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

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

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22   ABSTRACT

23   Climate change has resulted in upward elevational shifts in the distribution of animals and plants in

24   many high altitude areas. The potential consequences of such changes for alpine bird communities

25   were assessed by modelling data on breeding bird distributions along altitudinal gradients at

26   relatively high altitude (c. 1700-3100m) in the European Alps in relation to habitat, topography and

27   temperature. These models were used to assess the sensitivity of species to potential future

28   environmental change by estimating distributions under a range of scenarios of habitat and climate

29   change. Distributions of the majority of forest or shrub nesting species remained stable or increased

30   in response to climate change according to most scenarios as a result of elevational shifts in suitable

31   habitats. However, open habitat species may face a severe decrease in distribution as grasslands are

32   colonised by forest and shrubs, because much of the area considered is not at a sufficient altitude to

33   accommodate further elevational shifts. This may be exacerbated if upward shifts in vegetation are

34   constrained at high altitudes, leading to a habitat 'squeeze' caused by an asymmetric response of

35   vegetation zones to climate change at higher altitudes. Model outcomes suggested that

36   management to maintain open habitats may not be sufficient for a number of species if climate

37   change results in a mismatch between the distribution of suitable climates and suitable habitats. The

38   loss of open habitats due to differential responses of vegetation zones to climate change may

39   therefore present a serious conservation problem for mountain biodiversity in the future.

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

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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

69 tree lines (Harsch et al., 2009), may alter the distribution of habitats, leading to increased

70 fragmentation and eventual loss of habitats at higher altitude (e.g. Peñuelas and Boada, 2003;

71 Gonzalez et al., 2010). However, it should also be acknowledged that the European Alps at least are

72 subject to many pressures, including changes in agriculture, particularly the abandonment of

73 traditional seasonal grazing practices (Laiolo et al., 2004), and increased disturbance from human

74 leisure activities, especially winter sports (e.g. Rolando et al., 2007).

75   Elevational shifts in alpine plant communities in general are well studied ('alpine' here is

76 defined as high altitude mountainous areas at or above the elevational limit of the treeline), and

77 there is evidence that such shifts may not occur at the same rate across different altitudes, nor for

78 different geographical areas. Cannone et al. (2007), in common with many other studies, found

79 recent upward shifts in alpine grassland and shrubland, but they also observed that changes in plant

80 distribution were asymmetrical, and there was little change, and even decreases in vegetation cover,

81 at higher altitudes (<2800m). Recent research has also highlighted the potential negative impacts on

82 soil processes at high altitudes, in particular the likelihood that warmer temperatures could lead to

83 colder soils if snow cover, and its associated insulating properties, are reduced (Edwards et al., 2007;

84 Freppaz et al., 2010). Such an effect would prevent the development of vegetation, and in particular

85 sward-forming grasses, at high altitudes (in accord with Cannone et al., 2007), yet at the same time,

86 this habitat is likely to be lost at lower altitudes due to advancing treelines. There is therefore a

87 potential threat to alpine grasslands due to this differential response of vegetation zones to climate

88 change.

89   Predicting climate impacts on altitudinal distributions is complicated by the variation in

90 climate over small scales due to the steepness of the terrain (typically there is approximately a 0.5°C-

91 0.65°C decrease for every 100m increase in altitude; e.g. Hodkinson, 2005; Colwell et al. 2008), and

92 relatively few studies have attempted to assess likely consequences of environmental (including

93 climate) change on high alpine faunal biodiversity. Altitudinal gradients provide a good basis for

94   studying climate change (Shoo et al., 2006), as the climatic conditions vary over a small spatial scale,

95   thus spatial variations along the gradient provide a substitution for processes over time (Hodkinson,

96   2005), and macroecological influences that may complicate the interpretation of latitudinal studies

97   are reduced (Rahbek, 2005).

98   In this paper, we modelled the altitudinal distributions of breeding alpine bird species at

99   relatively high altitudes (c. 1700-3000m), surveyed along altitudinal transects, in relation to habitat,

100   topography and climate. These models were then used to assess the birds' sensitivity to future

101   climate warming by estimating change in potential breeding distribution according to scenarios of

102   climate and habitat change. Our over-arching goal was to identify species, and habitats with which

103   they are closely associated, that are likely to be sensitive to future environmental changes at high

104   elevations. Whilst elevational shifts due to climate change have typically been assessed at relatively

105   large scales (e.g. Jetz et al., 2007; Sekercioglu et al., 2008; Dirnböck et al., 2011), it is clear that much

106   finer scale-data is needed that more closely matches the climatic variation that occurs over small

107   spatial scales in alpine habitats (Sekercioglu et al. 2008). The extent to which changes in different

108   habitats, and in particular their differential responses to climate change, will affect high altitude

109   faunal distributions associated with the different vegetation zones has not, as far as we are aware,

110   been considered at appropriate spatial scales.

111

112   **2. Methods**

113

114   *2.1 Site and point selection*

115

116   The study area was high altitude habitat (minimum 1700m asl) in the western Italian Alps in

117   the province of Torino (Fig. 1), from the Pellice Valley in the south (44°43′11′′ N; 7°03′35′′) to the

118   Orco Valley in the north (45°30′42′′N; 7°16′25′′). This area is dominated by larch *Larix* spp. at lower

119   altitudes, and shrub species such as Juniper *Juniperus communis* and Alpenrose *Rhododendron*

120   *ferrugium*. Grasslands occur throughout the area, consisting of seasonal pastures and higher

121   altitude alpine grassland. Scree and rocky areas are dominant above c. 2700m.

122   Using land cover data and altitude from a DTM in Geographic Information Systems (GIS)

123   software package, ArcGIS 9.2 (ESRI, 2007), potentially suitable locations for survey sites were

124   identified that had larch-dominated forest at lower altitudes, and where the highest points were at

125   an altitude of at least 2500m. Villages (including tourist developments) and ski-pistes were avoided

126   (a minimum of 330m from the point location). Transects spaced at least 1-km apart were initially

127   selected at random, but due to the difficulty of the terrain, the nearest footpath to the initially

128   selected transect was usually used. Point counts were carried out along the transects with a

129   minimum spacing of 200m between points (or selecting the first suitable location after 200m).

130   Suitable points were those without any obvious disturbance (e.g. occupied human habitation,

131   livestock) or where detectability may have been affected (e.g. large cliffs, noisy streams in spate)

132   within 100m. Sampling took place over three years (2010-2012).

