Variations in Niche Breadth and Position of Alpine Birds along Elevation Gradients in the European Alps

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14 **Variations in niche breadth and niche position of alpine birds along elevation gradients in the**

15 **European Alps**

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ABSTRACT

Mountains support high levels of biodiversity, but they are also particularly vulnerable to climate change. Whilst studies on mountain biodiversity at the species level are common, studies that consider whole assemblages are scarce. We assessed how an alpine bird assemblage varied in terms of ecological habitat niche by surveying bird communities and habitat at point counts placed along elevation gradients in the Western Italian Alps. Niche breadth as measured by habitat use increased along the gradient, suggesting that being more generalist is an advantage in terms of survival at higher elevation. Niche position also increased with elevation, which means that species occurring at higher elevations use habitats that are atypical with respect to the average species in the community. Both niche breadth and position were negatively associated with habitat diversity, but these relationships were mainly driven by the species occurring at the very highest elevations (>2500 m), suggesting that true alpine specialist show a different pattern from the other species of the assemblage. Our results therefore generally supported the idea that having a wider niche breadth is useful in harsh environments, such as mountains, enabling the exploitation of a wider range of resources. The broader niche of many high elevation species may therefore indicate some degree of resilience to environmental change, as long as key habitat types are maintained.

INTRODUCTION

Climate change and land use changes are regarded as the major threats to biodiversity in the world (Travis, 2003; Stephens et al., 2016). The interaction between these two threats can intensify the impacts on biodiversity. Species are thus constrained to adjust their spatial distribution according to their ecological niches in order to have the resources they need to survive (Bani et al., 2019). It therefore follows that species with a broader niche ('generalists') will be better placed to adapt to

62   environmental changes (McKinney & Lockwood, 1999). Indeed, there are many examples of generalists

63   increasing their range in response to environmental changes, often accompanied by decreases in

64   narrow-niche specialists (e.g. Warren et al., 2001; Clavel et al., 2011). Studying niche breadth and niche

65   position is thus likely to give an insight into those species that may be more vulnerable to

66   environmental change in the future.

67   Birds are definitely a well-studied group regarding the impacts of environmental changes.

68   Nevertheless, compared to other habitats, bird distribution and population dynamics are less well

69   known in mountains (Chamberlain et al., 2012), mainly because of logistical constraints of working in

70   this type of environment (Chamberlain et al., 2012). Mountains are subject to several pressures such

71   as climate change (Gobiet et al., 2014), land-use change (Laiolo et al., 2004) and human disturbance

72   (Caprio et al., 2011; Brambilla et al., 2016). Mountain species are considered particularly vulnerable to

73   climate change, since opportunities to shift their distributions towards the mountain tops in response

74   to environmental changes are constrained by mountain orography (i.e. they effectively run out of

75   space on the 'escalator to extinction'; (Freeman et al., 2018), and dispersal to alternative suitable sites

76   may be limited by low connectivity with other mountain ranges (Lehikoinen et al., 2018).

77   Many species have already shown shifts in their distributions in response to environmental

78   changes, notably towards high latitudes and elevations (Maggini et al., 2011; Reif & Flousek, 2012; Bani

79   et al., 2019). These effects could have considerable consequences for mountain biodiversity

80   (Chamberlain et al., 2013, 2016), and it has been shown that birds of high elevation are already

81   declining in Europe (Lehikoinen et al., 2018). Given that habitat preference is one of the key ecological

82   traits of any bird species (Reif et al., 2010), analysing how niche breadth and niche position can affect

83   the distribution of species along environmental gradients is useful to understand and predict their

84   future responses to environmental change. It may help to identify which species (i.e. with narrower

85   niches, or that use less typical resources) may be negatively impacted by, and which species will be

86   resilient to, future environmental change, if our environmental gradient is considered as a space-for

87   time substitution (Hodkinson, 2005; Blois et al., 2013). In the absence of long-term monitoring data,

88   this approach can be useful to understand changes in the community.

89   Niche breadth and niche position are two complementary measures of specialisation. Niche

90   position assesses how typical the resource use of a particular species is relative to all other species and

91   the resources available. Thus, species with a high niche position use less typical resources, i.e. these

92   species are specialised compared to the community studied (Mac Nally, 1989). Niche breadth

93   measures the range of environmental conditions or habitat used by a species (Shugart & Patten, 1972).

