

1 **Alpine bird distributions along elevation gradients: the consistency of climate**
2 **and habitat effects across geographic regions**

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28 **Author contribution statement** – All authors contributed significantly to the conception and
29 planning of the paper. DEC took a lead on analysing the data and writing the paper. MB and EC
30 carried out data extraction in GIS. PP and AR managed fieldwork in Trentino and Piedmont
31 respectively.

32 Many species have shown recent shifts in their distributions in response to climate change. Patterns
33 in species occurrence or abundance along altitudinal gradients often serve as the basis for detecting
34 such changes and assessing future sensitivity. Quantifying the distribution of species along
35 altitudinal gradients acts as a fundamental basis for future studies on environmental change
36 impacts, but in order for models of altitudinal distribution to have wide applicability, it is necessary
37 to know the extent to which altitudinal trends in occurrence are consistent across geographically
38 separated areas. Such model transferability was assessed by fitting models of bird species
39 occurrence across altitudinal gradients in relation to habitat and climate variables in two separated
40 Alpine regions, Piedmont and Trentino. The ten species studied showed non-random altitudinal
41 distributions which in most cases were consistent across regions in terms of pattern. Trends in
42 relation to altitude and differences between regions could be explained mostly by habitat or a
43 combination of habitat and climate variables. Variation partitioning showed that most variation
44 explained by the models were attributable to habitat, and habitat and climate together, rather than
45 climate alone or geographic region. The shape and position of the altitudinal distribution curve is
46 important as it can be related to vulnerability where the available space is limited, i.e. where
47 mountains are of not sufficient altitude for expansion. This study therefore suggests that
48 incorporating habitat and climate variables should be sufficient to construct models with high
49 transferability for many Alpine species.

50 **Introduction**

51

52 Many species have shown recent shifts in their distributions in response to environmental change, in
53 particular climate change (Chen et al. 2011), which has led to shifts in the range of several species
54 (Parmesan and Yohe 2003), mostly towards higher latitudes and/or altitudes (Walther et al. 2002).
55 Investigating the effect of climate change on biodiversity and ecosystems has thus become a key
56 ecological research area, often underpinned by modelling approaches that seek to determine
57 relationships between species occurrence or population dynamics and climate, and to predict the
58 future response to climate change (Bellard et al. 2012). Such approaches have been frequently
59 applied to species distributions, which may be affected by a range of factors, but in particular by
60 climatic variation and habitat availability. The effect of environmental factors such as climate,
61 topography and land-cover are often considered for modelling species distribution (Guisan and
62 Thuiller 2005), typically using correlative models, which relate the occurrence of a species to a set of
63 environmental predictors, allowing for the re-projection of species occurrence under new, future
64 environmental conditions. A critical issue in this approach is represented by the extent to which a
65 given model can be generally applied over different spatial and temporal contexts (i.e. model
66 transferability). As it is impossible to test predictions on future data, model performance could be
67 evaluated by means of a space-for-time substitution (Araujo and Rahbek 2006), using data from
68 different regions and cross-checking models (e.g. Randin et al. 2006).

69 In mountain environments, where species distributions are often limited by temperature,
70 increased warming has been accompanied by upward shifts in the distributions of many species, e.g.
71 plants (Lenoir et al. 2008; Harsch et al. 2009), butterflies (Wilson et al. 2005), birds (Tryjanowski et
72 al. 2005; Reif and Flousek 2012) and small mammals (Moritz et al. 2008). For several cold-adapted
73 species, and in particular for those living in high altitude open habitats, such shifts may lead to a
74 reduction in range as areas of suitable climate and habitat become smaller and more fragmented as
75 they are pushed towards mountain summits. Such effects may have serious consequences for
76 mountain biodiversity in the future (Sekercoglu et al. 2008; Dirnbock et al. 2011; Chamberlain et al.
77 2013; Maggini et al. 2014; Brambilla et al. 2015), and indeed there is evidence that birds of high
78 altitude are already showing declines (Lehikoinen et al. 2014, Flousek et al. 2015). It should,
79 however, also be acknowledged that mountain biodiversity may be under other anthropomorphic
80 pressures (Chamberlain et al. in press), such as changes in grazing regimes (Laiolo et al. 2004) and
81 increasing disturbance (Caprio et al. 2011), although evidence for effects of these factors, either
82 positive or negative, on mountain bird population trends is so far lacking.

83 Patterns in species occurrence or abundance along altitudinal gradients often serve as the
84 basis for detecting changes (e.g. Maggini et al. 2011; Parnollet et al. 2015) and assessing future
85 sensitivity (Chamberlain et al. 2013) of mountain species to climate change. Generally speaking,
86 investigating elevational range limits is critical to understanding distributional patterns, and is
87 needed to predict the likely effects of (and responses to) climate change in mountain species
88 (Gifford and Kozak 2012). The altitudinal transect approach is useful for studying potential climatic
89 effects on species distributions, because the altitudinal gradient provides a space-for-time
90 substitution when considering conditions along the gradient (Hodkinson 2005), and also,
91 complications involving broader-scale biogeographic processes, evident in geographic distribution
92 shift studies, are largely avoided (Rahbek, 2005). However, given that conditions change rapidly
93 over fine spatial scales along altitudinal gradients, data collected needs to be of a sufficiently high-
94 resolution to be useful for monitoring and modelling distribution shifts (Chamberlain et al. 2012). In
95 areas with strong altitudinal gradients, the use of models developed at finer spatial scales is required
96 to avoid overestimation of habitat loss due to climate change (Randin et al. 2009).

