

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

**Microclimate affects the distribution of grassland birds, but not forest birds, in an Alpine environment**

**This is a pre print version of the following article:**

*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1736954> since 2020-04-22T12:16:40Z

*Published version:*

DOI:10.1007/s10336-020-01778-5

*Terms of use:*

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

1 **Microclimate Affects the Distribution of Grassland Birds, but not Forest Birds,**  
2 **in an Alpine Environment**

3

4 Susanne Jähnig<sup>1\*</sup>, Martha Maria Sander<sup>1</sup>, Enrico Caprio<sup>1</sup>, Domenico Rosselli<sup>2</sup>,  
5 Antonio Rolando<sup>1</sup>, Dan Chamberlain<sup>1</sup>

6

7 <sup>1</sup>Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy

8 <sup>2</sup>Ente di Gestione delle Aree Protette delle Alpi Cozie, Salbertrand, Italy

9

10 \*Corresponding author

11 Email: [susanne.jaehnig@gmail.com](mailto:susanne.jaehnig@gmail.com)

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29 **Abstract**

30 Predictions derived from species distribution models (SDMs) are strongly influenced by the  
31 spatial scale at which species and environmental data (e.g. climate) are gathered. SDMs of  
32 mountain birds usually build on large-scale temperature estimates. However, the topographic  
33 complexity of mountain areas could create microclimatic refuges which may alter species  
34 distributions at small spatial scales. To assess whether fine-scale data (temperature and/or  
35 topography) improve model performance when predicting species occurrence, we collected  
36 data on presence-absence of bird species, habitat and fine-scale temperature at survey points  
37 along an elevational gradient in the Alps (NW Italy). Large-scale temperature data, and both  
38 large- and fine-scale topography data, were extracted from online databases for each point.  
39 We compared species models (fine-scale vs large-scale) using an information-theoretic  
40 approach. Models including fine-scale temperature estimates performed better than  
41 corresponding large-scale models for all open habitat species, whereas most forest/ecotone  
42 species showed no difference between the two scales. Grassland birds such as Northern  
43 Wheatear *Oenanthe oenanthe* and Water Pipit *Anthus spinoletta* were positively associated  
44 with warmer microclimates. These results suggest that alpine grassland species are potentially  
45 more resistant to the impact of climate change than previously predicted, but that indirect  
46 effects of climate change such as habitat shifts (forest- and shrub encroachment at high  
47 elevations) pose a major threat. Therefore, active management of alpine grassland is needed  
48 to maintain open areas and to prevent potential habitat loss and fragmentation. SDMs based  
49 solely on large-scale temperatures for open habitat species in the Alps should be re-assessed.

50

51

52 **Key words:** information-theoretic approach, mountains, species distribution models,  
53 temperature, topography.

54

55 **Introduction**

56 Species distribution models (henceforth SDMs) are a widely used tool in conservation (Guisan  
57 and Thuiller 2005, Rodríguez et al. 2007, Franklin 2013) for a range of taxa (Ongaro et al.  
58 2018, Lewthwaite et al. 2018, Hof and Allen 2019). In the face of climate change, SDMs have  
59 become particularly important in predicting current and/or future distributions of species under  
60 different climate change scenarios (Avalos and Hernández 2015, Jackson et al. 2015,  
61 Lehtikoinen and Virkkala 2016). These studies usually rely on macroclimate data, which  
62 describe climatic conditions at a relatively large scale (approximately one square kilometre or  
63 more; Zellweger et al. 2019) derived from national networks, weather stations or online  
64 databases (e.g Worldclim; Hijmans et al. 2005).

65 However, mountain environments are often poorly represented by conventional climate  
66 station data, and uncertainty for interpolated climatic values is high (Hijmans et al. 2005).  
67 Furthermore, local temperature can vary substantially due to the topographic complexity in  
68 mountain areas (Scherrer and Körner 2010, Gunton et al. 2015), thus creating a mosaic of  
69 microclimatic conditions over small spatial scales. Depending on discipline, microclimates  
70 have been defined in various ways. In this study, we adopt the definition by Bramer et al. (2018)  
71 who defined microclimate as fine-scale climate variations at spatial resolutions of < 100m,  
72 which are influenced by fine-resolution biotic and abiotic variations (topography, soil type and  
73 vegetation). Topographic variables like aspect and slope can markedly alter microclimate by  
74 influencing the amount of incoming solar radiation between different exposed slopes. Between  
75 north and south exposed slopes, temperature can differ by approximately 1°C if slopes are  
76 gentle (<5°) but can increase up to 5°C if slopes are steep (40°; Gubler et al. 2011). Moreover,  
77 these differences could subsequently influence snow accumulation processes and thus the  
78 rate of snow melt in spring (Gubler et al. 2011).

79 There is mounting evidence of the importance of microclimate in influencing habitat  
80 selection. For example, Bramblings *Fringilla montifringilla* tend to rest in higher densities in  
81 areas with warm microclimatic conditions (Zabala et al. 2012). In Mountain Chickadees *Poecile*  
82 *gambeli*, microclimates influence the selection of foraging sites (Wachob 1996). Microclimates

83 can also act as thermal refuges, which enable individuals to persist despite unfavourable  
84 ambient conditions (Wilson et al. 2015). This has been shown in Northern Bobwhites *Colinus*  
85 *virginianus*, which mitigated thermal stress by seeking thermally-buffered microclimatic sites  
86 during hot days (Carroll et al. 2015). Furthermore, Northern Bobwhite nest site selection was  
87 proven to be influenced by microclimate: Individuals nested in cooler and moister microclimatic  
88 conditions compared to surrounding non-nesting locations (Tomecek et al. 2017, Carroll et al.  
89 2018).