94   As species that have a wide niche breadth show more tolerance to environmental conditions (Evans et

95   al., 2011), they should be better adapted to higher elevations than species with a narrow niche breadth

96   as conditions become harsher and less predictable (Körner, 2003). Furthermore, if species of high

97   elevation are considered more generalist because of the environmental conditions, they should have

98   a low niche position compared to other species. Furthermore, if niche trends only reflect habitat along

99   the elevation gradient (i.e. habitat availability corresponds to habitat use), we also expect some

100   relationship between habitat diversity and niche breadth.

101   Traditionally, the monitoring of biodiversity, including birds, has focused on the distribution or

102   the abundance of single species. However, studying a whole community through assemblages such as

103   habitat selection can be useful to assess ecosystem health (Siriwardena et al., 2019). We are unaware

104   of any studies that have considered potential drivers of bird species distributions (including habitat

105   and climate) along elevation gradients from a community perspective in the Alps. Here, we take an

106   assemblage approach to consider how habitat niche varies along elevation gradients in the Western

107   European Alps at relatively high elevation (1700-3100 m) using multi-species and multi-variate

108   analyses. We define habitat niche (henceforth 'niche') as the environmental conditions present within

109   a 100m radius (i.e. the point count area) in which a given species was detected, which include measures

110   of habitat, topography and climate. We assume therefore that a given species is using the habitat

111   resources as expressed by our niche measures at any point where it was recorded. This study focuses

112 on assessing the relationship (1) between niche (position and breadth) and elevation; (2) between

113 niche (position and breadth) and habitat diversity.

114

115 **METHODS**

116 *Study sites*

117 A database of the presence of bird species from several sites in the Western Alps was compiled from

118 two different bird surveys, carried out between 2010 and 2012 for the first, and in 2017 for the second.

119 In the majority of cases, points were only surveyed in a single year (92%). Sites were located in the far

120 north of Italy close to the French border (Appendix 1, Fig. S1). At a lower elevation, the European larch

121 *Larix decidua* is the dominant species in the study area. The natural treeline is around 2200-2300 m,

122 although in many areas, this limit is lower owing to pastoral activities. Juniper *Juniperus communis* and

123 rhododendron *Rhododendron ferrugineum* are the main shrub species in the area. Above the treeline,

124 alpine meadows and grasslands are found. Higher in elevation (>2700 m), rocks and scree are dominant

125 (Chamberlain et al., 2016; Jähnig et al., 2018).

126

127 *Point counts*

128 Full methods are given in Chamberlain et al. (2013), so only a summary is provided here. Point counts

129 were carried out from mid-May to mid-July along elevation gradients on transects that were a

130 minimum distance of 300 m apart. On a single transect, each point was separated from another by at

131 least 200 m to make sure two successive points did not overlap. All the points were above 1700 m

132 (minimum = 1717 m) and reached a maximum of 3056 m. The mean range in elevation for each

133 transect was 601 m $\pm$ 339 m (mean ± SD; n=39). At each point, for 10 minutes, all birds heard or seen

134 were recorded by the observer within a 100 m radius (estimated with the aid of a laser range finder),

135 and signs of potential breeding (e.g. singing, carrying nesting material or food for young, territorial

136 disputes) were noted. Transects were visited one to three times. The maximum count over all visits

137   was used in the analyses for each species for the relatively small proportion of points that had more

138   than one visit.

139   Both studies (i.e. from 2010-2012 and 2017) adopted the same point count method, except that

140   the early survey included a 5-minute settling period before the point count period started, which was

141   absent in the later surveys. However, previous work (Chamberlain & Rolando 2014) and additional

142   analyses (Appendix 2) has demonstrated that inclusion of the settling period makes very little

143   difference to estimations of species occurrence. Observer effects were minimised since all observers

144   were experienced in identifying Alpine birds by sight and song, and the two surveys (i.e. from 2010-

145   2012 and 2017) were not independent and done in a consistent manner (one observer took part in

146   both and led training days for all observers to standardize the recording methods).

147   Two data sets were created, one with all the species observed and another one with only the

148   species showing evidence of potential breeding. In total, 39 transects were studied for 309 point

149   counts. During the first bird survey (2010-2012), 271 points were carried out in 34 transects. In 2017,

150   a total of 194 points were carried out on 35 transects in a restricted area (Natural Park of Val Troncea).

