334 particular at lower elevations (Pozzi, 2009; Marty, 2013). Future projections suggest that other sites
 335 at medium and low elevations will probably be decommissioned (Pozzi, 2009; Marty, 2013), in
 336 keeping with our own results. Even if the use of artificial snow (a non-sustainable adaptation; Disch
 337 *et al.*, 2007) may to some extent buffer against decreased snow cover, it is likely that ski-pistes will
 338 contract towards higher elevations to track the availability of suitable temperatures and snow cover.

339

340 **Model assumptions**

341 We used scenarios derived from a single global climate model to evaluate potential conflicts with
 342 ski-pistes. Future species distribution models based on scenarios derived from an alternative global
 343 model (MIROC-ESM-CHEM; Watanabe *et al.*, 2011) led to consistent, though less severe,
 344 predictions (Appendix S2). Although this general agreement and the fact that the predictions about
 345 temperature increase in the Alps are rather consistent across different models (Giorgi & Lionello,
 346 2008; in our study area, the correlation between average temperature values according to the

347 scenario RCP +8.5 of the two climate models was 0.98), we cannot exclude some possible minor
 348 differences in future predictions according to scenarios taken from other global models. However,
 349 we used different scenarios (RCP +4.5/+8.5 W/m²) and different assumptions
 350 (restricted/unrestricted development of ski-pistes) to provide a range of scenarios, in keeping with
 351 our generally conservative approach (see below). It is unlikely that the possible variation from using
 352 different circulation models would be greater than that associated with different emission
 353 scenarios/RCP values used; whilst there would be some variation, we expect that the general
 354 patterns would very likely be the same.

355 In our approach, we assumed constant land cover over the period considered. Significant
 356 land cover changes due to climate change at high elevation can require a fairly long time to become
 357 discernible due to lagged responses (e.g. Cannone *et al.*, 2007), although there is clearly much
 358 geographic variation (e.g. Harsch *et al.*, 2009; Carlson *et al.*, 2014). Nevertheless, we feel our
 359 approach is justified in that it gives a conservative estimate of species distribution decrease, as the
 360 most likely scenario of climate-induced habitat change is loss of open grassland habitat as treelines
 361 continue to shift upslope. Without management intervention, this may cause potentially severe
 362 reductions in the area of alpine grasslands, and increased fragmentation of remaining patches, with
 363 subsequent negative impacts on grassland species (Chamberlain *et al.*, 2013). At the same time, ski-
 364 pistes are not likely to be constrained by habitat changes, as they can be constructed on any habitat
 365 that is topographically suitable. A model that considered both altitudinal shifts in the treeline in
 366 conjunction with expansion of ski-pistes to higher altitudes would therefore almost certainly result
 367 in more severe model outcomes compared to our conservative approach. It is all the more striking
 368 then that even under the relatively conservative scenarios adopted here, there are nonetheless some
 369 major declines and increased conflicts predicted.

370 We considered only ski-pistes, but their impact extends beyond the piste itself, as the
 371 development of a ski-area also includes the development of infrastructure (e.g. roads, hotels,
 372 restaurants; Rolando *et al.*, 2013). Off-piste skiing may also be expected to respond to climate

373 changes in the same way, which also has negative consequences for biodiversity (Arlettaz *et al.*,
 374 2007). The fact that wider impacts of development of infrastructure and of off-piste skiing were not
 375 explicitly included in the approach are further factors which makes the estimates of negative
 376 impacts fairly conservative. Our model outcomes can therefore be considered to be relatively
 377 optimistic given the underlying assumptions.

