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Assessing the sensitivity of alpine birds to potential future changes in habitat and climate

D.E. Chamberlain*, M. Negro, E. Caprio and A. Rolando

Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy

*Corresponding author. E-mail: dan.chamberlain99@gmail.com, tel. 0039 0116704534

ABSTRACT

Climate change has resulted in upward elevational shifts in the distribution of animals and plants in many high altitude areas. The potential consequences of such changes for alpine bird communities were assessed by modelling data on breeding bird distributions along altitudinal gradients at relatively high altitude (c. 1700-3100m) in the European Alps in relation to habitat, topography and temperature. These models were used to assess the sensitivity of species to potential future environmental change by estimating distributions under a range of scenarios of habitat and climate change. Distributions of the majority of forest or shrub nesting species remained stable or increased in response to climate change according to most scenarios as a result of elevational shifts in suitable habitats. However, open habitat species may face a severe decrease in distribution as grasslands are colonised by forest and shrubs, because much of the area considered is not at a sufficient altitude to accommodate further elevational shifts. This may be exacerbated if upward shifts in vegetation are constrained at high altitudes, leading to a habitat 'squeeze' caused by an asymmetric response of vegetation zones to climate change at higher altitudes. Model outcomes suggested that management to maintain open habitats may not be sufficient for a number of species if climate change results in a mismatch between the distribution of suitable climates and suitable habitats. The loss of open habitats due to differential responses of vegetation zones to climate change may therefore present a serious conservation problem for mountain biodiversity in the future.

Keywords – Altitudinal transect, climate change, grassland, species distribution, treeline, Water Pipit

1. Introduction

Climate change impacts on the distribution of animal and plants are well documented (e.g. Parmesan and Yohe 2003). Typically, as a result of general increases in temperature, poleward range shifts have been reported for a large number of organisms, including plants, birds and butterflies (e.g. Sturm et al., 2001; Thomas and Lennon, 1999; Settele et al., 2008). Analogously, altitudinal shifts have also been documented, most notably for plants (e.g. Grabherr et al., 1994; Harsch et al., 2009), but also for birds (Maggini et al., 2011; Reif and Flousek, 2012), butterflies (Wilson et al., 2005), and small mammals (Moritz et al., 2008).

Predicting impacts of climate change on biodiversity has become a key research topic (Bellard et al. 2012), and has particular importance in identifying, and making provision for, potential future conservation problems. For animals and plants, how their main habitats will change in response to climate change is a key question, and often it is assumed that habitats will shift in tandem with climate, although few models have tried to incorporate both climate and habitat change scenarios (Jeltsch et al. 2011). However, habitats may change for other reasons, particularly due to human intervention, and such changes may have more severe consequences than climate change (Jetz et al. 2007), but they may also interact with, and be amplified by, climate change (Mantyka-Pringle et al. 2012). Furthermore, differential shifts in climate and habitats may lead to a de-coupling of suitable climatic and suitable habitat conditions (e.g. Reif et al. 2010). An understanding of how habitat and climate interact is therefore needed in order to forecast likely future impacts on biodiversity (Barnagaud et al. 2012).

High altitude regions are expected to be especially vulnerable to climate change (Brunetti et al., 2009), and have shown a rate of warming approximately double the global average (Beniston et al., 1997; Böhm et al., 2001). The elevational range shifts that will occur as a consequence of climate warming are expected to have serious consequences for biodiversity at relatively high altitude (Sekercioglu et al., 2008; Dirnböck et al., 2011). Shifts in major habitat types, for example advancing tree lines (Harsch et al., 2009), may alter the distribution of habitats, leading to increased fragmentation and eventual loss of habitats at higher altitude (e.g. Peñuelas and Boada, 2003; Gonzalez et al., 2010). However, it should also be acknowledged that the European Alps at least are subject to many pressures, including changes in agriculture, particularly the abandonment of traditional seasonal grazing practices (Laiolo et al., 2004), and increased disturbance from human leisure activities, especially winter sports (e.g. Rolando et al., 2007).

Elevational shifts in alpine plant communities in general are well studied ('alpine' here is defined as high altitude mountainous areas at or above the elevational limit of the treeline), and there is evidence that such shifts may not occur at the same rate across different altitudes, nor for different geographical areas. Cannone et al. (2007), in common with many other studies, found recent upward shifts in alpine grassland and shrubland, but they also observed that changes in plant distribution were asymmetrical, and there was little change, and even decreases in vegetation cover, at higher altitudes (<2800m). Recent research has also highlighted the potential negative impacts on soil processes at high altitudes, in particular the likelihood that warmer temperatures could lead to colder soils if snow cover, and its associated insulating properties, are reduced (Edwards et al., 2007; Freppaz et al., 2010). Such an effect would prevent the development of vegetation, and in particular sward-forming grasses, at high altitudes (in accord with Cannone et al., 2007), yet at the same time, this habitat is likely to be lost at lower altitudes due to advancing treelines. There is therefore a potential threat to alpine grasslands due to this differential response of vegetation zones to climate change.

Predicting climate impacts on altitudinal distributions is complicated by the variation in climate over small scales due to the steepness of the terrain (typically there is approximately a 0.5°C-0.65°C decrease for every 100m increase in altitude; e.g. Hodkinson, 2005; Colwell et al. 2008), and relatively few studies have attempted to assess likely consequences of environmental (including climate) change on high alpine faunal biodiversity. Altitudinal gradients provide a good basis for studying climate change (Shoo et al., 2006), as the climatic conditions vary over a small spatial scale, thus spatial variations along the gradient provide a substitution for processes over time (Hodkinson, 2005), and macroecological influences that may complicate the interpretation of latitudinal studies are reduced (Rahbek, 2005).

In this paper, we modelled the altitudinal distributions of breeding alpine bird species at relatively high altitudes (c. 1700-3000m), surveyed along altitudinal transects, in relation to habitat, topography and climate. These models were then used to assess the birds' sensitivity to future climate warming by estimating change in potential breeding distribution according to scenarios of climate and habitat change. Our over-arching goal was to identify species, and habitats with which they are closely associated, that are likely to be sensitive to future environmental changes at high elevations. Whilst elevational shifts due to climate change have typically been assessed at relatively large scales (e.g. Jetz et al., 2007; Sekercioglu et al., 2008; Dirnböck et al., 2011), it is clear that much finer scale-data is needed that more closely matches the climatic variation that occurs over small spatial scales in alpine habitats (Sekercioglu et al. 2008). The extent to which changes in different habitats, and in particular their differential responses to climate change, will affect high altitude faunal distributions associated with the different vegetation zones has not, as far as we are aware, been considered at appropriate spatial scales.

2. Methods

2.1 Site and point selection

The study area was high altitude habitat (minimum 1700m asl) in the western Italian Alps in the province of Torino (Fig. 1), from the Pellice Valley in the south (44°43'11'' N; 7°03'35'') to the Orco Valley in the north (45°30'42''N; 7°16'25''). This area is dominated by larch *Larix* spp. at lower altitudes, and shrub species such as Juniper *Juniperus communis* and Alpenrose *Rhododendron ferrugium*. Grasslands occur throughout the area, consisting of seasonal pastures and higher altitude alpine grassland. Scree and rocky areas are dominant above c. 2700m.

Using land cover data and altitude from a DTM in Geographic Information Systems (GIS) software package, ArcGIS 9.2 (ESRI, 2007), potentially suitable locations for survey sites were identified that had larch-dominated forest at lower altitudes, and where the highest points were at an altitude of at least 2500m. Villages (including tourist developments) and ski-pistes were avoided (a minimum of 330m from the point location). Transects spaced at least 1-km apart were initially selected at random, but due to the difficulty of the terrain, the nearest footpath to the initially selected transect was usually used. Point counts were carried out along the transects with a minimum spacing of 200m between points (or selecting the first suitable location after 200m). Suitable points were those without any obvious disturbance (e.g. occupied human habitation, livestock) or where detectability may have been affected (e.g. large cliffs, noisy streams in spate) within 100m. Sampling took place over three years (2010-2012).

2.2. Field surveys

Standard point count methods were carried out (Bibby et al., 2000), using a ten minute count period preceded by a five minute settling period. At each point, the observer (DEC) recorded all birds seen and heard, including their activity using standard activity codes (Bibby et al., 2000). For each registration, the distance from the observer was estimated with the aid of a laser range finder. Simple habitat data were also collected at each point, including the percentage cover of canopy (i.e. above head height) and the number of mature trees (≥20cm in diameter) within a 50m radius. Point counts commenced 1 to 1.5 hours after sunrise and continued until 1300 hrs.

2.3 Habitat, topography and climate data

The cover of 5 relevant habitat types (i.e. those occurring above 1700m), selected based on the likely ecological importance for the species under consideration (according to standard works such as Snow and Perrins, 1998, and expert knowledge), was extracted from the Piani Forestali Territoriali (PFT) land cover database for the whole province (www.regione.piemonte.it/foreste/cms/foreste/pianificazione): coniferous forest, scrub, pasture (created as a result of human influence, relatively heavily grazed with a continuous and usually relatively dense sward), grass (natural, though often lightly grazed in late summer, interspersed with rocks, usually at higher altitudes) and rock/scree (details in online Appendix, Table A1). The treeline was simply defined as the perimeter of forest habitat within the study area. As the goal was to estimate species distributions at a relatively large scale, land cover data, rather than habitat data collected in the field, was used in the modelling. However, there were strong correlations between forest land cover and the comparable habitat variables canopy cover (Pearson correlation $r_{255} = 0.86$, $P > 0.0001$) and number of mature trees within 50m ($r_{255} = 0.77$, $P > 0.0001$) collected in the field, suggesting that the land cover data provided a good representation of habitat 'on the ground'.

Mean, minimum and maximum annual temperature, and mean monthly precipitation at a 1-km square scale were extracted from WorldClim (Hijmans et al., 2005). Topographic data (aspect and slope) were derived from the DTM elevation grid at a 1ha scale. Mean values were calculated for each 100m radius point count location. Easting and northing have been shown to have separate effects on alpine plant and animal distributions (Guisan et al., 1998; Rauter and Reyer, 2000), so both were considered, expressed as an index equal to $-\cos(A)$, where A is the aspect (east or south) expressed in radians (Bradbury et al., 2011). A value of 1 represents facing directly south or east, and -1 represents facing directly north or west. Altitude (expressed in m) at each point was recorded by the GPS in the field to an accuracy of at least ±20m (but usually ±5m).

2.4 Statistical methods

The presence of singing birds detected within 100m radius of the point count location was used to analyse the breeding distribution of alpine birds. This radius was selected to ensure no adjacent points were overlapping (the minimum distance apart being 200m). A total of 257 points along 33 transects was surveyed over 396 visits, covering an altitudinal range of 1717m to 3056m. Only species that were recorded on at least 35 points were considered for analysis (preliminary analyses suggested model fits were consistently poor below this value).

Prior to developing predictive models, points that were in habitats wholly outside a species' normal breeding range were removed ('bad zeros' which may cause model fitting problems whilst providing no useful information; Zuur et al., 2009). In practice, the species considered here can be divided into forest/shrub species and open habitat species. The former are those that require the presence of trees or shrubs for nesting, and wholly unsuitable habitats were hence simply defined as those with zero forest plus shrub cover, leaving a total sample of 150 points. Forest/shrub species with sufficient samples for analysis were Tree Pipit *Anthus trivialis* (singing birds present on 39 points), Dunnock *Prunella modularis* (n = 36), Wren *Troglodytes troglodytes* (n = 41), Coal Tit *Periparus ater* (n = 46), Willow Tit *Poecile montanus* (n = 39) and Chaffinch *Fringilla coelebs* (n = 93). Open habitat species with sufficient samples for analysis were Skylark *Alauda arvensis* (n = 41), Water Pipit *Anthus spinoletta* (n = 67), Wheatear *Oenanthe oenanthe* (n = 46) and Black Redstart *Phoenicurus ochruros* (n = 49). These species nest on or near the ground, and have been recorded as showing strong preferences for open habitats (Snow and Perrins, 1998), although a universal definition of open habitat was not really possible as such species may show varying levels of tolerance to forest or shrubs. The maximum forest cover of a given point in which the four species were recorded was 40% for Skylark, 4% for Wheatear, 0% for Water Pipit and 71% for Black Redstart. Based on these results, 'open' habitats were defined as those with less than 50% forest cover for

Skylark, less than 10% for Wheatear, 0% for Water Pipit and less than 80% for Black Redstart (sample sizes were respectively 197, 156, 170 and 224).