90 Only a few studies have investigated the role of microclimate within a mountain context.  
91 Frey et al. (2016) showed that fine-scale temperature metrics were strong predictors of bird  
92 distributions, with temperature effects being larger than vegetation effects on occupancy  
93 dynamics in mountain forests (but see Viterbi et al. 2013). In the Alps, the habitat of the alpine  
94 Rock Ptarmigan *Lagopus muta helvetica* is characterised by a wide variety of microclimates  
95 over small spatial scales with individuals choosing colder sites in summer (Visinoni et al. 2015).

96 Beside the direct impact on birds, microclimate also plays a crucial role in habitat selection  
97 in insects. It has been demonstrated that in *Parnassius apollo*, a mountain specialist butterfly,  
98 larval habitat selection is related to ambient temperature. Larvae selected warm microclimates  
99 when ambient temperatures fell below a threshold of 27°C, whereas cold microclimates were  
100 selected when this threshold was exceeded (Ashton et al. 2009). Microclimate can further  
101 influence oviposition (Stuhldreher et al. 2012), and the precise microclimatic conditions for  
102 thermoregulation are actively sought by montane species of the genus *Erebia* (Kleckova et al.  
103 2014). In this respect, microclimate won't only shape the distributions of these butterfly species,  
104 but it will also indirectly influence bird species which rely on caterpillars as a food source for  
105 chick rearing.

106 Microclimate thus has the potential to influence many aspects of an organism's life cycle.  
107 It could help to buffer or to compound the effects of climate change (Spasojevic et al. 2013).  
108 To assess the impact of climate change on current or future distributions of species it is crucial  
109 to gather climate data at the most appropriate scale in order to increase model accuracy  
110 (Barton et al. 2018, Randin et al. 2009). However, predictions for future geographic

111 distributions of mountain birds under a range of climate change scenarios have thus far been  
112 based on models which have considered climate variables measured at large scales, usually  
113 ca. 1 km<sup>2</sup> (Chamberlain et al. 2013, 2016, Brambilla et al. 2016, 2017a). Given the potential  
114 for bird responses to microclimatic conditions in mountains (Frey et al. 2016, Visoni et al.  
115 2014), it may be more appropriate to consider the role of climate measured at finer spatial  
116 resolutions in determining mountain bird distributions. This is particularly important given that  
117 environmental conditions in mountains typically change over very small spatial scales thanks  
118 to steep elevation gradients (Scherrer and Körner 2010, Gunton et al. 2015).

119 In this study, we investigated the role of microclimate for a range of Alpine ecotone and  
120 open habitat species. There were two specific aims. First, to evaluate if models including a  
121 microclimatic variable (in this case temperature) show better performance than models using  
122 large-scale climate estimates. This will inform future modelling studies, and should help to  
123 improve predictions of future impacts of climate change on Alpine birds where microclimatic  
124 effects are evident. Second, to assess if models including topographic variables (slope and  
125 aspect) in combination with climatic variables (fine and large scale) increase model  
126 performance. This will assess the extent to which topographic variables should be included in  
127 SDMs of alpine bird species. Based on previous studies, which showed that microclimate can  
128 influence bird distributions within mountain habitats (Frey et al. 2016, Visoni et al. 2015), we  
129 hypothesise that models using fine-scale temperature estimates will show better model  
130 performance than models using large-scale temperature estimates.

131

## 132 **Methods**

### 133 Study area and point selection

134 The study was carried out in Val Tronca Natural Park (44°57'28" N; 6°56'28" E) in the western  
135 Italian Alps. At lower elevations, the area is dominated by larch *Larix decidua*. The natural  
136 treeline is typically found at around 2200 m asl, but varies depending on local conditions.  
137 Typical shrub species are *Juniperus nana* (henceforth Juniper) and *Rhododendron*  
138 *ferrugineum* (henceforth Rhododendron) which rapidly encroached wide areas of grasslands

139 after the decline of agro-pastoral activities. Grasslands are mainly dominated by *Festuca*  
140 *curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky areas occur  
141 predominantly at higher elevations, above approximately 2700 m asl.

142 Point counts were carried out along an elevational gradient ranging from 1750 m to 2820  
143 m encompassing forest, ecotone and open habitats. Point count locations coincided with the  
144 centroids of a pre-existing grid at a scale of approximately 150 x 150 m (there was some  
145 variation, due to access constraints for example; Probo et al. 2014) along the western facing  
146 slope of the valley. All points were spaced a minimum of 200 m apart.

147

#### 148 Bird surveys

149 Point counts (n = 221) were carried out from mid-May to mid-July 2017 following the methods  
150 of Bibby et al. (2000), using a 10 minute count period. At each point count location, all individual  
151 birds seen or heard were recorded within a 100 m radius (estimated with the aid of a laser  
152 range finder). Point counts commenced 1-1.5 h after sunrise and continued until 1200 h.  
153 Surveys did not take place in excessively wet or windy conditions. Each point count location  
154 was visited once.