151   In order to avoid hyper-sampling from a single geographical location, only five transects comprising 38

152   points were selected, at random, from this latter data set. On average, there were 8 ± 4 (mean ± SD)

153   points per transect over the whole sample.

154   In order to carry out the multivariate analyses (CCA), points where no species were observed

155   (n=17 and n=35 respectively for complete and breeding data) and where habitat descriptions were

156   missing (n=15) were removed from both datasets, since this type of analysis cannot include zeros or

157   missing values. For the breeding data, 38 transects and 259 points were used, while for the complete

158   data, 38 transects and 277 points were used.

159

160   *Environmental data*

161   At each point count location, habitat was described within a 100 m radius (all variables are summarised

162   in Appendix 1). The percentage cover of each type of habitat was estimated by eye, including canopy

163   (vegetation above head height), shrubs (ligneous vegetation under head height), grassland (without

164   canopy), rock (unvegetated areas and screes), and snow (surface that was still covered by snow during

165   the survey). Such estimates have proven to match closely with those from remote-sensed land cover

166   datasets (Chamberlain et al., 2013). The presence or absence of water, footpaths and dung was

167   recorded. The number of mature trees (approximately greater than 20 cm in diameter at breast height)

168   was recorded within a 50-m radius (in forested areas, it was not possible to count trees at a greater

169   distance). The elevation of each point (in meters) was recorded with a GPS in the field. Topographic

170   data (slope and aspect) were extracted from a Digital Terrain Model of Northern Italy. Slope was

171   measured in degrees. Both northing and easting were considered and were expressed as an index

172   equal to $-\cos(x)$ where x is the aspect (north or east) in radians. A value of 1 indicates facing directly

173   south (or east) and a value of -1 indicates facing directly north (or west).

174   Climate data were obtained from Chelsa (Climatologies at High resolution for the Earth's Land

175   Surface Areas) Climate (Karger et al., 2017). Data comprised monthly precipitation and temperature

176   climatology for the period 1979-2013 and had a resolution of 30 arc sec. The mean monthly

177   precipitation for the breeding season (May-July) was used. For temperatures, three variables were

178   extracted: the minimum, maximum and mean monthly temperature for the breeding season.

179

180   *Data analysis*

181   All analyses were carried out in R 4.0.0 (R Core Team 2020). Preliminary analyses showed that including

182   rare species (that occurred in less than 1% of the points) often resulted in convergence problems,

183   hence these species were removed from the dataset in subsequent analyses (n=9 for complete data,

184   n=5 for breeding data).

185   Following Reif et al. (2010) and Evans et al. (2011), habitat niche position and niche breadth were

186   calculated using Canonical Correspondence Analysis (CCA) with environmental data (habitat and

187   climate). CCA was performed using the *cca* command in the *vegan* package (Oksanen et al., 2013). CCA

188   is a weighted ordination method, thus rare species have a low weight and do not have a great influence

189   in the rotation ordination. Elevation was not included as we were interested in explaining which

190   environmental variables were the key drivers of assemblage change that may explain elevational

191   trends. Using both habitat and climate variables to define the habitat niche of each species was

192   justified by the fact that usually, models combining habitat and climate performed best to study

193   species distribution along elevational gradients (Acharya et al., 2011; Chamberlain et al., 2016). The

194   CCA allowed the niche breadth and the niche position of each species along the first four axes of the

195   CCA (those explaining the largest proportion of variability in bird community structure) to be defined.

196   Niche position was considered as "the distance of the centroid of a species from that of the whole

197   assemblage (=mean of the coordinates of the species' centroids)". Niche breadth was calculated as the

198   standard deviation of each species' distribution of tolerance across each axis identified by the CCA,

199   providing estimates of niche breadth. The root mean-squared standard deviations across the first four

200   axes provided an overall estimate of niche breadth. To reduce the skew in their distribution and hence

201   approximate normal distributions, niche position and niche breadth were log-transformed prior to

202   analyses.

203   Habitat diversity was estimated at each point count with the percentage cover of each type of

204   habitat, calculating the Shannon diversity index with the function *diversity* from the *vegan* package.