As some points were visited more than once (44%), the probability of occurrence was modelled as a vector of presences and absences (i.e. the successes/failures syntax of Crawley, 2007) to account for variation in survey effort, using binomial logistic regression in a general linear mixed-modelling framework with the lmer command in the lme4 package in R. In order to account for potential spatial autocorrelation between points on the same transect, 'site' was fitted as a random term. In order to assess the predictive ability of the models, data were divided into model (70%) and test (30%) data sets.

Habitat variables expressed as a proportion were arcsine-square root transformed prior to analysis. This to some extent reduced linear dependence, but there were still some unacceptably high correlations amongst variables, in particular there was very high inter-correlation between all four climate variables (Pearson's correlation $|r| > 0.79$, $P < 0.001$ in each case). In order to reduce the level of collinearity prior to modelling, variance inflation factors (VIFs) were calculated, and the variable with the highest VIF was sequentially removed and VIFs re-calculated (following Zuur et al., 2009) until all variables had a VIF < 2.0. There was no strong evidence of spatial autocorrelation according Moran's I calculated from model residuals (online Appendix Table A2).

Once the final model variable set had been identified, model averaging (Burnham and Anderson 2002) was carried out using the MuMIn package in R (R Core Development Team, 2010), averaged parameter estimates being calculated across the set of models which accounted for 95% of the sum of all model weights. Predictive ability was assessed by calculating two different metrics (reliance on only a single measure of model fit is not recommended – Elith and Graham, 2009) calculated from the averaged models applied to the test data set. These were the area under the receiver operating characteristics (ROC) curve (AUC; Fielding and Bell 1997) and the True Skill

Statistic (TSS; Allouche et al., 2006). Models that had a predictive ability no better than random, considered as AUC < 0.60 or TSS < 0.10, were not used subsequently.

2.4.1 Scenarios of environmental change

Climate, topographic and habitat variables were derived for the whole province, and the mean value or percentage cover as appropriate was calculated for hexagons of 200m width (henceforth ‘cell’), hence maintaining the resolution at which the survey data was collected. Using parameter estimates derived from the modelling approach, the current probability of occurrence of each species was estimated for each cell for altitudes above 1700m, with wholly unsuitable habitats (see above) being assigned a zero probability. Different scenarios of habitat and climate change were then applied, and the change in estimated range of each species was calculated for each scenario.

To estimate the potential consequences of climate and habitat change, we considered three principal drivers: change in mean temperature, elevational shift in habitats and the response of the upper limit of the vegetation zone, basing scenarios on climate predictions for the year 2080 using the projections derived from the Hadley General Circulation Model (specifically HADCM3) available in WorldClim (Hijmans et al., 2005) for IPCC scenario B2A (medium rate of change). We intentionally adopted a conservative approach in selecting the least extreme projections of climate change available for the scale required. The average increase in temperature by 2080 (calculated at the cell level) for the study area according to B2A projections was 3.3°C.

Scenarios were based on logistic regression models to simulate natural variation in habitat cover due to climate and topography. The presence of each of the five habitat types in each cell was modelled separately in relation to topographic and climate variables, and all two way interactions between both linear and quadratic climate terms, for the whole province (i.e. the whole regional climatic range including all altitudes). Data were divided into model and test data sets and multi-model inference was used to derive model averaged parameter estimates, as for the bird data. The resulting estimates of the probability of occurrence for each habitat were used to calculate AUC and TSS from the test data, and to identify optimal thresholds for defining presence using the PresenceAbsence package in R (Freeman, 2007) for the study area (≥1700m in altitude), i.e. a habitat was considered present for a given cell if the estimated probability of occurrence was equal to or greater than the threshold.

The above procedure produced separate distributions for each of the five habitats, which partially overlapped one another. The next step was to combine these distributions into a current modelled habitat surface by first applying thresholds to the predicted probabilities for each habitat for each cell (see below), setting area to 0 for any habitat that did not have a probability above the threshold for a given cell. The sum of the probabilities of the remaining habitats was then calculated. The cover of an individual habitat type per cell was then its individual probability of occurrence divided by the total, hence the estimated cover of an individual habitat type was weighted by the probabilities of the other relatively important (i.e. above threshold) habitats in a given cell. In this way, it was possible to have a cell with mixed habitats as long as they had predicted probabilities greater than their respective thresholds. A number of different methods for defining thresholds are available, and we considered three that are considered to be among the best (Liu et al. 2005): the prevalence approach, the sensitivity-specificity sum maximization approach and the sensitivity-specificity equality approach. The combination of thresholds that resulted in the closest match to the observed habitat vertical distribution was identified (specifically the mean altitude was required to be within 100m of the observed altitude for each habitat). The best fit was generally provided by sensitivity-specificity sum maximization approach, although model tuning was necessary by using alternative thresholds for forest and rock.

A similar approach was undertaken for future scenarios, using constant topographic variables, but substituting climate variables from the B2A projections for 2080. For the initial scenario of rapid increase in forest extent (scenario 1), the thresholds were applied as for the final current model (online appendix). A second scenario (scenario 2) simply changed the threshold for forest to the highest available of those considered, which increased the cover of shrub and decreased the cover of forest, thus simulating a lag in the response of forest (e.g. Cannone et al., 2007).

In scenarios 1 and 2, it was assumed that alpine grassland can respond readily to climate warming and therefore its rate of elevational shift will be proportional to temperature. We consider further scenarios of vegetation development at the interface of the grass/bare rock zone for the open habitat species, assuming that ground vegetation formation is constrained by soil processes (Edwards et al., 2007; Freppaz et al., 2010), and hence no further elevational increase of this zone is possible. We define this zone as areas at or above 2800m, the altitude above which Cannone et al. (2007) found little evidence of vegetation change, and also where the cover of rock is 95% in the study area. Habitat above this altitude remained equal to the current scenario. This effect is applied to both scenarios 1 and 2, producing two further scenarios (scenario 3 and 4 respectively).

2.4.2 Estimating species distributions under different scenarios

The current distribution of each species was estimated for the whole study area based on model averaged parameter estimates. Species presence was defined as the probability equal to or greater than the threshold that optimised the match between predicted and observed prevalence, using the PresenceAbsence package in R (Freeman, 2007), one of the recommended methods of Lui et al. (2005). For each scenario, the change in distribution was estimated as the percentage change in predicted suitable cells relative to the current modelled habitat.

In estimating species distributions according to the scenarios, two assumptions were made. First, it was assumed that both climate and habitat dictate species distributions, hence temperature and habitat variables were included in the modelling procedure (‘combined models’). Second, it was assumed that species respond only to habitat change rather than climate change *per se*, hence only habitat variables were included (‘habitat models’), i.e. the same modelling approach without climate variables. In addition, we consider the case where species may respond to climate, but habitat cover does not change (which may mimic a situation where current habitat is maintained by management interventions under a changing climate). To estimate species distributions from these ‘climate models’, only temperature was altered according to the B2A projections for 2080, all other variables being equal to the current estimated values. Therefore, in summary, there were four scenarios for combined models, four scenarios for habitat models, and a single scenario for the climate model, giving a total of nine scenarios considered per species.

3. Results

Model fits were good for most species (AUC ≥ 0.7 and TSS ≥ 0.2), but less so for Wren (AUC = 0.66, TSS = 0.10). Model fit was no better than random for Black Redstart (both models) and Water Pipit (habitat model) and these were not considered further. A comparison of AIC between full models suggested that combined models were usually better (i.e. ΔAIC > 2) than habitat models for most species. However, there was no difference between models for Wren and Willow Tit (ΔAIC < 2), and the habitat model was better for Dunnock. (Full details of model-averaged parameter estimates and measures of model fit are given in the online Appendix, Tables A3 and A4).

3.1 Habitat change

Model averaged parameter estimates (online Appendix Table A5) for habitat showed good fit in terms of AUC and TSS (online Appendix Table A6). The estimated current habitat map gave a good match to the observed habitat cover (Table 1) and location of the treeline (Fig. 2), and the mean altitudes of observed and predicted habitats were in good agreement (all within 100m; online Appendix Table A7). The change in habitat cover relative to the current scenario is summarised in Table 1 for scenario 1 to 4. Under scenario 1, the area of forest more than doubles and there is a smaller increase in shrub cover, whilst under scenario 2, the increase in shrub and forest are more equitable and above 50%. Pasture increases relatively modestly in all scenarios. Under scenarios 1 and 2, cover of rock is lost because much of the study area is not high enough to accommodate habitat shifts, and also because other habitats are able to replace high altitude rock. Under scenario 3 and 4, where high altitude rock cannot be replaced, the decrease in rock cover is less marked, and as a consequence the loss of grass is greater as this habitat is squeezed between advancing tree and shrub habitats and an immovable rock zone (Table 1).

3.2 Estimated changes in species distribution

The estimated changes in distribution of forest/shrub species are given in Fig. 3. Coal Tit and Chaffinch showed estimated increases under each scenario, sometimes of considerable magnitude, due to a positive influence of both temperature and habitat. Willow Tit and Wren showed estimated increases in all except the climate scenario, suggesting that temperature increases that are not accompanied by habitat shifts would be detrimental to these species. However, there was a different pattern for Tree Pipit and Dunnock, where there were increases estimated by habitat models (an exception being Tree Pipit under scenario 2), but decreases or little difference for the combined models.

In contrast to forest/shrub species, decreases in the distribution of open habitat species were estimated under the majority of scenarios (Fig. 4). To a large extent, this was due to loss of open areas as they were encroached upon by forest and shrub. However, for Water Pipit, there was an additive effect of temperature in the combined models, indicating that some open habitats were climatically unsuitable under these scenarios. By contrast Skylark and Wheatear increased under warmer conditions, as shown by the estimated distribution under the climate model. For Wheatear, this was not enough to offset decreases caused by habitat loss under combined models. The model outcomes for Skylark were largely dependent on whether there was a greater upward shift in forest (resulting in declines) or shrub (resulting in increases). Including the further assumption that habitat would not change at high altitudes due to effects on soil processes (scenarios 3 and 4) led to a further loss in estimated distribution of c. 15% for Skylark, 7% for Wheatear (habitat models) and 10% for Water Pipit (combined model), although for the former two species, this effect was reversed under the combined model, with decreases respectively 10% and 15% less than under the habitat model.

4. Discussion

The goal of this study was to describe statistically the distribution of alpine bird species along an altitudinal gradient, and to use this information to assess the sensitivity of these species to potential habitat change induced by climate change. For the majority of species nesting in forest or in the transition zone between forest and alpine grasslands, their distribution remained constant or expanded according to the scenarios, because the amount of suitable habitat is likely to remain stable or increase in the study area in response to climate change at high altitude as a result of elevational shifts in forest and shrubs. However, open habitat species showed a decrease in distribution under most scenarios, suggesting that these species are facing a potentially severe loss of habitat as alpine grasslands are colonised by forest and shrubs. This is illustrated using as an example the change in the estimated distribution of Water Pipit (under a combined scenario) in Figure 5. The loss is exacerbated as much of the area considered is not at an altitude high enough to accommodate further elevational shifts – in effect, many mountain tops and ridges currently covered by grass are likely to be colonised by shrub or forest over the next century. The result is a much reduced and fragmented distribution of potentially suitable habitat (Fig. 5). Such effects will be even more pronounced if colonisation of higher unvegetated areas by grasslands is not possible due to constraints on soil formation (e.g. Freppaz et al., 2010). The effects of this 'squeeze' on natural grassland may therefore have potentially serious consequences for this habitat in the future.