97 Birds are undoubtedly a well-studied group in terms of impacts of environmental change
98 generally. However, relative to other habitats, the factors that dictate bird distributions, population
99 size and population trend in mountains are less well-known (EEA 2010), largely due to the logistical
100 constraints of working in such an environment (Chamberlain et al. 2012). Even basic, but
101 nonetheless essential, information on species distributions along altitudinal gradients are scarce. In
102 Europe, there is very little information on variation in bird distributions along altitudinal gradients in
103 mountains, with a few exceptions (Ring Ouzel *Turdus torquatus*, Marsh Tit *Poecile palustris* and
104 Bullfinch *Pyrrhula pyrrhula*, Maggini et al. 2011; Water Pipit *Anthus spinoletta*, Melendez and Laiolo
105 2014; Ptarmigan *Lagopus muta*, Parnollet et al. 2015). There is therefore a need to quantify the
106 distribution of more species along altitudinal gradients in order to act as a fundamental basis for
107 future studies on environmental change impacts. Furthermore, if models of altitudinal distribution
108 are to be used for drawing inferences on wider impacts of environmental change, then it is
109 necessary to know the extent to which altitudinal trends in occurrence are consistent across
110 geographically separated areas and therefore the extent to which a model derived from one area
111 can be used to make predictions in another (i.e. model transferability, Whittingham et al. 2007;
112 Schaub et al. 2011). Finally, it would be useful to know whether relatively simple models based on
113 altitude alone are sufficient to describe bird distributions along the gradient, or whether
114 environmental variables (habitat and climate) are essential elements to modelling elevational
115 distributions of birds.

116 This paper has three aims: (1) to describe the distributions of birds along altitudinal
117 gradients in the European Alps at relatively high altitude (c. 1700-3100m) and determine if they vary
118 between two geographically separated regions; (2) to assess the performance of models derived
119 across the whole study area in order to determine whether bird distributions can be better
120 explained by variations in altitude, habitat cover or climate, or combinations of these, along the
121 gradient; (3) to assess the extent of unexplained variation attributable to regional differences (i.e.
122 whether combinations of habitat and climate are sufficient to explain regional differences).

123

124

125 **Materials and methods**

126

127 Fieldwork was undertaken in two geographically distinct Alpine areas in northern Italy, Piedmont
128 and Trento (Fig 1). In Piedmont, the study area was in the western Italian Alps, mostly in the
129 province of Torino (there was a single site just outside of Piedmont in the Val d'Aosta region, Fig. 1).
130 In both areas, dominant shrub species are typically Juniper *Juniperus communis* and *Rhododendron*
131 spp. The natural treeline occurs at around 2200-2300m, although this varies depending on local
132 conditions. Furthermore, in many areas, the treeline is lower due to impacts of livestock grazing.
133 Grasslands occur throughout both areas, consisting of seasonal pastures and higher altitude alpine
134 meadows. Scree and rocky areas are common, especially at higher altitudes, and are typically
135 dominant above c. 2700m. In Piedmont, the dominant tree species is European Larch *Larix decidua*
136 whereas in Trentino it is Spruce *Picea abies*. In general, trends in the cover of major habitat types
137 were similar between the two regions, although there were some notable differences, e.g. greater
138 forest cover at lower altitudes (c. 1700-1900m) and higher rock cover throughout the gradient in
139 Trentino (Supplementary Material Fig. S1). There was little difference in temperature between the
140 two regions, although there was markedly higher precipitation in Piedmont (Fig. S2).

141

142 Bird and environmental data

143

144 Sampling took place over three years in Piedmont (2010-2012), and in a single year, 2011, in
145 Trentino. Identical field survey methods were undertaken in each region. Point counts were carried
146 out along transects in the two regions, which were selected based on accessibility, and which were
147 usually (although not always) along footpaths. Transects were separated by at least 1-km. A
148 minimum altitude of 1700m was defined in both areas. In the field, the start of each transect was
149 the closest suitable point above 1700m in altitude. Suitable points were those without any obvious

150 disturbance (e.g. occupied human habitation, livestock) or where detectability may have been
151 affected (e.g. large cliffs, noisy streams in spate) within 100m. Point locations were recorded on a
152 handheld Garmin GPS. The next selected point along the transect was then the next suitable location
153 after a minimum distance of 200m (i.e. to ensure no adjacent points were overlapping). Whilst a
154 random selection of points was not practically feasible, this systematic technique at least avoided
155 any possible selection based on the birds themselves.

156 Point counts (Bibby et al. 2000) were carried out from mid-May to mid-July, using a ten
157 minute count period preceded by a five minute settling period. At each point, the observer recorded
158 all birds seen and heard within a 100m radius (estimated with the aid of a laser range finder). Simple
159 habitat data were also collected at each point, including the percentage cover of canopy (i.e.
160 vegetation above head height), shrubs (woody vegetation below head height), open grassland (i.e.
161 no canopy), bare rock (including scree and other unvegetated areas) within 100m radius, and the
162 number of mature trees (approximately greater than 20cm in diameter) within a 50m radius (in
163 forested areas, it was not possible to count trees at a greater distance). Point counts commenced 1
164 to 1.5 hours after sunrise and continued until 13:00. No surveys were undertaken in wet or
165 excessively windy conditions.

166 Climate data were extracted from WorldClim (Hijmans et al. 2005), including five
167 temperature variables and five precipitation variables. The temperature variables were: mean
168 annual monthly temperature, maximum and minimum monthly temperature over the whole year,
169 mean monthly temperature for the breeding season and mean monthly temperature for the winter.
170 The precipitation variables were: and total annual precipitation, maximum and minimum monthly
171 precipitation over the whole year, mean monthly precipitation for the breeding season and mean
172 monthly precipitation for the winter. Topographic data (aspect and slope) were extracted from a
173 Digital Terrain Model of northern Italy at a 1ha scale, and calculated at the point level by calculating
174 mean values of the squares overlapping each 100m radius point count location. Both easting and
175 northing were considered, which were expressed as an index equal to $-\cos(A)$, where A is the aspect
176 (east or south) expressed in radians (following Bradbury et al. 2011), where a value of 1 represents
177 facing directly south or east, and -1 represents facing directly north or west. Altitude (expressed in
178 m) at each point was recorded by the GPS in the field. Slope was measured in degrees. (A full list of
179 environmental variables considered in the modelling procedure is presented in Table S1). All
180 variables were standardized to a mean of zero prior to analysis. All analyses were carried out in R
181 3.01 (R Development Core Team 2013).