378 Regarding the distribution models, the use of a rather coarse land-cover map, the lack of
 379 explicit information about model transferability, and the relatively small sample size for snowfinch
 380 should lead to some caution when interpreting the model outcomes. First, despite the low resolution
 381 of the Corine Land Cover map, the species-habitat relationships we modelled were all coherent with
 382 the basic species' ecology, and the reliable output we obtained (e.g. in terms of consistence with the
 383 observed distributions) further confirmed that at the scale considered, the use of such data coupled
 384 with climatic data provides valuable insights into species distributions. Second, although we did not
 385 explicitly evaluate model transferability across different sub-regions, the general consistency of the
 386 discriminatory ability of models across the geographically independent training and testing data
 387 (Table S5) suggested an overall validity of the species-environment relationships over the study
 388 area. Furthermore, consistency in the species trends along altitudinal gradients in different Alpine
 389 regions (unpubl. data) suggests that model transferability is likely to be high. Third, sample size was
 390 relatively low for the snowfinch ($N = 74$) compared to the other species. However, MAXENT is less
 391 sensitive to sample size than other methods (Wisz *et al.*, 2008), and there are several examples in
 392 the literature of robust MAXENT models with much lower sample sizes (e.g. Guisan *et al.*, 2007;
 393 Wisz *et al.*, 2008; Brambilla, 2015), and indeed, snowfinch models evaluated by visual assessment
 394 and by AUC had good predictive ability. Nevertheless, future insights based on a larger sample may
 395 potentially increase model accuracy and hence would be desirable for this scarce high altitude
 396 specialist.

397 Future specific work is required to further understand the ultimate mechanisms driving
 398 species occurrence. In common with the general climate envelope modelling approach, we

399 implicitly assume that climate, either directly or indirectly (e.g. via resources) is a key determinant
 400 of species distributions, although such approaches have limitations for estimating the true niche of a
 401 species (Schurr *et al.*, 2012). We can conclude little on the precise mechanisms that may influence
 402 species distributions. There is a need for further studies, especially in mountain environments which
 403 are poorly studied, to understand mechanisms underpinning apparently climate-limited species
 404 distributions and hence to identify potential compensatory or mitigation measures (Chamberlain *et*
 405 *al.* 2012).

406

407 **Applications**

408 Given the alarming range contractions forecast for high elevation species in general, and the
 409 increasing potential impact of ski-pistes on those species, it is essential to develop conservation
 410 strategies to safeguard high alpine habitats against negative effects of ski development. There is a
 411 need to promote better management of existing ski-pistes to minimise their negative impacts,
 412 through grassland restoration and minimization of deleterious management practices (Negro *et al.*,
 413 2013; Rixen & Rolando, 2013). However, the priority should be to secure the persistence of
 414 climatically and structurally suitable sites for those threatened species, unaltered by development.
 415 We identified c. 118 000 hectares that are currently suitable for the most threatened species
 416 (snowfinch) and/or for all the other species belonging to the species assemblage (mountain
 417 grassland birds), and that will remain suitable in the future, whatever the scenario considered; those
 418 areas should be regarded as conservation priorities, where the development of ski infrastructures
 419 should be avoided. Unfortunately, the potential pressure on those areas will be high, as two thirds of
 420 them will also be suitable for future ski-piste development. The scenarios which considered that
 421 potentially suitable areas for ski-pistes will only be in the proximity of existing ski-pistes predicted
 422 a consequently lower overlap with areas potentially suitable for high-elevation bird species.
 423 However, many areas close to and including existing ski-pistes may not be climatically suitable for
 424 adequate snow conditions in the future, hence there is likely to be further pressure to develop new

425 ski resorts far from existing ones.

426 The skiing industry provides economic benefits to local mountain communities which
427 otherwise could have limited economic capacity (Elsasser and Messerli, 2001), and it is already
428 adapting to climate changes, via a range of different measures adopted to offset adverse economic
429 impacts, putting new pressures on mountain environments (Marty, 2013). A clear conservation
430 strategy is thus required to preserve suitable conditions in the priority areas for the protection of
431 alpine biodiversity (Fig. 2). Given that there are some areas which are predicted to be potentially
432 suitable for ski-pistes, but which are not within the conservation priority areas, a way to minimize
433 the impact of new developments would be to perform a first selection of areas for new ski-pistes
434 among those sites. Clearly, other factors should then be taken into account (e.g. occurrence of other
435 species or habitats of conservation concern, accessibility, economic feasibility, etc.), but our outputs
436 could provide spatially explicit guidance in avoiding planned development in the most important
437 sites for the conservation of high-elevation biodiversity.