133

134   *2.2. Field surveys*

135

136   Standard point count methods were carried out (Bibby et al., 2000), using a ten minute

137   count period preceded by a five minute settling period. At each point, the observer (DEC) recorded

138   all birds seen and heard, including their activity using standard activity codes (Bibby et al., 2000). For

139   each registration, the distance from the observer was estimated with the aid of a laser range finder.

140   Simple habitat data were also collected at each point, including the percentage cover of canopy (i.e.

141   above head height) and the number of mature trees (≥20cm in diameter) within a 50m radius. Point

142   counts commenced 1 to 1.5 hours after sunrise and continued until 1300 hrs.

143

2.3 Habitat, topography and climate data

145

146   The cover of 5 relevant habitat types (i.e. those occurring above 1700m), selected based on

147   the likely ecological importance for the species under consideration (according to standard works

148   such as Snow and Perrins, 1998, and expert knowledge), was extracted from the Piani Forestali

149   Territoriali (PFT) land cover database for the whole province

150   (www.regione.piemonte.it/foreste/cms/foreste/pianificazione): coniferous forest, scrub, pasture

151   (created as a result of human influence, relatively heavily grazed with a continuous and usually

152   relatively dense sward), grass (natural, though often lightly grazed in late summer, interspersed with

153   rocks, usually at higher altitudes) and rock/scree (details in online Appendix, Table A1). The treeline

154   was simply defined as the perimeter of forest habitat within the study area. As the goal was to

155   estimate species distributions at a relatively large scale, land cover data, rather than habitat data

156   collected in the field, was used in the modelling. However, there were strong correlations between

157   forest land cover and the comparable habitat variables canopy cover (Pearson correlation $r_{255} = 0.86$,

158     $P > 0.0001$) and number of mature trees within 50m ($r_{255} = 0.77$, $P > 0.0001$) collected in the field,

159   suggesting that the land cover data provided a good representation of habitat 'on the ground'.

160   Mean, minimum and maximum annual temperature, and mean monthly precipitation at a 1-

161   km square scale were extracted from WorldClim (Hijmans et al., 2005). Topographic data (aspect

162   and slope) were derived from the DTM elevation grid at a 1ha scale. Mean values were calculated for

163   each 100m radius point count location. Easting and northing have been shown to have separate

164   effects on alpine plant and animal distributions (Guisan et al., 1998; Rauter and Reyer, 2000), so

165   both were considered, expressed as an index equal to –cos(A), where A is the aspect (east or south)

166   expressed in radians (Bradbury et al., 2011). A value of 1 represents facing directly south or east,

167   and -1 represents facing directly north or west. Altitude (expressed in m) at each point was

168   recorded by the GPS in the field to an accuracy of at least ±20m (but usually ±5m).

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

194 Skylark, less than 10% for Wheatear, 0% for Water Pipit and less than 80% for Black Redstart (sample

195 sizes were respectively 197, 156, 170 and 224).

196   As some points were visited more than once (44%), the probability of occurrence was

197 modelled as a vector of presences and absences (i.e. the successes/failures syntax of Crawley, 2007)

198 to account for variation in survey effort, using binomial logistic regression in a general linear mixed-

199 modelling framework with the lmer command in the lme4 package in R. In order to account for

200 potential spatial autocorrelation between points on the same transect, 'site' was fitted as a random

201 term. In order to assess the predictive ability of the models, data were divided into model (70%) and

202 test (30%) data sets.

203   Habitat variables expressed as a proportion were arcsine-square root transformed prior to

204 analysis. This to some extent reduced linear dependence, but there were still some unacceptably

205 high correlations amongst variables, in particular there was very high inter-correlation between all

206 four climate variables (Pearson's correlation $|r| > 0.79$, $P < 0.001$ in each case). In order to reduce

207 the level of collinearity prior to modelling, variance inflation factors (VIFs) were calculated, and the

208 variable with the highest VIF was sequentially removed and VIFs re-calculated (following Zuur et al.,

209 2009) until all variables had a VIF < 2.0. There was no strong evidence of spatial autocorrelation

210 according Moran's I calculated from model residuals (online Appendix Table A2).

211   Once the final model variable set had been identified, model averaging (Burnham and

212 Anderson 2002) was carried out using the MuMIn package in R (R Core Development Team, 2010),

213 averaged parameter estimates being calculated across the set of models which accounted for 95% of

214 the sum of all model weights. Predictive ability was assessed by calculating two different metrics

215 (reliance on only a single measure of model fit is not recommended – Elith and Graham, 2009)

216 calculated from the averaged models applied to the test data set. These were the area under the

217 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

11

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.

292   In estimating species distributions according to the scenarios, two assumptions were made.

293   First, it was assumed that both climate and habitat dictate species distributions, hence temperature

294   and habitat variables were included in the modelling procedure ('combined models'). Second, it was

295   assumed that species respond only to habitat change rather than climate change *per se*, hence only

296   habitat variables were included ('habitat models'), i.e. the same modelling approach without climate

297   variables. In addition, we consider the case where species may respond to climate, but habitat cover

298   does not change (which may mimic a situation where current habitat is maintained by management

299   interventions under a changing climate). To estimate species distributions from these 'climate

300   models', only temperature was altered according to the B2A projections for 2080, all other variables

301   being equal to the current estimated values. Therefore, in summary, there were four scenarios for

302   combined models, four scenarios for habitat models, and a single scenario for the climate model,

303   giving a total of nine scenarios considered per species.

304

305   **3. Results**

306

307   Model fits were good for most species (AUC ≥ 0.7 and TSS ≥ 0.2), but less so for Wren (AUC =

308   0.66, TSS = 0.10). Model fit was no better than random for Black Redstart (both models) and Water

309   Pipit (habitat model) and these were not considered further. A comparison of AIC between full

310   models suggested that combined models were usually better (i.e. ΔAIC > 2) than habitat models for

311   most species. However, there was no difference between models for Wren and Willow Tit (ΔAIC <

312   2), and the habitat model was better for Dunnock. (Full details of model-averaged parameter

313   estimates and measures of model fit are given in the online Appendix, Tables A3 and A4).