A range of scenarios were considered under two main assumptions: that species respond only to changes in habitat type (habitat models), and that they respond to changes in both climate and habitat type (combined models). Whilst there was little difference in model estimates for most species under these two assumptions, there were two that showed markedly different estimates depending on whether temperature was included in the models. Tree Pipit and Dunnock mostly showed declines in distribution under combined models due to a mismatch between suitable climate conditions and suitable habitat, but clear increases under habitat models. The extent to which climate in addition to habitat determines bird distribution is therefore crucial in assessing potential sensitivity to environmental change for these species. Certainly for many species, temperature accounted for additional variation in the models, suggesting that its effects are likely to reflect finer-scale variations in habitat or resources, or both, which themselves may well be directly limited by climate, and that are important determinants of bird distribution. However, there is some evidence that climate may directly affect Water Pipit distribution (Rauter and Reyer, 2000; Rauter et al., 2002). The extent to which climate *per se* may be important for the other species considered warrants further research.

4.1 Model predictions

Model fits were generally good, exceptions being Black Redstart and Water Pipit (habitat model), suggesting key variables were not considered in the model for the former species, and that the latter species' distribution could not be predicted from habitat and topography alone. For the other species, model performance strongly suggested that distributions could be adequately predicted by a combination of habitat cover, temperature and topography. We used the smallest-scale climate data available (1km^2), which was larger than the unit of analysis (100m radius). Although the addition of smaller scale topographic variables will to some extent have effectively provided finer-scale adjustments, there is evidence that there is significant climatic variation at smaller scales which has a major influence on plant distribution (e.g. Scherrer et al. 2011) and invertebrate, though not bird, diversity (Viterbi et al., 2013). Furthermore, for five species (Skylark, Water Pipit, Wheatear, Coal Tit and Chaffinch), substituting altitude for temperature in our models improved model fit (ΔAIC > 2). Altitude was strongly correlated with both temperature and precipitation (r_{255} = -0.79 and 0.83 respectively, $P < 0.001$), but it was measured at a much finer scale than climate variables, and its effects are likely to reflect finer-scale variations in habitat or resources, or both, which themselves may be directly limited by climate. Although models were generally good in terms of predictive ability, it is likely that finer-scale measures of habitat or climate would prove even better tools for some species. Further detailed autecological studies to identify the key resources of the species of interest would be necessary for such approaches.

In modelling species responses to climate, it is advisable to consider as much as possible of a species' range (Barbet-Massin et al., 2010). This would be major logistical challenge at the scales considered, i.e. those appropriate in considering altitudinal shifts. For higher altitude habitats, the conclusions of this study should not be affected by the restricted altitudinal range if the assumptions of forest and shrub advancement used in the scenarios are confirmed (see below) – there is little doubt that the strong negative effects of forest in particular will lead to loss of suitable areas for open habitat species. There is also an assumption in the approach that the upper limit of the distribution was sampled, and that birds would not breed in habitats and/or climates at higher altitudes. This is probably reasonable for the species considered – maximum altitudes for open habitat species (Skylark = 2574m, Water Pipit = 2861m, Wheatear = 2754m) were somewhat lower than the maximum altitude surveyed (3058m).

The extent of species range sampled is more of an issue with forest/shrub species, because the models predict climates for the lower areas (larch-dominated forest at c. 1700m-2000m) for 2080 that are outside of the current study area. However, suitable climate for broadleaf forest (especially Beech *Fagus sylvaticus*) would likely occur at the altitudes considered under future scenarios. Several species considered are also commonly found in broadleaved forests, such as Wren and Chaffinch, although Coal Tit and Willow Tit are much more widespread in alpine coniferous forests (Snow and Perrins, 1998). These two species in particular may have had overestimated increases due to the restricted study area, and consequently habitat, considered in the scenarios.

4.2 Scenario development

In constructing the scenarios of future change, we have intentionally adopted a relatively simple approach as our goal was to produce scenarios against which to test the sensitivity of different species to potential climate change-induced habitat shifts. Nevertheless, the approach adopted predicted well the current habitat distribution. Given the levels of uncertainty in both potential responses of habitat to climate change, and in the projections of climate change themselves, we feel that this is an appropriate approach to take, and that the results are very likely to reflect the relative sensitivity of alpine birds (and their habitats) to potential climate change, although we stress that the estimates of change should be taken as a relative guide to potential sensitivity, rather than predictions of actual change.

The scenarios were developed to incorporate natural variation in habitat cover due to climate and topography. The estimated annual rate of forest advance until 2080 relative to the current modelled habitat varied between 2.43m and 2.81m for the different scenarios, which are within the range of observed rates of treeline shifts for the European Alps: 0.28 m per year (Paulsen et al. 2000) to 3.16 m per year (Gehrig-Fasel et al., 2007) respectively. Our scenarios therefore represent plausible rates of forest expansion based on published estimates. Whether treelines shift in response to climate change, and the rate of that change, depend on several factors (Gehrig-Fasel et al., 2007; Harsch et al., 2009). In our study area, the abandonment of traditional grazing practices is increasingly common (Laiolo et al., 2004), and is a factor that is likely to have increased the rate of treeline shift over the past few decades in addition to climate effects (Gehrig-Fasel et al., 2007). Furthermore, the trend towards increased urbanisation and development of ski resorts may well increase in the future, bringing further detrimental effects (e.g. Caprio et al., 2011). Whilst it is difficult to formally incorporate such effects in the scenario development (indeed, developed habitats were specifically not included), it should be noted that all of these anthropomorphic impacts are likely to negatively impact on high alpine habitats, especially open grasslands. This, and the use of B2A climate projections, means our scenario outcomes are as a consequence conservative.

4.3 Conservation implications

The results presented here suggest strongly that open habitat species will be most sensitive to habitat shifts induced by climate change, especially Water Pipit and Wheatear, which showed estimated declines in all scenarios for both habitat and combined models. The loss of open grassland habitats may therefore present a serious conservation problem in the future, which could be even more marked if climate change progresses at rates in line with other, possibly more likely, projections than the relatively conservative ones used here. Of those species predicted to be most sensitive to climate change, Water Pipit is likely to represent the biggest potential conservation problem as it is very much a mountain specialist throughout most of Europe, and it also seems completely intolerant of forest, and was most sensitive to potential differential shifts in habitats in response to climate change. Clearly this is a species that may be at particular risk and is therefore worthy of further investigations.

Effects of successional changes caused by climate change may be ameliorated by direct management intervention, which in this case would consist of maintaining open areas (e.g. by clearing trees and shrubs and/or increasing grazing intensity) at threat of shrub and forest encroachment. The extent to which this may be successful depends on whether species are sensitive to climate (directly or indirectly) in addition to habitat. The outcomes of the climate models, whereby current habitat is maintained but the temperature changes according to the projections, show estimated declines for a number of species (Figs 3 and 4), suggesting that even if open habitats are maintained at the current level, the climatic conditions will become less favourable. This again includes Water Pipit, and also Tree Pipit, Dunnock, Wren and Willow Tit. Management intervention to maintain current habitat cover may therefore not be sufficient for several species.

The approach here is restricted to the European Alps of the province of Torino. The extent to which the inferences arising from this work can be applied to alpine habitats in general is unknown. Large-scale biogeographic effects, and local habitat conditions, may influence distributions, in effect causing significant region by habitat/climate interactions, resulting in a species having different sensitivities in different areas. If such models are to have wider applicability, especially from a conservation perspective, then they need to be tested in different regions (Whittingham et al., 2007). We therefore urge similar work to be carried out in other alpine regions in order to determine whether species sensitivities to potential climate change are consistent across larger areas. Nevertheless, the processes of habitat shifts illustrated here, especially when there are differential responses of vegetation zones to climate change, are likely to be highly relevant to any mountain areas with analogous altitudinal zonation of habitats and their associated animal communities.

5. Conclusions

Here, we have used birds to illustrate how possible changes in habitats and climate may affect species distributions in high alpine habitats in the future. The results are in accord with those of Dirnböck et al. (2011) who predicted that areas of endemism for vascular plants and several invertebrate groups were at high risk of future habitat loss due to forest expansion. Therefore, in a more general sense, open habitat bird species illustrate the potential threat to wider biodiversity of alpine grasslands which are likely to host a high diversity of a number of groups, such as flowers, carabid beetles, dung beetles and butterflies (e.g. Nagy et al., 2003; Tocco et al., 2013), not to mention other high altitude specialist bird species which were recorded too infrequently for analysis (e.g. Ptarmigan *Lagopus muta*, Alpine Accentor *Prunella collaris*, Snow Finch *Fringilla montifringilla*). The potential for loss of alpine grassland under future climate change seems high, especially if upward shifts are constrained, either due to a lack of higher altitude areas or due to a habitat 'squeeze' caused by an asymmetric response of vegetation zones to climate change at higher altitudes. Continued monitoring and research should be prioritised for this potentially threatened habitat, in particular at the interface between the grassland and bare rock habitats at higher altitudes where soil responses may be crucial for vegetation communities and consequently possible distributional shifts of alpine fauna.

Whilst we believe our modelling approach was fit for purpose in terms of assessing likely sensitivity of alpine birds to environmental change, we also acknowledge that there are many other potential approaches which could be worth considering, especially if additional data in the form of repeat visits could be obtained (e.g. use of hierarchical state-space models; Buckland et al., 2004). More broadly, such 'static' species distribution models (including those used in this paper) have a number of limitations in estimating the true niche of a species, and hence in making predictions for potential future impacts of environmental change (Schurr et al., 2012), as they cannot incorporate more complex processes such as dispersal, biotic interactions and range dynamics (Pearson and Dawson, 2003; Holt, 2009), nor indeed can they account for the potential adaptation of species to novel conditions (Pearson and Dawson, 2003). In order to address such issues and therefore better understand the actual demographic processes underlying species' distributions, the adoption of a process-based dynamic range modelling framework would be ideal (Schurr et al., 2012). However, such complex models require complex data in terms of spatio-temporal demographic rates. The paucity of such data for the European Alps (Chamberlain et al., 2012), and for mountain regions in general, currently precludes such approaches, but detailed demographic monitoring should be made a priority for the future if we are to better understand factors determining bird species distributions at high altitude, and therefore make improved predictions on impacts of environmental change.

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Table 1

The percentage of observed cover and current modelled cover of each habitat type in the study area ≥1700m asl, and the percentage change in cover according to each scenario relative to the current model (so a 100% increase would indicate a doubling in area covered). Scenario 1 represents a rapid response of forest extent to climate change (based on the B2A projections), scenario 2 represents a slower response of forest with greater subsequent shrub expansion. Scenarios 3 and 4 are the same as scenarios 1 and 2 respectively, except that vegetation development is constrained at high altitudes, therefore habitat cover is equal to the current scenario above 2800m for both.

