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

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

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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).

169 *2.4 Statistical methods*

170

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

177 Prior to developing predictive models, points that were in habitats wholly outside a species'
178 normal breeding range were removed ('bad zeros' which may cause model fitting problems whilst
179 providing no useful information; Zuur et al., 2009). In practice, the species considered here can be
180 divided into forest/shrub species and open habitat species. The former are those that require the
181 presence of trees or shrubs for nesting, and wholly unsuitable habitats were hence simply defined as
182 those with zero forest plus shrub cover, leaving a total sample of 150 points. Forest/shrub species
183 with sufficient samples for analysis were Tree Pipit *Anthus trivialis* (singing birds present on 39
184 points), Dunnock *Prunella modularis* (n = 36), Wren *Troglodytes troglodytes* (n = 41), Coal Tit
185 *Periparus ater* (n = 46), Willow Tit *Poecile montanus* (n = 39) and Chaffinch *Fringilla coelebs* (n = 93).
186 Open habitat species with sufficient samples for analysis were Skylark *Alauda arvensis* (n = 41),
187 Water Pipit *Anthus spinoletta* (n = 67), Wheatear *Oenanthe oenanthe* (n = 46) and Black Redstart
188 *Phoenicurus ochruros* (n = 49). These species nest on or near the ground, and have been recorded as
189 showing strong preferences for open habitats (Snow and Perrins, 1998), although a universal
190 definition of open habitat was not really possible as such species may show varying levels of
191 tolerance to forest or shrubs. The maximum forest cover of a given point in which the four species
192 were recorded was 40% for Skylark, 4% for Wheatear, 0% for Water Pipit and 71% for Black Redstart.
193 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

218 Statistic (TSS; Allouche et al., 2006). Models that had a predictive ability no better than random,
219 considered as AUC < 0.60 or TSS < 0.10, were not used subsequently.
220
221 *2.4.1 Scenarios of environmental change*
222
223 Climate, topographic and habitat variables were derived for the whole province, and the
224 mean value or percentage cover as appropriate was calculated for hexagons of 200m width
225 (henceforth 'cell'), hence maintaining the resolution at which the survey data was collected. Using
226 parameter estimates derived from the modelling approach, the current probability of occurrence of
227 each species was estimated for each cell for altitudes above 1700m, with wholly unsuitable habitats
228 (see above) being assigned a zero probability. Different scenarios of habitat and climate change
229 were then applied, and the change in estimated range of each species was calculated for each
230 scenario.
231 To estimate the potential consequences of climate and habitat change, we considered three
232 principal drivers: change in mean temperature, elevational shift in habitats and the response of the
233 upper limit of the vegetation zone, basing scenarios on climate predictions for the year 2080 using
234 the projections derived from the Hadley General Circulation Model (specifically HADCM3) available
235 in WorldClim (Hijmans et al., 2005) for IPCC scenario B2A (medium rate of change). We intentionally
236 adopted a conservative approach in selecting the least extreme projections of climate change
237 available for the scale required. The average increase in temperature by 2080 (calculated at the cell
238 level) for the study area according to B2A projections was 3.3°C.
239 Scenarios were based on logistic regression models to simulate natural variation in habitat
240 cover due to climate and topography. The presence of each of the five habitat types in each cell was
241 modelled separately in relation to topographic and climate variables, and all two way interactions
242 between both linear and quadratic climate terms, for the whole province (i.e. the whole regional

243 climatic range including all altitudes). Data were divided into model and test data sets and multi-
244 model inference was used to derive model averaged parameter estimates, as for the bird data. The
245 resulting estimates of the probability of occurrence for each habitat were used to calculate AUC and
246 TSS from the test data, and to identify optimal thresholds for defining presence using the
247 PresenceAbsence package in R (Freeman, 2007) for the study area (≥1700m in altitude), i.e. a habitat
248 was considered present for a given cell if the estimated probability of occurrence was equal to or
249 greater than the threshold.

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

267 A similar approach was undertaken for future scenarios, using constant topographic
268 variables, but substituting climate variables from the B2A projections for 2080. For the initial
269 scenario of rapid increase in forest extent (scenario 1), the thresholds were applied as for the final
270 current model (online appendix). A second scenario (scenario 2) simply changed the threshold for
271 forest to the highest available of those considered, which increased the cover of shrub and
272 decreased the cover of forest, thus simulating a lag in the response of forest (e.g. Cannone et al.,
273 2007).

274 In scenarios 1 and 2, it was assumed that alpine grassland can respond readily to climate
275 warming and therefore its rate of elevational shift will be proportional to temperature. We consider
276 further scenarios of vegetation development at the interface of the grass/bare rock zone for the
277 open habitat species, assuming that ground vegetation formation is constrained by soil processes
278 (Edwards et al., 2007; Freppaz et al., 2010), and hence no further elevational increase of this zone is
279 possible. We define this zone as areas at or above 2800m, the altitude above which Cannone et al.
280 (2007) found little evidence of vegetation change, and also where the cover of rock is 95% in the
281 study area. Habitat above this altitude remained equal to the current scenario. This effect is applied
282 to both scenarios 1 and 2, producing two further scenarios (scenario 3 and 4 respectively).