155

#### 156 Habitat data collection

157 At each point count location, habitat data were collected through the visual estimation of the  
158 percentage cover of canopy (i.e. vegetation above head height), the dominant shrub species,  
159 open grassland and bare rock (including scree and unvegetated areas) within a 100 m radius  
160 of the point's centre. The dominant shrub species were defined into four groups:  
161 Rhododendron, Juniper, bilberry (*Vaccinium myrtillus* and *V. gaultherioides*) and other (e.g.  
162 Green Alder *Alnus viridis*, Willow *Salix spp*, and also including young trees less than two  
163 meters in height, mostly European Larch *Larix decidua*). Furthermore, the number of mature  
164 trees (greater than c. 20 cm in diameter at breast height) within a 50 m radius of a point count  
165 location was counted. These estimates have been shown to correlate well with estimates of

166 land cover derived from remote sensing and have been used as the basis of predictive models  
167 for several species considered here (Chamberlain et al. 2013, 2016, Jähnig et al. 2018).

168

169 Temperature measurements

170 At each point count location, temperature was measured with hygro buttons (Plug & Track™),  
171 using methods based on Frey et al. (2016). Each button was stuck on the bottom of a small  
172 plastic cup, which was attached upside down to a bamboo stick to protect the button against  
173 wind, direct sunlight and water. Mean button height was 40.89 cm (min = 28 cm, max = 47  
174 cm). Hygro buttons were programmed to record temperature every 5 minutes. They were  
175 placed 24 hours before a point count commenced and were collected 24 hours after the point  
176 count ended, which resulted in a total recording time of 48 hours. At every hygro button  
177 location, button height, distance to slope, substrate and canopy presence/absence was  
178 recorded.

179

180

181 Statistical analysis

182 *Temperature modelling*

183 For each point count location, minimum, maximum and mean temperatures were derived over  
184 the 48 hour recording period. All temperature measurements were checked for collinearity by  
185 calculating Pearson's correlation coefficient. Mean temperature was strongly correlated with  
186 both minimum ( $r = 0.80$ ) and maximum temperature ( $r = 0.73$ ) over the recording period.  
187 Therefore, temperature modelling was undertaken with mean temperature values. The same  
188 procedure was repeated for night-time temperatures. Minimum, maximum and mean night-  
189 time temperatures were obtained for the time period between 23.00 pm and 03.00 am over the  
190 same recording period at each point. There was a strong positive correlation of mean night-  
191 time temperature between minimum ( $r = 0.97$ ) and maximum night-time temperature ( $r = 0.89$ ).

192 The objective of the first analysis was to model temperature in relation to date and  
193 elevation. This model was then used to predict a standardised temperature at each point count

194 location, set at a fixed date, which was representative of the fine-scale temperature at that  
195 point controlling for seasonal effects. This procedure provided data which was analogous to  
196 the larger scale temperature data (see below). This standardised temperature was then used  
197 subsequently as a variable in species distribution models. Note that all subsequent modelling  
198 steps were performed separately for mean temperature and mean night-time temperature.  
199 However, models with night-time temperature were very similar to those using mean  
200 temperature, so we focus on the latter. Further details on night-time temperature models are  
201 given in the Electronic Supplementary Material (ESM) Table S1.

202 First, to investigate if temperature recording was influenced by characteristics of the hygro  
203 button's position, it was analysed using a generalised linear model in relation to button height,  
204 distance to slope, substrate underneath the button and canopy presence/absence, specifying  
205 a normal error distribution. None of the variables showed a significant effect on mean  
206 temperature ( $p > 0.05$ ), therefore they were not considered further in the analysis.

207 In the next modelling step, standardised temperature estimates were derived separately  
208 for open Alpine grassland and forest/ecotone habitat, i.e. models were used to estimate  
209 temperature for a given elevation whilst accounting for seasonal variation. Points were  
210 classified as Alpine grassland if there was no canopy within 100m radius of the point count  
211 centre (following Chamberlain et al. 2013). For open habitat points ( $n = 93$ ), temperature was  
212 modelled in relation to date and elevation. Date was described as the number of days passed  
213 since the start of the field season, where day 1 = 27-May-2017. Canopy cover was added to  
214 the model structure for points located in forest and ecotone habitat ( $n = 128$ ). In both cases, a  
215 normal distribution was specified. Prior to modelling, all variables were scaled and centred  
216 using the scale function in R. Collinearity was assessed using Variance inflation factors (VIFs),  
217 calculated using the 'corvif' function (package 'AED', Zuur et al. 2009), and by considering  
218 Spearman correlations between continuous variables. All variables had  $VIF < 3$ , and no pair of  
219 variables showed a correlation  $> 0.7$ , indicating low levels of inter-correlation. These models  
220 were used to derive a standardised temperature for each point, based on the elevation at that  
221 point, the canopy cover (for forest/ecotone habitat) and for a date fixed at 15<sup>th</sup> June.

222

### 223 *Species distribution models*

224 Birds detected within a 100-m radius of a point count location were used to analyse species  
225 distribution (presence/absence of individual species). Bird species were considered in the  
226 modelling process if they were present on at least 15 % of the points; below this threshold  
227 model performance is consistently poor (Chamberlain et al. 2013).