Class	Observed	Current	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Forest	18	19	+136	+85	+133	+84
Shrub	12	16	+27	+59	+18	+50
Past	20	20	+22	+37	+13	+28
Grass	18	19	-55	-49	-65	-59
Rock	32	26	-94	-94	-72	-72

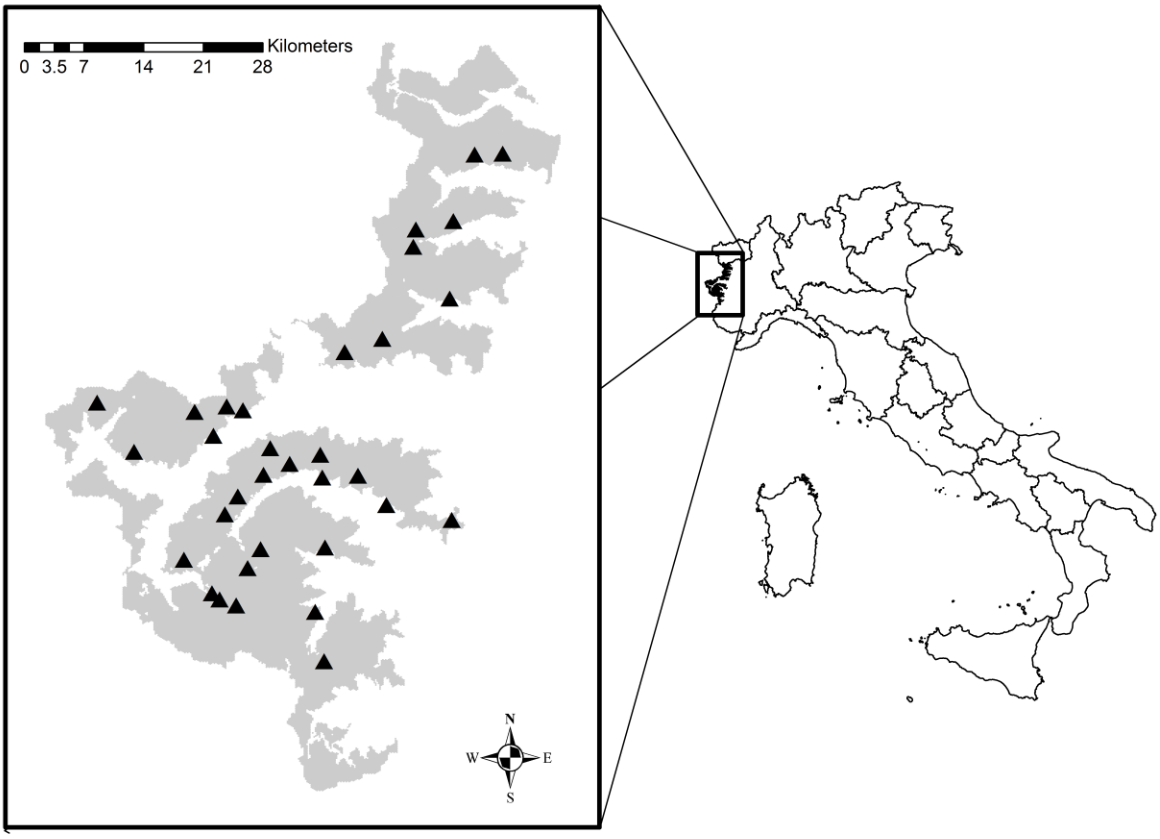

Fig. 1. Location of the study area in northern Italy, showing the area considered (altitude ≥1700m) in grey and locations of survey transects (black triangles). The extent of the study area was 1331 km^2.

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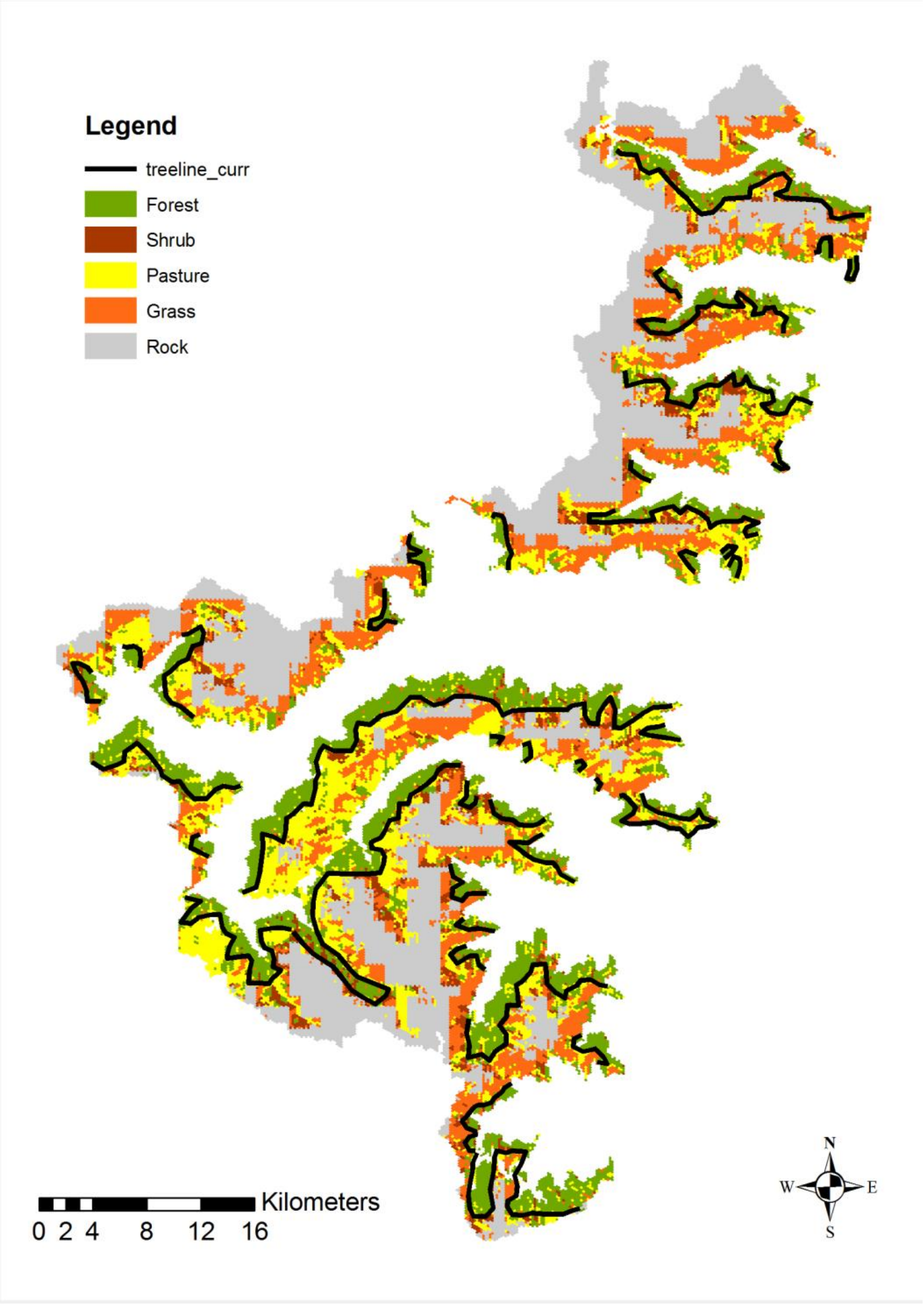

Fig. 2. Land cover predicted from modelling the presence of five habitat types (forest, shrub, pasture, grass and rock) in relation to temperature, aspect and slope. Predictions were made in 42398 hexagonal cells of 200m width for the Province of Torino at altitudes ≥ 1700m. The observed treeline ('treeline_curr') estimated from PFT data is also shown.

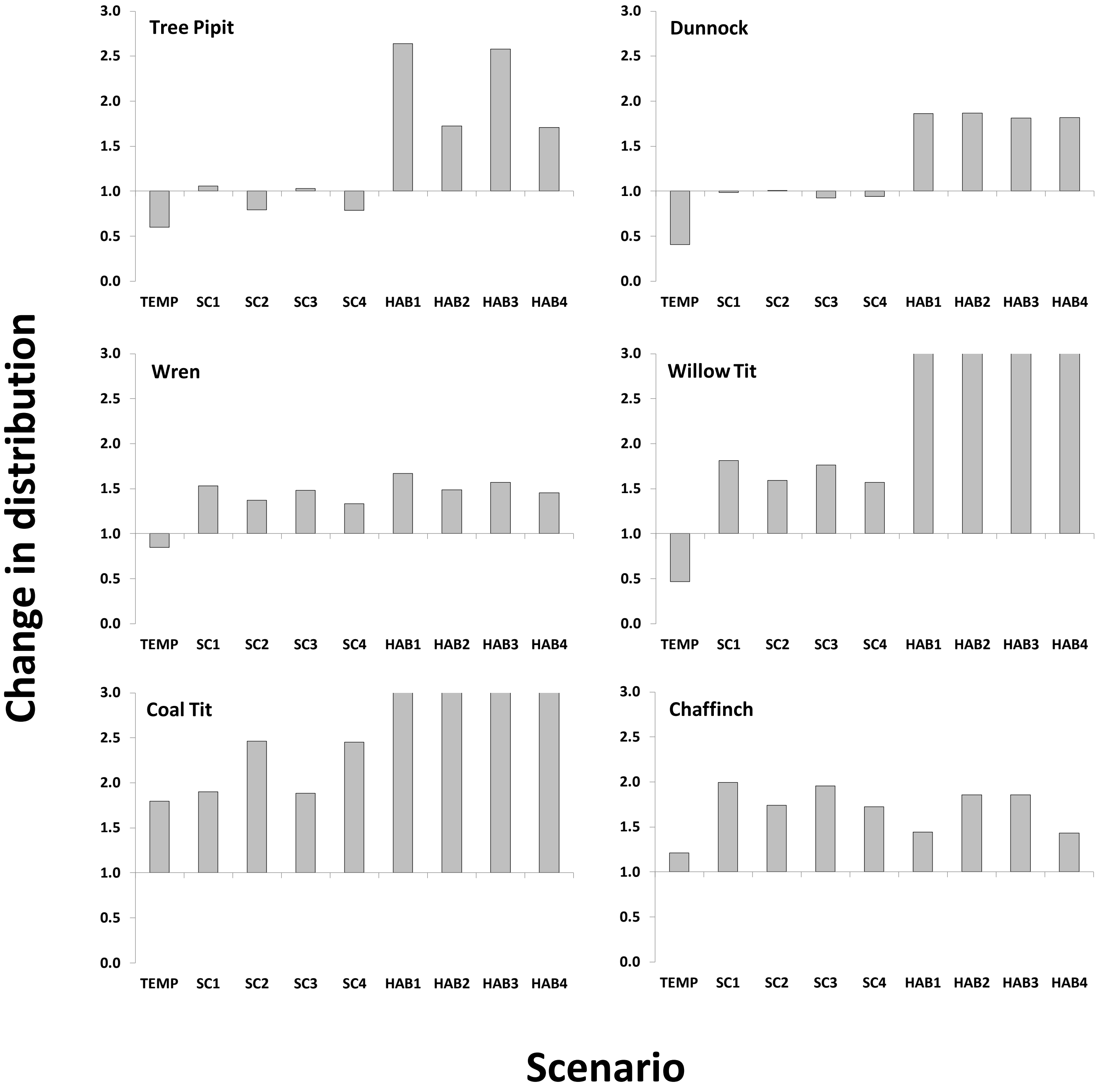

Fig. 3. Change in the distribution of forest/shrub bird species at high altitude (≥1700m) in the western Italian Alps estimated from various scenarios of future environmental change by 2080. The climate model (TEMP) assumes habitat stays constant, but species respond to temperature changes; SC1-SC4 are derived from scenarios 1 to 2 (Table 1) for combined models where species respond to both habitat and temperature changes; HAB1- HAB4 are derived from scenarios 1 to 2 for habitat models where species respond only to change in habitat. Change is expressed as the proportion of the current estimated distribution relative to the distribution estimated under each scenario (so values <1 indicate a decrease and values >1 indicate an increase). Note that for presentational purposes, increases greater than 3 are not shown for HAB1-HAB4 for Willow Tit (respective values = 5.96, 4.93, 5.91 and 4.90) and Coal Tit (respective values = 6.22, 5.03, 6.19 and 5.00).