283

284 *2.4.2 Estimating species distributions under different scenarios*

285

286 The current distribution of each species was estimated for the whole study area based on
287 model averaged parameter estimates. Species presence was defined as the probability equal to or
288 greater than the threshold that optimised the match between predicted and observed prevalence,
289 using the PresenceAbsence package in R (Freeman, 2007), one of the recommended methods of Lui
290 et al. (2005). For each scenario, the change in distribution was estimated as the percentage change
291 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

366 of habitat as alpine grasslands are colonised by forest and shrubs. This is illustrated using as an
367 example the change in the estimated distribution of Water Pipit (under a combined scenario) in
368 Figure 5. The loss is exacerbated as much of the area considered is not at an altitude high enough to
369 accommodate further elevational shifts – in effect, many mountain tops and ridges currently
370 covered by grass are likely to be colonised by shrub or forest over the next century. The result is a
371 much reduced and fragmented distribution of potentially suitable habitat (Fig. 5). Such effects will
372 be even more pronounced if colonisation of higher unvegetated areas by grasslands is not possible
373 due to constraints on soil formation (e.g. Freppaz et al., 2010). The effects of this 'squeeze' on
374 natural grassland may therefore have potentially serious consequences for this habitat in the future.
375 A range of scenarios were considered under two main assumptions: that species respond
376 only to changes in habitat type (habitat models), and that they respond to changes in both climate
377 and habitat type (combined models). Whilst there was little difference in model estimates for most
378 species under these two assumptions, there were two that showed markedly different estimates
379 depending on whether temperature was included in the models. Tree Pipit and Dunnock mostly
380 showed declines in distribution under combined models due to a mismatch between suitable
381 climate conditions and suitable habitat, but clear increases under habitat models. The extent to
382 which climate in addition to habitat determines bird distribution is therefore crucial in assessing
383 potential sensitivity to environmental change for these species. Certainly for many species,
384 temperature accounted for additional variation in the models, suggesting that its effects are likely to
385 reflect finer-scale variations in habitat or resources, or both, which themselves may well be directly
386 limited by climate, and that are important determinants of bird distribution. However, there is some
387 evidence that climate may directly affect Water Pipit distribution (Rauter and Reyer, 2000; Rauter et
388 al., 2002). The extent to which climate *per se* may be important for the other species considered
389 warrants further research.
390

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 ($\Delta AIC > 2$). 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

416 doubt that the strong negative effects of forest in particular will lead to loss of suitable areas for
417 open habitat species. There is also an assumption in the approach that the upper limit of the
418 distribution was sampled, and that birds would not breed in habitats and/or climates at higher
419 altitudes. This is probably reasonable for the species considered – maximum altitudes for open
420 habitat species (Skylark = 2574m, Water Pipit = 2861m, Wheatear = 2754m) were somewhat lower
421 than the maximum altitude surveyed (3058m).
422 The extent of species range sampled is more of an issue with forest/shrub species, because
423 the models predict climates for the lower areas (larch-dominated forest at c. 1700m-2000m) for
424 2080 that are outside of the current study area. However, suitable climate for broadleaf forest
425 (especially Beech *Fagus sylvaticus*) would likely occur at the altitudes considered under future
426 scenarios. Several species considered are also commonly found in broadleaved forests, such as
427 Wren and Chaffinch, although Coal Tit and Willow Tit are much more widespread in alpine
428 coniferous forests (Snow and Perrins, 1998). These two species in particular may have had
429 overestimated increases due to the restricted study area, and consequently habitat, considered in
430 the scenarios.
431
432 *4.2 Scenario development*
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434 In constructing the scenarios of future change, we have intentionally adopted a relatively
435 simple approach as our goal was to produce scenarios against which to test the sensitivity of
436 different species to potential climate change-induced habitat shifts. Nevertheless, the approach
437 adopted predicted well the current habitat distribution. Given the levels of uncertainty in both
438 potential responses of habitat to climate change, and in the projections of climate change
439 themselves, we feel that this is an appropriate approach to take, and that the results are very likely
440 to reflect the relative sensitivity of alpine birds (and their habitats) to potential climate change,

