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14 The contribution of broadscale and finescale habitat structure to the distribution and diversity
15 of birds in an Alpine forest-shrub ecotone

16

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34 distribution models · Habitat mosaic · *Rhododendron ferrugineum*

35

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41 **Abstract**

42 In a mountain context, the forest-shrub ecotone is an area of high biodiversity. Relatively
43 little is known about the habitat requirements of birds in this habitat, yet it is facing potential
44 threats from changes in grazing practices and climate change. Moreover, it is not clear at
45 which scale habitat associations should be assessed in Alpine birds. Further information on
46 key habitat components affecting bird communities of the ecotone are needed in order to
47 inform management strategies to counteract potential habitat loss, and to better inform
48 predictions of how bird communities may be affected by future environmental change. Data
49 on bird occurrence and broadscale (land cover) and finescale (vegetation structure and
50 shrub species composition) habitat variables were collected in an Alpine forest-shrub
51 ecotone in Val Troncea (northwestern Italian Alps) in order to address two objectives: to
52 identify the key habitat variables associated with the occurrence of individual species and
53 with the diversity of the bird community; and, to assess which scale of habitat measurement
54 (broad-scale, finescale or both combined) is needed to model bird occurrence. Broad-scale
55 variables, or combinations of broad- and finescale variables, tended to have the best
56 performing models. When combined models performed best, shrub species identity was
57 included in many cases. Shrubs also played an important role in explaining variations in
58 species diversity and richness. Vegetation structure was of relatively little importance, either
59 for individual bird species or for species richness and diversity. These findings suggest that
60 management should strive to maintain a mosaic of habitats whilst minimizing forest
61 encroachment, which could be achieved through targeted grazing. Broad-scale habitat data
62 and data on shrub species composition should provide a sufficient basis for identifying
63 relevant species-specific habitat parameters in a mountain environment in order to model
64 future scenarios of effects of habitat change on the bird community of the alpine forest-shrub
65 ecotone.

66 **Introduction**

67 Mountain biodiversity is under a range of environmental pressures, including land use
68 change (Laiolo et al. 2004), increased human leisure activities (Rolando et al. 2007; Arlettaz
69 et al. 2007), climate change (Sekercioglu et al. 2008; Dirnböck et al. 2011), and interactions
70 between these factors (e.g. Brambilla et al. 2016). Climate change may be a particular
71 problem given that the rate of warming in mountains is approximately double the global
72 average, a trend that is expected to continue (Böhm et al. 2001). A consequence of climate
73 change is that vegetation zones are likely to shift upwards – for example, the upper forest
74 limit has shifted to higher elevations in many mountain regions in line with rising
75 temperatures (Harsch et al. 2009). The loss of high altitude open habitats as a consequence
76 of such vegetation shifts has been identified as a potential future conservation problem
77 (Sekercioglu et al. 2008; Chamberlain et al. 2013), especially as the proportion of species of
78 conservation concern tends to increase with elevation (Viterbi et al. 2013). However,
79 vegetation shifts in some areas have also been due to abandonment of grazing which
80 maintained the forest limit at a lower altitude than would be possible under only climatic
81 constraints. This effect has had a greater effect than climate change on treeline shifts in the
82 European Alps (Gehrig-Fasel et al. 2007).

83 The ecotone between the forest and the alpine grassland zone is characterized by a
84 high structural diversity, typically being a mix of open grassland areas, pioneer forest and
85 shrub species. It is therefore often an area of high biodiversity (Dirnböck et al. 2011). Whilst
86 abandonment of grazing and vegetation shifts due to climate change may, at least initially,
87 have the capacity to create new habitats, in particular through the colonization by shrub
88 species (Laiolo et al. 2004), there are also threats to this habitat. First, it seems plausible to
89 expect that structural diversity is a key factor driving the relatively high biodiversity of the
90 ecotone (e.g. MacArthur and MacArthur 1961), and grazing is likely to maintain a habitat
91 mosaic that underpins the structural diversity, hence further abandonment of grazing may be
92 detrimental. Second, many mountainous areas do not reach altitudes that are high enough

93 to maintain the ecotone habitat given the likely magnitude of vegetation shifts (Dirnböck et
94 al. 2011) – such areas are likely to be mostly forest in the future. Third, it cannot be assumed
95 that all components of the vegetation community will respond simultaneously to climate
96 change (Theurillat and Guisan 2001). For example, there is evidence that vegetation zones
97 respond differentially to warming temperatures in the Alps (Cannone et al. 2008), and that
98 trees and shrubs may respond differentially to reduced snow cover resulting from climate
99 change. Snow has insulating properties that benefit some shrub species from frost damage
100 (Neuner 2014), and lower snow cover or earlier snow melt could potentially lead to a net loss
101 of ecotone habitat.

102 Within the gradient of alpine habitats from mountain forest to the highest altitude nival
103 zone (Kapos et al. 2000, Körner & Ohsawa 2006), the highest biodiversity is typically found
104 in the forest-shrub ecotone, yet it has been little studied in an avian context. Whilst common
105 species such as Dunnock *Prunella modularis*, Linnet *Carduelis cannabina*, Lesser
106 Whitethroat *Sylvia curruca* and Wren *Troglodytes troglodytes* have been studied in lowland
107 habitats (usually at higher latitudes), the few studies that have assessed habitat associations
108 in these species in mountain habitats have considered only broadscale, usually remote-
109 sensed, habitat data and have not considered more detailed measures of habitat complexity
110 (Chamberlain et al. 2013, 2016). With a few exceptions, notably Black Grouse *Tetrao tetrix*
111 (e.g. Patthey et al. 2012, Braunisch et al. 2016) and Ring Ouzel *Turdus torquatus* (von dem
112 Bussche et al. 2008), there is as yet insufficient information to determine at which scale
113 species-habitat associations should be assessed in order to plan conservation actions for
114 the majority of common Alpine ecotone species in the context of environmental changes.
115 Furthermore, such studies would also allow the improvement in our ability to forecast
116 potential effects of future environmental change for ecotone species. Species distribution
117 models for typical ecotone species such as Dunnock, Wren and Tree Pipit *Anthus trivialis*
118 show generally less good model performance, and greater inconsistency in model outcomes
119 between different scenarios of change, compared with forest and grassland species
120 (Chamberlain et al. 2013, 2016). This may be because these species are more dependent

121 on finescale habitat characteristics, such as vegetation structure, and hence are not well-
122 described by land cover and topographic variables that typically underpin many species
123 distribution models.

124 Heterogeneity plays an important role for bird species diversity in a range of different
125 habitats, including farmland (Benton et al. 2003), rain- (Guerta and Cintra 2014) and
126 temperate forests (Freemark and Merriam 1986) and grasslands (Hovick et al. 2014).
127 However, the role of heterogeneity in the forest-shrub ecotone is still not well understood.
128 We would expect that, based on the influence of habitat diversity and structural vegetation
129 diversity, species richness in the ecotone would be positively associated with measures of
130 habitat heterogeneity. A recent study on Black Grouse in the Swiss Alps showed that
131 horizontal and vertical structural heterogeneity was the best predictor for the occurrence of
132 the species (Patthey et al. 2012). We similarly expect that ecotone species will in general be
133 positively associated with habitat complexity. In this study, we consider complexity in terms
134 of the diversity of vegetation structure, the heterogeneity in vegetation height, and also in
135 terms of the habitat mosaic formed by shrubs, grassland and forest. We focus in particular
136 on non-linear relationships between the bird community and shrub cover as a measure of
137 the habitat mosaic, the expectation being that bird diversity and individual species
138 occurrences will peak at intermediate values of shrub cover.

139 The specific objectives of this study are (i) to assess key habitat attributes that
140 influence bird diversity and individual species occurrence in an Alpine forest-shrub ecotone,
141 and (ii) to determine whether habitat cover and altitude are adequate to model species
142 distributions in the ecotone, or if more detailed information on vertical vegetation structure
143 and shrub species composition is needed.