228 The commonest species were modelled in relation to four different variable sets: (i) habitat  
229 (HABITAT), (ii) habitat + temperature (TEMP), (iii) habitat + topography (TOPO), (iv) habitat +  
230 temperature + topography (COMB; Table 2). Temperature and topographic variables were  
231 used at two different scales (large-scale/ fine-scale). Fine-scale temperature estimates were  
232 derived from the temperature modelling approach described above, whereas large-scale  
233 temperature data for each point were extracted from the Worldclim database (Hijmans et al.  
234 2005) by calculating the average temperature within a 1000 m radius of the point count centre.  
235 Topographic variables (aspect and slope) were derived from a Digital Elevation Model (DEM)  
236 at a spatial resolution of 10 metres. Aspect was transformed as  $x = -1 * \cos[\varnothing(\pi/180)]$ , where  $\varnothing$   
237 is measured in degrees. Values ranged from 1 where solar insolation was higher (south-facing  
238 slopes) to -1 (north-facing slopes) where it was lower.

239 The mean aspect (transformed values) and slope was calculated within a 100 m (fine-  
240 scale) and a 1000 m (large-scale) radius of the point count centre for the analysis. Habitat  
241 variables were kept at a constant scale in the models (as the objective was to test scale effects  
242 in temperature and topography).

243 Habitat models of Lesser Whitethroat *Sylvia curruca* and Dunnock *Prunella modularis*  
244 were tested for non-linear relationships with Rhododendron and Juniper cover as suggested  
245 by previous work (Jähnig et al. 2018). Habitat models with and without quadratic terms for shrub  
246 species cover were compared using AIC. Lesser Whitethroat models showed lower AIC values  
247 for the habitat model without quadratic terms. Therefore these were omitted in further modelling  
248 steps. The addition of the quadratic term for Rhododendron cover reduced the AIC of the  
249 habitat model for Dunnock by  $\Delta AIC > 2$ , hence it was included in the next modelling steps.

250 The occurrence probability of each species was modelled in relation to the different  
251 variable sets using a binomial logistic regression, after controlling for potential collinearity (as  
252 above). In the case of open habitat species, we found high VIFs for the variables rock and  
253 grass cover. After the removal of rock cover, all VIFs were below the threshold of three. As a  
254 result, rock cover was removed from all models for open habitat species.

255 Data were analysed using an information theoretic approach with the MuMIn package in  
256 R version 3.5.2; (R Development Core Team 2018, Bartón 2013). This entailed deriving full  
257 models for each variable set at each scale (except habitat which was kept constant in all  
258 models) using generalised linear models (R package lme4; Bates et al. 2015). This approach  
259 served two goals. First, model-averaged parameter estimates were derived for all  
260 combinations of variables in each full model set in order to identify variables that were most  
261 closely associated with bird distribution.  $p$ -values derived from the model-averaged parameter  
262 estimates and their SEs were considered to represent significant effects when  $p < 0.05$ .  
263 Second, the Akaike information criterion corrected for small sample size (AICc) was  
264 determined for each individual model and was used to assess model performance for different  
265 variable combinations at different scales in the full model. In this way it was possible to assess  
266 which combination of the four different variable sets produced the best models, and at which  
267 scale.

268 At each scale, the residuals for all full models were extracted and tested for spatial  
269 autocorrelation using Moran's  $I$  (Moran 1950). Significant spatial autocorrelation was found for  
270 models of Eurasian Skylark *Alauda arvensis*, Tree Pipit *Anthus trivialis* and Water Pipit. For  
271 these species, spatial effects were incorporated by modelling their distributions using  
272 Generalized Additive Models (GAMs) from the mgcv package (Wood 2011) by fitting smoothed  
273 terms for latitude and longitude in the model, following Wood (2017).

274

## 275 **Results**

276 In total, 862 individuals of 40 species were recorded in 221 point counts over an elevational  
277 range of 1750 – 2800 m a.s.l. There were seven species that were recorded on at least 15%

278 of the points within forest and ecotone habitat: Dunnock, Lesser Whitethroat, Chaffinch  
279 *Fringilla coelebs*, Mistle Thrush *Turdus viscivorus*, Coal Tit *Parus ater*, rock bunting *Emberiza*  
280 *cia*, Tree Pipit and three species within open habitat: Eurasian Skylark, Water Pipit and  
281 Northern Wheatear.

282 The best model to predict rock bunting occurrence was always the null model for each  
283 model set at each scale, with no model-averaged parameter estimates being significant.  
284 Therefore, this species was not considered further in the analysis.

285

286 Forest and ecotone species

287 Habitat variables such as trees and shrubs were the variables most commonly associated with  
288 species occurrence within the HABITAT model for forest and ecotone species. In general, the  
289 results of the HABITAT models were in line with previous findings by Jähnig et al. (2018).  
290 Juniper showed a positive relationship with Coal Tit, Dunnock and Lesser Whitethroat, but was  
291 negatively related to Tree Pipit presence. Rhododendron was positively associated with Mistle  
292 Thrush and Lesser Whitethroat presence, whereas it showed a non-linear relationship with  
293 Dunnock presence. The number of mature trees showed a positive relationship with forest  
294 species (Chaffinch, Mistle Thrush and Coal Tit). Habitat associations among the species  
295 remained mostly constant in TEMP, TOPO and COMB models (for full details see ESM Table  
296 S2, S4).