182

183 Statistical analysis

184

185 The presence of a given species detected at each point count location was used to analyse the
186 distribution of alpine birds along the altitudinal gradient. Initial analyses suggested that species with
187 occurrence rates < 15% had consistently poor model performance (see below) and often, problems
188 with model fitting (e.g. lack of convergence), therefore a species was only considered if it occurred
189 on at least 15% of the sample for the relevant open or closed habitat type. For each species, we
190 considered only the likely nesting habitat, which we defined broadly into 'closed' and 'open' habitats
191 following Chamberlain et al. (2013). The former was defined as any habitat where the cover of
192 canopy + shrubs > 0. Open habitats were defined as any habitat where the number of mature trees
193 was zero – these species to some extent tolerate some woody vegetation (e.g. young trees, shrubs),
194 but tend to avoid mature trees and other vertical structures. Applying this 'habitat mask' had the
195 advantage of focussing only on likely breeding habitat (and thus omitting isolated records of non-
196 breeding and/or dispersing individuals) and omitting redundant zeros which may cause model fitting
197 problems (Zuur et al. 2009). Black Redstart *Phoenicurus ochrurus* was recorded in a range of
198 habitats, so for this species, the entire data set was considered.

199

200 *General modelling approach* - Bird distributions were analysed using logistic regression with the
201 lme4 package in R (Bates 2015). Multiple visits were made to some points in Piedmont, which was
202 accounted for by using a successes/failures syntax (Crawley 2013). Transect was fitted as a random
203 factor in all models to account for non-independence of points along the same transect. In all cases,
204 model fitting was preceded by a procedure to detect and reduce the effect of collinearity between
205 the variables. This was done by calculating Variance Inflation Factors (VIFs) for the variables and
206 sequentially deleting the variable with the highest VIF, as described by Zuur et al. (2009), using a cut-
207 off value of 3.0. The final variable sets, with minimal levels of collinearity, were used for model
208 averaging (see below).

209

210 *Altitudinal trends across regions (Aim 1)* - In order to determine variations in species distributions in
211 relation to altitude and region, a statistical hypothesis testing framework was adopted, with the null
212 hypothesis that bird species were distributed randomly in relation to altitude and region. Both linear
213 and quadratic terms were included in the models. 'Region' was included as a two-level factor
214 (Piedmont or Trentino). The interactions between region and both altitude and altitude² were
215 included in the initial model for each species, where significant interactions indicate differing trends
216 along the gradient between regions. These initial models were subject to a model reduction

217 procedure whereby non-significant terms were sequentially dropped from a model until only
218 significant ($P \leq 0.05$) terms remained.

219

220 *Model performance (Aim 2)* - Altitude may be a proxy for a multitude of effects operating at various
221 scales (Hodkinson 2005). The extent to which either habitat, climate or altitude, either alone or in
222 combination, could predict bird distributions was assessed by testing the performance of different
223 models derived from a randomly selected data set from 70% of observations against the observed
224 distributions from the remaining 30% of observations. Models were derived from the model data
225 set (i.e. 70% of the observations) for altitude (ALT), habitat (HAB – habitat cover and topographic
226 variables), climate (CLIM – temperature and rainfall) and combined habitat and climate (HAB+CLIM)
227 variables for each species (see Table S1 for a complete list of variable sin each set). In each case,
228 variables causing inflated VIFs (see above) were omitted. Non-linear effects were included in models
229 following visual assessment of scatterplots (following Zuur et al. 2009). Altitude and temperature,
230 and altitude and precipitation (which were highly collinear) were not modelled together. In total,
231 there were ten climate variables considered, and there was also a high level of collinearity within
232 this data set. A preliminary step was therefore undertaken to select the best fitting temperature
233 and best rainfall variable for each species by comparing univariate models (i.e. only one climate
234 variable at a time) using AIC. The climate variables used in CLIM and HAB+CLIM models were then
235 those whose univariate models had the lowest AIC (see OSM for further details).

236 For each model type (ALT, HAB, CLIM, HAB+CLIM), a model averaging approach, considering
237 all combinations of models, was used to derive parameter estimates using the shrinkage method
238 with the MuMIn package in R (Bartoń 2013). These were then used to predict the probability of
239 presence in the test data set (i.e. 30% of observations). Observed presences were compared with
240 the probability estimates from the model, and AUC was calculated from the package
241 PresenceAbsence (Freeman 2015) to test the ability of the models to correctly predict observed
242 presence. Models with $AUC < 0.70$ are considered to have limited predictive capacity (e.g. Swets
243 1988). To aid interpretation, we further classified models as having adequate ($0.70 \leq AUC < 0.80$)
244 and good ($AUC \geq 0.80$) predictive capacity.

245

246 *Variation partitioning (Aim 3)* – The categorical variable ‘region’ was added to HAB+CLIM models
247 from the above procedure – these models containing, habitat, climate and region were defined as
248 ‘full’ models. Variation partitioning for generalized linear models (e.g. Ficetola et al. 2007) was then
249 carried out on the full models in order to assess the amount of variation explained by HAB and CLIM
250 variables, and by the categorical variable region. A large amount of variation attributable to region

251 indicates that overall differences between regions are not attributable to the other model variables
252 (i.e. HAB and CLIM). Marginal R^2 values (fixed effects) for generalized linear mixed effects models
253 (Nagakawa & Schieleth 2013) were calculated for the full model, and for HAB variables, CLIM
254 variables, region, and combinations of these for each species using the `r.squareGLMM` command in
255 R package MuMIn (Bartoń 2013). The variation attributable to each component was determined
256 using the approach outlined by Legendre (2008). Altitude was not considered in this analysis due to
257 strong collinearity with climate variables.

