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Original article

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

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ABSTRACT

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

Location Italian Alps.

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

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

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

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

INTRODUCTION

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

High-mountain regions harbour a relatively high biodiversity (Dirnböck *et al.*, 2011) and a high percentage of both endemic (Essl *et al.*, 2009) and vulnerable species (Viterbi *et al.*, 2013). Many species are restricted to the upper elevations of their former range because of human pressures (Martin, 2001) and thus careful management of mountains is crucial for conservation (Rolando *et al.*, 2013). Mountain regions are particularly threatened by climate change (Brunetti *et al.*, 2009) and show a higher rate of warming compared to the global average (Böhm *et al.*, 2001). Species and habitats are already undergoing elevational range shifts due to climate warming, which is predicted to have important impacts on biodiversity at high elevation (Sekercioglu *et al.*, 2008; Dirnböck *et al.*, 2011; Chamberlain *et al.*, 2013). However, habitat changes caused by human action may have more severe consequences than climate change (Jetz *et al.*, 2007), or may interact with it, showing synergistic effects (Mantyka-Pringle *et al.*, 2012).

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

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

We aim to describe the increase in the potential impact of ski-pistes on alpine biodiversity by modelling the potential future distributions of both species and ski-pistes in relation to projected climate changes in the European Alps. Our goal is to highlight where conflicts between downhill skiing and nature conservation are most likely to occur over the next decades, by constructing spatially explicit models of conflict zones between ski-pistes for downhill skiing and wildlife (Braunisch *et al.*, 2011), using high-elevation birds as an example group. We first model the current and future distribution of some high-altitude bird species potentially vulnerable to ski-piste development in relation to climate, habitat and topography. Then, we model the current and future distribution of ski-pistes in relation to climate and topography; finally, we adopt an approach to reduce possible future conflicts by evaluating where they may arise. Among the areas that should be considered as high-priority for the conservation of high-elevation species in a warmer climate, we identify those which are likely to be suitable for ski-pistes in the future, and hence those where ski-developments should be restricted or regulated.

MATERIALS AND METHODS

Study area, fieldwork and model species

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

Modelling species distributions

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

To make distribution models as general and robust as possible, we applied the approach proposed by Radosavljevic & Anderson (2014), adopting a masked geographically structured evaluation of models. We divided our study area into four longitudinal belts (see Fig. S8 in Appendix S2), and used records and background points (10 000) from eastern and central-western portions to build models (training data), and records from western and central-eastern portions to evaluate models (test data).

Environmental variables included land cover, bioclimatic and topographical variables (Table S3). Ten land cover types were selected from the CORINE Land Cover (CLC2006; EEA, 2007) database in order to describe the habitat composition of each cell, assuming constant land cover over the time period (up to 2050). Two bioclimatic variables, annual temperature and precipitation, were calculated for each grid cell from the values downloaded from WorldClim v.1.4 (Hijmans *et al.*, 2005; http://www.worldclim.org; resolution 30 arc-seconds, corresponding to less than 1-km at this latitude). Slope and solar radiation (calculated taking 21st June as the reference day), were extracted from a Digital Terrain Model (resolution 20 m) of the study area. Before distribution modelling, we checked for multicollinearity among environmental predictors in order to minimize the risk of overfitting species' responses to climate. Variance Inflation Factors (VIFs) were evaluated, and highly collinear variables (VIF > 5) were omitted, following Zuur et al. (2009). This procedure included an evaluation of seasonal, in addition to annual, bioclimatic variables, but the former showed high levels of collinearity, therefore only annual values were used in distribution modelling (see below).

All environmental variables were calculated for 40 m x 40 m cells; for each cell, values represented i) the sum of cover (total area) per each type of land cover, ii) the average slope, and iii) the mean solar radiation, all referring to a radius of c. 100 m from each cell. For bioclimatic variables, we assigned to each 40 m x 40 m cell the value of the 30 arc-seconds cell with which it overlapped. Given the raster structure, this resulted in variables measured over an area of slightly more than 2 ha, a grain that matches fairly well with the supposed territory sizes, and hence the main areas of activity, of the species considered (Cramp, 1998; Gustin *et al.*, 2010). To reduce the risk of overfitting, we fitted models considering only linear and quadratic terms (dropping interaction, threshold and hinge functions), irrespective of sample size.

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

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

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

Future distribution models

To simulate future conditions under climate warming, we chose two scenarios with different values of representative concentration pathways (RCPs; van Vuuren *et al.*, 2011), with respectively low and high rates of climate change. We selected the RCP values of +4.5 and +8.5 W/m^2 (Brambilla *et al.*, 2015), corresponding to an average increase of +1.4 and 2.0˚C respectively in global temperature (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).