314

315   *3.1 Habitat change*

316

317   Model averaged parameter estimates (online Appendix Table A5) for habitat showed good

318   fit in terms of AUC and TSS (online Appendix Table A6). The estimated current habitat map gave a

319   good match to the observed habitat cover (Table 1) and location of the treeline (Fig. 2), and the

320   mean altitudes of observed and predicted habitats were in good agreement (all within 100m; online

321   Appendix Table A7). The change in habitat cover relative to the current scenario is summarised in

322   Table 1 for scenario 1 to 4. Under scenario 1, the area of forest more than doubles and there is a

323   smaller increase in shrub cover, whilst under scenario 2, the increase in shrub and forest are more

324   equitable and above 50%. Pasture increases relatively modestly in all scenarios. Under scenarios 1

325   and 2, cover of rock is lost because much of the study area is not high enough to accommodate

326   habitat shifts, and also because other habitats are able to replace high altitude rock. Under scenario

327   3 and 4, where high altitude rock cannot be replaced, the decrease in rock cover is less marked, and

328   as a consequence the loss of grass is greater as this habitat is squeezed between advancing tree and

329   shrub habitats and an immovable rock zone (Table 1).

330

331   *3.2 Estimated changes in species distribution*

332

333   The estimated changes in distribution of forest/shrub species are given in Fig. 3. Coal Tit and

334   Chaffinch showed estimated increases under each scenario, sometimes of considerable magnitude,

335   due to a positive influence of both temperature and habitat. Willow Tit and Wren showed estimated

336   increases in all except the climate scenario, suggesting that temperature increases that are not

337   accompanied by habitat shifts would be detrimental to these species. However, there was a

338   different pattern for Tree Pipit and Dunnock, where there were increases estimated by habitat

339   models (an exception being Tree Pipit under scenario 2), but decreases or little difference for the

340   combined models.

341   In contrast to forest/shrub species, decreases in the distribution of open habitat species

342   were estimated under the majority of scenarios (Fig. 4). To a large extent, this was due to loss of

343   open areas as they were encroached upon by forest and shrub. However, for Water Pipit, there was

344   an additive effect of temperature in the combined models, indicating that some open habitats were

345   climatically unsuitable under these scenarios. By contrast Skylark and Wheatear increased under

346   warmer conditions, as shown by the estimated distribution under the climate model. For Wheatear,

347   this was not enough to offset decreases caused by habitat loss under combined models. The model

348   outcomes for Skylark were largely dependent on whether there was a greater upward shift in forest

349   (resulting in declines) or shrub (resulting in increases). Including the further assumption that habitat

350   would not change at high altitudes due to effects on soil processes (scenarios 3 and 4) led to a

351   further loss in estimated distribution of c. 15% for Skylark, 7% for Wheatear (habitat models) and

352   10% for Water Pipit (combined model), although for the former two species, this effect was reversed

353   under the combined model, with decreases respectively 10% and 15% less than under the habitat

354   model.

355

356   **4. Discussion**

357

358   The goal of this study was to describe statistically the distribution of alpine bird species

359   along an altitudinal gradient, and to use this information to assess the sensitivity of these species to

360   potential habitat change induced by climate change. For the majority of species nesting in forest or

361   in the transition zone between forest and alpine grasslands, their distribution remained constant or

362   expanded according to the scenarios, because the amount of suitable habitat is likely to remain

363   stable or increase in the study area in response to climate change at high altitude as a result of

364   elevational shifts in forest and shrubs. However, open habitat species showed a decrease in

365   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

391   *4.1 Model predictions*

392

393   Model fits were generally good, exceptions being Black Redstart and Water Pipit (habitat

394   model), suggesting key variables were not considered in the model for the former species, and that

395   the latter species' distribution could not be predicted from habitat and topography alone. For the

396   other species, model performance strongly suggested that distributions could be adequately

397   predicted by a combination of habitat cover, temperature and topography. We used the smallest-

398   scale climate data available (1km^2), which was larger than the unit of analysis (100m radius).

399   Although the addition of smaller scale topographic variables will to some extent have effectively

400   provided finer-scale adjustments, there is evidence that there is significant climatic variation at

401   smaller scales which has a major influence on plant distribution (e.g. Scherrer et al. 2011) and

402   invertebrate, though not bird, diversity (Viterbi et al., 2013). Furthermore, for five species (Skylark,

403   Water Pipit, Wheatear, Coal Tit and Chaffinch), substituting altitude for temperature in our models

404   improved model fit (ΔAIC > 2). Altitude was strongly correlated with both temperature and

405   precipitation (r_{255} = -0.79 and 0.83 respectively, P < 0.001), but it was measured at a much finer scale

406   than climate variables, and its effects are likely to reflect finer-scale variations in habitat or

407   resources, or both, which themselves may be directly limited by climate. Although models were

408   generally good in terms of predictive ability, it is likely that finer-scale measures of habitat or climate

409   would prove even better tools for some species. Further detailed autecological studies to identify

410   the key resources of the species of interest would be necessary for such approaches.

411   In modelling species responses to climate, it is advisable to consider as much as possible of a

412   species' range (Barbet-Massin et al., 2010). This would be major logistical challenge at the scales

413   considered, i.e. those appropriate in considering altitudinal shifts. For higher altitude habitats, the

414   conclusions of this study should not be affected by the restricted altitudinal range if the assumptions

415   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*

433

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

491   regions (Whittingham et al., 2007). We therefore urge similar work to be carried out in other alpine

492   regions in order to determine whether species sensitivities to potential climate change are

493   consistent across larger areas. Nevertheless, the processes of habitat shifts illustrated here,

494   especially when there are differential responses of vegetation zones to climate change, are likely to

495   be highly relevant to any mountain areas with analogous altitudinal zonation of habitats and their

496   associated animal communities.

497

498   **5. Conclusions**

499

500   Here, we have used birds to illustrate how possible changes in habitats and climate may

501   affect species distributions in high alpine habitats in the future. The results are in accord with those

502   of Dirnböck et al. (2011) who predicted that areas of endemism for vascular plants and several

503   invertebrate groups were at high risk of future habitat loss due to forest expansion. Therefore, in a

504   more general sense, open habitat bird species illustrate the potential threat to wider biodiversity of

505   alpine grasslands which are likely to host a high diversity of a number of groups, such as flowers,

506   carabid beetles, dung beetles and butterflies (e.g. Nagy et al., 2003; Tocco et al., 2013), not to

507   mention other high altitude specialist bird species which were recorded too infrequently for analysis

508   (e.g. Ptarmigan *Lagopus muta*, Alpine Accentor *Prunella collaris*, Snow Finch *Fringilla montifringilla*).