297 Each variable set at each scale performed equally well for Lesser Whitethroat, Mistle  
298 Thrush and Coal Tit (Table 3). (Note that full details of all models are given in ESM Table S3).  
299 Large-scale temperature and topographic variables were included in the best performing  
300 model for Dunnock, temperature being negatively associated with Dunnock presence (Table  
301 4, Fig. 1). In contrast, large-scale temperature showed a positive relationship with Chaffinch  
302 presence in models including only large-scale temperature (Table 4, Fig. 1), or in models  
303 including a combination of large-scale temperature and topographic variables. In both species,  
304 large-scale model sets performed better than their fine-scale equivalents. Large-scale models  
305 for TOPO and COMB were the best performing models for Tree Pipit, whose presence was

306 more closely associated with large-scale topographic variables such as aspect, for which it  
307 showed a strong negative relationship indicating a preference for westerly over southerly  
308 slopes (Fig. 2). Beside Tree Pipit, only Mistle Thrush showed a negative association with  
309 aspect. No other species showed any association with slope or aspect. Furthermore, Tree Pipit  
310 was the only species that showed better model performance ( $\Delta AICc \leq 2$ ) for the large-scale  
311 TOPO model compared to all fine-scale models and the large-scale TEMP model. All other  
312 species showed better (Chaffinch) or equal model performance of TEMP models compared to  
313 TOPO models at both scales.

314

315 Open habitat species

316 The HABITAT model for each open species did not show any habitat associations among the  
317 recorded variables. However, all fine-scale models (TEMP, TOPO and COMB) showed a  
318 positive association between grass cover and Skylark presence while Juniper cover was only  
319 positively associated in the TEMP and COMP models.

320 Models including fine-scale temperature and topography performed best ( $\Delta AICc \leq 2$ ) for  
321 Northern Wheatear. The best performing models of Skylark and Water Pipit included both fine-  
322 scale TEMP and COMB models. Fine-scale temperature was positively associated with Water  
323 Pipit and Northern Wheatear presence, whereas Eurasian Skylark presence was negatively  
324 associated (Table 4, Fig. 3).

325 At a fine scale, TEMP models showed better model performance than TOPO models for  
326 Northern Wheatear and Water Pipit, whereas on a large scale, model sets for TEMP and TOPO  
327 were overlapping (Northern Wheatear, Water Pipit). The large-scale TOPO model showed  
328 equal model performance compared to the large-scale TEMP model for Skylark, but  $AIC_c$  was  
329 still higher compared to fine-scale COMB. In addition, aspect showed a positive relationship  
330 with Northern Wheatear (Fig.2, fine-scale COMB model) and Skylark presence (large-scale  
331 TOPO model) while slope was positively related to Skylark presence in the fine-scale TOPO  
332 model.

333

334 **Discussion**

335 Models including fine-scale temperature estimates (TEMP, COMB) showed better model  
336 performance ( $\Delta AIC_c < 2$ ) than corresponding large-scale models for all three open habitat  
337 species. Northern Wheatear and Water Pipit were both positively associated with warm  
338 microclimates while Skylark presence was negatively associated with fine-scale temperature.  
339 These results contrast with previous findings from the same region of the Alps (Chamberlain  
340 et al. 2013, 2016), where model predictions were based on large-scale climatic variables. In  
341 these studies, SDMs (based on temperature change and assuming no change in habitat)  
342 suggested that under warmer conditions, Skylark and Northern Wheatear would show an  
343 increase in their distribution whereas Water Pipit distribution would decrease. Therefore, for  
344 Water Pipit and Skylark distributions, our findings suggest opposite associations between fine-  
345 scale and large-scale temperature.

346 Differences in model predictions at different spatial scales have been reported for a range  
347 of studies, and thus identifying the appropriate scale represents a major problem when  
348 forecasting suitable habitat in order to inform conservation planning (Elith and Leathwick 2009,  
349 Randin et al. 2009, Franklin et al. 2013, Logan et al. 2013, Scridel et al. 2018). To improve  
350 SDMs, it is therefore necessary to carefully select predictors (e.g. temperature variables) and  
351 their spatial resolution. In the case of microclimate, local topography could create areas with  
352 suitable climatic conditions under which it would still be possible for a species to persist under  
353 the impact of climate change. Through the use of large-scale climate data, these areas might  
354 not be recognised by SDMs (Austin et al. 2011). Besides affecting the future distribution of a  
355 species, microclimate can also influence many other aspects of a species' life cycle.

356 There is evidence that microclimate can be important in influencing habitat selection in  
357 mountain birds which may explain our findings. For example, it has been shown that Horned  
358 Larks *Eremophila alpestris* adjusted the amount of incubation time in response to microclimatic  
359 conditions (Camfield and Martin 2009) by spending less time on the nest as temperatures in  
360 the nest surrounding increased, which may imply energy savings in warmer microclimates.  
361 Furthermore, microclimate and aspect strongly influenced nestling survival in Water Pipits

362 (Rauter et al. 2002). Nests which were located at ENE-facing slopes (temperature maximum  
363 in the morning) had more fledglings than those on WSW-facing slopes (temperature maximum  
364 in the afternoon). In contrast, foraging habitat selection by alpine White-winged Snowfinches  
365 *Montifringilla nivalis*, a high altitude specialist, was influenced by solar radiation (Brambilla et  
366 al. 2017b). Snowfinches preferred to forage at colder sites (low solar radiation) throughout the  
367 season. These studies illustrate that behaviour, foraging habitat selection and choice of nest  
368 sites could be driven by microclimatic conditions thereby affecting bird species distributions.  
369 Therefore, we would strongly recommend considering microclimate as a predictor in future  
370 SDMs for open habitat Alpine species.