144

145 **Methods**

146 **Study area and point selection**

147 The study was carried out in Val Troncea Natural Park (44°57'28" N; 6°56'28" E) in the
148 western Italian Alps. At lower altitudes the area is dominated by larch *Larix decidua*. The
149 natural treeline is typically found at around 2200 m asl, but varies depending on local
150 conditions. Typical shrub species are *Juniperus nana* (henceforth Juniper) and
151 *Rhododendron ferrugineum* (henceforth Rhododendron) which rapidly encroached wide
152 areas of grasslands after the decline of agro-pastoral activities. Grasslands were mainly
153 dominated by *Festuca curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky
154 areas occur predominantly at higher altitudes, above approximately 2700 m asl.

155 Point counts were carried out in the forest-shrub ecotone, which we defined as the
156 transition zone between forest and alpine grasslands. We included both natural ecotones
157 where the treeline is limited by climatic conditions, and areas where open grassland has
158 been maintained at lower altitudes, mostly due to grazing by domestic livestock, but also due
159 to avalanches in some locations. Point count locations coincided with the centroids of a pre-
160 existing grid at a scale of approximately 150 x 150 m (there was some variation, due to
161 access constraints for example; Probo et al. 2014) along the western facing slope of the
162 valley. Points were selected that had a minimum shrub cover of 5 % and a maximum tree
163 cover of 70 % (i.e. thus presenting the forest-shrub ecotone) within 100 m radius according
164 to vegetation surveys (see below). All points were spaced a minimum of 200 m apart.

165

166 **Bird surveys**

167 Point counts (n = 79) were carried out from mid-May to mid-July over a period of 2 years (46
168 in 2015 and 33 in 2016) following the methods of Bibby et al. (2000), using a 10 minute
169 count period. At each point count location, all individual birds seen or heard were recorded
170 within a 100 m radius (estimated with the aid of a laser range finder). Point counts
171 commenced 1-1.5 h after sunrise and continued until 1200 h. Surveys did not take place in
172 excessively wet or windy conditions. Each point count location was visited once.

173

174 **Broadscale and finescale habitat**

175 Habitat data were defined into two categories representing 'broadscale' habitat data (land
176 cover, altitude and other variables estimated at a resolution of the whole point count
177 location) and 'finescale' habitat data (vegetation structure and shrub species composition
178 estimated from plots at a finer scale of resolution within the point count location). Broadscale
179 habitat comprised visual estimation of the percentage cover of canopy (i.e. vegetation above
180 head height), shrubs (woody vegetation below head height), open grassland and bare rock
181 (including scree and unvegetated areas) within a 100 m radius of the point's centre. The
182 number of mature trees (greater than c. 20 cm in diameter at breast height) within a 50 m
183 radius of a point count location was also counted. These estimates have been shown to
184 correlate well with estimates of land cover derived from remote sensing and have been used
185 as the basis of predictive models for several species considered here (Chamberlain et al.
186 2013, 2016).

187 Finescale habitat data on vegetation structure and composition were collected at the
188 centre of the point count location and along two 100 m long transects, each divided into 5
189 plots spaced 20 m apart originating at the point's centre (therefore there were eleven plots
190 sampled per point count location including the central point). The compass bearing of each
191 transect from the centre of the point to its perimeter was selected at random, the only
192 constraint being that there had to be an angle greater than 90° between two transects at the
193 same point. Following Bibby et al. (2000), at each plot, vegetation density was measured at
194 three different heights (0 m; 0.5 m; 1 m) using a chequered board (50 cm x 30 cm), divided
195 into 10 x 10 cm square subdivisions, placed vertically into the vegetation, the bottom of the
196 board coinciding with the appropriate height class. To produce an index of vegetation
197 density, an estimate was made of the number of squares of the board that were obscured by
198 vegetation observed from a distance of 5 m. A square was considered obscured by
199 vegetation when <50 % of it was visible. The diversity of vegetation density over all 11 plots
200 was then calculated with the Shannon index $H' = - \sum p_i \ln p_i$, where p_i is the proportion of
201 squares obscured at the i th plot. Data were also collected on grass and shrub height (if
202 present), and the standard deviation of height calculated across the 11 plots was used as a

203 measure of vegetation height heterogeneity for each point. The dominant shrub species at
204 each plot within a 1 m radius was recorded, defined into four groups: Rhododendron,
205 Juniper, bilberry (*Vaccinium myrtillus* and *V. gaultherioides*) and other (e.g. Green Alder
206 *Alnus viridis*, Willow *Salix spp*, and also including young trees less than two meters in height,
207 mostly European Larch *Larix decidua*). The frequency of plots in which a given group was
208 present was calculated for each point (i.e. the maximum frequency was 11). All habitat
209 variables used in the analysis are listed in Table 1 (a complete list of variables measured in
210 the field, but not included in the models due to collinearity, are given in Electronic
211 Supplementary Material (ESM) Table S1).

212

213 **Data analysis**

214 Birds detected within a 100 m radius of a point count location were used to analyse species
215 richness (simply the number of species detected on each point count), species diversity
216 (expressed using the Shannon index) and species distribution (presence/absence of
217 individual species) with regard to habitat composition and structure within the forest-shrub
218 ecotone.

219 Data were analysed using an information theoretic approach with the MuMIn package
220 in R (R v.3.3.2, R Development Core Team 2016; Bartoń 2013). This entailed first deriving
221 full models at each scale and for each dependent variable (richness, diversity or species
222 presence) using a mixed modelling approach in the R package lme4 (Bates et al. 2015).
223 Model-averaged parameter estimates were derived for all combinations of variables in each
224 full model in order to identify variables that were most closely associated with bird
225 distribution and diversity. P-values derived from the model-averaged parameter estimates
226 and their standard errors were considered to represent significant effects when $P < 0.05$. In
227 addition, the Akaike Information Criterion corrected for small sample size (AICc) was
228 determined for each individual model and was used to assess model performance at
229 different scales (see below).

230 Prior to modelling, all variables within each set (i.e. broad- or finescale) were scaled
231 and centred. Variance inflation factors (VIFs) were calculated using the 'corvif' function
232 (package 'AED', Zuur et al. 2009) to assess collinearity between continuous explanatory
233 variables. All variables with a VIF > 3 were sequentially removed from the variable set until
234 all VIFs were < 3. Intercorrelations between remaining variables were then checked, and for
235 those with Spearman correlation coefficients > 0.50, one of the pair was subsequently
236 omitted (variables with a large proportion of zeroes were preferentially omitted, otherwise the
237 choice was random). As a final check, variables that had been removed in the procedure to
238 minimise collinearity were substituted for closely correlated variables (in particular between
239 overall shrub cover or frequency, and the frequency of individual shrub species). Cases
240 where the model with the substituted variable had a lower AICc were used in the final full
241 model. As we were particularly interested in how the shrub-grassland habitat mosaic
242 affected the bird community, we included a quadratic effect of variables representing shrub
243 cover (including the frequency of individual shrub species) in all models. For other variables,
244 non-linear effects were included in the models following visual assessment of scatterplots
245 (following Zuur et al. 2009). Year was specified as random effect in every model to account
246 for possible inter-annual effects.

247 Species richness and species diversity were analysed using generalised linear mixed
248 models in relation to habitat variables, specifying a Poisson and a normal error distribution
249 respectively. The occurrence probability of the commonest species (present on 15 % of
250 points – Chamberlain et al. 2013 found that models performed persistently poorly below this
251 threshold) in relation to habitat was analysed using binomial logistic regression, each
252 species being recorded as either present or absent per point. At each scale, the residuals for
253 all full models were extracted and tested for spatial autocorrelation using Moran's I (Moran
254 1950). There was no strong evidence of spatial autocorrelation across species or scales
255 (see details ESM Table S6 and S7), therefore this was not considered further.