509   The potential for loss of alpine grassland under future climate change seems high, especially if

510   upward shifts are constrained, either due to a lack of higher altitude areas or due to a habitat

511   'squeeze' caused by an asymmetric response of vegetation zones to climate change at higher

512   altitudes. Continued monitoring and research should be prioritised for this potentially threatened

513   habitat, in particular at the interface between the grassland and bare rock habitats at higher

514   altitudes where soil responses may be crucial for vegetation communities and consequently possible

515   distributional shifts of alpine fauna.

516   Whilst we believe our modelling approach was fit for purpose in terms of assessing likely

517   sensitivity of alpine birds to environmental change, we also acknowledge that there are many other

518   potential approaches which could be worth considering, especially if additional data in the form of

519   repeat visits could be obtained (e.g. use of hierarchical state-space models; Buckland et al., 2004).

520   More broadly, such 'static' species distribution models (including those used in this paper) have a

521   number of limitations in estimating the true niche of a species, and hence in making predictions for

522   potential future impacts of environmental change (Schurr et al., 2012), as they cannot incorporate

523   more complex processes such as dispersal, biotic interactions and range dynamics (Pearson and

524   Dawson, 2003; Holt, 2009), nor indeed can they account for the potential adaptation of species to

525   novel conditions (Pearson and Dawson, 2003). In order to address such issues and therefore better

526   understand the actual demographic processes underlying species' distributions, the adoption of a

527   process-based dynamic range modelling framework would be ideal (Schurr et al., 2012). However,

528   such complex models require complex data in terms of spatio-temporal demographic rates. The

529   paucity of such data for the European Alps (Chamberlain et al., 2012), and for mountain regions in

530   general, currently precludes such approaches, but detailed demographic monitoring should be made

531   a priority for the future if we are to better understand factors determining bird species distributions

532   at high altitude, and therefore make improved predictions on impacts of environmental change.

533

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540

541   **References**

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678

679   **Table 1**

680   The percentage of observed cover and current modelled cover of each habitat type in the study area

681   ≥1700m asl, and the percentage change in cover according to each scenario relative to the current

682   model (so a 100% increase would indicate a doubling in area covered). Scenario 1 represents a rapid

683   response of forest extent to climate change (based on the B2A projections), scenario 2 represents a

684   slower response of forest with greater subsequent shrub expansion. Scenarios 3 and 4 are the same

685   as scenarios 1 and 2 respectively, except that vegetation development is constrained at high

686   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
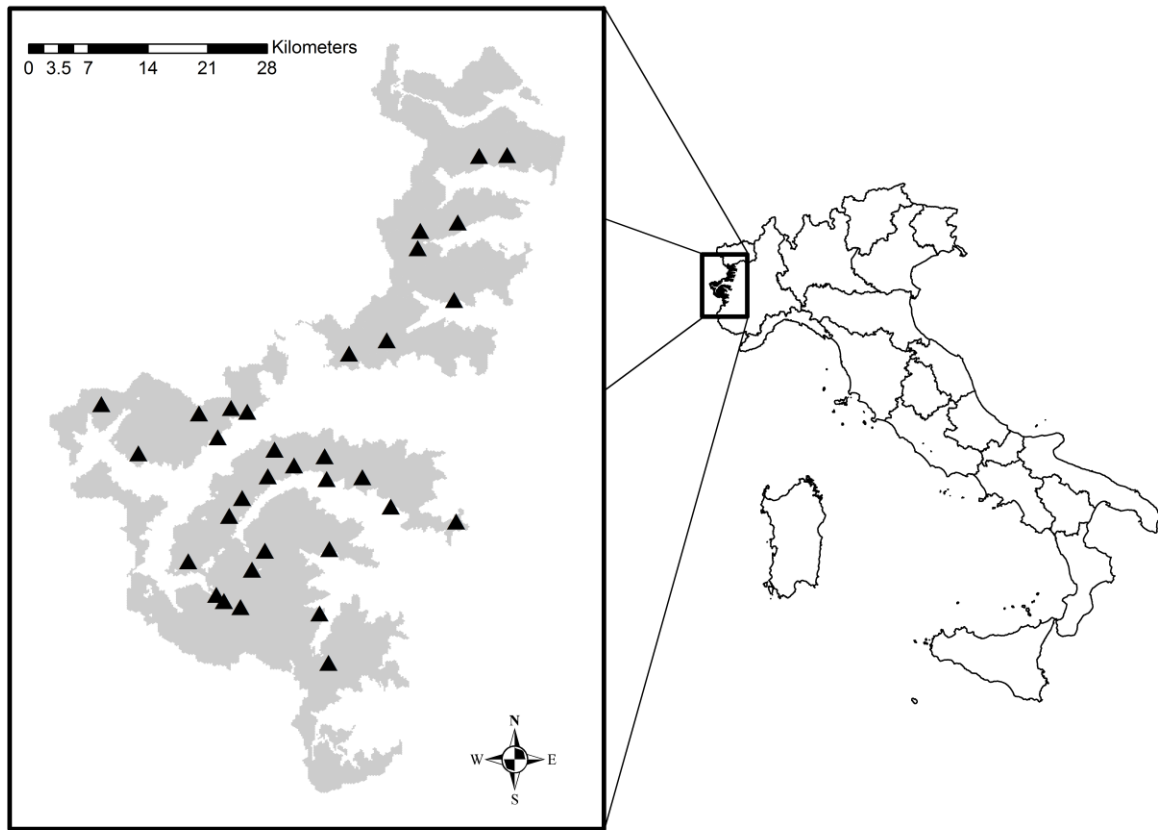
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Fig. 1. Location of the study area in northern Italy, showing the area considered (altitude ≥1700m) in grey and locations of survey transects (black triangles). The extent of the study area was 1331 km^2.