371 In contrast to the open habitat species considered, forest and ecotone species showed no  
372 association with fine-scale temperature. One possible reason might be the buffering effect of  
373 vegetation. Körner et al. (2007) showed that temperature can vary strongly between forest and  
374 open alpine grassland along the elevation gradient with intermediate values at the treeline  
375 ecotone. Furthermore, canopies can buffer the diurnal amplitude of air temperature in the forest  
376 (Chen et al. 1999).

377 For two species (Dunnock and Chaffinch) large-scale models including temperature (TEMP,  
378 COMB) performed better than fine-scale models. The probability of occurrence of Chaffinch  
379 was positively associated with large-scale temperature, whereas the probability of Dunnock  
380 presence was negatively affected. A future increase in temperature could therefore affect the  
381 distribution of Chaffinches by expanding its range towards higher elevations. In contrast, the  
382 distribution of Dunnocks might be severely limited. Bani et al. (2019) demonstrated that  
383 Dunnock distribution experienced a lower range contraction along the elevational gradient  
384 during the last 35 years, but a simple dispersal into higher elevations as a response to  
385 environmental change might not be possible because it's preferred nesting habitat in our study  
386 area, *Rhododendron*, has a slow rate of colonisation to the extent that treeline shifts towards  
387 higher elevations are likely to be more rapid than upwards shifts in this species (Komac et al.  
388 2016).

389 The mismatch between temperature and available future habitat can also affect open  
390 habitat species considered in this study. Due to increasing temperatures, shifts in major habitat  
391 types (i.e. forest and shrub encroachment; Harsch et al. 2009) may lead to habitat  
392 fragmentation and/or loss of open alpine grassland at higher elevations. This process might  
393 even be exacerbated by the abandonment of pastoral activities which formerly have  
394 maintained the forest limit at lower elevations than would be possible under climatic constraints  
395 only (Gehrig- Fasel et al. 2007).

396

### 397 Topography

398 For the majority of species, COMB models performed equally well in comparison with TEMP  
399 models at both spatial scales. Combining temperature with topographic variables increased  
400 model performance only for Northern Wheatear and Skylark at a fine scale. For the former  
401 species, occurrence was more closely related with south-facing slopes. At a large scale, the  
402 probability of Tree Pipit presence was higher on westerly slopes. However, in general  
403 topographic variables were rarely associated with species occurrence. The influence of aspect  
404 on the occurrence of some species could be explained by its effect on snow melt patterns  
405 during spring. Thermal differences among slopes with different exposition, which are caused  
406 by the amount of received solar radiation, could lead to an early snow melt on south-exposed  
407 slopes whereas north-exposed slopes might stay snow covered for a longer period (Keller et  
408 al. 2005). These early snow free areas could potentially benefit Northern Wheatears by making  
409 suitable nesting sites available earlier. Furthermore, it has been shown that differences in  
410 temperature among slopes can influence plant species diversity in temperate mountains  
411 (Winkler et al. 2016) with south-exposed slopes favouring a higher degree of species richness  
412 and diversity which may in turn influence insect availability.

413

### 414 Conservation implications

415 Previous studies from the Italian Alps have indicated that increasing temperatures could have  
416 detrimental effects for certain Alpine species in the future (Chamberlain et al. 2013), with some

417 species being potentially impacted by both temperature and habitat shifts (Water Pipit), while  
418 for others, loss of habitat due to forest and shrub encroachment will likely be more important  
419 (Northern Wheatear, Skylark).

420         However, our results have shown that species such as Water Pipit and Northern  
421 Wheatear are positively associated with warm microclimates which could indicate that both  
422 species are potentially more resistant to the impact of a warming climate than previously  
423 emphasised by large-scale temperature modelling (e.g. Chamberlain et al. 2013). As a  
424 consequence, our results imply that changes in habitat in the form of advancing treelines and  
425 the encroachment of formerly open areas by shrubs and trees (Gehrig-Fasel et al. 2007,  
426 Leonelli et al. 2011) are currently the major threat to those Alpine species, rather than direct  
427 effects of temperature. Therefore, it becomes particularly important to actively manage open  
428 areas within mountain environments. This could be achieved by targeted grazing techniques  
429 such as mineral mix supplements (Pittarello et al. 2016) or temporary night camp areas (Tocco  
430 et al.2013). Both techniques lead to the mechanical damage of shrubs (including saplings) and  
431 eventually result in a reduction of shrub cover (Probo et al. 2013, 2014).

432

433

434

### 435 **Acknowledgements**

436 We thank all rangers and staff of Val Troncea Natural Park for their great help and we are  
437 grateful to Nadja Schäfer and Riccardo Alba for help with the field work.

438

### 439 **Figure legends**

440

441 **Fig. 1** Relationship between large-scale temperature and the probability of occurrence of  
442 Dunnock and Chaffinch based on the large-scale COMB model. Shading indicates the 95%  
443 confidence interval.

444

445 **Fig. 2** Relationship between aspect and the probability of occurrence for Tree Pipit and  
446 Northern Wheatear for the large-scale TOPO and the fine-scale COMB model, respectively.  
447 Note that aspect was modelled as an index from 1 (south-facing) to -1 (north facing), but here  
448 we present the axis as the equivalent cardinal direction for ease of interpretation. Shading  
449 indicates the 95% confidence interval.

450

451 **Fig. 3** Relationship between fine-scale temperature and probability of occurrence for open  
452 habitat species for the fine-scale COMB model. Shading indicates the 95% confidence interval.