256 At the end of the above process, for species richness and diversity and for each
257 individual species, candidate models with model averaged parameter estimates were

258 derived for each combination of variables based on the full model for broad- and finescale
259 habitat variables separately. The next step was then to derive combined models based on
260 the most important variables from both broadscale and finescale models, defined as those
261 variables which were either significant ($p \leq 0.05$) or which approached significance ($p \leq 0.1$)
262 from the broad- and finescale model sets. In the few cases where no variables had $P < 0.10$,
263 those with a high Akaike weight (> 0.50) in each scale-specific model were used in the
264 combined model. The new data set was again subject to variable set reduction according to
265 VIFs and correlation coefficients, and subsequently combined models were derived, which
266 were again subject to model averaging.

267 The extent to which broadscale or finescale habitat structure, or a combination of the
268 two, was necessary to model species diversity and distributions was assessed using AICc.
269 At each scale (finescale, broadscale and combined) and for each dependent variable,
270 models were ordered according to the AICc, where lower values indicate better performing
271 models. Change in AICc relative to the top ranked model was calculated as $\Delta AICc$. Models
272 with $\Delta AICc < 2$ were considered equivalent. Models from all three scales were compared in
273 order to assess whether high model performance was associated with either broadscale or
274 finescale habitat variables, or a combination of both. The importance of each variable at
275 each scale was assessed by calculating Akaike weights based on all combinations of
276 models (Burnham and Anderson 2002), which are expressed as the likelihood contribution of
277 each model as a proportion of the summed likelihood contributions of all models. The weight
278 for each variable is the sum of model weights for all models in which a given variable was
279 present (Burnham and Anderson 2002).

280

281 **Results**

282 In total, 263 individuals of 29 species were recorded in 79 point counts over an altitudinal
283 range of 1800-2600 m asl. There were eight species that were recorded on at least 15 % of
284 the points: Tree Pipit, Water Pipit *Anthus spinoletta*, Dunnock, Northern Wheatear *Oenanthe*

285 *oenanthe*, Lesser Whitethroat, Wren, Chaffinch *Fringilla coelebs*, Rock Bunting *Emberiza*
286 *cia*. No significant model averaged parameter estimates could be identified to predict Rock
287 Bunting occurrence for broad- or finescale models, therefore this species was not
288 considered in further analyses.

289

290 **Broadscale habitat structure**

291 Details of model-averaged parameters of the model set for broadscale habitat structure are
292 given in ESM Table S2. Bird species richness and diversity showed a positive relationship
293 with the number of mature trees. Shrub cover showed a quadratic effect on bird diversity
294 whereby diversity increased initially with the percentage of shrub cover, but declined after a
295 shrub cover of approximately 55 % was reached. Furthermore, diversity was negatively
296 associated with altitude. Among individual species, Dunnocks showed a positive linear
297 association with shrub cover, whereas both Lesser Whitethroat and Wren showed a
298 quadratic association, where the probability of occurrence of Lesser Whitethroat and Wren
299 peaked at c. 45% and c. 50% shrub cover respectively. The number of mature trees showed
300 a positive relationship with Chaffinch presence. There was also a negative effect of rock
301 cover on Tree Pipit occurrence. Altitude was the only variable within the full model which
302 was not linked to vegetation cover, and had different effects on the occurrence probability of
303 Chaffinch, Wren (negative) and Northern Wheatear and Water Pipit (positive).

304

305 **Finescale habitat structure**

306 Details of model-averaged parameters of the model set for finescale habitat structure are
307 given in the ESM Table S3. A number of dependent variables showed significant quadratic
308 effects (e.g. probability of occurrence or diversity peaking at intermediate frequencies), either
309 for all shrubs (Northern Wheatear), or for individual shrub species (Wren and Juniper
310 frequency, Dunnock and Rhododendron frequency, species diversity and Bilberry
311 frequency). Shrub height heterogeneity was positively correlated with Wren and Tree Pipit
312 presence. A positive relationship of canopy presence was found for bird species richness

313 and diversity, as well as for Chaffinch presence. In contrast, it showed a negative
314 association with Northern Wheatear presence. Structural vegetation diversity was not
315 selected in any model set (see ESM Table S3).

316

317

318 **Combination of broadscale and finescale habitat structure**

319 Details of significant model-averaged parameters of the final combined model sets are given
320 in Table 2 (for a full list of parameters see ESM Table S4). In line with our expectation on
321 effects of habitat mosaics on ecotone species, we here focus on shrub cover, but graphs of
322 all significant variables in combined models are presented in ESM, Fig. S1. Shrub cover, as
323 a broadscale variable, occurred in the combined model set for bird species diversity (Fig. 1)
324 and Lesser Whitethroat (ESM Fig. S1). In a number of cases, individual bird species
325 occurrences were closely associated either with shrub species identity or with shrub
326 frequency (Table 2). Quadratic relationships between shrub species and bird species
327 occurrence were found for Dunnock (Rhododendron), Wren (Juniper) and bird species
328 diversity (Bilberry, see Fig. 2). Tree Pipit occurrence declined with increasing Rhododendron
329 frequency (Fig. 2). Shrub height heterogeneity was closely related to Tree Pipit and Wren
330 occurrences.

331 The frequency of canopy or the number of mature trees was retained in the combined
332 models for bird species diversity, bird species richness and Chaffinch occurrence (positive
333 associations) as well as for Dunnock occurrence (negative association). Altitude showed a
334 negative relationship with the occurrence of Wren and Chaffinch, while it was positively
335 associated with Northern Wheatear presence.

336

337 **Model comparison**

338 A summary of the ten highest ranked models for each species and each diversity measure
339 across scales is shown in Fig. 3. The higher ranked models were mostly based on combined
340 models (i.e. combinations of broad- and finescale variables), or broadscale models alone.

341 The best models ($\Delta AICc < 2$) for Dunnock, Lesser Whitethroat, Northern Wheatear, Tree
342 Pipit, Chaffinch, Wren and species diversity contained only combined models. Finescale
343 models were in the best model set only for species richness, but combined and broadscale
344 models performed equally well (i.e. $\Delta AICc < 2$). Figure 3 also illustrates that, for many
345 species, there was a high degree of model uncertainty in that there were often several
346 models where $\Delta AICc < 2$. In general, finescale habitat variables of high weight that were
347 present in the combined (best) models were related to the presence of shrubs either overall
348 (Northern Wheatear) or of specific shrub species (Dunnock, Lesser Whitethroat, Tree Pipit,
349 Wren and bird species richness and diversity; Table 3).

350

351

352 **Discussion**

353 The aim of this study was to describe species-specific habitat requirements within a
354 mountainous forest-shrub ecotone in order to assess the relationships between the diversity
355 and distributions of birds and environmental variables measured at different scales, and
356 hence to identify potential conservation priorities and to inform future modelling methods.
357 Through the combination of broad- and finescale habitat data in final models, we determined
358 key habitat characteristics which shaped bird species richness and diversity. Furthermore, it
359 enabled us to pinpoint habitat elements which are specifically required by common ecotone
360 species. Our expectations of positive associations between bird community measures
361 (diversity and individual species occurrence) and habitat complexity were partially met in
362 terms of shrub cover and to a lesser extent shrub height heterogeneity, but there was no
363 evidence that the diversity of vegetation structure was important.

364

365 **Comparison of model scales**

366 For making management recommendations, the identification of key habitat characteristics
367 (e.g. vegetation structure or plant species composition) supporting bird species diversity or

368 target species is essential. The decision at which scale this objective will be addressed
369 varies among studies representing a trade-off between broadscale (remote sensing
370 techniques, Braunisch et al. 2016) and finescale data collection (detailed vegetation
371 measurements in the field, Patthey et al. 2012). Both techniques show advantages and
372 disadvantages. Collecting broadscale data (for example, through remote-sensed data bases)
373 allows large areas to be covered, but has the potential to miss relevant habitat features.
374 Data collection in the field provides more detailed information, but is time consuming and
375 only applicable for smaller areas. Therefore choosing the appropriate scale is crucial as it
376 directly determines the outcome of the study. The model scale comparison (broadscale,
377 finescale or combined) applied on the same data allowed the assessment of the scale of
378 data collection needed to identify habitat parameters determining bird species diversity or
379 species specific habitat requirements in the forest-shrub ecotone.