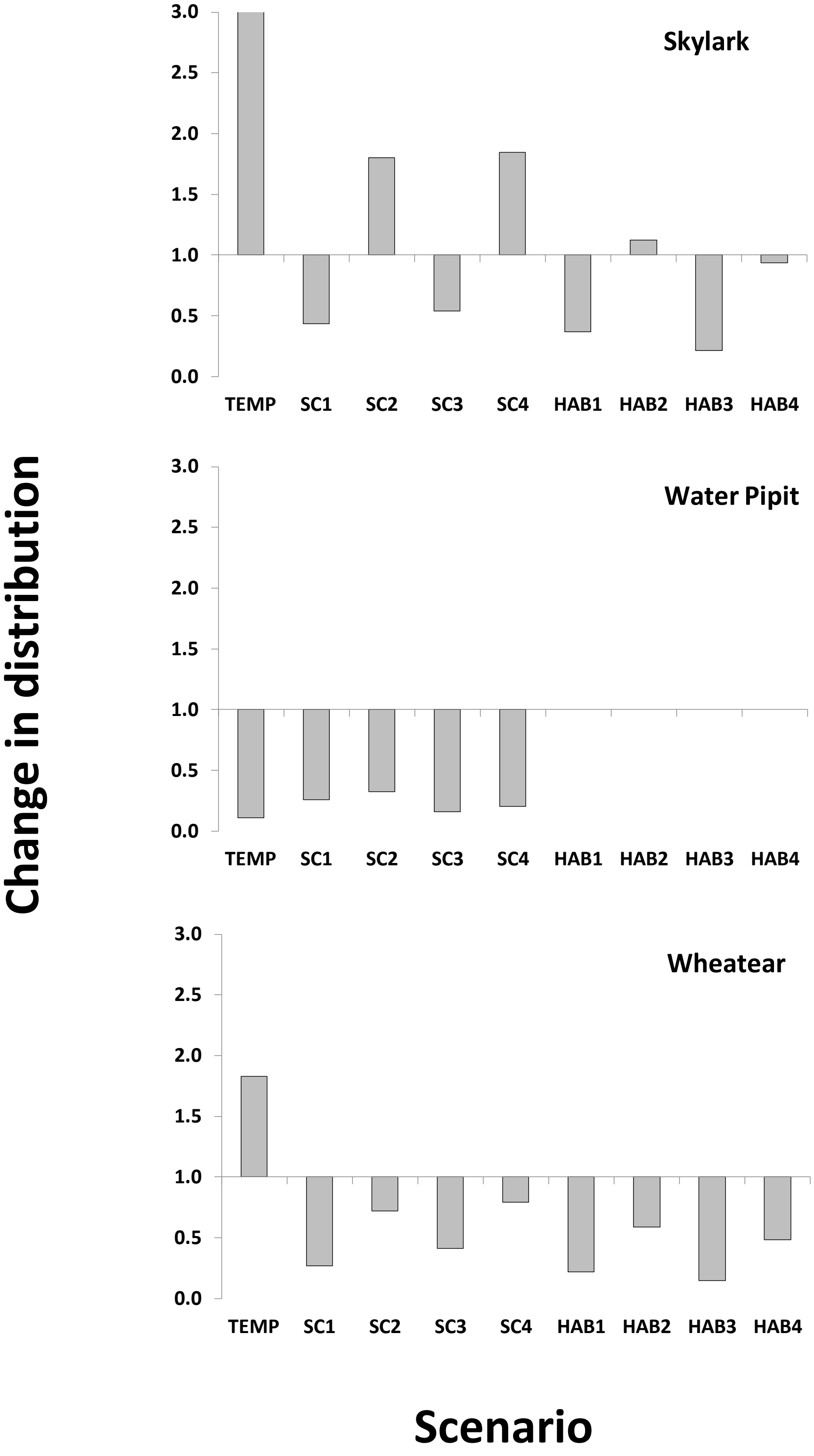

Fig. 4. Change in the distribution of open habitat bird species at high altitude (≥1700m) in the western Italian Alps estimated from various scenarios of future environmental change by 2080. Estimated changes are based on the climate model (TEMP), scenarios 1 to 4 from combined models (SC1-SC4) and habitat models (HAB1-HAB4). No valid habitat model was produced for Water Pipit. Other details are as per Fig. 3. Note that for presentational purposes, increases > 2 are not shown for Skylark (TEMP, change = 5.29).

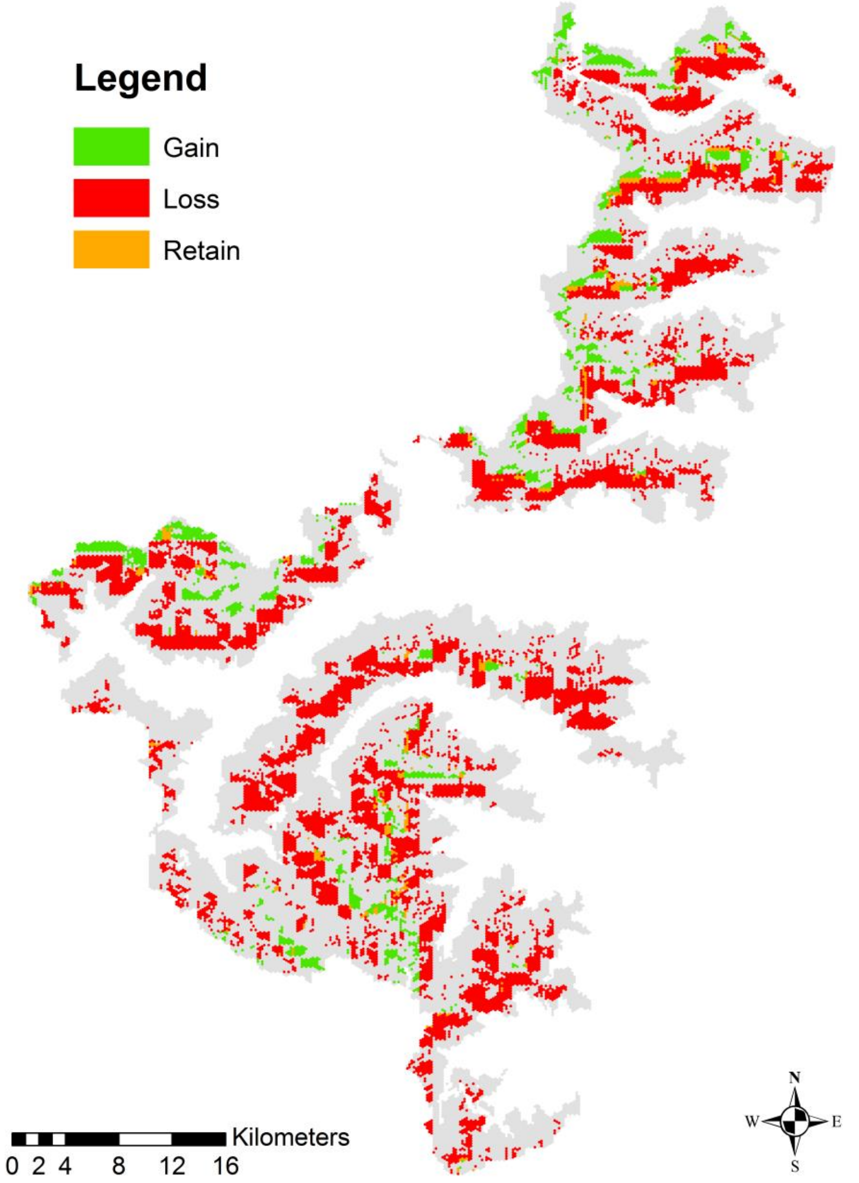

Fig. 5. Change in the predicted distribution of Water Pipit between the current predicted distribution and that under scenario 3 (combined model, rapid response of forest to temperature increase, no expansion of vegetation above 2800m). Grey areas indicate predicted absences in both current and future scenarios.

Table and figure legends

Table 1

The percentage of observed cover and current modelled cover of each habitat type in the study area ≥1700m asl, and the percentage change in cover according to each scenario relative to the current model (so a 100% increase would indicate a doubling in area covered). Scenario 1 represents a rapid response of forest extent to climate change (based on the B2A projections), scenario 2 represents a slower response of forest with greater subsequent shrub expansion. Scenarios 3 and 4 are the same as scenarios 1 and 2 respectively, except that vegetation development is constrained at high altitudes, therefore habitat cover is equal to the current scenario above 2800m for both.

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Online Appendix

Further details on habitat variables, bird and habitat models and scenario development

1. Habitat variables

The five habitat variables were based on 15 relevant land cover types (i.e. those occurring above 1700m) extracted from the Piani Forestali Territoriali (PFT) land cover database for the whole province (www.regione.piemonte.it/foreste/cms/foreste/pianificazione). PFT data are backed-up by a high level of ground-truthing and they provided a much better visual fit when overlaid on Google Earth images of the study area compared to the commonly used CORINE (CO-oRdination of INformation on the Environment) land cover database. Variable definitions are given in Table A1. PFT was therefore considered more suitable for a study of medium-low geographical scale. For each point, the percentage cover of these five variables was extracted in ArcGIS 9.3 (ESRI, 2008). The approximate location of the current treeline (Fig. A1) was estimated as the perimeter of forest habitat within the study area, although small patches (<10h) and relatively small gaps between areas of forest (<400m) were ignored.

As the goal was to estimate species distributions at a relatively large scale, land cover data, rather than habitat data collected in the field, was used in the modelling. For the latter, some simple data (estimated 'by eye') were collected at each point, including the percentage cover of canopy (i.e. above head height) and the number of mature trees (≥20cm in diameter) within a 50m radius. However, there were strong correlations between forest land cover and the comparable habitat variables canopy cover (Pearson correlation $r_{255} = 0.86$, $P > 0.0001$) and number of mature trees within 50m ($r_{255} = 0.77$, $P > 0.0001$) collected in the field, suggesting that the land cover data provided a good representation of habitat 'on the ground'.

Table A1

Definitions and summary statistics of variables (including land cover categories used to define habitats) used in the analysis. Code is used to identify variables in the models (Table A3). The mean value was calculated from the total sample of points (n = 257). The description includes the data source where GPS = field reading from Geographical Positioning System, PFT = Piani Forestali Territoriali land cover database, DTM = Digital Terrain Model (www.mais.sinanet.isprambiente.it), WC = WorldCLim database (summarised at 1-km^2 scale). CORINE land cover classes were also considered, but visual overlays of land cover classes on GoogleEarth images of the study points found a much better concordance with PFT than with CORINE.

Variable	Code	Mean ± sd	Description
Altitude (m)	ALT	2231 ± 317	Altitude of the point above sea level (GPS)
Rock (%)	ROC	16.35 ± 31.46	Rock, scree and areas devoid of vegetation (PFT)
Pasture (%)	PAS	32.96 ± 38.21	Alpine meadows with a continuous sward, seasonally grazed pasture and abandoned pastures (PFT)
Alpine grassland (%)	GRA	14.62 ± 28.97	Semi-natural grassland, intermediate rock/grassland mosaic, comprising rocky and stony areas interspersed with sparse grass cover or other ground vegetation (PFT)
Shrubs (%)	SHR	13.49 ± 28.69	Sub-alpine shrubs, scrub, pioneer or regenerating forest and dwarf trees (including *Pinus uncinata*) (PFT)
Forest (%)	FOR	22.54 ± 34.84	*Larix* spp, *Pinus sylvestris* and *P.cembra* (PFT)
Slope (°)	SLO	23.81 ± 8.29	Gradient of the slope at a 1 ha scale (DTM)
South-facing aspect (index)	aspectS	0.46 ± 0.64	Direction that a point faces at a 1 ha scale, expressed as an index between 1 (facing directly south) and -1 (facing directly north) (DTM).
East-facing aspect (index)	aspectE	0.35 ± 0.61	Direction that a point faces at a 1 ha scale, expressed as an index between 1 (facing directly east) and -1 (facing directly west) (DTM).
Temperature (°C)	TEMP	2.32 ± 1.89	Mean annual temperature (calculated as mean

			of monthly means) at 1-km^2 scale (WC).
Maximum temperature (°C)	TMAX	5.32 ± 1.98	Maximum temperature at 1-km^2 scale (WC).
Minimum temperature (°C)	TMIN	-1.59 ± 1.43	Maximum temperature at 1-km^2 scale (WC).
Precipitation (mm)	RAIN	121.70 ± 13.88	Mean annual precipitation (calculated as mean of monthly mean accumulated precipitation) at 1-km^2 scale (WC).