441 although we stress that the estimates of change should be taken as a relative guide to potential
442 sensitivity, rather than predictions of actual change.
443 The scenarios were developed to incorporate natural variation in habitat cover due to
444 climate and topography. The estimated annual rate of forest advance until 2080 relative to the
445 current modelled habitat varied between 2.43m and 2.81m for the different scenarios, which are
446 within the range of observed rates of treeline shifts for the European Alps: 0.28 m per year (Paulsen
447 et al. 2000) to 3.16 m per year (Gehrig-Fasel et al., 2007) respectively. Our scenarios therefore
448 represent plausible rates of forest expansion based on published estimates. Whether treelines shift
449 in response to climate change, and the rate of that change, depend on several factors (Gehrig-Fasel
450 et al., 2007; Harsch et al., 2009). In our study area, the abandonment of traditional grazing practices
451 is increasingly common (Laiolo et al., 2004), and is a factor that is likely to have increased the rate of
452 treeline shift over the past few decades in addition to climate effects (Gehrig-Fasel et al., 2007).
453 Furthermore, the trend towards increased urbanisation and development of ski resorts may well
454 increase in the future, bringing further detrimental effects (e.g. Caprio et al., 2011). Whilst it is
455 difficult to formally incorporate such effects in the scenario development (indeed, developed
456 habitats were specifically not included), it should be noted that all of these anthropomorphic
457 impacts are likely to negatively impact on high alpine habitats, especially open grasslands. This, and
458 the use of B2A climate projections, means our scenario outcomes are as a consequence
459 conservative.
460
461 *4.3 Conservation implications*
462
463 The results presented here suggest strongly that open habitat species will be most sensitive
464 to habitat shifts induced by climate change, especially Water Pipit and Wheatear, which showed
465 estimated declines in all scenarios for both habitat and combined models. The loss of open

466 grassland habitats may therefore present a serious conservation problem in the future, which could
467 be even more marked if climate change progresses at rates in line with other, possibly more likely,
468 projections than the relatively conservative ones used here. Of those species predicted to be most
469 sensitive to climate change, Water Pipit is likely to represent the biggest potential conservation
470 problem as it is very much a mountain specialist throughout most of Europe, and it also seems
471 completely intolerant of forest, and was most sensitive to potential differential shifts in habitats in
472 response to climate change. Clearly this is a species that may be at particular risk and is therefore
473 worthy of further investigations.

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

485 The approach here is restricted to the European Alps of the province of Torino. The extent
486 to which the inferences arising from this work can be applied to alpine habitats in general is
487 unknown. Large-scale biogeographic effects, and local habitat conditions, may influence
488 distributions, in effect causing significant region by habitat/climate interactions, resulting in a
489 species having different sensitivities in different areas. If such models are to have wider
490 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