380 The comparison revealed that combined and/or broadscale models always performed
381 better than finescale models for individual species. When combined models performed best,
382 variables linked to shrub species identity (finescale variables) were included in several cases
383 (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity).
384 Other finescale variables were rarely included in the combined model set for individual bird
385 species, or alternatively could be substituted by equivalent broadscale variables which had
386 been excluded from the modelling process because of high collinearity between variables
387 (e.g Canfreq, a finescale variable which was highly correlated with canopy cover measured
388 at the broadscale). Furthermore, finescale models were only included in the best model set
389 (i.e. $\Delta AICc < 2$) for species richness, but combined and broadscale models performed
390 equally well. Variables that described vegetation structural heterogeneity or diversity were
391 only rarely included in the best model sets: SDshrubs was in the best model set for Wren,
392 Tree Pipit and species diversity, although for the latter, the variable was not significant and
393 was of low variable weight (ESM Tables S4 and S5).

394 These results therefore suggest that structural vegetation may be less important for
395 the identification of factors determining species diversity and species distribution in the

396 majority of cases. However, to further our understanding of individual species and bird
397 species diversity, data collection in the field should focus on habitat data which considers
398 horizontal vegetation cover collected at a broad scale, but which includes species-specific
399 estimates of cover of relevant shrub species in the area in order to model distributions of
400 birds in the shrub-forest ecotone. The assessment of horizontal habitat cover can be done
401 quickly and easily by eye from a single location for the whole area of a point count, including
402 cover of easily recognizable shrub species such as Juniper and Rhododendron, whereas
403 detailed structural vegetation measurements (as undertaken here) require considerable
404 effort and access to a much greater area of a given point. The results further suggest that
405 land cover datasets analogous to the data collected here should also be adequate for
406 species distribution modelling in the studied habitat if they are able to estimate the cover of
407 the dominant shrub species. Thus, broadscale habitat data and data on shrub species
408 composition should provide a sufficient basis in identifying relevant species-specific habitat
409 parameters in a mountain environment. Future species distribution models should seek to
410 incorporate species-specific estimates of shrub cover, especially as the dominant species in
411 the area are likely to respond differently to future climate change (Theurillat and Guisan
412 2001; Neuner 2014).

413

414 **Factors affecting bird diversity and distribution at different habitat scales**

415 There was some support that a habitat mosaic was beneficial for some individual species in
416 that Dunnock, Lesser Whitethroat and Wren showed significant non-linear associations with
417 either shrub cover or shrub species frequency in at least one model. Furthermore, shrub
418 cover and frequency occurred in two final models and were positively correlated with bird
419 species diversity (shrub cover) as well as Northern Wheatear presence (shrub frequency).
420 The general overall importance of shrubs can easily be understood as they provide nesting
421 habitat for shrub-nesting species, provide shelter in harsh weather conditions and can shield
422 birds from predators.

423 In addition to overall shrub cover, individual shrub species were also important for
424 some bird species. Bilberry cover was negatively related to bird species diversity,
425 presumably because, in contrast to the other shrub species present, this species does not
426 provide dense cover that could be suitable for nesting. Only Wren was positively associated
427 with Juniper frequency. It was also negatively associated with altitude, which may suggest a
428 link to the different growth characteristics of Juniper along the altitudinal gradient (Hallinger
429 et al. 2010). At high altitudes (>2000m), this shrub species typically grows fairly low to the
430 ground (10-30 cm; Aeschimann et al. 2004), which may make it unsuitable for nesting (due
431 to predation risk for example). Suitable Wren nesting habitat may only be found at lower
432 altitudes (1800 – 2000 m), where Juniper tends to be taller, and possibly less dense.

433 In contrast to Juniper, Rhododendron can still grow up to heights suitable for nesting
434 (30 – 120 cm; Aeschimann et al. 2004) in the upper fringe of the ecotone and could therefore
435 be seen as an attractive alternative for shrub-nesting species. In the combined models,
436 Rhododendron showed a non-linear association with Dunnock presence, which seems to be
437 preferred as a nesting habitat over other shrub species (pers. obs.). In the Alps,
438 Rhododendron can form very large and dense patches on north, west and northwest-facing
439 slopes within the subalpine belt (Pornon and Bernard 1996). Its distribution depends highly
440 on winter snow cover which serves as a protective layer against excessive irradiation and
441 frost (Neuner et al. 1999). However, due to climate change, snow cover is predicted to
442 decrease by the end of the century (Beniston et al. 2003). Taking potential snow
443 accumulation into account, Komac et al. (2016) showed that Rhododendron could
444 experience an important reduction in its realized niche, and that its future habitat could be
445 confined to areas which are today scree and rocky hillside habitats. This outcome suggests
446 that, even if current habitat is maintained, climatic conditions might become less favourable
447 for the persistence of Rhododendron and that suitable habitat for shrub-nesting species in
448 the forest-shrub ecotone will disappear.

449

450 **Conservation implications**

451 The loss of open habitats due to abandonment of grazing (Gehrig-Fasel et al. 2007; Roura-
452 Pascual et al. 2004; MacDonald et al. 2000) and climate change (Lenoir et al. 2008; Pauli et
453 al. 2007) is likely to continue in the future to the extent that significant areas of more open
454 habitats, including the shrub-grassland ecotone, will be replaced by forest. To maintain
455 ecotone habitat, it may therefore be necessary to counteract shrub and indeed forest
456 encroachment in targeted areas in order to keep a heterogeneous character of the forest-
457 shrub ecotone. Possible methods to counteract shrub-encroached areas could be
458 mechanical shrub clearance or the re-establishment of grazing (e.g rotational grazing
459 systems with appropriate stocking level; Probo et al. 2014). However, mechanical shrub
460 clearance can only be applied if the required equipment can be transported to the
461 encroached areas, but accessibility by road is often limited in mountain areas. Moreover,
462 encroached areas are frequently characterized by a steep terrain, which influences the
463 effectiveness of traditional grazing practices, as livestock tends to concentrate in flat areas
464 and avoids steep slopes (Bailey et al. 1996, Mueggler 1965). Therefore, more specific
465 pastoral practices involving targeted grazing are needed. The strategic placement of mineral
466 mix supplements (MMS) would be one viable management option to be used in rugged
467 shrub-encroached locations (Pittarello et al. 2015). The placement of MMS would lead to
468 increased trampling in the surrounding 100 m of MMS site and therefore would reduce shrub
469 cover (Probo et al. 2013). A further more targeted option is the use of temporary night camp
470 areas (TNCA), where cows are fenced for up to two nights in shrub-encroached areas.
471 Through intense trampling within the fenced area, shrubs get mechanically damaged and
472 subsequently decrease in cover (Tocco et al. 2013; Pittarello et al. 2016, Probo et al. 2016).
473 In the long-term, this pastoral technique has the additional advantage that it increases plant
474 diversity (Pittarello et al. 2016), which in turn might positively influence invertebrate
475 availability (Tocco et al. 2013) for birds. Any such initiatives would have to be managed
476 carefully so as to open-up encroached areas whilst maintaining a reasonable level of shrub
477 cover. Similarly, grazing also has the potential to maintain open areas above the ecotone,
478 which is important for Northern Wheatear and Water Pipit which both are open habitat

479 species at high altitudes. Although, grazing could represent a viable management option in
480 forest-ecotone areas, it is still unknown which potential direct or indirect effects it can have
481 on different bird species groups (e.g. grassland, ecotone, forest) as it is likely that some
482 species might be more affected than others. Moreover, grazing management targeted in the
483 wrong areas, or applied at intensive levels, could also be detrimental to biodiversity.