258

259

260 **Results**

261

262 The occurrence rates for the commonest species (present on 15% of points in both regions) are
263 shown in Table 1, along with the classification into 'open' and 'closed' habitat species. There were 10
264 species that were recorded on at least 15% of points in both regions (for a total of 847 records
265 relative to those species).

266

267 Altitudinal trends across regions (Aim 1)

268

269 All ten species considered showed significant variation in probability of occurrence in relation to
270 altitude (Fig. 2). Two, Robin and Willow Tit, showed a significant interaction between region and
271 altitude. Robin showed significant linear decreases in probability of occurrence with altitude in both
272 regions, although the decrease was steeper in Trentino compared to Piedmont (Fig. 2D). Willow Tit
273 showed a non-linear relationship with altitude in Piedmont, occurrence peaking at c. 1900m, but a
274 decline in Trentino (Fig. 2I). Overall probability of occurrence varied significantly between regions for
275 several species and was higher for Water Pipit, Wheatear and Chaffinch in Piedmont and higher for
276 Dunnock and Robin in Trentino. In general therefore, trends across the elevation gradient were
277 similar for most species in the two regions, although overall occurrence rates often varied.

278 Based on Fig. 2, the species can be broadly defined into lower altitude species (those
279 showing a decline along the gradient), transition zone species (those showing a non-linear trend with
280 a peak in probability of occurrence around the treeline) and open habitat species (either showing a
281 peak in probability of occurrence in open grassland or an increase with altitude). The majority of
282 species were closed habitat species showing a significant decrease with altitude: Wren, Robin,
283 Chiffchaff, Coal Tit and Chaffinch (Fig. 2). In addition to Willow Tit in Piedmont, Dunnock also
284 showed an intermediate peak at the transition zone (c. 1900m, Fig. 2C). Both open habitat species

285 considered showed a non-linear trend, with a peak in probability of occurrence at intermediate
286 altitudes: Water Pipit (c. 2205m, Fig. 2A) and Wheatear (c. 2350m, Fig. 2F). Black Redstart was the
287 only species considered initially to be a habitat generalist and therefore analysed across all habitats.
288 This species showed a peak in probability of occurrence at relatively high altitudes (c. 2650m, Fig. 2E)
289 suggesting it was more of an open habitat species. However, when the species was analysed
290 considering only open habitats, there was no significant effect of altitude, suggesting that the
291 significant variation in Fig. 2E is largely driven by the contrast in species occurrence between open
292 and closed habitats.

293

294 Model performance (Aim 2)

295

296 AUC values for ALT, HAB, CLIM, and combined habitat and HAB+CLIM models, are given in Table 2
297 (details of the highest ranked model for each species are given in Table S2). For Black Redstart,
298 model fits were considered inadequate (AUC < 0.70) for all models. There were also three species
299 where no models were classified as 'good', Dunnock, Wheatear and Chiffchaff. Forest species
300 tended to have better performing models than species of more open habitats. Considering the best
301 performing model (i.e. the highest AUC value, regardless of classification) for each species, it was
302 clear that models which included habitat were better than those without, and in particular
303 combinations of habitat and climatic variables (HAB+CLIM models) tended to have relatively high
304 AUC values (Fig. 3A). When considering models classified according to AUC (i.e. poor, adequate or
305 good), again it was clear that HAB+CLIM models tended to perform best, followed by HAB models.
306 ALT and CLIM models performed less well (Fig. 3B).

307

308 Variation partitioning (Aim 3)

309

310 Variation partitioning was used to assess the contribution of each of HAB variables, CLIM variables
311 and region in the full models (parameter estimates are given in Table S3). There was a wide range of
312 variation explained by the fixed effects of the full model, from 0.20 in Water Pipit to 0.75 in Robin
313 (Table 3). Much of the variation was attributable to habitat variables, and to a lesser extent climate
314 (with the notable exception of Robin). The pure effect of region was very low in most models,
315 suggesting regional differences (e.g. Fig. 2) could be explained largely on the basis of habitat and
316 climate. The variation attributable to interactions between region and climate variables was,
317 however, reasonably high, and likely arose due to the sometimes marked differences in climate
318 between the two regions (OSM Fig. S2).

319

320

321 **Discussion**

322

323 Altitudinal trends

324

325 Alpine bird species show marked patterns in distribution along altitudinal gradients. For the widely
326 distributed species considered (i.e. those occurring relatively commonly in both Piedmont and
327 Trentino), these patterns were generally consistent across regions (Wren, Chiffchaff, Coal Tit),
328 although there were some species for which overall rates of occurrence varied, but the shape of the
329 relationship between probability of occurrence and altitude was the same between regions (Water
330 Pipit, Dunnock, Wheatear, Chaffinch). This has important implications for modelling species
331 distributions, as it suggests model transferability for several species, i.e. a model derived from one
332 region could be used to project relative elevational shifts in a wider area. There were two species
333 that showed significant differences in altitudinal trend between region, Robin and Willow Tit.
334 Differences in habitat, and in particular the number of trees may explain these patterns, especially
335 for Willow Tit, where the patterns in species occurrence match very closely with trends in number of
336 trees across the two regions (compare Fig. 2i and Fig. S3a).

337 Observer effects may be important in such surveys (e.g. Sauer et al. 1994; Farmer et al.
338 2014), and we cannot rule out that these may have influenced overall between-region differences
339 for some species. However, we believe such effects are likely to have been minimised as methods
340 were identical in the two areas, the species involved were relatively easily identifiable by song, and
341 the use of a fairly coarse measure, presence/absence, will have reduced subjectivity that might arise
342 from making estimates of abundance. It is also notable that differences were not uni-directional –
343 there were some species with higher occurrence rates in Trentino (Dunnock, Robin) and others with
344 higher occurrence rates in Piedmont (Water Pipit, Wheatear, Willow Tit, Chaffinch). There were also
345 differences in survey effort between regions in that many points were subjected to two or more
346 visits in Piedmont, but there was only a single visit in Trentino. However, there was no evidence that
347 this affected the outcome of the results (Supplementary Material Fig. S4).