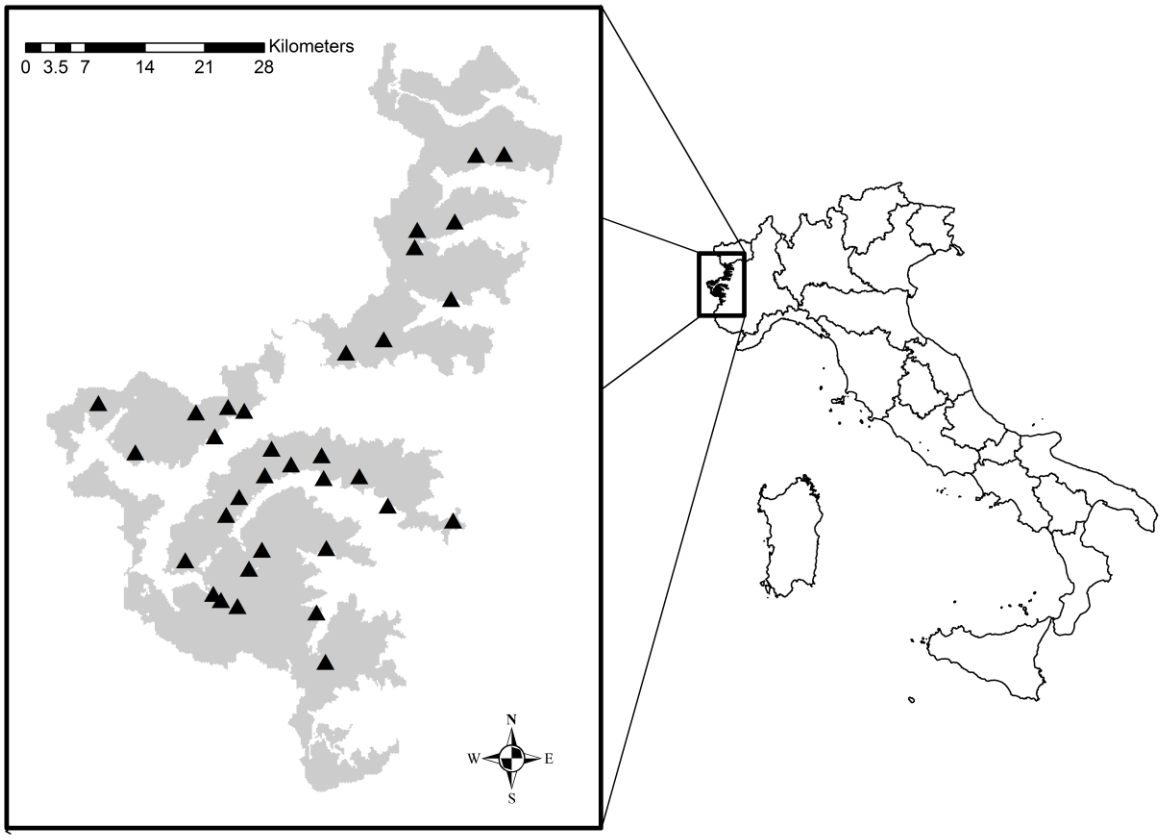

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Fig. 1. Location of the study area in northern Italy, showing the area considered (altitude ≥1700m) in grey and locations of survey transects (black triangles). The extent of the study area was 1331 km^2.

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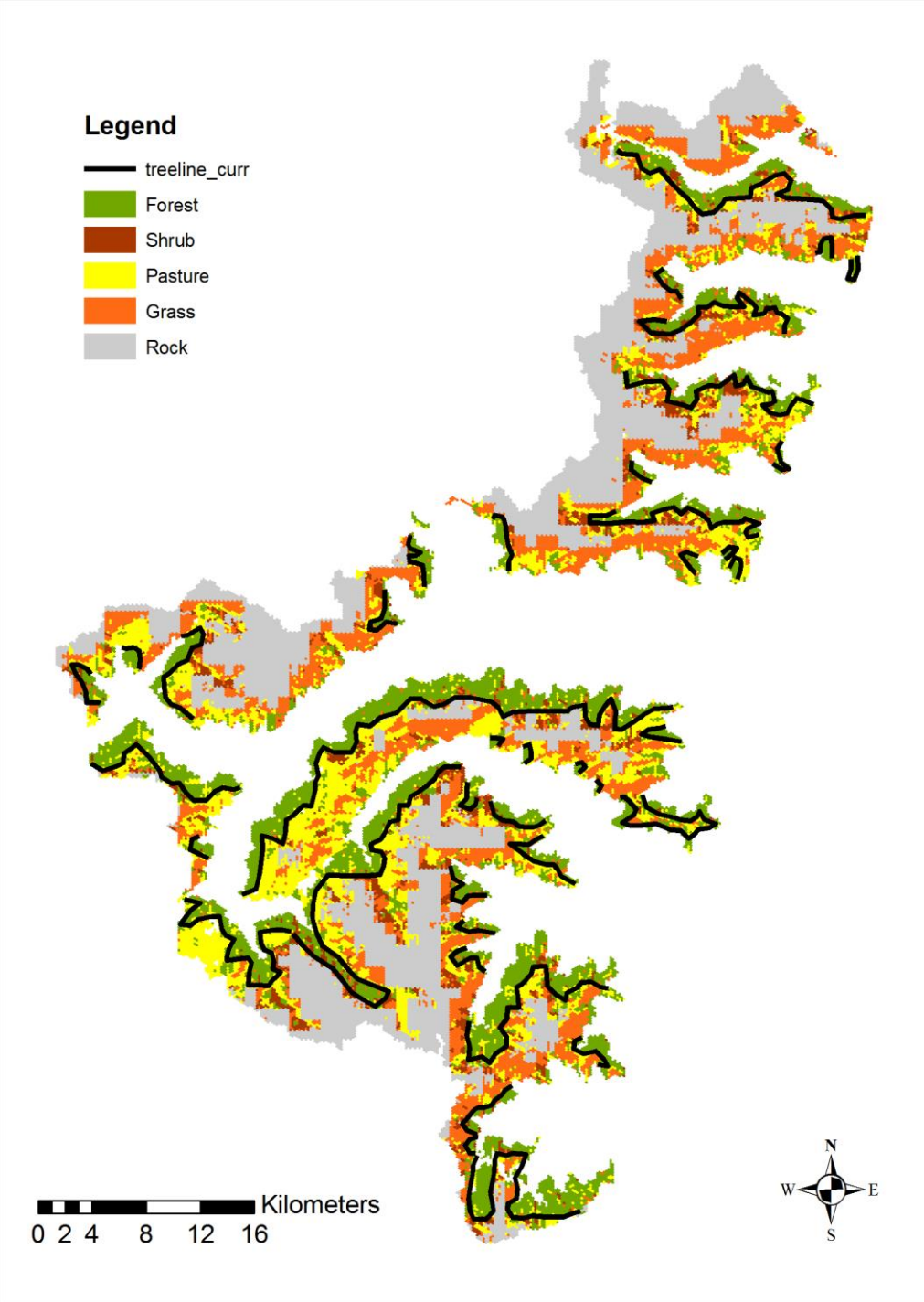

Fig. 2. Land cover predicted from modelling the presence of five habitat types (forest, shrub, pasture, grass and rock) in relation to temperature, aspect and slope. Predictions were made in 42398 hexagonal cells of 200m width for the Province of Torino at altitudes ≥ 1700m. The observed treeline ('treeline_curr')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