484 It should be noted that habitat requirements among the most common bird species
485 within the forest-shrub ecotone can differ considerably. Chamberlain et al. (2013) argued
486 that management for the maintenance of high altitude grassland would be preferable to
487 allowing forest expansion due to the high proportion of specialist species and species of
488 conservation concern that could be negatively impacted. However, our data showed that
489 forested areas with high shrub cover had the highest bird diversity. Nevertheless, the
490 ecotone holds important bird species that were not well covered by our methods (von dem
491 Bussche et al. 2008; Braunisch et al. 2016), and also has a high biodiversity of other taxa
492 (Dirnböck et al. 2011). In order to meet a range of species-specific habitat requirements, it
493 might therefore be important to sustain a high level of heterogeneity and to maintain a
494 habitat mosaic within the ecotone (Patthey et al. 2012). Management recommendations
495 need to be adopted for areas differing in altitude, topography, shrub species composition
496 and the degree of shrub encroachment at appropriate scales (Braunisch et al. 2016).
497 Depending on the targeted area, it might therefore be necessary to apply a combination of
498 different management techniques and to adjust the time period of application to promote
499 heterogeneity. There is the possibility of managing for diverse landscapes that can
500 incorporate a range of needs for different habitat types which facilitates species resilience
501 and resistance to environmental change (e.g. Brambilla et al. 2017), but further work is
502 needed on the most appropriate scale of management by which this can be achieved.

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

642 The broadscale category was measured at the whole point count location scale and

643 finescale category was measured at the plot level (n = 11 for each point)

644

Parameter	Category	Description
Canopy	Broadscale	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Shrubs	Broadscale	Percentage cover of shrubs within a radius of 100 m of the point count centre
Trees	Broadscale	Number of mature (greater than c. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Rocks	Broadscale	Percentage cover of rocks within a radius of 100 m of the point count centre
HCOV	Broadscale	Shannon Index of broadscale habitat diversity ($H' = - \sum p_i \ln p_i$, where p_i is the percentage cover of the different habitat types)
Alt	Broadscale	Altitude of the point count location in meters asl. estimated from a GPS
H1	Finescale	Shannon Index of vegetation density diversity at 1 m above the ground
H05	Finescale	Shannon Index of vegetation density diversity at 0,5 m
SDShrub	Finescale	Shrub height heterogeneity measured as the standard deviation of the average shrub height at the point count location
Canfreq	Finescale	Frequency of vegetation sampling points for a point count location where canopy was present
Shrubfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs were present
Rodfreq	Finescale	Proportion of vegetation sampling points for a point count location where Rhododendron was the dominant shrub species
Junfreq	Finescale	Frequency of vegetation sampling points for a point count location where Juniper was the dominant shrub species
Bilfreq	Finescale	Frequency of vegetation sampling points for a point count location where bilberry was the dominant shrub species

645

646 **Table 2** Final significant model-averaged parameters of the model set derived by combining
647 significant model-averaged parameters of broadscale and finescale habitat structure model
648 sets for bird diversity, richness and the commonest species in the study area. The scale (B =
649 broadscale, F= finescale), estimate, standard error (SE), test value (z) and p value are given
650 for each parameter. Full details for all species and parameters are given in Table S4
651

Dependent Variable	Parameter	Scale	Estimate \pm SE	z	p
Lesser Whitethroat	Shrubs	B	2.171 \pm 0.729	2.930	0.003
	Shrubs ²	B	-2.041 \pm 0.823	2.439	0.015
Tree Pipit	Rock	B	-1.416 \pm 0.648	2.151	0.032
	SDshrub	F	1.438 \pm 0.514	2.754	0.006
	Rodfreq	F	-1.120 \pm 0.480	2.296	0.022
Dunnock	Trees	B	-0.939 \pm 0.471	1.963	0.050
	Rodfreq	F	1.601 \pm 0.672	2.351	0.019
	Rodfreq ²	F	-1.363 \pm 0.589	2.286	0.022
Northern Wheatear	Alt	B	2.872 \pm 0.482	5.873	\leq 0.000
	Shrubfreq	F	-2.325 \pm 0.469	4.884	\leq 0.000
	Shrubfreq ²	F	-0.618 \pm 0.031	19.595	\leq 0.000
Wren	Alt	B	-2.435 \pm 0.875	2.747	0.006
	Junfreq ²	F	0.583 \pm 0.291	1.974	0.048
	SDshrub	F	1.096 \pm 0.549	1.969	0.049
Chaffinch	Alt	B	-1.533 \pm 0.409	3.687	\leq 0.000
	Canfreq	F	1.238 \pm 0.404	3.016	0.003
Species richness	Canfreq	F	0.169 \pm 0.059	2.838	0.005
Species diversity	Shrubs	B	0.221 \pm 0.062	3.508	\leq 0.000
	Canfreq	F	0.131 \pm 0.053	2.451	0.014
	Bilfreq	F	-0.171 \pm 0.056	2.990	0.003
	Bilfreq ²	F	-0.063 \pm 0.025	2.491	0.013

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654 **Table 3** Variables with the highest importance (Akaike weight > 0.70) for combined models,
 655 derived from all combinations of models for each dependent variable, grouped according to
 656 whether they were broad- or finescale. Full details are given in ESM Table S5. A dash
 657 indicates Akaike weight < 0.70 for a given scale. Variable codes are given in Table 1 and
 658 Table S1

659

Variable	Broadscale	Finescale
Tree Pipit	Rock, Shrubs ²	SDShrub, Rodfreq
Water Pipit	Alt	Canfreq
Dunnock	Trees	Rodfreq, Rodfreq ²
Northern Wheatear	Alt	Shrubfreq
Lesser Whitethroat	Shrubs, Shrubs ²	-
Wren	Alt, Shrubs	SDShrub, Junfreq ²
Chaffinch	Alt	Canfreq
Species richness	-	Canfreq
Species diversity	Shrubs	-

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661 **Figure legends**

662 **Fig. 1**

663 Relationship between shrub cover (%) and bird species diversity based on the combined
664 model. Black circles represent the H-value in relation to shrub cover for a given point count,
665 where the size of the circle is proportional to the number of points for a given H-value at a
666 particular level of shrub cover

667 **Fig. 2**

668 Relationship between shrub species frequency (Rhododendron, Juniper, bilberry) and the
669 probability of occurrence for individual bird species (Dunnock, Tree Pipit, Wren) and bird
670 species diversity based on combined models. Black circles represent the point counts where
671 a species was present/absent in relation to shrub species frequency, and the size of the
672 circle is proportional to the number of points for a given category of presence/absence at a
673 particular level of shrub frequency. For bird species diversity, black circles represent the H-
674 value in relation to bilberry frequency, where the size of the circle is again proportional to the
675 number of points for a given H-value at a particular level of bilberry frequency.

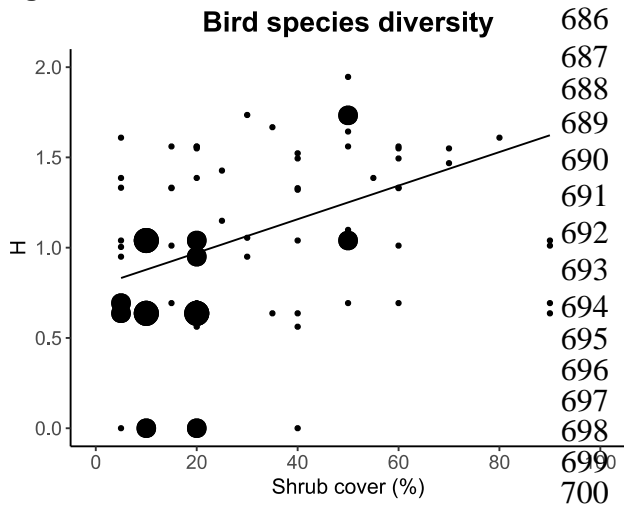
676 **Fig. 3** The ten best ranked models according to AICc (where smaller AICc values indicate
677 better performing models) for individual species, and for species richness and diversity.
678 Each model is classified according to whether variables were finescale (white bars),
679 broadscale (black bars) or a combination of the two (grey bars) in each model. The dashed
680 horizontal line indicates $\Delta AICc = 2$ (i.e. models below the line are considered to be in the
681 best model set)