453

454

455

456

457

458

459

460

461

462

463

464

465

466

467

**Table 1** Variables considered in the analysis, and the scale at which they were measured.

Parameter	Scale	Description
Canopy	fine	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Rod	fine	Percentage cover of Rhododendron within a radius of 100 m of the point count centre
Jun	fine	Percentage cover of Juniper within a radius of 100 m of the point count centre
Vac	fine	Percentage cover of bilberry within a radius of 100 m of the point count centre
Oth	fine	Percentage cover of shrubs different from Juniper, Rhododendron and bilberry within a radius of 100 m of the point count centre
Grass	fine	Percentage cover of grass within a radius of 100 m of the point count centre
Rock	fine	Percentage cover of rock within a radius of 100 m of the point count centre
Trees	fine	Number of mature (greater than ca. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Temp	fine	Modelled fine-scale standardised average temperature of the point count centre
Temp	large	Large-scale average temperature within 1000 m of the point count centre extracted from WorldClim.
Aspect	fine	The average direction a slope is facing within a 100 m radius of the point count centre transformed as $x = -1 \cdot \cos[\varnothing(\pi/180)]$ , where $\varnothing$ is measured in degrees.
Aspect	large	The average direction a slope is facing within a 1000 m radius of the point count centre transformed as $x = -1 \cdot \cos[\varnothing(\pi/180)]$ , where $\varnothing$ is measured in degrees.
Slope	fine	The average inclination of the surface within a 100 m radius of the point counts centre measured in degrees.
Slope	large	The average inclination of the surface within a 1000 m radius of the point counts centre measured in degrees.

**Table 2** Variable combinations for each model set. Model sets for TEMP, TOPO and COMB were considered at two different scales (fine and large) and included temperature, slope and

Full models	Parameter
HABITAT	Rod + Jun + Vac + Oth + Grass + (Rock) + (Trees)
TEMP	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Temp
TOPO	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Slope + Aspect
COMB	Rod + Jun + Vac + Oth * Grass + (Rock) + (Trees) + Temp + Slope + Aspect

aspect at their matching scale. The variables Rock and Trees were omitted from the habitat model for open habitat species (Northern Wheatear, Water Pipit and Skylark).



**Table 3**  $\Delta AIC_c$  value for each model set at each scale for all species. A  $\Delta AIC_c$  value of zero indicates the best performing model. Note that in some cases, the best performing models were identical in different model sets, hence a value of zero can appear more than once for a given species. Original  $AIC_c$  values are listed in ESM Table S3.

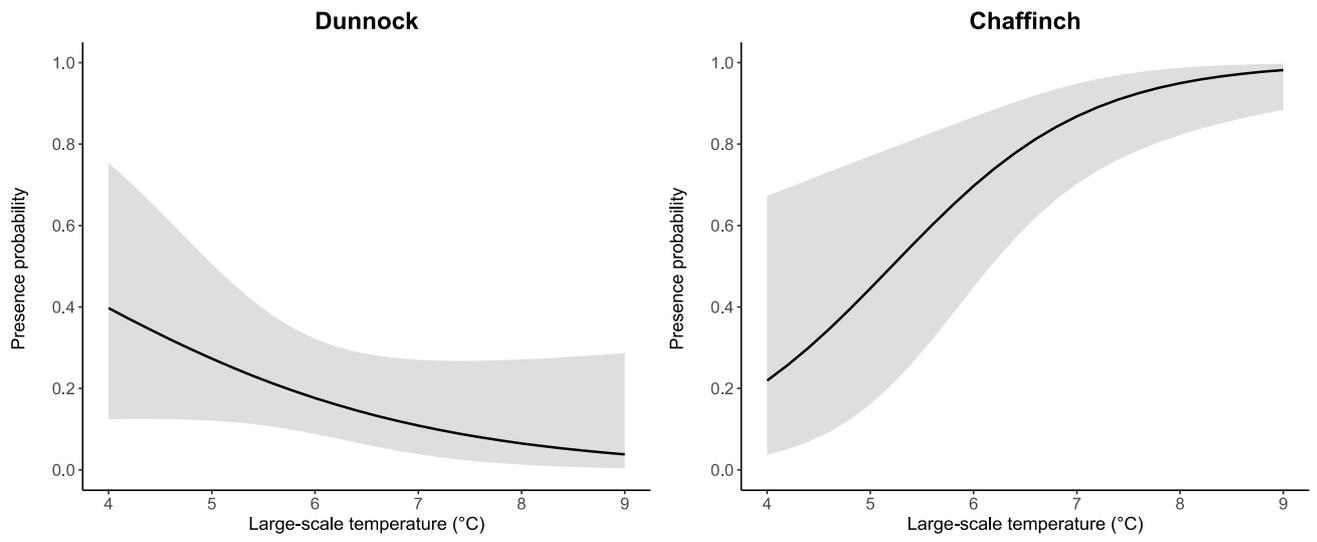
<b>Species</b>	<b>HABITAT</b>		<b>TEMP</b>		<b>TOPO</b>		<b>COMB</b>	
	fine-scale	fine-scale	large-scale	fine-scale	large-scale	fine-scale	large-scale	
<i>Prunella modularis</i>	3.9	2.7	0.8	3.9	3.9	2.7	0	
<i>Sylvia curruca</i>	0	0	0	0	0	0	0	
<i>Parus ater</i>	1.4	1.4	0	1.4	1.4	1.4	0	
<i>Turdus viscivorus</i>	1.2	1.2	1.2	0	1.2	0	1.2	
<i>Fringilla coelebs</i>	13.9	6.3	0	13.1	12.9	6.3	0	
<i>Anthus trivialis</i>	10	8.5	10	9.8	0	8.4	0	
<i>Oenanthe oenanthe</i>	7.7	3.5	7.7	5.8	6.5	0	6.5	
<i>Anthus spinoletta</i>	4.6	0.9	4.6	3.2	4.6	0	4.6	
<i>Alauda arvensis</i>	6.0	0.9	2.7	2.3	4.8	0	2.7	