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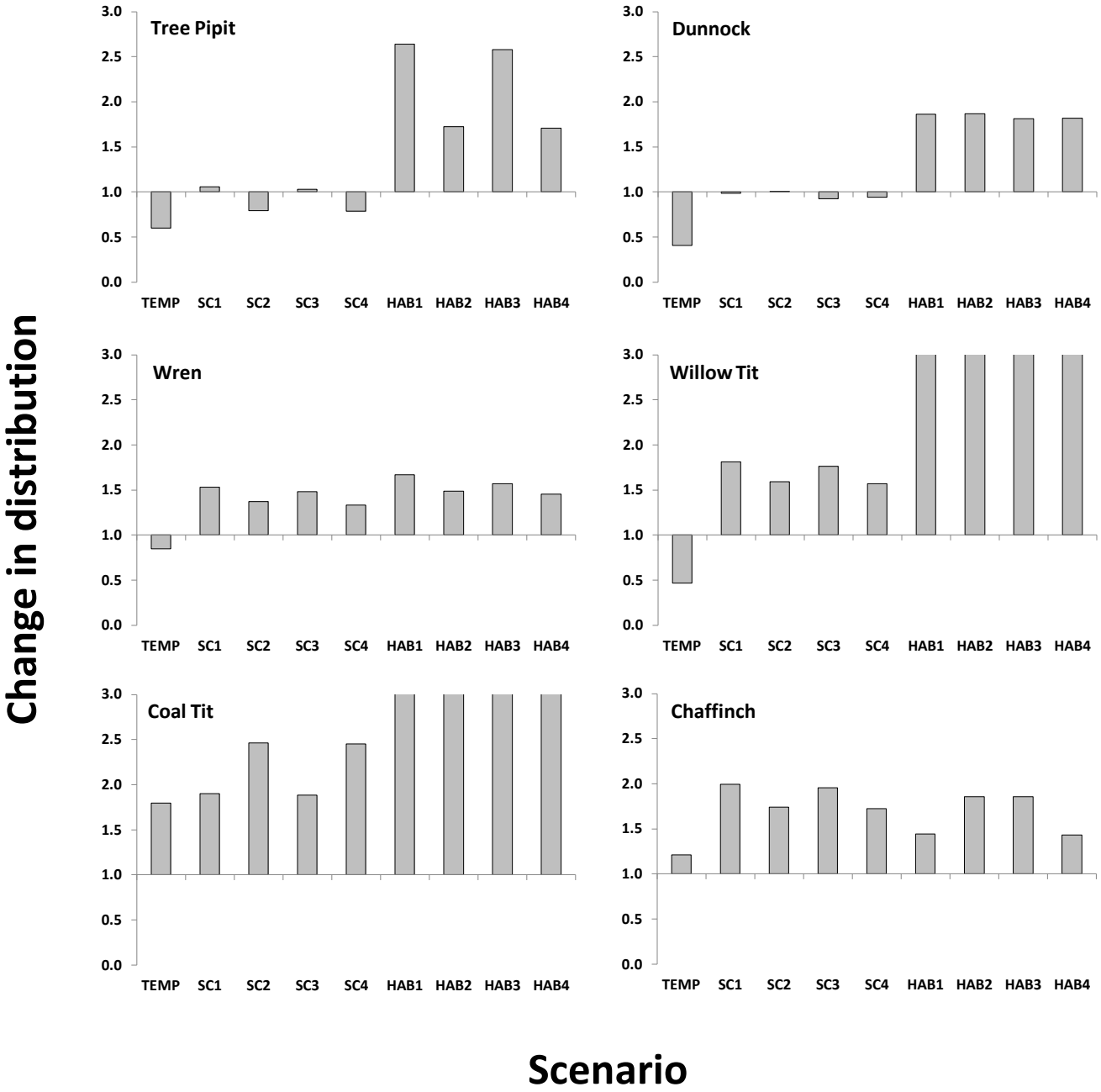

Fig. 3. Change in the distribution of forest/shrub bird species at high altitude (≥1700m) in the western Italian Alps estimated from various scenarios of future environmental change by 2080. The climate model (TEMP) assumes habitat stays constant, but species respond to temperature changes; SC1-SC4 are 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).