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685 **Fig. 1**



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Fig. 2

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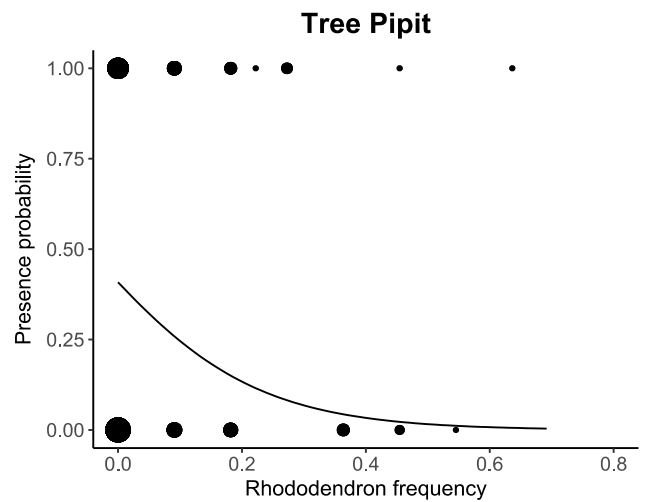
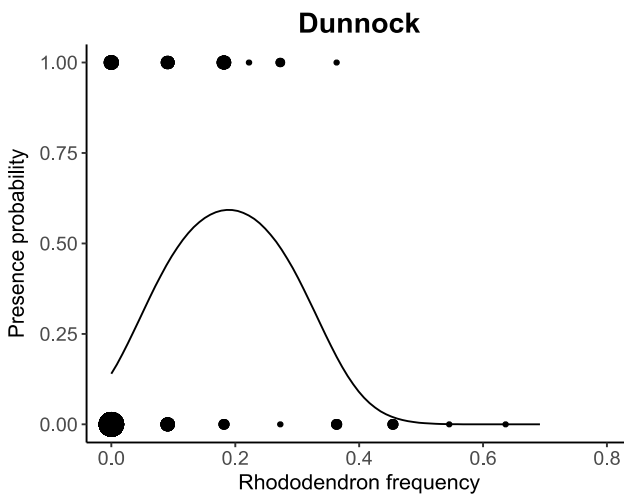
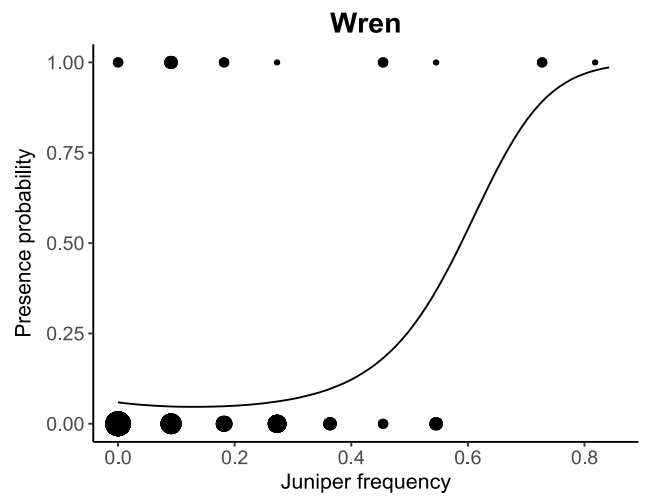
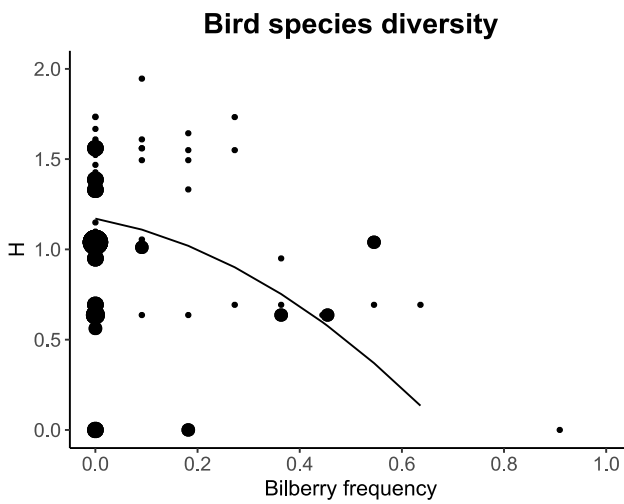
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727 **Electronic Supplementary Material – Journal of Ornithology**

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729 **The contribution of broadscale and finescale habitat structure to the distribution and**
730 **diversity of birds in an Alpine forest-shrub ecotone**

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755 **Table S1** Variables which were removed after VIF and correlation coefficient calculations, or
 756 during the model reduction process. The broadscale category was measured at the whole
 757 point count location scale and finescale category was measured at the plot level (n = 11 for
 758 each point)

Parameter	Category	Description
Grass	Broadscale	Percentage cover of grass within a radius of 100 m of the point count centre
H0	Finescale	Shannon-Index of vegetation density diversity at ground level
Altgrs	Finescale	Average grass height across the plots at each point count location
Altshrub	Finescale	Average shrub height across the plots at each point count location
SDgrs	Finescale	Standard deviation of the average grass height at the point count location
Othfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs different from Juniper, Rhododendron and bilberry were the dominant shrub species

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761 **Table S2** Model-averaged estimates of the model set for broadscale habitat structure
 762 presented for bird diversity, richness and the commonest species in the study area. The
 763 estimate, standard error (SE), test value (z) and p value are given for each parameter
 764

Dependent Variable	Parameter	Estimate \pm SE	z	p
Tree Pipit	Alt	-0.559 \pm 0.355	1.552	0.121
	Trees	0.247 \pm 0.308	0.790	0.429
	Shrubs	0.292 \pm 0.497	0.583	0.560
	Shrubs ²	0.905 \pm 0.480	1.857	0.063
	Rock	-1.403 \pm 0.616	2.243	0.025
	HCOV	0.445 \pm 0.420	1.047	0.295
Water Pipit	Alt	2.095 \pm 1.014	2.036	0.042
	Trees	-18.384 \pm 16.692	1.085	0.278
	Shrubs	-0.851 \pm 0.777	1.081	0.280
	Shrubs ²	-0.418 \pm 0.849	0.485	0.627
	Rock	0.185 \pm 0.769	0.238	0.812
	HCOV	-0.714 \pm 0.661	1.065	0.287
Dunnock	Alt	0.547 \pm 0.468	1.154	0.249
	Trees	-1.136 \pm 0.511	2.191	0.028
	Shrubs	1.029 \pm 0.466	2.183	0.029
	Shrubs ²	-0.335 \pm 0.387	0.857	0.391
	Rock	-0.693 \pm 0.527	1.298	0.194
	HCOV	0.585 \pm 0.423	1.365	0.172
Northern Wheatear	Alt	1.907 \pm 0.789	2.384	0.017
	Trees	-2.382 \pm 1.658	1.418	0.156
	Shrubs	-1.661 \pm 1.020	1.613	0.107
	Shrubs ²	-0.453 \pm 0.988	0.452	0.651
	Rock	-0.774 \pm 0.768	0.997	0.319
	HCOV	1.071 \pm 0.908	1.168	0.243
Lesser Whitethroat	Alt	0.331 \pm 0.496	0.658	0.511
	Trees	-0.257 \pm 0.397	0.639	0.523
	Shrubs	1.914 \pm 0.757	2.492	0.013
	Shrubs ²	-1.758 \pm 0.834	2.075	0.038
	Rock	0.048 \pm 0.480	0.098	0.922
	HCOV	0.731 \pm 0.550	1.313	0.189
Wren	Alt	-2.263 \pm 0.663	3.358	0.001
	Trees	0.015 \pm 0.385	0.039	0.969
	Shrubs	2.204 \pm 0.897	2.421	0.015
	Shrubs ²	-1.351 \pm 0.630	2.109	0.035