2. Details of bird distribution models

In order to assess the predictive ability of the models (see below), data were divided into model (70%) and test (30%) data sets. The probability of the occurrence of singing birds (which were therefore assumed to be potential breeders) from the model data set was modelled using binomial logistic regression in a general linear mixed-modelling framework with the lmer command in the lme4 package in R. In order to account for potential spatial autocorrelation between points on the same transect, 'site' was fitted as a random term. Some points (44%) were subject to more than one visit, so to account for variation in survey effort, bird occurrence per points was expressed as a vector of presences and absences (i.e. the successes/failures syntax of Crawley, 2007). All predictor variables initially considered are shown in Table A1.

Habitat variables expressed as a proportion were arcsine-square root transformed prior to analysis. There were some high correlations amongst variables, in particular there was very high inter-correlation between all four climate variables (Pearson's correlation $|r| > 0.79$, $P < 0.001$ in each case). Prior to modelling, the degree of collinearity was assessed by calculating variance inflation factors (VIFs). Following the procedure of Zuur et al. (2009), we calculated VIFs for all linear variables. The variable with the highest VIF was sequentially removed and VIFs re-calculated (following Zuur et al., 2009) until all variables had a VIF < 2.0. Quadratic terms were included if scatter plots of species occurrence per point (the proportion presence/visits) indicated possible non-linear effects. As a final check, variables that had been removed in the VIF procedure were substituted for closely correlated variables (in particular mean temperature, maximum temperature and precipitation, rock and pasture cover, and forest and shrub cover) and models were compared with AIC. Cases where the model with the substituted variable had a lower AIC, and where VIF for each was less than 2, were used as the final full models. The resulting model, which included a set of variables, including climate variables, with a low degree of collinearity, was termed the full combined model. The procedure was repeated without climate variables, and the resulting model was termed the full habitat model.

To assess the level of spatial autocorrelation in the data, Moran's I was calculated on the residuals from the full combined model for each species at various scales. There was no evidence of significant autocorrelation with the exception of Black Redstart (Table A2), where Moran's I was significant at larger scales, even though the magnitude of the effects were very small. Such a result may suggest large-scale geographic variation which may be accounted for by including an appropriate additional variable in the model (Zuur et al., 2009) We defined a further factor 'region' which comprised three groups based on the main valleys in the study area, Chisone, Susa and Lanzo, which was specified as a random factor in the model. Addition of this factor improved the fit (ΔAIC = -7.92) and Moran's I was no longer significant (Table A2). The model including region was therefore subsequently used for Black Redstart.

Multi-model inference (Burnham and Anderson, 2002) was used to derive model averaged parameter estimates based on the full models, whereby the suite of models containing all combinations of variables were determined, and model weights were calculated (which express the weight of evidence that a given model is likely to be the best predictive model). Model averaged parameter estimates were calculated across the set of models which accounted for 95% of the sum of all model weights (Table A3).

Thresholds for bird presence were defined according to the prevalence approach (Liu et al., 2005), i.e. a bird was considered present if its estimated probability exceeded the predefined threshold for the species. (Note that whilst threshold choice affected the actual magnitude of predicted change in the number of cells in which a species was present, the proportional change did not vary greatly according to the method of threshold derivation selected). In order to assess the predictive ability of the models, AUC and TSS were calculated based on how well the models derived from the model data sets predicted observed presence in the test data sets. In general model fits were good (AUC ≥ 0.70 and TSS ≥ 0.20; Table A4), although they were less good for Wren, and poor for Black Redstart and Water Pipit (habitat model). In the latter two cases, predictive ability was considered no better than random (AUC < 0.60 and TSS < 0.10) an so they were not considered for assessing scenario outcomes.

Table A2

Moran's I statistic calculated from residuals derived from the full combined model for each species at various scales. Values in bold indicate significance (P < 0.05). 'Black Redstart (reg)' is Moran's I for the model including the three level factor 'region' specified as a random effect.

<table>
<tr><th>Species</th><th>10km</th><th>20km</th><th>30km</th><th>40km</th><th>50km</th></tr>
<tr><td>Skylark</td><td>-0.022</td><td>-0.013</td><td>>|0.001|</td><td>>|0.001|</td><td>>|0.001|</td></tr>
<tr><td>Water Pipit</td><td>0.004</td><td>0.007</td><td>>|0.001|</td><td>>|0.001|</td><td>>|0.001|</td></tr>
<tr><td>Tree Pipit</td><td>0.011</td><td>0.003</td><td>-0.003</td><td>>|0.001|</td><td>>|0.001|</td></tr>
<tr><td>Wheatear</td><td>-0.022</td><td>-0.013</td><td>>|0.001|</td><td>>|0.001|</td><td>>|0.001|</td></tr>
<tr><td>Black Redstart</td><td>**0.018**</td><td>**0.004**</td><td>**0.004**</td><td>**-0.001**</td><td>-0.006</td></tr>
<tr><td>Black Redstart (reg)</td><td>0.017</td><td>0.006</td><td>0.006</td><td>-0.007</td><td>-0.005</td></tr>
<tr><td>Dunnock</td><td>-0.027</td><td>-0.005</td><td>-0.015</td><td>-0.001</td><td>>|0.001|</td></tr>
<tr><td>Wren</td><td>-0.036</td><td>0.002</td><td>>|0.001|</td><td>>|0.001|</td><td>>|0.001|</td></tr>
<tr><td>Willow Tit</td><td>0.017</td><td>-0.008</td><td>>|0.001|</td><td>>|0.001|</td><td>>|0.001|</td></tr>
<tr><td>Coal Tit</td><td>0.011</td><td>-0.018</td><td>-0.013</td><td>-0.001</td><td>>|0.001|</td></tr>
<tr><td>Chaffinch</td><td>-0.037</td><td>-0.027</td><td>-0.012</td><td>-0.001</td><td>>|0.001|</td></tr>
</table>

Table A3

Model averaged parameter estimates (Est.) for the probability of occurrence of alpine birds along point transects. Upper and lower 95% confidence limits (UCL and LCL respectively) and model weights (*W*) for the model set comprising 95% of total model weights are also presented. A multi-model inference approach (Burnham & Anderson, 2002) was used to derive estimates and weights from binomial logistic regression models of climate, topography and habitat (combined models), and topography and habitat only (habitat models), on species presence, specifying random site effects. In addition, the three-level factor ‘region’ was fitted as a random factor for the Black Redstart model. Variables considered were selected for modelling based on VIFs, and vary according to species. Temperature was expressed in degrees centigrade, aspect as an index from 1 (directly facing the aspect in question) to -1 (directly opposite to the aspect in question), slope in angular degrees and habitat cover (forest, scrub, sparse vegetation and rock) as arcsine-square root transformed proportions. – indicates a variable not considered in the modelling procedure for a given species (or not applicable in the case of *W* for intercepts).

Species	Variable	Combined models				Habitat models			
		W	Est.	LCL	UCL	*W*	Est.	LCL	UCL
Skylark	Intercept	–	-3.430	-5.970	-0.879	–	-1.880	-4.040	0.287
	East	0.51	0.386	-0.661	1.430	0.30	0.064	-0.758	0.885
	Forest	1.00	-6.760	-12.000	-1.560	1.00	-5.230	-9.560	-0.891
	Grass	0.59	0.686	-0.872	2.240	0.32	0.146	-0.664	0.955
	Rock	–	–	–	–	0.87	-1.480	-3.370	0.417
	Shrub	0.84	-1.510	-3.560	0.538	0.56	-0.654	-2.260	0.952
	Slope	0.36	-0.019	-0.121	0.084	0.32	-0.016	-0.126	0.093
	Slope^2	0.34	-0.0002	-0.002	0.002	0.30	-0.00003	-0.002	0.002
	South	–	–	–	–	0.83	1.170	-0.484	2.820
	Temp	1.00	1.270	-0.055	2.600	–	–	–	–
	Temp^2	0.65	-0.122	-0.368	0.125	–	–	–	–
Water Pipit	Intercept	–	0.458	-2.600	3.510	–	0.243	-2.700	3.190
	East	0.30	0.073	-0.474	0.621	0.28	0.070	-0.403	0.542
	Grass	0.24	-0.019	-0.453	0.416	0.26	0.056	-0.391	0.504

	Rock	0.45	-0.340	-1.400	0.719	0.42	-0.248	-1.050	0.550
	Shrub	0.49	-0.380	-1.440	0.674	0.61	-0.502	-1.590	0.582
	Slope	0.43	-0.070	-0.320	0.181	0.46	-0.067	-0.300	0.167
	Slope^2	0.41	0.001	-0.004	0.006	0.41	0.001	-0.003	0.006
	South	0.60	0.470	-0.551	1.490	0.48	0.277	-0.519	1.070
	Temp	0.64	0.391	-0.451	1.230	–	–	–	–
	Temp^2	0.99	-0.196	-0.413	0.020	–	–	–	–
Tree Pipit	Intercept	–	-9.850	-20.700	0.990	–	-4.130	-12.800	4.550
	East	0.52	0.539	-0.654	1.730	0.41	0.254	-0.629	1.140
	Grass	0.26	0.178	-0.946	1.300	0.21	0.007	-0.763	0.778
	Pasture	0.44	0.390	-0.811	1.590	0.29	0.132	-0.597	0.861
	Rock	0.29	-0.380	-2.430	1.660	0.35	-0.562	-2.910	1.790
	Shrub	0.98	-2.570	-5.070	-0.075	1.00	-3.270	-5.680	-0.863
	Slope	0.47	0.201	-0.469	0.872	0.56	0.261	-0.476	0.997
	Slope^2	0.44	-0.004	-0.017	0.010	0.52	-0.005	-0.020	0.010
	Temp	0.92	3.020	-0.766	6.810	–	–	–	–
	Temp^2	0.86	-0.343	-0.810	0.125	–	–	–	–
Dunnock	Intercept	–	-3.520	-10.700	3.660	–	-3.550	-10.500	3.430
	East	0.30	-0.101	-0.676	0.474	0.30	-0.101	-0.675	0.473
	Grass	0.48	-0.756	-3.010	1.500	0.47	-0.706	-2.890	1.480
	Pasture	0.25	-0.072	-0.773	0.629	0.26	-0.077	-0.793	0.639
	Rock	0.95	-76.900	-41000	40800	0.97	-78	-41400	41300
	Shrub	0.28	0.093	-0.482	0.668	0.30	0.107	-0.478	0.693
	Slope	0.47	0.173	-0.421	0.766	0.46	0.164	-0.415	0.743
	Slope2	0.46	-0.003	-0.015	0.008	0.46	-0.003	-0.015	0.008
	Temp	0.26	-0.032	-0.477	0.414	–	–	–	–
	Temp^2	0.25	-0.002	-0.064	0.060	–	–	–	–
Wren	Intercept	–	-11.400	-22.500	-0.277	–	-10.600	-20.900	-0.281