348

349 Model performance across regions

350

351 Altitude correlates with gradients in habitat cover and with trends in climate, and is therefore
352 thought to be a good general surrogate for the multiple environmental variables that are likely to

353 dictate species distributions (e.g. Hodkinson 2005) and therefore to be a good basis for studying
354 environmental, and in particular climate, change (Shoo et al. 2006). Although the species here
355 showed clear variations along the altitudinal gradient, altitude models with a simple habitat mask
356 (i.e. removing unsuitable nesting habitat prior to modelling) did not perform especially well (only
357 Coal Tit had an altitude model considered 'good'; Table 2). Schaub et al. (2011), working across a
358 longer, but lower, altitudinal gradient also found only weak evidence that altitude was a good
359 predictor of farmland bird density. Similarly, climate-only models performed relatively poorly, and
360 there was no species that had a 'good' climate model (Table 2). For both climate and altitude
361 models, there were several species whose models were considered adequate, so it should not be
362 concluded that such models, masked for wholly inappropriate habitats, are of no value. However, it
363 is clear that incorporation of habitat cover in the models resulted in improved model performance in
364 many species. Whilst models using climate alone have proved useful in estimating species
365 distributions at broad scales (e.g. Huntley et al. 2007), in many situations (and particularly when
366 considering finer scales) climate and bird distributions are unlikely to be very tightly linked when
367 vegetation distribution is subject to other limiting factors (in particular, grazing by domestic
368 livestock) and when complex topography may mean strong influences of microclimatic conditions.
369 Data derived from relatively broad scales may therefore be inadequate to model distributions over
370 steep altitudinal gradients where mean climates can change over short distances. Climatic data
371 collected in the field at scales more appropriate to the activity of the birds (e.g. delimited by
372 territory size, foraging range or nest site) may therefore provide the basis of more informative
373 climate-only models. However, given the effort involved in collecting such data, it is difficult to
374 envisage a situation where simple habitat variables modelled in conjunction with larger-scale climate
375 variables would not prove to be the best option in terms of both effort and model performance.

376 There was very little variation attributable to region compared to climate and habitat
377 variables. This is likely because most of the variation caused by region (e.g. Fig. 2) is in fact due to
378 habitat and climatic differences already taken into account in the models, so inclusion of region in
379 addition to climate does not add any useful information. This is further evidence (along with the
380 consistency in altitudinal trends) that habitat and climate act on species distributions in a consistent
381 way across geographic regions. It also implies that other unmeasured differences, such as geology,
382 soil type, current and past land management, and disturbance (e.g. through winter sports or
383 hunting), either are unimportant in dictating bird distributions, or they do not vary sufficiently across
384 regions. Of course, we would caution against assuming such relationships are consistent across
385 other regions with widely differing environmental pressures. Our results suggest model

386 transferability for the Southern Alps for several widespread species, but it would be worthwhile to
387 repeat the study on distribution data from regions in different countries.

388

389 Wider implications

390

391 The relatively poor performance of climate-only models (models were 'adequate' for five species
392 and inadequate for the rest) implies that climate alone does not have a major role in directly limiting
393 species distributions along the altitudinal gradient. Habitat, or a combination of habitat and climate,
394 showed better performing models, suggesting that habitat management can be used to some extent
395 to improve conditions, potentially mitigating the negative effects of climate change for some species
396 (Braunisch et al. 2014). Habitat degradation and loss are often considered to be the key threats to
397 biodiversity, rather than climate change *per se* (e.g. Sala et al. 2000; Jetz et al. 2007; Chamberlain et
398 al. in press), and indeed in an alpine context, there are a number of environmental pressures which
399 are likely to affect habitat quality (e.g. winter sports, Rolando et al. 2007; land abandonment, Laiolo
400 et al. 2004), but whose effects could be ameliorated via habitat management. Nevertheless, climate
401 change is also a major driver of habitat change in the Alps, in particular via effects on shifts in
402 vegetation zones (e.g. Cannone et al. 2007) which may have consequences for bird distributions in
403 the future (Chamberlain et al. 2013). Whilst climate apparently plays a relatively minor role in
404 limiting current species distributions at the altitudes and at the fine spatial scale considered here, it
405 is very likely to be of greater importance over broader contexts – a longer altitudinal gradient and/or
406 a broader spatial scale may well have revealed a greater importance of climate in the models.
407 Although not the goal of this paper, identifying the point along the altitudinal distribution at which
408 climate becomes limiting would help to improve longer-term forecasts of potential effects of climate
409 change.

410 Although overall occurrence rates often varied between regions, the species studied showed
411 non-random altitudinal distributions which for most species were consistent across regions in terms
412 of pattern, which is a key finding in terms of evaluation of the potential effects of climate change
413 and associated habitat shifts (Araújo and Rahbek 2006). The shape and position of the altitudinal
414 distribution curve is important as it can be related to vulnerability where the available space is
415 limited, i.e. where mountains are of not sufficient altitude for expansion (e.g. Chamberlain et al.
416 2014; Pernolet et al. 2015). This study therefore suggests general consistency in response in terms
417 of the shape of the curve, and that regional differences are largely driven by habitat and climate.
418 Incorporating these variables should be sufficient to construct models with high transferability for
419 many Alpine species, a particularly relevant finding in terms of modelling species response to habitat

420 characteristics and environmental change (Randin et al. 2006). However, despite adequate model
421 performance in many cases, there was nonetheless often a large amount of unexplained variation,
422 suggesting that there is considerable scope for improving model performance further. We suggest
423 that further detailed autecological studies of alpine bird species are needed in order to improve our
424 ability to describe their distributions, in particular in terms of understanding what specific factors
425 mostly affect their occurrence. This would help understand the capacity of bird species to buffer the
426 effects of climate change by means of (micro)habitat selection (Moritz and Agudo 2013). Such
427 knowledge would contribute to evaluate the species' sensitivity (Chamberlain et al. 2013) and
428 adaptation potential (Bellard et al. 2012), and ultimately to build more precise models on which to
429 base future scenarios of environmental change and conservation planning. This is particularly
430 compelling for alpine habitats and species, as fine-scaled modelling is highly desirable in areas with
431 strong altitudinal gradients, where coarse models may overestimate the potential habitat loss due to
432 climate change (Randin et al. 2009).