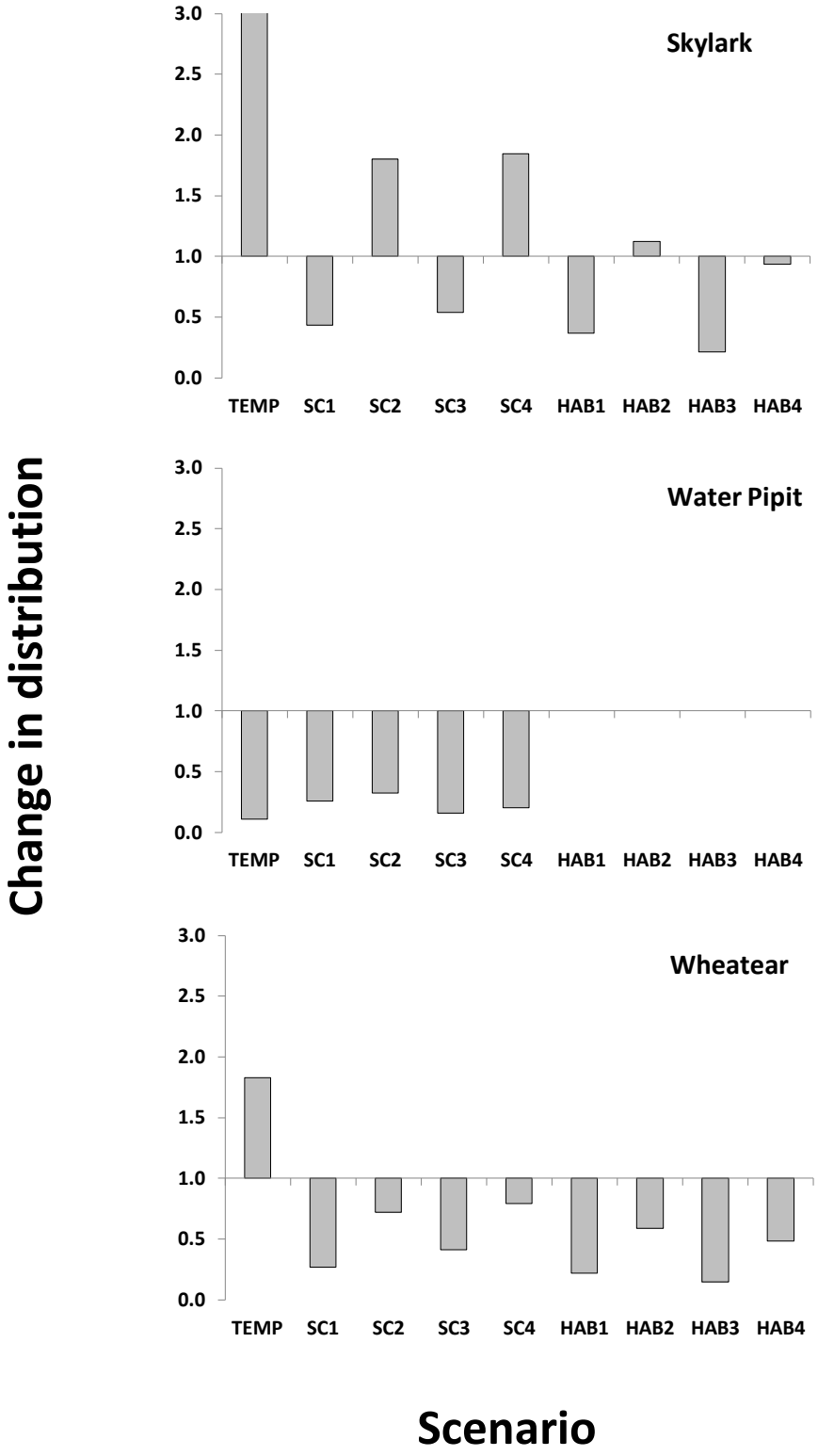

Fig. 4. Change in the distribution of open habitat bird species at high altitude (≥1700m) in the western Italian Alps estimated from various scenarios of future environmental change by 2080. Estimated changes are based on the climate model (TEMP), scenarios 1 to 4 from combined models (SC1-SC4) and habitat 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).