	East	1.00	-3.430	-5.310	-1.550	1.00	-3.400	-5.260	-1.550
	Forest	0.79	1.580	-0.820	3.980	0.79	1.430	-0.753	3.620
	Grass	0.60	1.480	-1.760	4.730	0.61	1.510	-1.730	4.760
	Pasture	0.80	-1.980	-4.820	0.871	0.82	-2.010	-4.790	0.772
	Rock	0.27	-0.279	-2.740	2.180	0.27	-0.323	-2.810	2.160
	Slope	0.93	0.677	-0.131	1.480	0.93	0.647	-0.135	1.430
	Slope^2	0.91	-0.012	-0.026	0.003	0.90	-0.011	-0.025	0.003
	Temp	0.33	0.328	-1.580	2.240	–	–	–	–
	Temp^2	0.37	-0.060	-0.342	0.223	–	–	–	–
Wheatear	Intercept	–	-0.682	-4.120	2.760	–	-0.401	-3.210	2.410
	East	0.34	-0.162	-0.852	0.527	0.37	-0.183	-0.901	0.535
	Forest	0.78	-7.450	-19.200	4.320	0.73	-6.170	-17.200	4.850
	Grass	0.23	-0.003	-0.516	0.511	0.23	-0.011	-0.526	0.504
	Rock	0.28	-0.020	-0.779	0.739	0.38	-0.230	-1.090	0.629
	Shrub	0.46	-0.388	-1.540	0.769	0.36	-0.226	-1.150	0.704
	Slope	0.50	-0.075	-0.317	0.166	0.45	-0.056	-0.256	0.145
	Slope^2	0.42	0.001	-0.003	0.005	0.38	0.001	-0.003	0.004
	South	0.24	-0.033	-0.565	0.500	0.23	-0.004	-0.492	0.484
	Temp	0.78	0.798	-0.553	2.150	–	–	–	–
	Temp^2	0.72	-0.166	-0.469	0.137	–	–	–	–
Black Redstart	Intercept	–	-2.750	-4.970	-0.526	–	-3.220	-5.710	-0.722
	East	0.23	-0.007	-0.343	0.330	0.26	-0.051	-0.487	0.384
	Forest	0.60	-0.777	-2.510	0.952	0.87	-1.540	-3.430	0.355
	Grass	0.32	0.129	-0.510	0.769	0.36	0.179	-0.604	0.961
	Rock	0.34	0.168	-0.595	0.931	0.36	0.193	-0.653	1.040
	Shrub	0.42	0.239	-0.564	1.040	0.46	0.305	-0.641	1.250
	Slope	0.61	0.042	-0.076	0.160	0.65	0.057	-0.097	0.210

	Slope^2	0.50	0.0003	-0.002	0.002	0.48	-0.00002	-0.003	0.003
	Temp	0.40	-0.077	-0.355	0.202	–	–	–	–
	Temp^2	0.27	0.001	-0.044	0.046	–	–	–	–
Willow Tit	Intercept	–	-1.050	-3.740	1.650	–	-0.763	-1.960	0.437
	East	0.24	-0.032	-0.451	0.387	0.24	-0.034	-0.456	0.389
	Grass	0.92	-2.410	-5.180	0.357	0.94	-2.380	-5.010	0.256
	Pasture	0.29	-0.131	-0.869	0.608	0.29	-0.135	-0.884	0.613
	Rock	0.40	-0.684	-3.210	1.840	0.40	-0.671	-3.160	1.820
	Shrub	0.96	-1.470	-2.820	-0.112	0.97	-1.420	-2.700	-0.145
	Slope	0.23	-0.001	-0.055	0.053	0.24	-0.002	-0.056	0.053
	Slope^2	0.24	-0.0001	-0.001	0.001	0.24	-0.0001	-0.001	0.001
	Temp	0.36	0.256	-1.080	1.590	–	–	–	–
	Temp2	0.40	-0.043	-0.229	0.143	–	–	–	–
Coal Tit	Intercept	–	-4.450	-7.520	-1.370	–	-2.950	-4.330	-1.560
	East	0.28	-0.104	-0.632	0.424	0.28	-0.082	-0.547	0.384
	Forest	1.00	1.630	0.616	2.630	1.00	1.970	1.060	2.890
	Grass	0.28	-0.211	-1.550	1.130	0.28	-0.222	-1.540	1.100
	Pasture	0.26	-0.100	-0.888	0.688	0.23	0.049	-0.598	0.697
	Rock	0.34	0.439	-1.420	2.300	0.37	0.509	-1.390	2.410
	Slope	0.26	-0.008	-0.088	0.072	0.24	-0.001	-0.052	0.050
	Slope^2	0.28	0.0002	-0.001	0.002	0.25	0.0001	-0.001	0.001
	Temp	0.74	0.574	-0.840	1.990	–	–	–	–
	Temp^2	0.50	-0.015	-0.192	0.163	–	–	–	–
Chaffinch	Intercept	–	-3.680	-6.180	-1.170	–	-2.510	-4.290	-0.725
	East	0.43	0.291	-0.630	1.210	0.41	0.255	-0.602	1.110
	Forest	1.00	2.930	1.770	4.090	1.00	3.610	2.500	4.720
	Grass	0.24	-0.077	-0.908	0.754	0.28	-0.151	-1.100	0.803

Pasture	0.40	0.336	-0.836	1.510	0.66	0.817	-0.729	2.360
Rock	0.37	-0.683	-3.310	1.950	0.33	-0.478	-2.650	1.690
Slope	0.30	0.005	-0.070	0.080	0.27	0.006	-0.050	0.063
Slope^2	0.33	0.0003	-0.001	0.002	0.28	0.0002	-0.001	0.001
Temp	0.70	0.471	-0.546	1.490	–	–	–	–
Temp^2	0.46	0.014	-0.128	0.157	–	–	–	–

Table A4

Measures of model performance, based on predicting the probability of species presence in a test data set (30% of the sample) using models derived from a model data set (70% of the sample). Model performance was measured as the area under the ROC curve (AUC) and the True Skill Statistic (TSS). The subscript 'comb' indicates combined models including topography, habitat cover and temperature, 'hab' indicates habitat models including only topography and habitat . ΔAIC = difference in AIC between the full combined model and the full habitat model (i.e. so minus indicates the combined model is better). AUC is given ± sd derived from the PresenceAbsence package in R (Freeman, 2007).

Species	AUC_{comb}	AUC_{hab}	TSS_{comb}	TSS_{hab}	ΔAIC
(a) Forest/shrub					
Tree Pipit	0.79 ± 0.08	0.74 ± 0.09	0.31	0.44	-7.35
Dunnock	0.77 ± 0.08	0.75 ± 0.08	0.32	0.37	3.57
Wren	0.65 ± 0.09	0.66 ± 0.09	0.10	0.10	1.15
Willow Tit	0.83 ± 0.07	0.81 ± 0.08	0.52	0.43	1.30
Coal Tit	0.81 ± 0.07	0.78 ± 0.08	0.50	0.50	-5.99
Chaffinch	0.93 ± 0.04	0.93 ± 0.04	0.62	0.81	-3.41
(b) Open habitat					
Skylark	0.82 ± 0.06	0.81 ± 0.06	0.18	0.30	-7.40
Water Pipit	0.70± 0.08	0.52 ± 0.09	0.39	0.13	-6.63
Wheatear	0.78 ± 0.07	0.70 ± 0.08	0.24	0.51	-5.06
Black Redstart	0.62 ± 0.09	0.58 ± 0.10	-0.16	-0.12	0.44

3. Habitat modelling and scenario development

A range of approaches have been used to model vegetation responses to climate change in alpine environments, but these typically are undertaken at relatively small scales, consider individual species, and have not as far as we are aware yet included predictions for responses of high altitude soils to climate change. Land cover data are available over a large area and for the most part define general structural vegetation types rather than individual species (with the exception of some mature tree species), which are nonetheless likely to be appropriate for predicting altitudinal distributions of bird species. Scenario development was a two stage process described in detail below. In summary, the first stage was to estimate the probability of occurrence of each habitat type per cell using logistic regression models in relation to climate and topography. In the second stage, the model outputs were then combined into a continuous surface for each cell by (i) eliminating habitats with predicted probabilities of occurrence lower than pre-defined thresholds (Liu et al. 2005) and (ii) calculating the sum of probabilities of all remaining habitats, and defining habitat cover as the proportion made up by each individual habitat for a given cell.

3.1 Logistic regression

The presence of each of five habitat types (forest, shrub, pasture, grass and rock; see Table A1 for full definitions) in each cell was modelled separately in relation to topographic and climate variables (slope, aspect (east), aspect (south), mean, minimum and maximum temperature and precipitation, and the quadratic of each climate variable). Models were derived from the whole province (i.e. the whole regional climatic range including all altitudes), and data were randomly divided into model (70%) and test (30%) data. Prior to modelling, the degree of collinearity was assessed by calculating variance inflation factors (VIFs) in the same way as for the bird data (see above). In the event, all climate variables were highly correlated so the final variable set only ever had a single climate variable. However, these variables were interchangeable in the models (i.e. there were no effects on the VIFs of topographic variables), so models were compared with each climate variable in turn. All models also included all two way interactions between both linear and quadratic climate terms. Models were compared using AIC and the model with the lowest AIC (termed the full model) was used to make predictions of the probability of presence of each habitat type per cell. The full model for each habitat type was used as the basis for model averaging in order to derive averaged parameter estimates, as for the bird data (see above). These are given in Table A5. The performance of the resulting models derived from the model data set were then assessed using the test data set by calculating AUC and TSS. Model fits were good (AUC > 0.70 and TSS > 0.20) showing that they had good predictive ability (Table A6).

3.2 Combining model outputs

The above procedure produced separate distributions for each of the five habitats, which partially overlapped one another. The next step was to combine these distributions into a current modelled habitat surface that best approximated to the observed current habitat distribution. The estimates of the probability of occurrence from the logistic regression models for each habitat were used to identify optimal thresholds for defining habitat presence using the PresenceAbsence package in R (Freeman, 2007) for the study area (≥1700m in altitude), i.e. a habitat was considered present for a given cell if the estimated probability of occurrence was equal to or greater than the threshold. This package provides a range of methods for identifying optimal thresholds – in this case, three methods were used which gave a relatively broad range of values, the prevalence approach, the sensitivity-specificity sum maximization approach and the sensitivity-specificity equality approach, all of which were among those recommended by Liu et al. (2005). These were used as the basis for fitting the current predicted habitat cover.

Habitat cover per cell was determined by first omitting any habitat whose probability of occurrence was lower than the threshold for that habitat. The sum of the probabilities of the remaining habitats was then calculated. The cover of an individual habitat type per cell was then its individual probability of occurrence divided by the total, e.g. if a cell had three habitat types with probabilities above their specified thresholds, and if each had an estimated probability of 0.5, then the cover of each habitat in the cell would be 0.5/1.5 = 0.33. This procedure allows for the simulation of mixed cell habitats, the proportion of which is weighted by the probabilities of other habitats also occurring in that cell. It therefore creates a more realistic landscape in particular for ecotone species such as Tree Pipit and Dunnock which are characteristic of transitional treeline habitats.

The model was tuned by varying the combinations of thresholds available from the three methods until the mean altitude of all habitats was within 100m of that observed. The best fit was generally provided by sensitivity-specificity sum maximization approach, although model tuning was necessary by using alternative thresholds for two habitats, forest and rock (thresholds are given in Table A6). Following this process, there were 257 (0.6%) cells unclassified due to low estimated probabilities for all habitat in a given cell. In these cases, all thresholds were lowered by 50% and the process re-applied, which resulted in all cells being classified. This gave a very good fit to the current data in terms of both altitude (Table A7), area covered (main paper, Table 1) and the approximate location of the treeline (Fig. A1).