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 2), 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 S4 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, 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 was used to evaluate relative variable importance (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 ha ± 3 877 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 variables representing the distribution of target species considering: 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).

Ski-piste expansion is more likely to occur in the proximity of already existing ski-resorts, because of accessibility and other practical reasons. Therefore, we re-ran the above analyses for each species, limiting areas potentially suitable for ski-pistes to within 5-km of existing ski-pistes (i.e. considering the 610 points mapped to define the current occurrence of ski-pistes; see above). We selected the 5 km buffer as this figure matched the average linear extent of existing ski-resorts (mean 4.75 km ± 3.00 SD, N = 48). In summary, four different scenarios were considered, low and high rates of warming where any climatically and topographically suitable area could be considered for future ski-piste development, and low and high rates of warming where only climatically and topographically suitable areas within close proximity of an existing ski-piste could be considered for future ski development.

RESULTS

Average temperature had consistently high contributions to predicting distributions across species (Appendix S2). Consequently, all species were projected to undergo a more or less marked reduction in potentially suitable areas in the future, ranging from 24% (black redstart, RCP +4.5) to 97% (snowfinch, RCP +8.5) of the current range, with an average decrease across species of 58% - 67% according to the two scenarios, with the scenario of higher rates of warming having the highest impact (Table 1). As expected for species tied to grassland and rocky habitats, a negative effect of forest habitats and/or a positive effect of natural grassland and other open habitats was found in all species (Table S4).

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

In addition to the overall contractions in species range, for some species the models also predicted a decrease in the proportion of species distributions unsuitable for ski-piste developments, i.e. the overlap between areas potentially suitable for alpine birds and areas potentially suitable for ski-pistes will increase. This was the case for water pipit, alpine accentor and snowfinch (under the RCP +4.5 scenario), whereas the potential overlap for black redstart was predicted to decrease (Table 1). The areas potentially suitable for all the target species were projected to undergo a large decline (91%-97% according to scenario), and the potential conflict with ski-pistes for these areas to increase, from 66% to 68%-70%. Similar results were found for the areas potentially suitable for three out of four species, with a less dramatic overall decrease (44%-60%) coupled with a greater increase in potential conflict with ski-pistes, from 44% to 61%-64% (Table 2). The pattern of variation in areas suitable for all species combined except snowfinch was similar, although of lower magnitude: a decrease in potentially suitable areas of 56%-70% and an increase in potential overlap with ski-pistes from 60% to 63%-65% were predicted.

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

Repeating the analyses for areas within 5 km of existing ski-pistes, the pattern of variation in overlap between areas suitable for a given species (or for a given number of species) and the areas suitable for ski-pistes mirrored the general pattern, although overlap was obviously lower (Tables 3 and 4). The potential overlap between priority areas and areas suitable for pistes was projected to increase from 16% to 20%-21%. This projected increase in overlap was found despite a 51%-63% decrease in the areas suitable for pistes (from 172 448 ha to 83 907-63 656 ha) within the adjacent 5-km area, i.e. fewer areas adjacent to ski-pistes will be potentially suitable for ski-piste development, but there will still be an increase in the overlap with areas potentially suitable for bird species.

DISCUSSION

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

Black redstart makes wide use of urban habitats in addition to open mountain habitats, unlike the other species considered, and is projected to disappear from middle-elevation sites, but to retain a reasonable extent of potentially suitable areas both at high elevations and in urban habitats. However, the other three species are projected to lose a large part of their potential distribution. Some of these species are already declining or contracting their range in Italy (Gustin *et al.*, 2010; Rete Rurale Nazionale & LIPU, 2014; Nardelli *et al.*, 2015), and as a result of such shifts, the status of mountain grassland birds is particularly concerning (Chamberlain *et al*., 2013; Rete Rurale Nazionale & LIPU, 2014). The pattern of range contraction was projected to be quite similar across species (Appendix S2), and it is likely that a similar distributional change may also be relevant to other high-elevation species of open habitats in the future, including birds (e.g. rock ptarmigan *Lagopus muta helvetica*) and other taxa for which high altitude grasslands hold a high diversity and/or species of conservation interest (e.g. flowers, butterflies, carabids, dung beetles - Nagy *et al*., 2003; Tocco *et al*., 2013). To that extent, our results can be considered to represent threats not just to alpine birds, but to biodiversity of high altitude open habitats in general.