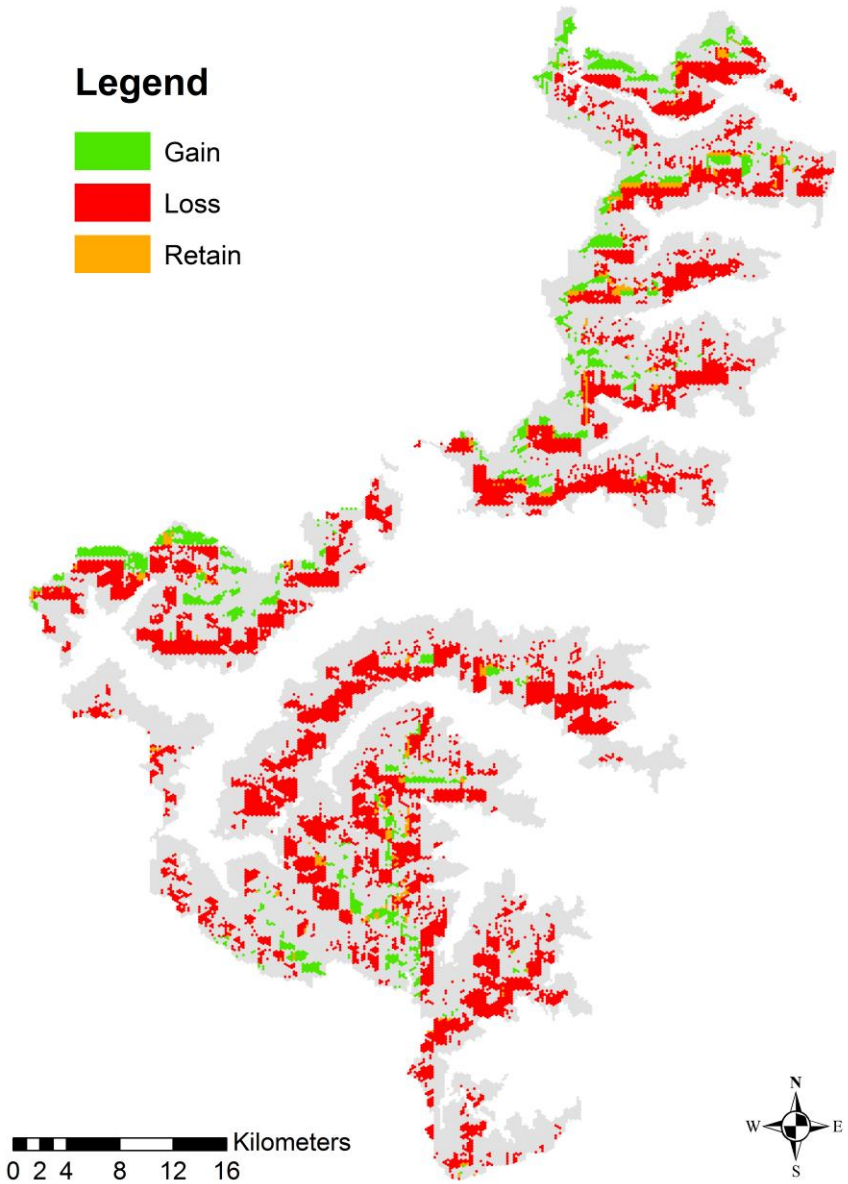

Fig. 5. Change in the predicted distribution of Water Pipit between the current predicted distribution and that under scenario 3 (combined model, rapid response of forest to temperature increase, no expansion of vegetation above 2800m). Grey areas indicate predicted absences in both current and future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

Table and figure legends

Table 1

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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

806 combined model. The procedure was repeated without climate variables, and the resulting model
807 was termed the full habitat model.
808 To assess the level of spatial autocorrelation in the data, Moran's I was calculated on the
809 residuals from the full combined model for each species at various scales. There was no evidence of
810 significant autocorrelation with the exception of Black Redstart (Table A2), where Moran's I was
811 significant at larger scales, even though the magnitude of the effects were very small. Such a result
812 may suggest large-scale geographic variation which may be accounted for by including an
813 appropriate additional variable in the model (Zuur et al., 2009) We defined a further factor 'region'
814 which comprised three groups based on the main valleys in the study area, Chisone, Susa and Lanzo,
815 which was specified as a random factor in the model. Addition of this factor improved the fit (ΔAIC =
816 -7.92) and Moran's I was no longer significant (Table A2). The model including region was therefore
817 subsequently used for Black Redstart.
818 Multi-model inference (Burnham and Anderson, 2002) was used to derive model averaged
819 parameter estimates based on the full models, whereby the suite of models containing all
820 combinations of variables were determined, and model weights were calculated (which express the
821 weight of evidence that a given model is likely to be the best predictive model). Model averaged
822 parameter estimates were calculated across the set of models which accounted for 95% of the sum
823 of all model weights (Table A3).
824 Thresholds for bird presence were defined according to the prevalence approach (Liu et al.,
825 2005), i.e. a bird was considered present if its estimated probability exceeded the predefined
826 threshold for the species. (Note that whilst threshold choice affected the actual magnitude of
827 predicted change in the number of cells in which a species was present, the proportional change did
828 not vary greatly according to the method of threshold derivation selected). In order to assess the
829 predictive ability of the models, AUC and TSS were calculated based on how well the models derived
830 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.

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

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

900 had a single climate variable. However, these variables were interchangeable in the models (i.e.
901 there were no effects on the VIFs of topographic variables), so models were compared with each
902 climate variable in turn. All models also included all two way interactions between both linear and
903 quadratic climate terms. Models were compared using AIC and the model with the lowest AIC
904 (termed the full model) was used to make predictions of the probability of presence of each habitat
905 type per cell. The full model for each habitat type was used as the basis for model averaging in order
906 to derive averaged parameter estimates, as for the bird data (see above). These are given in Table
907 A5. The performance of the resulting models derived from the model data set were then assessed
908 using the test data set by calculating AUC and TSS. Model fits were good (AUC > 0.70 and TSS > 0.20)
909 showing that they had good predictive ability (Table A6).