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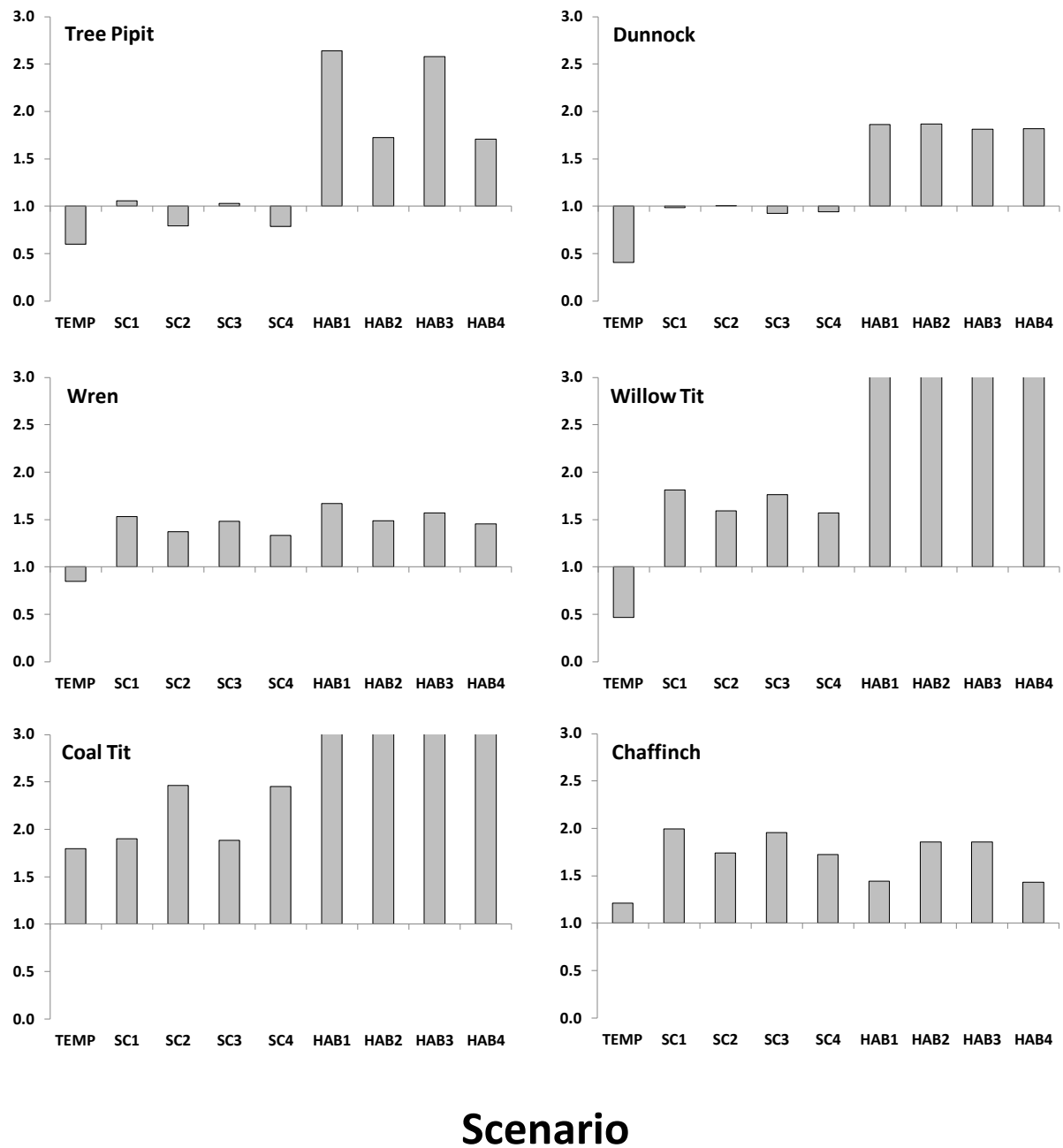
Fig. 3. Change in the distribution of forest/shrub bird species at high altitude (≥1700m) in the western Italian Alps estimated from various scenarios of future environmental change by 2080. The climate model (TEMP) assumes habitat stays constant, but species respond to temperature changes; SC1-SC4 are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

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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).

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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.

708   Table and figure legends

709

710   **Table 1**
711   The percentage of observed cover and current modelled cover of each habitat type in the study area
712   ≥1700m asl, and the percentage change in cover according to each scenario relative to the current
713   model (so a 100% increase would indicate a doubling in area covered). Scenario 1 represents a rapid
714   response of forest extent to climate change (based on the B2A projections), scenario 2 represents a
715   slower response of forest with greater subsequent shrub expansion. Scenarios 3 and 4 are the same
716   as scenarios 1 and 2 respectively, except that vegetation development is constrained at high
717   altitudes, therefore habitat cover is equal to the current scenario above 2800m for both.

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

720   **Fig. 2.** Land cover predicted from modelling the presence of five habitat types (forest, shrub,
721   pasture, grass and rock) in relation to temperature, aspect and slope. Predictions were made in
722   42398 hexagonal cells of 200m width for the Province of Torino at altitudes ≥ 1700m. The observed
723   treeline ('treeline_curr') estimated from PFT data is also shown.