205   Habitat diversity was estimated in elevation bands of 100 m (e.g. 1800-1899m) by calculating the mean

206   Shannon index of all point counts located in each band.

207   Niche breadth and habitat niche position were modelled separately in relation to elevation,

208   considering both linear and quadratic effects. The niche breadth and position of each species

209   (extracted from the CCA – see above) were related to the median elevation (centred and scaled) across

210   all points at which each species was recorded. In the same way, the relationship between niche

211   breadth of each species and the standard deviation of elevation (centred and scaled) was analysed in

212   order to see if species with a greater elevational range also have a wider niche breadth. Then, niche

213   breadth and niche position were analysed in relation to habitat diversity along the elevation gradient.

214   In order to account for the non-independence of species due to a shared ancestry, we used a

215 Phylogenetic Generalised Least Squared (PGLS) approach for the analysis of niche breath and niche

216 position. Closely related species are expected to have more similar traits because of their shared

217 evolutionary history, and hence to produce more similar residuals from least squares regression. PGLS

218 provides estimates of this covariance and includes it in a statistical model (Symonds & Blomberg,

219 2014). The PGLS approach was carried out in R using the *caper* package (Orme, 2018) and the

220 phylogeny of Jetz et al. (2012).

221   Outliers were defined visually with a qq-plot (Mundry, 2014) and if outliers were detected, models

222 were run again without these points. Both linear and quadratic models were fitted, and their

223 performance was assessed using Akaike's Information Criterion (AIC). The model with the lowest AIC

224 was presented in the Results, unless the difference in AIC (ΔAIC) was less than 2, in which case they

225 were considered as equivalent (Burnham & Anderson, 2010).

226

227 **RESULTS**

228 In total, 47 species were recorded, but only 34 of them showed signs of breeding (Table 1). There were

229 38 species recorded on at least 1% of the points (i.e. at least 3 records), of which 29 species showed

230 evidence of potential breeding. Models were run for both datasets (complete and breeding records),

231 but since the results were similar, only results for the complete dataset are presented here (see

232 Appendix 3 for the main results with the breeding dataset).

233

234 *Species-habitat associations*

235 The first four axes of the CCA accounted for 76.5% of the variation in the data and represented the

236 following gradients: (1) an elevation gradient from closed habitats (forest and shrubland) with light

237 precipitation and relatively warm temperatures to open habitats (grasslands and rocks) with low

238 temperatures and heavy precipitation (explaining 44.9% of the variation in the data); (2) from grassy

239 and south exposed slope to rocky areas (14,9%); (3) from shrubby habitats to all other habitats (10,7%);

240 (4) from steep slopes with heavy precipitation to less steep areas with dung proving the presence of

241 cattle (6.1%; see Appendix 4 for figures and Appendix 5 for the habitat scores on each axis).

242

243 *Niche position and niche breadth along the elevation gradient*

244 Niche position varied non-linearly with elevation (Fig. 1A; Appendix 6, Table S5), while niche breadth

245 showed no association with elevation. However, after removal of one detected outlier (Snowfinch

246 *Montifringilla nivalis*), there was a positive association between niche breadth and elevation (Fig. 1B;

247 Table S5). Niche breadth was positively associated with the standard deviation of elevation in both

248 linear and quadratic models (Fig. 2A) which performed equally (ΔAICc<2; Table S5). Although

249 Snowfinch was again identified as an influential outlier in the linear regression, its removal did not

250 affect the outcome of the model (Table S5). Niche position varied non-linearly with the standard

251 deviation of elevation (Fig. 2B, Table S5).

252

253 *Habitat niche position and niche breadth along the habitat diversity gradient*

254 Habitat niche position was negatively and linearly related to habitat diversity as measured by the

255 Shannon index (Table S5). However, this relationship seemed to be mainly driven by three species

256 (Alpine Accentor *Prunella collaris*, Snowfinch and Alpine Chough *Pyrrhocorax graculus*; Appendix 7, Fig.

257 S3A). When these species were removed, habitat niche position was still negatively linked with habitat

258 diversity, but the relationship was less strong (Table S5). Habitat niche breadth did not show any

259 association with habitat diversity. However, an outlier was detected (Snowfinch), and removing this

260 species resulted in a negative relationship between niche breadth and habitat diversity (Table S5). As

261 previously, this trend was driven by few species (Alpine Accentor and Alpine Chough; Fig. S3B). When

262 they were removed, there was no longer an evidence of a relationship between niche breadth and

263 habitat diversity.