910 *3.2 Combining model outputs*

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

923 Habitat cover per cell was determined by first omitting any habitat whose probability of
924 occurrence was lower than the threshold for that habitat. The sum of the probabilities of the

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

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

942 *3.3 Future scenarios*

943 The probability of occurrence of each habitat type was estimated from the logistic
944 regression models under a future scenario of moderate climate change based on the IPCC4 B2A
945 scenario (based on a relatively moderate rate of global population increase and intermediate levels
946 of economic development). This was the most conservative scenario available at the scales
947 necessary (1km^2), which was in keeping with our goal of assessing sensitivity against scenarios of less
948 extreme climate change. Climate values used in the current model were substituted for values for
949 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

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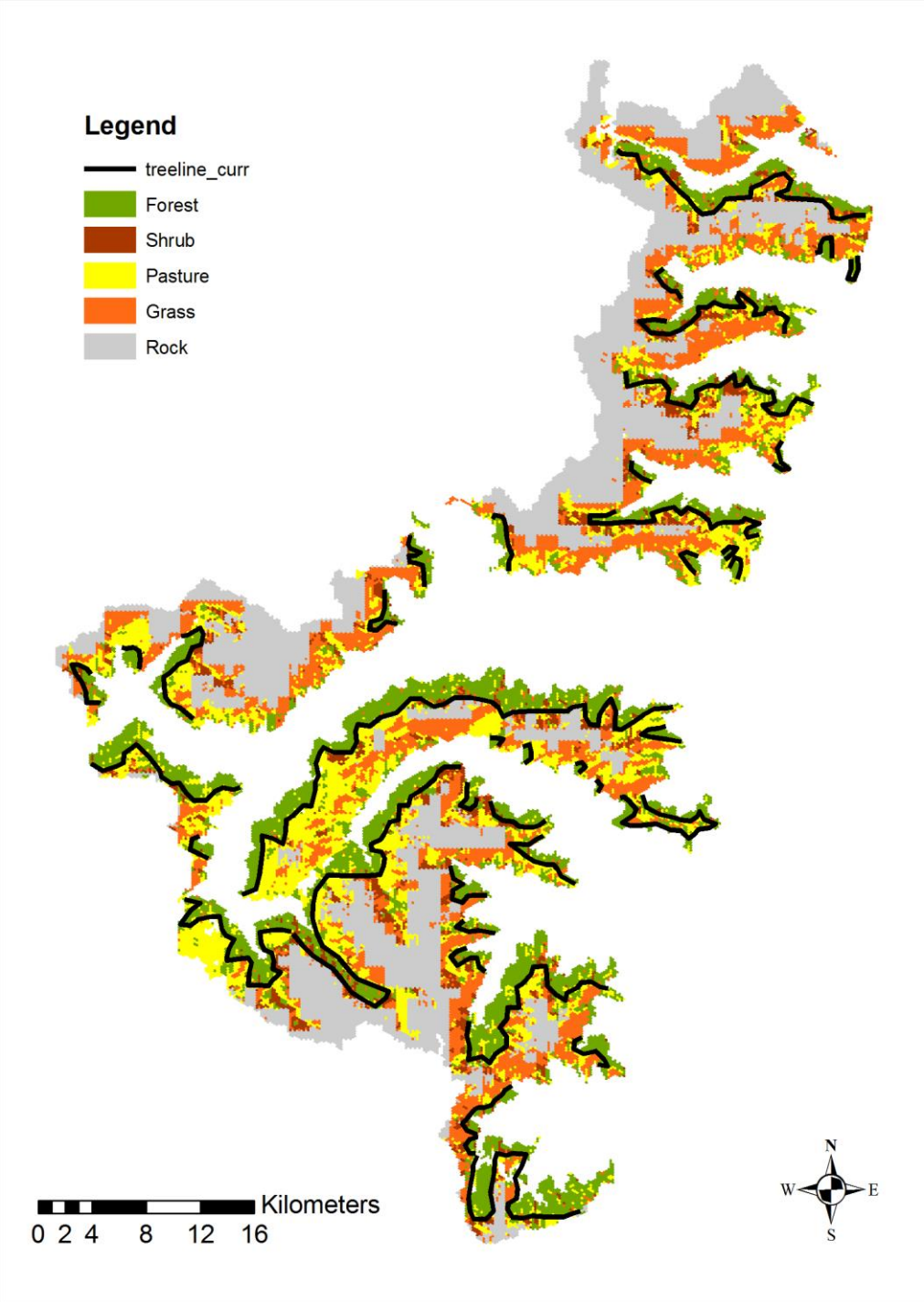

Fig. A1. Land cover predicted from modelling the presence of five habitat types (forest, shrub, pasture, grass and rock) in relation to temperature, aspect and slope. Predictions were made in 42398 hexagonal cells of 200m width for the Province of Torino at altitudes ≥ 1700m. The observed treeline ('treeline_curr')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