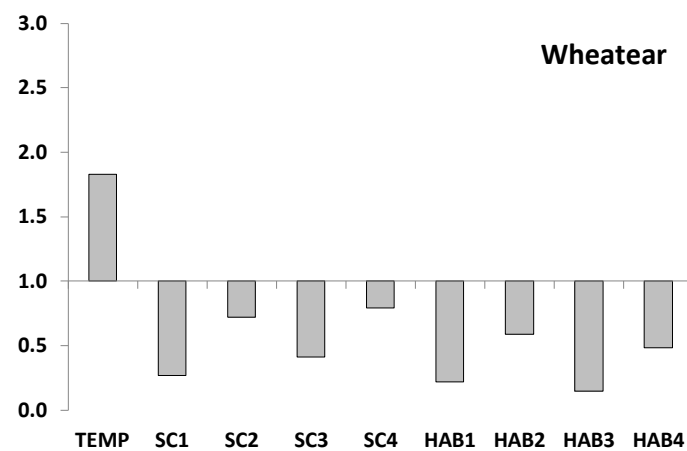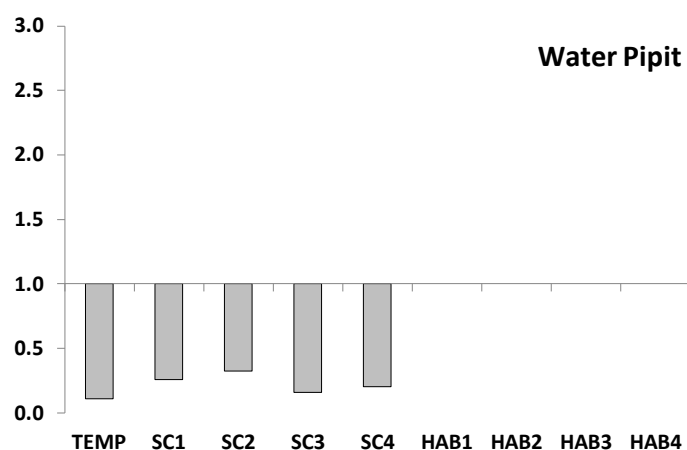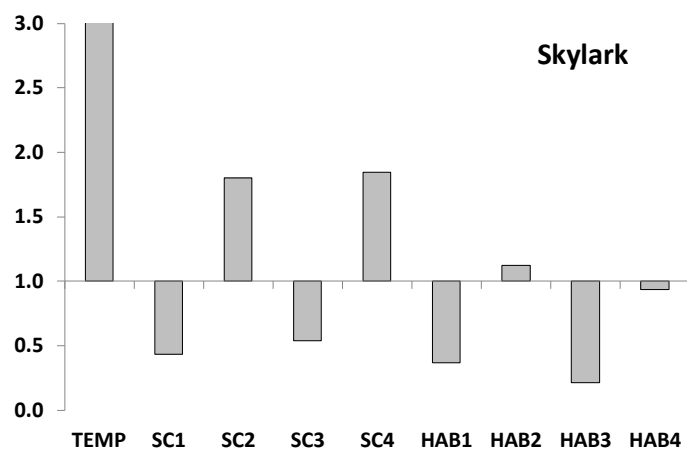724   **Fig. 3.** Change in the distribution of forest/shrub bird species at high altitude (≥1700m) in the
725   western Italian Alps estimated from various scenarios of future environmental change by 2080. The
726   climate model (TEMP) assumes habitat stays constant, but species respond to temperature changes;
727   SC1-SC4 are derived from scenarios 1 to 2 (Table 1) for combined models where species respond to
728   both habitat and temperature changes; HAB1- HAB4 are derived from scenarios 1 to 2 for habitat
729   models where species respond only to change in habitat. Change is expressed as the proportion of
730   the current estimated distribution relative to the distribution estimated under each scenario (so
731   values <1 indicate a decrease and values >1 indicate an increase). Note that for presentational
732   purposes, increases greater than 3 are not shown for HAB1-HAB4 for Willow Tit (respective values =
733   5.96, 4.93, 5.91 and 4.90) and Coal Tit (respective values = 6.22, 5.03, 6.19 and 5.00).

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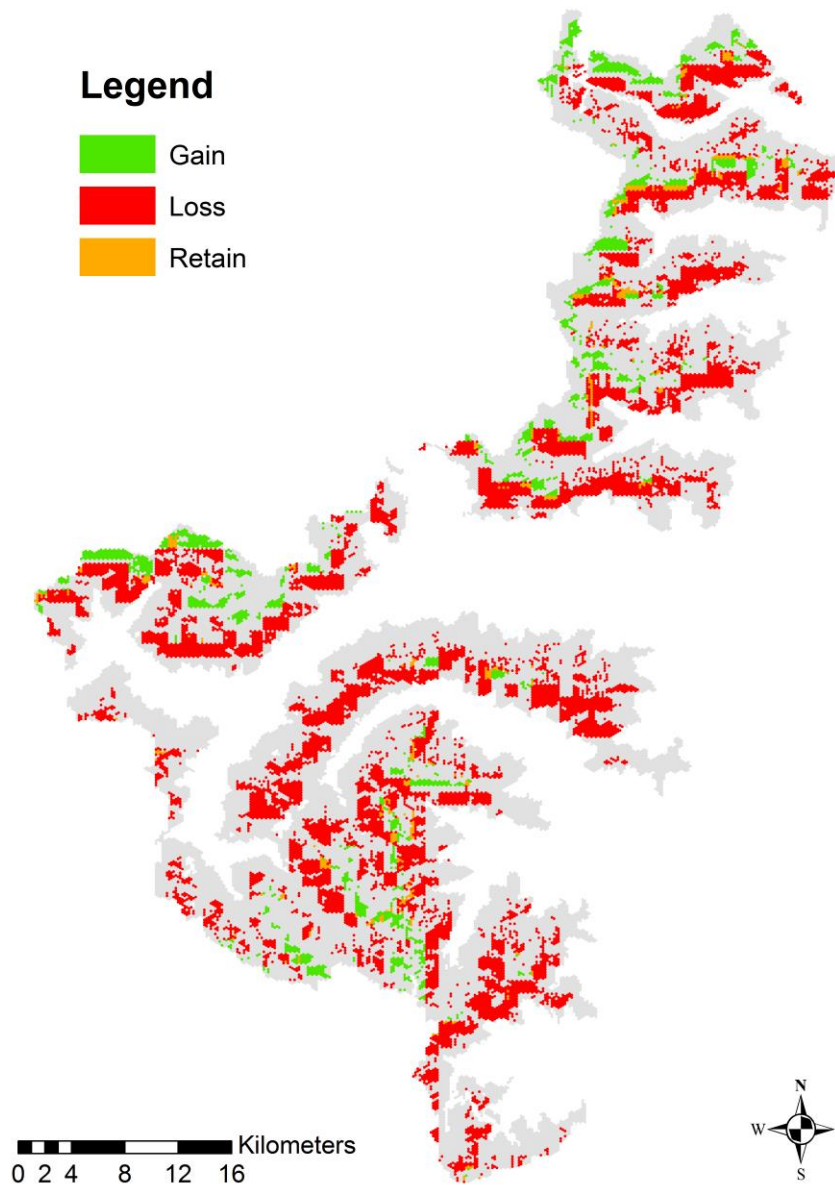739   for Skylark (TEMP, change = 5.29).