264

265 **DISCUSSION**

266 *Habitat niche position and niche breadth along the elevation gradient*

267 Habitat niche position increased with increasing elevation, suggesting that species occurring at higher

268 elevations are associated with atypical habitats compared to the rest of the community, characterised

269 by high precipitation, low temperatures, rock and grass. This result represents the turnover of species

270 along the elevation gradient from forest species such as Chaffinch *Fringilla coelebs* and Tree Pipit

271 *Anthus trivialis* to open habitat species such as Northern Wheatear *Oenanthe oenanthe* and finally high

272 elevation species including Alpine Chough, Snowfinch and Alpine Accentor. García-Navas et al. (2020)

273 showed that the alpine bird community (>2000 m) constituted a group distinct from lower elevation

274 species (from 500 m to 2000 m) in terms of functional richness. However, they defined the treeline as

275 the division between these two groups, whereas we found a continuum from forest species to open

276 grassland species (from 1700 m to 2500 m), and then a more marked division for high elevation species

277 (>2500 m).

278   Habitat niche breadth increased with increasing elevation, which supported our hypothesis that

279 it is an advantage to be more generalist in a harsh environment, i.e. to be able to exploit a wider range

280 of resources. Blondel & Farré (1988) found that specialisation of birds was more important in the early

281 stages of ecological succession in open and semi-open forest than in mature forest. At first glance, the

282 elevational gradient is similar to this ecological succession, with high elevation open habitat analogous

283 to early stages and forests analogous to later stages at lower elevation. Thus, habitat niche breadth

284 should have decreased with elevation. However, specialisation is only possible when environmental

285 conditions are stable, and with increasing elevation the variability of some (particularly climatic)

286 conditions increases. The elevation niche breadth hypothesis based on ecological succession as

287 analogous to the habitat-elevation gradient is thus not supported. As for insects (Rasmann et al., 2014),

288 a wider niche breadth is an advantage for birds at higher elevations. Furthermore, a narrower niche

289 breadth at lower elevation could be explained by interspecific competition. Indeed, more species are

290 living at low elevation and thus compete for the available resources. Due to competition between

291 species, they have to reduce their niche (Fuller, 2012b).

292   For higher elevation species, the results indicate both a wide niche breadth and a use of less

293   typical habitats (i.e. a high niche position). These two results may at first sight seem contradictory, but

294   they arise because high elevation species use a range of habitats, but these habitats are not used by

295   the other species. Thus our high elevation species use a broad range of habitats, but these habitats are

296   atypical compared to the average species in the community.

297   Niche breadth and niche position increased with increasing standard deviation of elevation,

298   indicating as expected that species occupying a wider elevation range use a greater range of habitats

299   that are more typical of the community as a whole. Quintero & Jetz (2018) showed that there is globally

300   a mid-elevation peak in bird richness along elevation gradients which is mainly driven by wide-ranging

301   species. We did not observe this peak since our elevation gradient was not complete and already

302   started at relatively high elevation (c. 1700 m). When a species has a greater elevational range, it is

303   more likely that it will occupy a wider range of habitats since the elevational gradient is characterised

304   by a succession of habitats from forests to rocky and snowy areas.

305

306   *Habitat niche position and niche breadth along the habitat diversity gradient*

307   Habitat niche position was negatively associated with habitat diversity, but this trend was mainly

308   driven by three species of high elevation (Alpine Accentor, Alpine Chough and Snowfinch). At lower

309   elevations, more species are present because of a greater availability of resources while at higher

310   elevations, the number of species is very scarce. These species of high elevation differ a lot from the

311   whole assemblage of species in terms of habitat use and they usually occupy habitats with a low

312   diversity. Habitat niche breadth only showed an association with habitat diversity when species of high

313   elevation were included in the model. If habitat availability had matched perfectly with habitat use,

314   then we would have seen a positive relationship between habitat niche breadth and habitat diversity.

315   Instead the results imply that other factors also drive species distribution along this habitat diversity

316   gradient. Where habitat diversity is greater, more resources are available and it is likely that more

317   species can use them, but interspecific competition likely also increases with habitat diversity resulting

318   in species exploiting a narrower range of resources (i.e. having a narrower niche breadth; (Fuller,

319   2012b). Species of high elevation are less numerous (lower species richness) and thus the competition

320   between them is lower, allowing them to exploit a wider range of resources (although Snowfinch was

321   the exception to this pattern). Finally, there was little evidence for a gradient from low diversity habitat

322   with 'generalist' species (broad niche breadth) to high diversity habitat 'specialist' species (narrow

323   niche breadth); rather, there was an indication of a threshold that separated species of high elevation

324   from the others. These species correspond to alpine specialists as defined by Thompson et al. (2012).