433

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440

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Table 1 Species occurrence (proportion of points where present) for species which occurred on at least 15% of points in at least one region. Species were defined according to general nesting habitat (see text for details). Species occurrence is based on the total points surveyed per habitat. n is the number of points for each habitat and region.

Species	Hab	Total	n	Piedmont	n	Trento	n
Water Pipit <i>Anthus spinoletta</i>	OPEN	0.46	246	0.57	140	0.30	106
Wren <i>Troglodytes troglodytes</i>	CLOSED	0.22	305	0.26	191	0.17	114
Dunnock <i>Prunella modularis</i>	CLOSED	0.30	305	0.20	191	0.46	114
Robin <i>Erithacus rubecula</i>	CLOSED	0.15	305	0.15	191	0.18	114
Black Redstart <i>Phoenicurus ochrurus</i>	ALL	0.21	453	0.24	271	0.16	182
Wheatear <i>Oenanthe oenanthe</i>	OPEN	0.35	246	0.45	140	0.22	106
Chiffchaff <i>P. collybita</i>	CLOSED	0.21	305	0.18	191	0.25	114
Coal Tit <i>Parus ater</i>	CLOSED	0.28	305	0.27	191	0.28	114
Willow Tit <i>Poecile montanus</i>	CLOSED	0.30	305	0.37	191	0.18	114
Chaffinch <i>Fringilla coelebs</i>	CLOSED	0.42	305	0.54	191	0.21	114

Table 2 Model performance of different models describing probability of occurrence of species along altitudinal gradients. Values presented are AUC \pm se . ALT includes altitude and altitude²; HAB includes only habitat and topographic variables (after variable reduction according to VIF); CLIM includes climate variables (temperature and precipitation). HAB+CLIM includes both habitat and climate variables. AUC is coded according to thresholds of inadequate (white), adequate (shaded, normal text) and good (shaded, bold text) model performance.

Species	ALT	HAB	CLIM	HAB+CLIM
Water Pipit	0.74 \pm 0.06	0.74 \pm 0.06	0.79 \pm 0.05	0.84 \pm 0.05
Wren	0.71 \pm 0.06	0.67 \pm 0.07	0.68 \pm 0.07	0.57 \pm 0.07
Dunnock	0.65 \pm 0.06	0.56 \pm 0.06	0.75 \pm 0.05	0.76 \pm 0.05
Robin	0.78 \pm 0.06	0.76 \pm 0.07	0.64 \pm 0.07	0.77 \pm 0.06
Black Redstart	0.59 \pm 0.05	0.67 \pm 0.05	0.65 \pm 0.06	0.64 \pm 0.06
Wheatear	0.74 \pm 0.06	0.51 \pm 0.08	0.75 \pm 0.06	0.65 \pm 0.07
Chiffchaff	0.60 \pm 0.07	0.76 \pm 0.06	0.60 \pm 0.06	0.74 \pm 0.06
Coal Tit	0.87 \pm 0.04	0.83 \pm 0.05	0.77 \pm 0.05	0.89 \pm 0.05
Willow Tit	0.68 \pm 0.06	0.87 \pm 0.04	0.59 \pm 0.06	0.84 \pm 0.04
Chaffinch	0.69 \pm 0.06	0.90 \pm 0.04	0.77 \pm 0.05	0.91 \pm 0.03

Table 3. Variation partitioning based on R^2 for generalised linear models (Nagakawa & Schielzeth 2013) derived from the fixed effects of full models, i.e. including habitat variables (HAB), climate variables (CLIM) and region (REG). The variation attributable to each individual group of variables is given by REG, CLIM and HAB. The variation attributable to interacting pairs of variables is given by REGHAB (region and habitat), CLIMHAB (climate and habitat) and REGCLIM (region and climate). The variation attributable to the interaction between all three variables is given as 3-WAY. Negative values are interpreted as zeros (Legendre 2008).

Species	Full	REG	CLIM	HAB	REGHAB	CLIMHAB	REGCLIM	3-WAY
Water Pipit	0.200	0.004	0.028	0.114	-0.001	0.011	0.054	-0.010
Wren	0.299	0.001	0.022	0.148	0.002	0.119	0.128	-0.121
Dunnock	0.471	0.001	0.117	0.105	0.009	0.094	0.248	-0.103
Robin	0.755	0.061	0.309	0.107	0.028	0.328	0.278	-0.356
Black Redstart	0.522	0.016	0.008	0.374	-0.018	0.137	0.124	-0.119
Wheatear	0.321	0.000	0.113	0.161	0.000	0.022	0.047	-0.022
Chiffchaff	0.429	0.015	0.069	0.180	0.016	0.138	0.165	-0.154
Coal Tit	0.549	0.022	0.154	0.171	-0.009	0.217	0.202	-0.208
Willow Tit	0.394	0.047	0.051	0.119	-0.012	0.164	0.177	-0.152
Chaffinch	0.648	0.004	0.030	0.200	-0.004	0.274	0.414	-0.270