	Rock	-0.080 ± 0.784	0.100	0.920
	HCOV	0.208 ± 0.649	0.317	0.751
Chaffinch	Alt	-1.638 ± 0.509	3.177	0.001
	Trees	1.141 ± 0.497	2.261	0.024
	Shrubs	0.458 ± 0.399	1.129	0.259
	Shrubs ²	0.181 ± 0.338	0.530	0.596
	Rock	-0.234 ± 0.474	0.486	0.627
	HCOV	0.561 ± 0.467	1.185	0.236
Rock Bunting	Alt	-0.388 ± 0.419	0.912	0.362
	Trees	0.380 ± 0.353	1.062	0.288
	Shrubs	0.672 ± 0.492	1.348	0.178
	Shrubs ²	-0.152 ± 0.378	0.398	0.690
	Rock	0.746 ± 0.376	1.955	0.051
	HCOV	0.376 ± 0.376	0.987	0.324
Species diversity	Alt	-0.125 ± 0.053	2.320	0.020
	Trees	0.139 ± 0.054	2.524	0.012
	Shrubs	0.221 ± 0.081	2.706	0.007
	Shrubs ²	-0.116 ± 0.049	2.317	0.021
	Rock	-0.044 ± 0.060	0.721	0.471
	HCOV	0.084 ± 0.063	1.319	0.187
Species richness	Alt	-0.097 ± 0.082	1.170	0.242
	Trees	0.134 ± 0.064	2.066	0.039
	Shrubs	0.180 ± 0.095	1.876	0.061
	Shrubs ²	-0.103 ± 0.075	1.359	0.174
	Rock	-0.023 ± 0.079	0.282	0.778
	HCOV	0.057 ± 0.090	0.621	0.535

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767 **Table S3** Model-averaged parameters of the model set for finescale habitat structure
768 presented for bird diversity, richness and the commonest species in the study area. The
769 estimate, standard error (SE), test value (z/t) and p value are given for each parameter
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Dependent Variable	Parameter	Estimate \pm SE	z / t	p
Lesser Whitethroat	SDshrub	0.144 \pm 0.296	0.477	0.633
	Bilfreq	-0.375 \pm 0.681	0.543	0.587
	Bilfreq ²	-1.364 \pm 1.199	1.119	0.263
	H05	0.251 \pm 0.256	0.966	0.334
	H1	0.290 \pm 0.272	1.047	0.295
	Canfreq	0.069 \pm 0.318	0.214	0.831
Tree Pipit	SDshrub	1.564 \pm 0.534	2.889	0.004
	Rodfreq	-1.007 \pm 0.544	1.827	0.068
	Rodfreq ²	0.167 \pm 0.278	0.593	0.553
	H05	0.481 \pm 0.387	1.223	0.221
	H1	0.415 \pm 0.344	1.187	0.235
	Canfreq	0.090 \pm 0.315	0.280	0.779
Dunnock	SDshrub	-0.614 \pm 0.497	1.215	0.224
	Rodfreq	2.036 \pm 0.670	2.995	0.003
	Rodfreq ²	-1.665 \pm 0.551	2.974	0.003
	H05	0.086 \pm 0.309	0.275	0.783
	H1	0.002 \pm 0.377	0.006	0.995
	Canfreq	-0.181 \pm 0.356	0.501	0.617
Rock Bunting	SDshrub	-0.220 \pm 0.447	0.486	0.627
	Shrubfreq	-0.270 \pm 0.357	0.746	0.456
	Shrubfreq ²	-0.300 \pm 0.357	0.827	0.408
	H05	-0.063 \pm 0.335	0.184	0.854
	H1	-0.168 \pm 0.364	0.453	0.650
	Canfreq	0.442 \pm 0.328	1.328	0.184
Northern Wheatear	SDshrub	-0.925 \pm 0.727	1.253	0.210
	Shrubfreq	-0.646 \pm 0.570	1.115	0.265
	Shrubfreq ²	-1.077 \pm 0.491	2.157	0.031
	H05	0.254 \pm 0.403	0.620	0.535
	H1	0.075 \pm 0.669	0.110	0.912
	Canfreq	-2.454 \pm 0.932	2.592	0.010
Wren	SDshrub	0.970 \pm 0.416	2.329	0.020
	Junfreq	0.113 \pm 0.565	0.198	0.843
	Junfreq ²	0.502 \pm 0.236	2.128	0.033
	H05	-0.012 \pm 0.351	0.032	0.974

	H1	0.252 ± 0.312	0.795	0.427
	Canfreq	0.205 ± 0.401	0.505	0.614
Chaffinch	SDshrub	-0.027 ± 0.389	0.070	0.945
	Shrubfreq	-0.462 ± 0.328	1.389	0.165
	Shrubfreq ²	0.328 ± 0.313	1.031	0.303
	H05	-0.337 ± 0.313	1.061	0.289
	H1	-0.279 ± 0.384	0.716	0.474
	Canfreq	1.738 ± 0.444	3.855	≤ 0.000
Water Pipit	SDshrub	0.340 ± 0.676	0.582	0.561
	Bilfreq	0.600 ± 0.466	1.270	0.204
	Bilfreq ²	0.020 ± 0.250	0.079	0.937
	H05	1.105 ± 3288.174	0.000	1.000
	H1	11.995 ± 2901.247	0.004	0.997
	Canfreq	-51.512 ± 8599.602	0.006	0.995
Species diversity	SDshrub	0.110 ± 0.064	1.699	0.089
	Bilfreq	-0.100 ± 0.065	1.526	0.127
	Bilfreq ²	-0.054 ± 0.023	2.350	0.019
	H05	-0.094 ± 0.052	1.769	0.078
	H1	0.040 ± 0.062	0.642	0.521
	Canfreq	0.178 ± 0.053	3.293	0.001
Species richness	SDshrub	0.068 ± 0.071	0.945	0.345
	Bilfreq	-0.057 ± 0.116	0.483	0.629
	Bilfreq ²	-0.073 ± 0.050	1.444	0.149
	H05	-0.065 ± 0.069	0.936	0.349
	H1	0.024 ± 0.068	0.358	0.721
	Canfreq	0.153 ± 0.064	2.349	0.019

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773 **Table S4** Final model-averaged parameters of the model set derived by combining
774 significant model-averaged parameters of broadscale and finescale habitat structure, and
775 top model sets for bird diversity, richness and the commonest species in the study area. The
776 scale (B = broadscale, F= finescale), estimate, standard error (SE), test value (z) and p
777 value are given for each parameter
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Dependent Variable	Parameter	Scale	Estimate ± SE	z	p
Lesser Whitethroat	Shrubs	B	2.171 ± 0.729	2.930	0.003
	Shrubs ²	B	-2.041 ± 0.823	2.439	0.015
	Bilfreq	F	-0.893 ± 0.685	1.284	0.199
	Bilfreq ²	F	-0.926 ± 0.960	0.949	0.343
Tree Pipit	Rock	B	-1.416 ± 0.648	2.151	0.032
	SDshrub	F	1.438 ± 0.514	2.754	0.006
	Shrubs	B	0.222 ± 0.457	0.478	0.632
	Shrubs ²	B	0.748 ± 0.427	1.721	0.085
Dunnock	Rodfreq	F	-1.120 ± 0.480	2.296	0.022
	Trees	B	-0.939 ± 0.471	1.963	0.050
	Shrubs	B	0.808 ± 0.485	1.646	0.010
	Rodfreq	F	1.601 ± 0.672	2.351	0.019
Northern Wheatear	Rodfreq ²	F	-1.363 ± 0.589	2.286	0.022
	Alt	B	2.872 ± 0.482	5.873	≤ 0.000
	Shrubfreq	F	-2.325 ± 0.469	4.884	≤ 0.000
	Shrubfreq ²	F	-0.618 ± 0.031	19.595	≤ 0.000
Wren	Canfreq	F	-1.239 ± 0.700	1.742	0.082
	Alt	B	-2.435 ± 0.875	2.747	0.006
	SDshrub	F	1.096 ± 0.549	1.969	0.049
	Shrubs	B	1.649 ± 0.923	1.765	0.078
	Shrubs ²	B	-1.095 ± 0.712	1.516	0.129
	Junfreq	F	0.306 ± 0.761	0.399	0.690
Chaffinch	Junfreq ²	F	0.583 ± 0.291	1.974	0.048
	Alt	B	-1.533 ± 0.409	3.687	≤ 0.000
	Canfreq	F	1.238 ± 0.404	3.016	0.003
Water Pipit	Alt	B	1.926 ± 0.985	1.925	0.054
	Canfreq	F	-48.267 ± 14751.960	0.003	0.997
Species richness	Shrubs	B	0.095 ± 0.063	1.481	0.139
	Canfreq	F	0.169 ± 0.059	2.838	0.005
Species diversity	Alt	B	-0.065 ± 0.062	1.039	0.299