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

Model assumptions

We used scenarios derived from a single global climate model to evaluate potential conflicts with ski-pistes. Future species distribution models based on scenarios derived from an alternative global model (MIROC-ESM-CHEM; Watanabe et al. 2011) led to consistent, though less severe, predictions (Appendix 2). Although this general agreement and the fact that the predictions about temperature increase in the Alps are rather consistent across different models (Giorgi & Lionello, 2008; in our study area, the correlation between average temperature values according to the scenario RCP +8.5 of the two climate models was 0.98), we cannot exclude some possible minor differences in future predictions according to scenarios taken from other global models. However, we used different scenarios (RCP +4.5 and +8.5 W/m^2) and different assumptions (restricted or unrestricted development of ski-pistes) to provide a range of scenarios, in keeping with our generally conservative approach (see below). It is unlikely that the possible variation from using different circulation models would be greater than that associated with different emission scenarios/RCP values used – whilst there would be some variation, we expect that the general patterns would very likely be the same.

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

We considered only ski-pistes, but their impact extends beyond the piste itself, as the development of a ski-area also includes the development of infrastructure (e.g. roads, hotels, restuarants; Rolando *et al.*, 2013). Off-piste skiing may also be expected to respond to climate changes in the same way, which also has negative consequences for biodiversity (Arlettaz *et al*., 2007). The fact that wider impacts of development of infrastructure and of off-piste skiing were not explicitly included in the approach are further factors which makes the estimates of negative impacts fairly conservative. Our model outcomes can therefore be considered to be relatively optimistic given the underlying assumptions.

Regarding the distribution models, the use of a rather coarse land-cover map, the lack of explicit information about model transferability, and the relatively small sample size for snowfinch should lead to some caution when interpreting the model outcomes. First, despite the low resolution of the Corine Land Cover map, the species-habitat relationships we modelled were all coherent with the basic species' ecology, and the reliable output we obtained (e.g. in terms of high AUC values) further confirmed that at the scale considered, the use of such data coupled with climatic data provides valuable insights into species distributions. Second, although we did not explicitly evaluate model transferability across different sub-regions, the general consistency of the discriminatory ability of models across the geographically independent training and testing data (Table S4) suggested an overall validity of the species-environment relationships over the study area. Furthermore, consistency in the species trends along altitudinal gradients in different Alpine regions (unpubl. data) suggests that model transferability is likely to be high. Third, sample size was relatively low for the snowfinch (N = 74) compared to the other species. However, MaxEnt is less sensitive to sample size than other methods (Wisz *et al.*, 2008), and there are several examples in the literature of robust MaxEnt models with much lower sample sizes (e.g. Guisan *et al.*, 2007; Wisz *et al.*, 2008; Brambilla, 2015), and indeed, snowfinch models evaluated by visual assessment and by AUC had good predictive ability. Nevertheless, future insights based on a larger sample may potentially increase model accuracy and hence would be desirable for this scarce high altitude specialist.

Future specific work is required to further understand the ultimate mechanisms driving species occurrence. In common with the general climate envelope modelling approach, we implicitly assume that climate, either directly or indirectly (e.g. via resources) is a key determinant of species distributions, although such approaches have limitations on estimating the true niche of a species (Schurr *et al.*, 2012). We can conclude little on the precise mechanisms that may influence species distributions. There is a need for further studies, especially in mountain environments which are relatively poorly studied, to understand mechanisms underpinning apparently climate-limited species distributions and hence to identify potential compensatory or mitigation measures (Chamberlain et al. 2012).

Applications

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

The skiing industry provides economic benefits to local mountain communities which otherwise could have limited economic capacity (Elsasser and Messerli 2001). Adaptation of skiing activities in response to climate change via the construction of pistes in more climatically suitable areas could be therefore desirable for the local economy. Given that there are some areas which are predicted to be potentially suitable for ski-pistes, but which are not within the conservation priority areas, a way to minimize the impact of new developments would be to perform a first selection of areas for new ski-pistes among those sites. Clearly, other factors should then be taken into account (e.g. occurrence of other species or habitats of conservation concern, accessibility, economic feasibility, etc.), but our outputs could provide spatially explicit guidance in avoiding planned development in the most important sites for the conservation of high-elevation biodiversity.

A clear conservation strategy is required to preserve suitable conditions in the priority areas for the protection of alpine biodiversity (Fig. 2). The winter tourism industry is already adapting to climate changes, via a range of different measures adopted to offset adverse economic impacts, putting new pressures on mountain environments (Marty, 2013). Consequently, effective conservation strategies, implemented at a landscape scale, need to consider prevention of ski-piste construction in sites characterized by high conservation value. The approach developed here provides a means by which such a strategy could be formulated.

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Supporting Information

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

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

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

BIOSKETCH

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

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

Table 1 Predicted decrease in species range and overlap with cells potentially suitable for ski-pistes 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%

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

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%

Figure 1 Location of the study area in Italy, defined as the provinces included in the Alpine Convention in Piedmont, Lombardy and Trentino. Extent 40,569 km^2, elevation range 30-4,600 m asl.

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