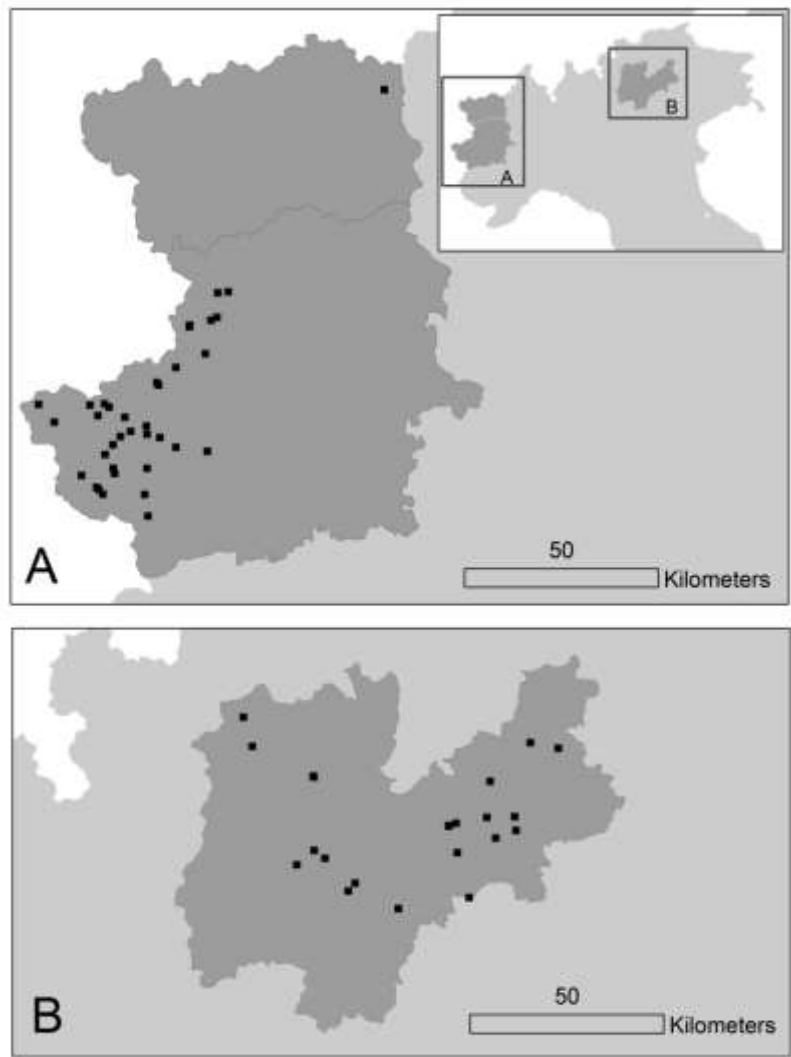


Fig. 1 Location of the transects in the provinces of Turin (Piedmont) (A) and Trentino (B).