SDshrub	F	0.066 ± 0.060	1.090	0.276
H05	F	-0.081 ± 0.048	1.657	0.097
Shrubs	B	0.221 ± 0.062	3.508	≤ 0.000
Shrubs ²	B	-0.083 ± 0.047	1.739	0.082
Canfreq	F	0.131 ± 0.053	2.451	0.014
Bilfreq	F	-0.171 ± 0.056	2.990	0.003
Bilfreq ²	F	-0.063 ± 0.025	2.491	0.013

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796 **Table S5** Variables weights across all combinations of models, considering either
 797 broadscale, finescale or combined models. Weights were calculated based on Akaike
 798 weights for each model, which is expressed as the likelihood contribution of each model as a
 799 proportion of the summed likelihood contributions of all models. The weight for each variable
 800 is the sum of model weights for all models in which a given variable was present (Burnham &
 801 Anderson 2002). Output is shown only if a given model type was amongst the top model set
 802 (i.e. $\Delta AICc < 2$). For example, no broadscale or finescale models were in the best model set
 803 for Dunnock (see Fig. 3), hence variable weights are presented only for combined models. A
 804 missing value indicates that a variable was not included in the model averaging procedure
 805 for that particular species/scale. Variables are defined in Table 1 and Table S3

806 (a) Broadscale

Variable	Alt	HCOV	Rock	Shrubs	Shrubs ²	Trees
Water Pipit	0.92	0.40	0.28	0.45	0.29	0.90
Species richness	0.42	0.33	0.26	0.78	0.52	0.71

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808 (b) Finescale

Variable	Canfreq	H05	H1	Bilfreq	Bilfreq ²	SDshrub
Species richness	0.82	0.34	0.26	0.35	0.57	0.35

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811 (c) Combined

Variable	Broadscale					Finescale										
	Alt	Rock	Shrubs	Shrubs ²	Trees	Shrubfreq	Shrubfreq ²	H05	Canfreq	Junfreq	Junfreq ²	Rodfreq	Rodfreq ²	SDshrub	Bilfreq	Bilfreq ²
Tree Pipit	-	0.97	0.26	0.84	-	-	-	-	-	-	-	0.94	-	0.99	-	-
Lesser Whitethroat	-	-	1.00	1.00	-	-	-	-	-	-	-	-	-	-	0.51	0.52
Dunnock	-	-	0.60	-	0.80	-	-	-	-	-	-	0.86	0.97	-	-	-
Northern Wheatear	1.00	-	-	-	-	1.0	0.39	-	0.50	-	-	-	-	-	-	-
Wren	1.00	-	0.74	0.63	-	-	-	-	-	0.34	0.82	-	-	0.88	-	-
Water Pipit	0.98	-	-	-	-	-	-	-	0.97	-	-	-	-	-	-	-
Chaffinch	1.00	-	-	-	-	-	-	-	0.99	-	-	-	-	-	-	-
Species diversity	0.07	-	0.95	0.13	-	-	-	0.13	0.48	-	-	-	-	0.08	0.67	0.25
Species richness	-	-	0.51	-	-	-	-	-	0.95	-	-	-	-	-	-	-

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819 **Table S6** Observed and expected values of Moran's I and associated P-values to test for
 820 spatial autocorrelation. Tests were based on residuals from the full model for each scale and
 821 each species

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Species	Broadscale			Finescale			Combined		
	obs	exp	p	obs	exp	p	obs	exp	p
Lesser Whitethroat	0.014	-0.013	0.073	0.028	-0.013	0.007	0.022	-0.013	0.022
Tree Pipit	0.012	-0.013	0.954	-0.019	-0.013	0.707	-0.015	-0.013	0.886
Dunnock	0.002	-0.013	0.345	0.001	-0.013	0.356	0.004	-0.013	0.272
Chaffinch	0.003	-0.013	0.529	0.008	-0.013	0.166	0.014	-0.013	0.076
Wren	0.003	-0.013	0.518	-0.019	-0.013	0.680	-0.013	-0.013	0.988
Northern Wheatear	0.002	-0.013	0.455	-0.021	-0.013	0.578	-0.020	-0.013	0.619
Water Pipit	0.008	-0.013	0.721	-0.017	-0.013	0.802	0.006	-0.013	0.210
Species diversity	0.020	-0.013	0.646	-0.022	-0.013	0.542	-0.027	-0.013	0.347
Species richness	0.023	-0.013	0.503	-0.016	-0.013	0.849	-0.020	-0.013	0.628

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827 There was only a single significant result, for the finescale model for Lesser Whitethroat. In
 828 this case, models were re-run accounting for spatial effects by adding a smoothed interactive
 829 effect of latitude and longitude in a Generalized Additive Mixed Model using the gamm
 830 command in the package gamm4 (Wood & Scheipl 2017). This made no difference to the
 831 model outcome in terms of significance levels (Table S6), and parameter estimates were
 832 similar. We therefore conclude that for this species, the significant spatial autocorrelation
 833 detected did not have an effect on model outcomes.

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838 **Table S7** A comparison of models predicting Lesser Whitethroat occurrence in relation to
 839 finescale habitat variables without (standard model) and with (spatial model) accounting for
 840 spatial effects. For variable definitions, see Table 1
 841

Variable	Standard model				Spatial model			
	Parameter	SE	z	P	Parameter	SE	z	P
Intercept	-0.711	0.601	-1.183	0.237	-0.887	0.678	-1.130	0.195
H05	0.205	0.274	0.749	0.454	0.058	0.305	0.191	0.849
H1	0.273	0.316	0.874	0.382	0.516	0.368	1.399	0.166
Bilfreq	0.143	0.757	0.189	0.850	0.184	0.827	0.222	0.825
Bilfreq ²	-1.547	1.290	-1.119	0.230	-1.639	1.349	-1.215	0.229
SDshrub	0.025	0.334	0.074	0.941	0.093	0.358	0.259	0.797
Canfreq	-0.059	0.353	-0.168	0.867	-0.158	0.390	-0.450	0.687

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845 **Reference**

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847 Wood S, Scheipl F (2017) Generalized Additive Mixed Models using 'mgcv' and 'lme4'. R
 848 package version 0.2-2, URL <http://CRAN.R-project.org/package=gamm4>

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853 **Electronic Supplementary Material – Journal of Ornithology**

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855 **The contribution of broadscale and finescale habitat structure to the**
856 **distribution and diversity of birds in an Alpine forest-shrub ecotone**

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871 **ESM Fig. S1**

872 Relationship between significant model-averaged parameters of the combined model
873 set for bird species richness, diversity and individual bird species. For individual bird
874 species, black circles represent the point counts where a species was present/absent
875 in relation to the relevant variable. The size of the circle is proportional to the number
876 of points for a given category of presence/absence at a particular level of the
877 respective variable. For bird species richness and diversity, black circles represent
878 the H-value (diversity) or the number of bird species (richness) in relation to canopy
879 frequency for a given point count, where the size of the circle is proportional to the
880 number of points for a given H-value (diversity) or species number (richness) at a
881 particular level of canopy frequency.

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