325   Alpine specialists are confined to the alpine zone (i.e. the major part of the population breeds in this

326   zone), while alpine generalists breed in mountains, but they can also breed at lower elevation in

327   different habitats. This result suggests that mountain generalists and mountain specialists may not

328   show the same pattern regarding the link between habitat niche and habitat diversity.

329

330   *Wider implications*

331   The species with smaller habitat niches at lower elevations tended to be forest species. Although this

332   may reflect a greater specialisation, these species are thought to be less threatened by climate change

333   as upslope shifts in treelines are unlikely to result in a net loss of suitable habitats (or indeed suitable

334   climates) in these species (Chamberlain et al., 2013). Species with a wider habitat niche breadth may

335   adapt better to environmental change than species with a narrower habitat niche breadth (e.g. Evans

336   et al., 2011), since they can exploit a larger range of resources. Indeed, there is evidence that generalist

337   bird species are adapting to climate change better than specialist species (Davey et al., 2012; Pearce-

338   Higgins et al., 2015; Bowler et al., 2019). Given that we found that habitat niche breadth increased

339   with elevation, species at higher elevation should be fairly resilient to environmental change. This

340   therefore suggests that high elevation species will have some capacity to adapt to environmental

341   changes, including some currently relatively widespread grassland species likely to be negative

342   affected by future climate change, e.g. Water Pipit *Anthus spinoletta*, Wheatear (Chamberlain et al.,

343   2013), and Ring Ouzel *Turdus torquatus* (Beale et al., 2006). However, the greatest impact of climate

344   change for such species is likely to be the loss of suitable habitat caused by forest encroachment

345   (García-Navas et al. 2020), hence such species may have some resilience, but only within habitat of

346   suitable structure. Furthermore, according to our results, these habitats are atypical and hence only

347   associated with higher elevation that are under threat from upslope shifts in vegetation zones.

348   Strategies to minimise gross changes in habitat (e.g. maintaining open grasslands) may therefore be

349   beneficial to these species, despite increases in temperature. In addition, some species occurring at

350   the highest elevations did not seem to follow the general pattern. For example, among the three

351   species occurring above 2500 m, Snowfinch, a scarce species, had a notably low habitat niche breadth,

352   suggesting that this true high alpine specialist may indeed be particularly threatened (as per Scridel et

353   al., 2018). Nevertheless, the two other species, Alpine Accentor and Alpine Chough, had particularly

354   wide habitat niche breadths suggesting that they could adapt more easily to future environmental

355   changes. Alpine Chough is indeed known to be adaptable and able to exploit anthropogenic habitats

356   even at high elevation (Vallino et al., 2019).

357   Our results could be slightly biased by some factors. First, we were not able to account for

358   detectability of species. Thus, we cannot know whether a species is rare because it has a low

359   probability of detection or because it is indeed very scarce. That is particularly true for Snowfinch which

360   was rarely contacted during the surveys and seemed to be specialised on high elevation habitats.

361   Second, and similarly, some species known to be present in the area were detected only rarely, or not

362   at all. For example, species such as Tengmalm's Owl *Aegolius funereus*, Black Grouse *Lyrurus tetrix* or

363   Rock Ptarmigan *Lagopus muta* have a lower detectability and are probably not suited to the point

364   count method used. It would be interesting to get more data for these species in order to assess their

365   influence on our analyses. Third, median elevation at which species occurred could be more accurately

366   assessed if the abundance of each species had been estimated. Indeed, bird distributions do not show

367   symmetric patterns along elevation gradients (Chamberlain et al., 2016), thus weighting presence of a

368   species by the abundance would give a more precise median elevation for the species.

Finally, given that in theory, a species can vary remarkably in its occupancy rate of identical

patches in different landscape contexts (Fuller, 2012a), more studies are needed in other regions of

the Alps in order to corroborate our results and assess the transferability of our models. As

Chamberlain et al. (2016) showed, species distribution is mainly driven by habitat and climate (and

thus elevation), but much variation was still unexplained by their models, suggesting that other factors

affected bird occurrence. Studying which factors (diet for example) can modulate bird occurrence

along the elevation gradient could be the subject of further ecological studies on alpine birds.