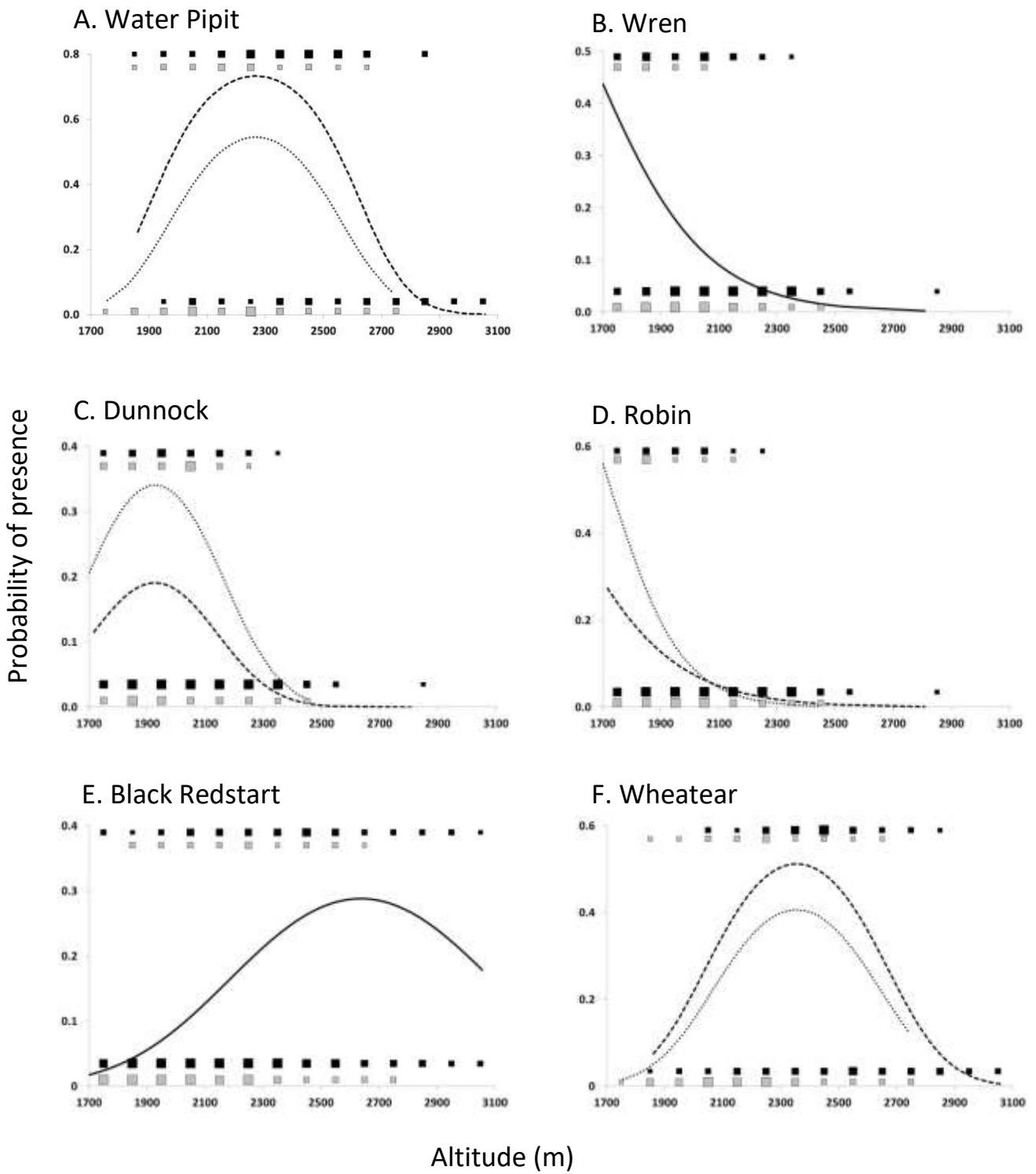


Fig. 2 Trends in the probability of occurrence in relation to altitude. Where there was an effect of region, or where a species was analysed in only one region, dashed lines indicate Piedmont and dotted lines indicate Trentino. A solid line indicates a trend fitted from both regions combined (i.e. where there was no significant difference). Observed presences and absences are shown as black squares (Piedmont) and grey squares (Trentino) on the y-axis maximum and minimum respectively. These are summarised into frequencies for each category (region and presence/absence) calculated at each 100m interval. Symbol size is representative of the number of points, divided into five groups, where 1 (i.e. the smallest) = 1 point, 2 = 2-5 points, 3 = 6-10 points, 4 = 11-15 points and 5 = 16 points or greater.

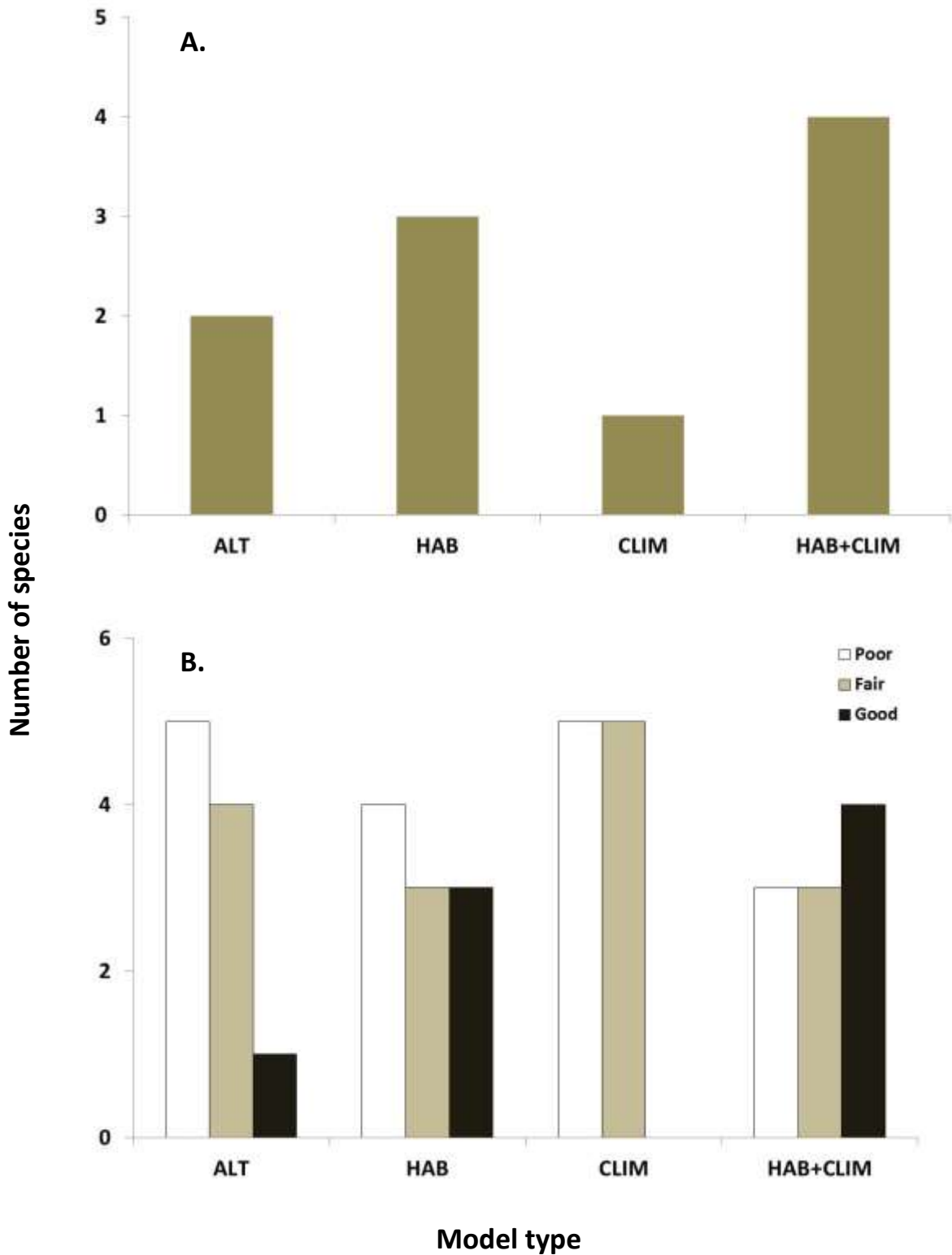


Fig. 3 Performance of different models measured by AUC. A. Number of species for which a given model had the maximum value of AUC. B. Number of species for which a given model was classified as having inadequate ($AUC < 0.70$, white bars), adequate ($0.70 \leq AUC < 0.80$, grey bars) and good ($AUC \geq 0.80$, black bars) predictive capacity. ALT = altitude only, HAB = habitat only, CLIM = climate variables only, HAB+CLIM= combined habitat and climate variables.