438 Consequently, effective conservation strategies, implemented at a landscape scale, need to
439 consider prevention of ski-piste construction in sites characterized by high conservation value. The
440 approach developed here provides a means by which such a strategy could be formulated.

441

442 **ACKNOWLEDGMENTS**

443

444 G. Assandri, E. Bassi, M. Belardi, A. Iemma provided additional field data. Two anonymous
445 reviewers provided useful comments on previous drafts of the article. MB was partly supported by
446 the LIFE+ project "LIFE11 NAT/IT/044 GESTIRE". Most of data from Trento province have been
447 made available through the WebGIS developed within the LIFE+ project "LIFE11/IT/187 T.E.N."
448 and MB and PP were also partly supported by this project and by the Accordo di Programma per la
449 Ricerca PAT/MUSE 2014. DEC was funded by the People Programme (Marie Curie Actions) of the
450 European Union's Seventh Framework Programme FP7/2007-2013/.

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640 **Supporting Information**

641 Additional Supporting Information may be found in the online version of this article:

642 S.1. Dataset of bird occurrence and selection of target species

643 S.2. Modelling distribution of ski-piste and bird species

644

645 **BIOSKETCH**

646 Our research focus is on animal ecology and conservation in high altitude habitats, with particular
647 emphasis on the effects of environmental change and of direct and indirect human impacts on alpine
648 faunal biodiversity.

649 Author contributions: M.B. and D.E.C. collected part of the field data; P.P. and A.R. managed
650 fieldwork in Trentino and Piemonte, respectively; M.B. took a lead on the analyses; M.B. and
651 D.E.C. wrote a first draft of the paper; all authors contributed to the final version of the paper.

652

653 **Editor:** Richard Ladle

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Table 1 Predicted decrease in species range and overlap with cells potentially suitable for ski-pistes in Italy in current and future scenarios according to the climates predicted under RCPs of +4.5 and +8.5 (general overlap and overlap considering sites potentially suitable for ski-pistes only within 5 km from existing ones).

	Suitable area (ha*1000)			Distribution change		Overlap with areas suitable for ski-pistes			Overlap with areas suitable for ski-pistes (< 5 km)		
	current	+4.5	+8.5	+4.5	+8.5	current	+4.5	+8.5	current	+4.5	+8.5
Water pipit	617	264	184	-57%	-70%	53%	61%	64%	17%	19%	20%
Alpine accentor	615	261	193	-57%	-69%	43%	48%	49%	14%	15%	15%
Black redstart	902	685	622	-24%	-31%	47%	31%	26%	16%	10%	9%
Snowfinch	318	27	10	-91%	-97%	42%	47%	42%	14%	15%	15%

660 **Table 2** Suitable area for different levels of species richness, and the relative overlap in Italy with
 661 areas potentially suitable for skiing under current and future conditions (general overlap and overlap
 662 considering sites potentially suitable for ski-pistes only within 5 km from existing ones).

663

No. of species	Area (ha * 1000)			Overlap with ski			Overlap with ski (< 5 km)		
	current	+4.5	+8.5	current	+4.5	+8.5	current	+4.5	+8.5
1	431	476	473	24%	13%	11%	9%	5%	4%
2	161	87	68	40%	51%	52%	7%	28%	16%
3	308	171	124	44%	61%	64%	14%	19%	20%
4	193	18	6	66%	70%	68%	23%	23%	25%

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667 **Figure 1** Location of the study area in Italy, defined as the provinces included in the Alpine
668 Convention in Piedmont, Lombardy and Trentino. Extent 40,569 km², elevation range 30-4,600 m
669 asl.

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674 **Figure 2** Spatial relationship between conservation priority sites (sites suitable for snowfinch and/or
675 all the other high-elevation species in 2050) and sites suitable for ski-pistes in 2050 (upper: RCP
676 +4.5; lower: RCP: +8.5), in the southern Alps, and in two sample areas (for RCP +4.5), Val d'Ossola
677 (left) and Valtellina (right).