Species	Mode	Scale	Parameter	Estimate	SE	z	p
<i>Prunella modularis</i>	COM B	large	Rod	1.285	0.618	2.068	
			Jun	0.818	0.308	2.632	0.038
			Oth	0.580	0.270	2.126	0.008
			Temp	- 0.886	0.406	2.163	0.033
							0.030
<i>Sylvia curruca</i> *	TEM P	fine	Rod	1.029	0.265	3.835	≤
			Jun	0.624	0.265	2.332	0.001
			Rock	- 1.174	0.467	2.487	0.019
							0.012
<i>Parus ater</i> *	COM B	large	Jun	0.677	0.333	2.017	
			Oth	0.657	0.277	2.351	0.043
			Grass	0.938	0.434	2.145	0.018
			Trees	1.126	0.303	3.678	0.031
							≤
							0.001
<i>Turdus viscivorus</i> *	TOP O	fine	Vac	- 1.700	0.823	2.049	
			Aspect	- 0.644	0.316	2.017	0.040
							0.043

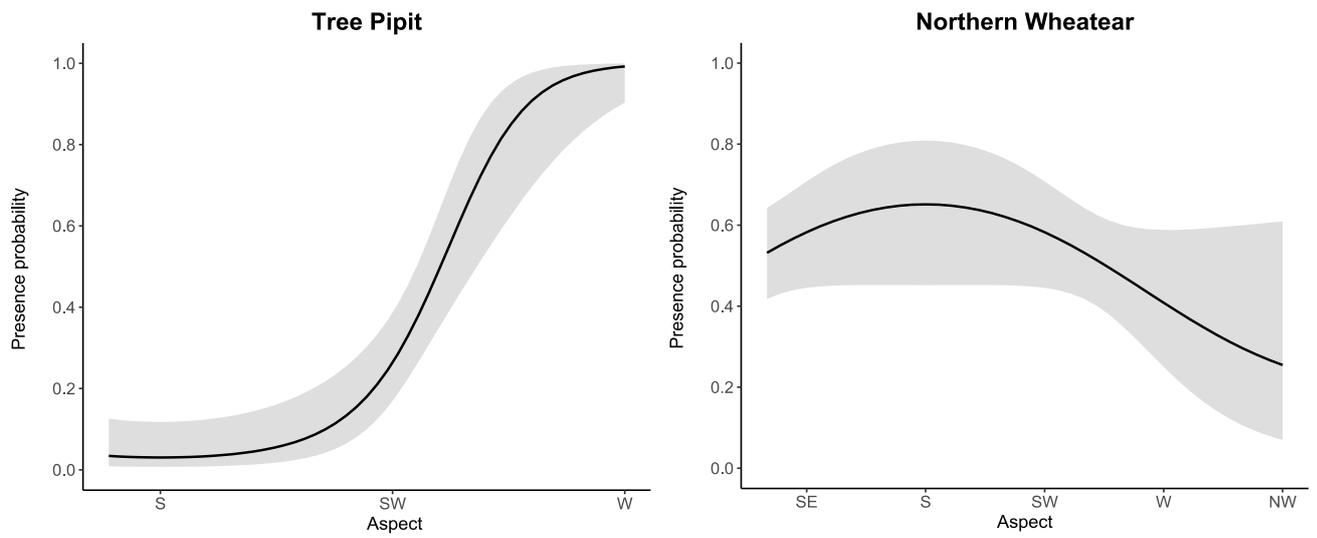
<i>Fringilla coelebs</i>	TEM	large	Trees	2.453	0.809	3.004	
	P						0.002
			Temp	1.500	0.462	3.218	
							0.001
<i>Anthus trivialis</i>	TOP	large	Jun	- 1.187	0.399	2.939	
	O						0.003
			Aspect	- 2.614	0.644	4.022	≤
							0.001
<i>Oenanthe oenanthe</i>	COM	fine	Temp	0.736	0.305	2.386	
	B						0.017
			Aspect	0.622	0.288	2.133	
							0.032
<i>Anthus spinoletta</i>	COM	fine	Temp	1.336	0.577	2.281	
	B						0.022
<i>Alauda arvensis</i>	COM	fine	Jun	0.616	0.282	2.158	
	B						0.030
			Grass	1.010	0.436	2.289	
							0.022
			Temp	-	0.447	1.980	
				0.896			0.047

**Table 4** Significant model averaged parameters of the best model for each species. The model type, scale (large or fine), estimate, standard error (SE), test value (z) and *p*-value are given for each parameter. Note that species where there was more than one model in the best model set (i.e.  $\Delta AIC_c < 2$ ) are marked with \*. In these cases, the model with the lowest  $AIC_c$  is presented, but competing models are shown in ESM, Table S3, along with full details for all species.

**Figure 1**



**Figure 2**



**Figure 3**