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

744

745   **Online Appendix**

746

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

748   **1. Habitat variables**

749   The five habitat variables were based on 15 relevant land cover types (i.e. those occurring

750   above 1700m) extracted from the Piani Forestali Territoriali (PFT) land cover database for the whole

751   province (www.regione.piemonte.it/foreste/cms/foreste/pianificazione). PFT data are backed-up by

752   a high level of ground-truthing and they provided a much better visual fit when overlaid on Google

753   Earth images of the study area compared to the commonly used CORINE (CO-oRdination of

754   INformation on the Environment) land cover database. Variable definitions are given in Table A1.

755   PFT was therefore considered more suitable for a study of medium-low geographical scale. For each

756   point, the percentage cover of these five variables was extracted in ArcGIS 9.3 (ESRI, 2008). The

757   approximate location of the current treeline (Fig. A1) was estimated as the perimeter of forest

758   habitat within the study area, although small patches (<10h) and relatively small gaps between areas

759   of forest (<400m) were ignored.

760   As the goal was to estimate species distributions at a relatively large scale, land cover data,

761   rather than habitat data collected in the field, was used in the modelling. For the latter, some simple

762   data (estimated 'by eye') were collected at each point, including the percentage cover of canopy (i.e.

763   above head height) and the number of mature trees (≥20cm in diameter) within a 50m radius.

764   However, there were strong correlations between forest land cover and the comparable habitat

765   variables canopy cover (Pearson correlation $r_{255} = 0.86$, $P > 0.0001$) and number of mature trees

766   within 50m ($r_{255} = 0.77$, $P > 0.0001$) collected in the field, suggesting that the land cover data

767   provided a good representation of habitat 'on the ground'.

768

Table A1

771 Definitions and summary statistics of variables (including land cover categories used to define

772 habitats) used in the analysis. Code is used to identify variables in the models (Table A3). The mean

773 value was calculated from the total sample of points (n = 257). The description includes the data

774 source where GPS = field reading from Geographical Positioning System, PFT = Piani Forestali

775 Territoriali land cover database, DTM = Digital Terrain Model (www.mais.sinanet.isprambiente.it),

776 WC = WorldCLim database (summarised at 1-km^2 scale). CORINE land cover classes were also

777 considered, but visual overlays of land cover classes on GoogleEarth images of the study points

778 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).

779

780

781

2. Details of bird distribution models

783   In order to assess the predictive ability of the models (see below), data were divided into

784   model (70%) and test (30%) data sets. The probability of the occurrence of singing birds (which were

785   therefore assumed to be potential breeders) from the model data set was modelled using binomial

786   logistic regression in a general linear mixed-modelling framework with the lmer command in the

787   lme4 package in R. In order to account for potential spatial autocorrelation between points on the

788   same transect, 'site' was fitted as a random term. Some points (44%) were subject to more than one

789   visit, so to account for variation in survey effort, bird occurrence per points was expressed as a

790   vector of presences and absences (i.e. the successes/failures syntax of Crawley, 2007). All predictor

791   variables initially considered are shown in Table A1.

792   Habitat variables expressed as a proportion were arcsine-square root transformed prior to

793   analysis. There were some high correlations amongst variables, in particular there was very high

794   inter-correlation between all four climate variables (Pearson's correlation $|r| > 0.79$, $P < 0.001$ in

795   each case). Prior to modelling, the degree of collinearity was assessed by calculating variance

796   inflation factors (VIFs). Following the procedure of Zuur et al. (2009), we calculated VIFs for all linear

797   variables. The variable with the highest VIF was sequentially removed and VIFs re-calculated

798   (following Zuur et al., 2009) until all variables had a VIF < 2.0. Quadratic terms were included if

799   scatter plots of species occurrence per point (the proportion presence/visits) indicated possible non-

800   linear effects. As a final check, variables that had been removed in the VIF procedure were

801   substituted for closely correlated variables (in particular mean temperature, maximum temperature

802   and precipitation, rock and pasture cover, and forest and shrub cover) and models were compared

803   with AIC. Cases where the model with the substituted variable had a lower AIC, and where VIF for

804   each was less than 2, were used as the final full models. The resulting model, which included a set of

805   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

831   were good (AUC ≥ 0.70 and TSS ≥ 0.20; Table A4), although they were less good for Wren, and poor

832   for Black Redstart and Water Pipit (habitat model). In the latter two cases, predictive ability was

833   considered no better than random (AUC < 0.60 and TSS < 0.10) an so they were not considered for

834   assessing scenario outcomes.

835

836 **Table A2**

837 Moran's I statistic calculated from residuals derived from the full combined model for each species

838 at various scales. Values in bold indicate significance ($P < 0.05$). 'Black Redstart (reg)' is Moran's I for

839 the model including the three level factor 'region' specified as a random effect.

840

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|

841

842

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	–	–	–	–

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Table A4

863 Measures of model performance, based on predicting the probability of species presence in a test

864 data set (30% of the sample) using models derived from a model data set (70% of the sample).

865 Model performance was measured as the area under the ROC curve (AUC) and the True Skill Statistic

866 (TSS). The subscript 'comb' indicates combined models including topography, habitat cover and

867 temperature, 'hab' indicates habitat models including only topography and habitat . ΔAIC =

868 difference in AIC between the full combined model and the full habitat model (i.e. so minus indicates

869 the combined model is better). AUC is given ± sd derived from the PresenceAbsence package in R

870 (Freeman, 2007).

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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

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877 **3. Habitat modelling and scenario development**

878   A range of approaches have been used to model vegetation responses to climate change in

879 alpine environments, but these typically are undertaken at relatively small scales, consider individual

880 species, and have not as far as we are aware yet included predictions for responses of high altitude

881 soils to climate change. Land cover data are available over a large area and for the most part define

882 general structural vegetation types rather than individual species (with the exception of some

883 mature tree species), which are nonetheless likely to be appropriate for predicting altitudinal

884 distributions of bird species. Scenario development was a two stage process described in detail

885 below. In summary, the first stage was to estimate the probability of occurrence of each habitat

886 type per cell using logistic regression models in relation to climate and topography. In the second

887 stage, the model outputs were then combined into a continuous surface for each cell by (i)

888 eliminating habitats with predicted probabilities of occurrence lower than pre-defined thresholds

889 (Liu et al. 2005) and (ii) calculating the sum of probabilities of all remaining habitats, and defining

890 habitat cover as the proportion made up by each individual habitat for a given cell.