3.3 Future scenarios

The probability of occurrence of each habitat type was estimated from the logistic regression models under a future scenario of moderate climate change based on the IPCC4 B2A scenario (based on a relatively moderate rate of global population increase and intermediate levels of economic development). This was the most conservative scenario available at the scales necessary (1km^2), which was in keeping with our goal of assessing sensitivity against scenarios of less extreme climate change. Climate values used in the current model were substituted for values for the 2080s under the B2A scenario (topographic variables were constant), and probabilities for each cell were calculated. The process of combining the habitat types based on thresholds was applied exactly as before which produces a general elevational shift in habitat types which were in line with those already observed, e.g. the mean altitude of forest was predicted to increase by 197m by the 2080s, a rate of 2.81m per year, which is within the minimum (0.28m per year, Paulsen et al., 2000) and maximum (3.16m per year, Gehrig-Fasel et al., 2007) rates already observed for treeline shifts in the European Alps. This was scenario 1. Scenario 2 simulated a situation where forest developed less rapidly, but instead there was greater shrub development. This scenario was constructed by substituting the best fitting forest threshold for the highest available threshold of those considered. This had the effect of constraining the spread of forest, and increasing the area of shrub. Scenario 3 and 4 were analogous to scenario 1 and 2 respectively, except that due to soil forming processes it was assumed that there would be no further vegetation development above 2800m, hence habitat cover above this height was held equal to that in the current model.

Table A5

Parameter estimates (Est.) and lower and upper 95& confidence limits (LCL and UCL respectively) for the effects of environmental variables on the probability of occurrence of different habitat types derived from model averaging of binomial logistic regression models based on climate and topographic variables. Model averaging (Burnham & Anderson, 2002) was based on the set of models that contributed 95% of total model weight, with the exception of shrub, where there was a single outstanding model (the full model, which accounted for 98% of model weight, and ΔAIC = 12.53 compared to the next best model). *W* is the model weight for each variable derived for the model set comprising 95% of total model weights (- indicates not applicable). Variables considered were selected for modelling based on VIFs (Zuur et al., 2009), and vary according to habitat. Mean temperature (Temp) and maximum temperature (Tmax) were expressed in degrees centigrade, aspect as an index from 1 (directly facing the aspect in question) to -1 (directly opposite to the aspect in question), considering both southerly (S) and easterly (E) aspects, and slope in angular degrees.

Habitat type	Variable	*W*	Est.	LCL	UCL
Forest	E	1.00	-0.379	-0.442	-0.316
	S	1.00	-0.318	-0.433	-0.203
	SLOPE	1.00	-0.010	-0.019	-0.001
	Temp	1.00	1.720	1.610	1.820
	Temp*E	0.34	0.003	-0.009	0.015
	Temp*S	1.00	-0.125	-0.175	-0.075
	Temp*SLOPE	1.00	-0.009	-0.013	-0.005
	$Temp^2$	1.00	-0.171	-0.181	-0.161
	$Temp^2$*E	0.27	0.0002	-0.001	0.001
	$Temp^2$*S	1.00	0.018	0.013	0.023
	$Temp^2$*SLOPE	1.00	0.001	0.001	0.002
	Intercept	-	-3.030	-3.270	-2.800
Shrub	E	-	-0.398	-0.592	-0.204
	S	-	-0.277	-0.465	-0.088

	SLOPE	-	-0.035	-0.049	-0.021
	Tmax	-	0.445	0.353	0.537
	Tmax*E	-	0.125	0.074	0.176
	Tmax*S	-	-0.146	-0.194	-0.097
	Tmax*SLOPE	-	0.015	0.011	0.018
	Tmax^2	-	-0.029	-0.034	-0.023
	Tmax^2*E	-	-0.006	-0.009	-0.003
	Tmax^2*S	-	0.015	0.012	0.018
	Tmax^2*SLOPE	-	-0.001	-0.001	-0.001
	Intercept	-	-3.133	-3.501	-2.765
Pasture	E	1.00	-0.168	-0.221	-0.114
	S	1.00	0.230	0.175	0.285
	SLOPE	1.00	-0.043	-0.047	-0.039
	Temp	1.00	0.635	0.586	0.683
	Temp*E	1.00	0.041	0.016	0.066
	Temp*S	1.00	0.079	0.053	0.104
	Temp*SLOPE	1.00	-0.008	-0.010	-0.006
	Temp^2	1.00	-0.066	-0.070	-0.061
	Temp^2*E	0.46	-0.001	-0.004	0.002
	Temp^2*S	1.00	-0.011	-0.013	-0.008
	Temp^2*SLOPE	1.00	0.001	0.0003	0.001
	Intercept	-	0.063	-0.045	0.170
Grass	E	1.00	0.147	0.024	0.270
	S	1.00	-0.085	-0.228	0.057
	SLOPE	1.00	-0.052	-0.062	-0.043
	Tmax	1.00	-0.061	-0.158	0.036

	Tmax*E	1.00	0.032	-0.009	0.074
	Tmax*S	1.00	0.154	0.103	0.205
	Tmax*SLOPE	0.79	0.021	0.017	0.024
	$Tmax^2$	1.00	-0.031	-0.039	-0.023
	$Tmax^2$*E	0.42	0.001	-0.003	0.004
	$Tmax^2$*S	1.00	-0.006	-0.010	-0.002
	$Tmax^2$*SLOPE	1.00	-0.001	-0.001	-0.001
	Intercept	-	-0.062	-0.324	0.200
Rock	E	1.00	-0.247	-0.413	-0.081
	S	1.00	-0.416	-0.532	-0.300
	SLOPE	1.00	0.024	0.015	0.033
	Tmax	1.00	-0.888	-0.957	-0.820
	Tmax*E	1.00	0.109	0.062	0.157
	Tmax*S	0.34	0.078	0.050	0.105
	Tmax*SLOPE	1.00	0.0005	-0.002	0.003
	$Tmax^2$	1.00	0.023	0.019	0.028
	$Tmax^2$*E	1.00	-0.006	-0.009	-0.003
	$Tmax^2$*S	0.29	-0.0002	-0.002	0.001
	$Tmax^2$*SLOPE	1.00	0.0003	0.0001	0.0005
	Intercept	-	3.020	2.770	3.270

Table A6

Model performance of predictive habitat models according to AUC and TSS for the study area (>1700m). Thresholds used to define habitat presence are also presented. For forest, the threshold used for Scenarios 2 and 4 is given in parentheses.

Habitat	AUC	TSS	Threshold
Forest	0.85±0.003	0.56	0.28 (0.46)
Shrub	0.79±0.005	0.32	0.22
Pasture	0.71±0.005	0.32	0.36
Grass	0.72±0.005	0.26	0.39
Rock	0.85±0.003	0.56	0.34

Table A7

Mean altitude (m) ± SD of each class per scenario. OBS = Observed data, CURRENT = current modelled habitat cover, Scenario 1 represents a rapid response of forest extent to climate change (based on the B2A projections), scenario 2 represents a slower response of forest with greater subsequent shrub expansion. Scenarios 3 and 4 are the same as scenarios 1 and 2 respectively, except that vegetation development is constrained at high altitudes, therefore habitat cover is equal to the current scenario above 2800m for both.

Class	OBS	CURRENT	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Forest	1962±170	1998±201	2196±299	2175±271	2181±284	2168±263
Shrub	2074±229	2054±239	2256±304	2243±309	2250±272	2219±277
Past	2121±255	2083±247	2278±318	2262±325	2241±285	2226±291
Grass	2281±279	2246±288	2562±306	2558±310	2475±254	2471±258
Rock	2563±315	2609±250	2930±314	2900±361	2928±213	2916±242

997

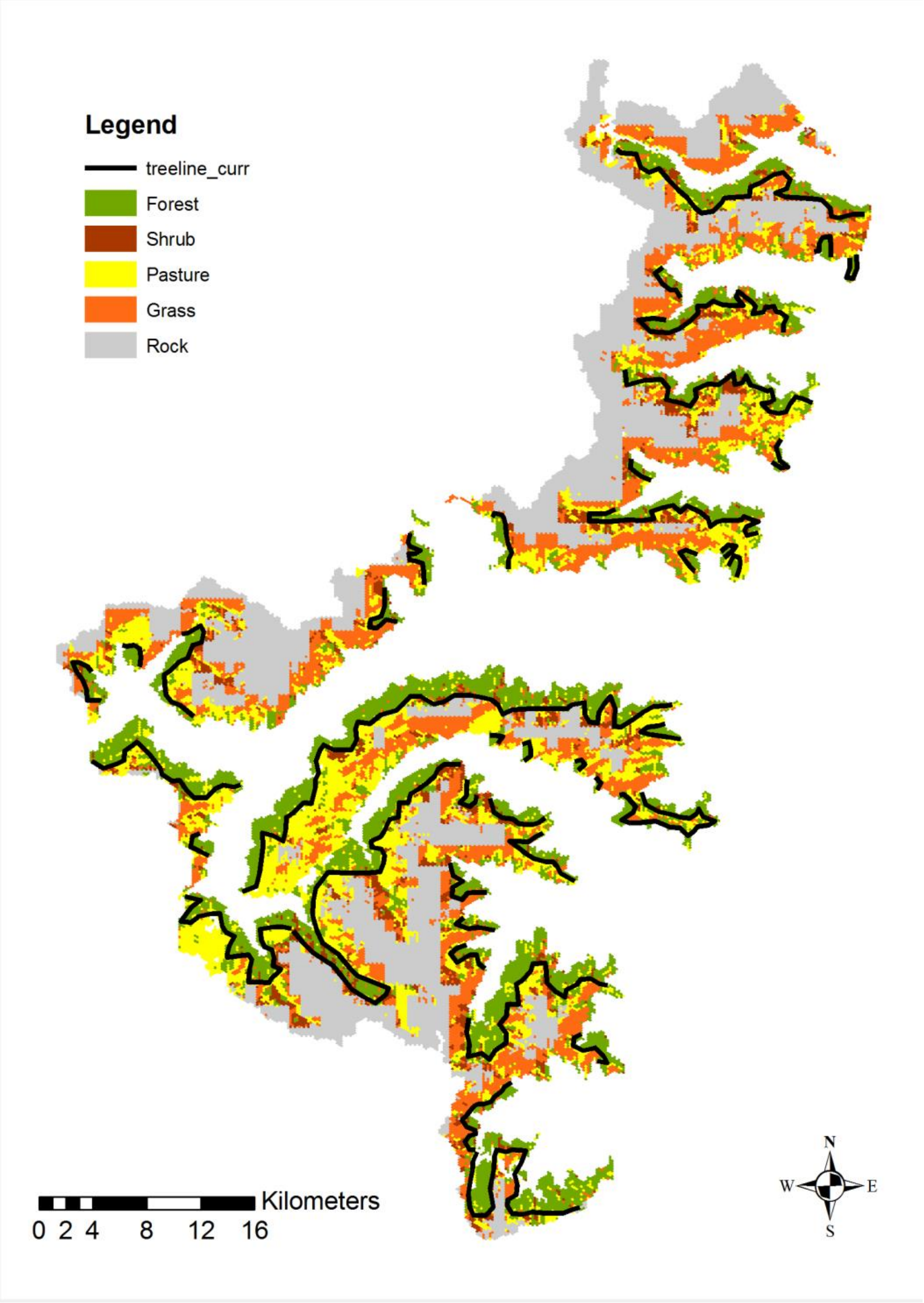

Fig. A1. Land cover predicted from modelling the presence of five habitat types (forest, shrub, pasture, grass and rock) in relation to temperature, aspect and slope. Predictions were made in 42398 hexagonal cells of 200m width for the Province of Torino at altitudes ≥ 1700m. The observed treeline ('treeline_curr') estimated from PFT data is also shown.