891 *3.1 Logistic regression*

892   The presence of each of five habitat types (forest, shrub, pasture, grass and rock; see Table

893 A1 for full definitions) in each cell was modelled separately in relation to topographic and climate

894 variables (slope, aspect (east), aspect (south), mean, minimum and maximum temperature and

895 precipitation, and the quadratic of each climate variable). Models were derived from the whole

896 province (i.e. the whole regional climatic range including all altitudes), and data were randomly

897 divided into model (70%) and test (30%) data. Prior to modelling, the degree of collinearity was

898 assessed by calculating variance inflation factors (VIFs) in the same way as for the bird data (see

899 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

950   cell were calculated. The process of combining the habitat types based on thresholds was applied

951   exactly as before which produces a general elevational shift in habitat types which were in line with

952   those already observed, e.g. the mean altitude of forest was predicted to increase by 197m by the

953   2080s, a rate of 2.81m per year, which is within the minimum (0.28m per year, Paulsen et al., 2000)

954   and maximum (3.16m per year, Gehrig-Fasel et al., 2007) rates already observed for treeline shifts in

955   the European Alps. This was scenario 1. Scenario 2 simulated a situation where forest developed

956   less rapidly, but instead there was greater shrub development. This scenario was constructed by

957   substituting the best fitting forest threshold for the highest available threshold of those considered.

958   This had the effect of constraining the spread of forest, and increasing the area of shrub. Scenario 3

959   and 4 were analogous to scenario 1 and 2 respectively, except that due to soil forming processes it

960   was assumed that there would be no further vegetation development above 2800m, hence habitat

961   cover above this height was held equal to that in the current model.

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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

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981 **Table A6**
982 Model performance of predictive habitat models according to AUC and TSS for the study area
983 (>1700m). Thresholds used to define habitat presence are also presented. For forest, the threshold
984 used for Scenarios 2 and 4 is given in parentheses.
985

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

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988 **Table A7**
989 Mean altitude (m) ± SD of each class per scenario. OBS = Observed data, CURRENT = current
990 modelled habitat cover, Scenario 1 represents a rapid response of forest extent to climate change
991 (based on the B2A projections), scenario 2 represents a slower response of forest with greater
992 subsequent shrub expansion. Scenarios 3 and 4 are the same as scenarios 1 and 2 respectively,
993 except that vegetation development is constrained at high altitudes, therefore habitat cover is equal
994 to the current scenario above 2800m for both.

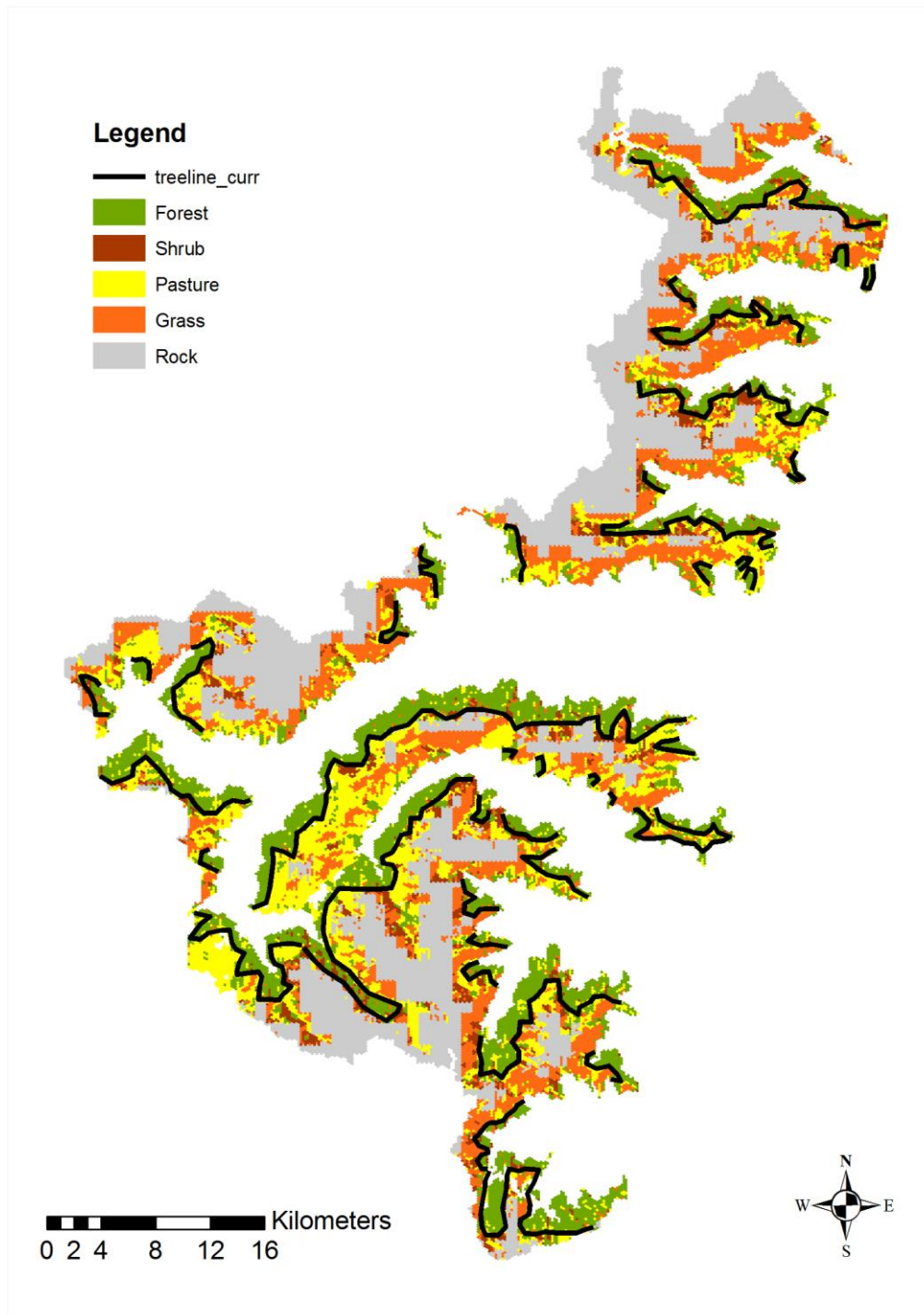| Class	OBS	CURRENT	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Forest	1962±170	1998±201	2196±299	2175±271	2181±284	2168±263
Shrub	2074±229	2054±239	2256±304	2243±309	2250±272	2219±277
Past	2121±255	2083±247	2278±318	2262±325	2241±285	2226±291
Grass	2281±279	2246±288	2562±306	2558±310	2475±254	2471±258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

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