Furthermore, since niche space is multidimensional, it would also be useful to study the relationship

between niche and elevation by using a broader niche definition including other factors such as diet or

foraging substrate.

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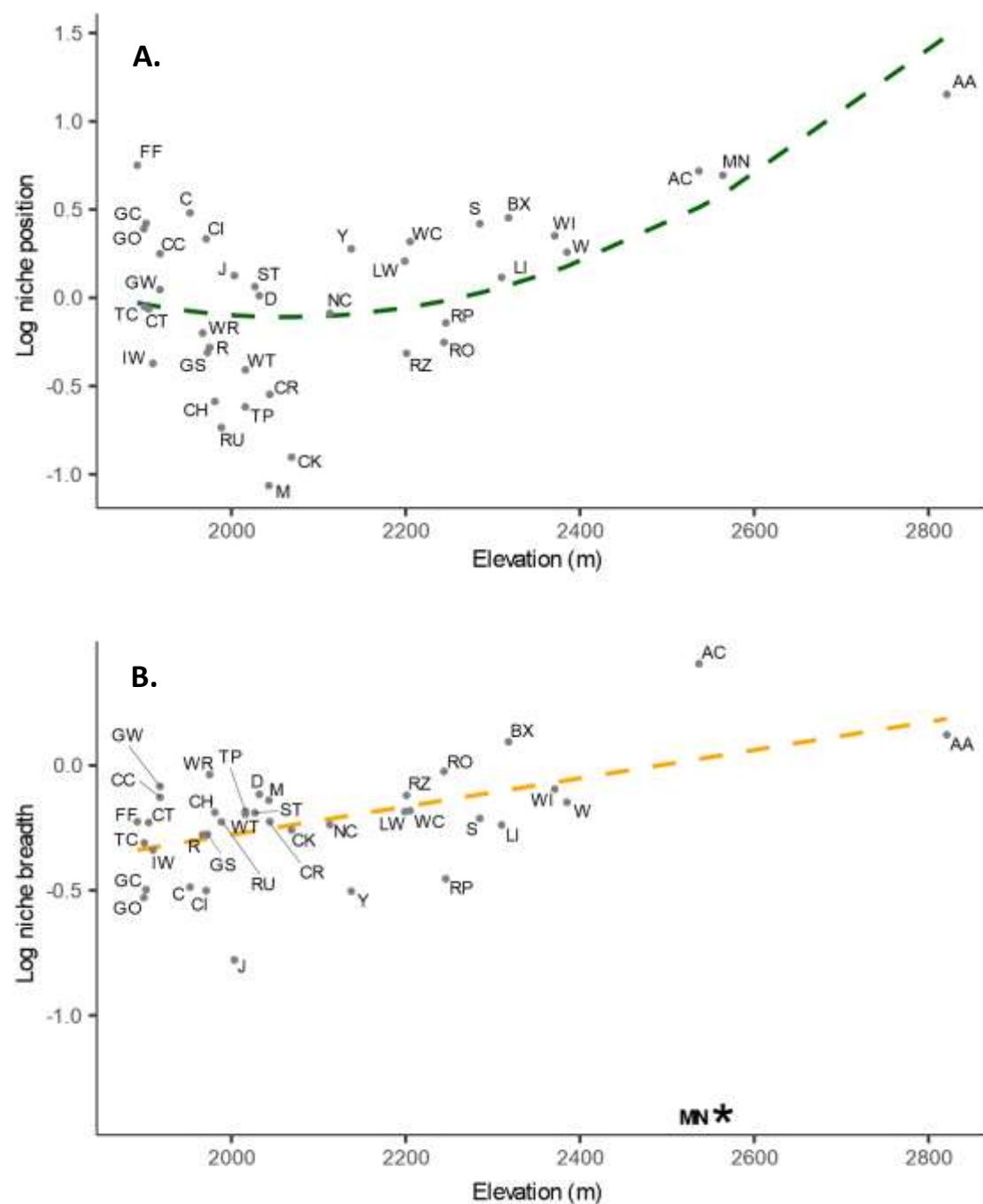505   65–69.
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Fig. 1 Niche position (A) and niche breadth (B) in relation to the median elevation of each

species' range. The dashed lines are fitted from the models given in Table S2. For niche

breadth, the influential outlier is represented by a bold black star with code in bold

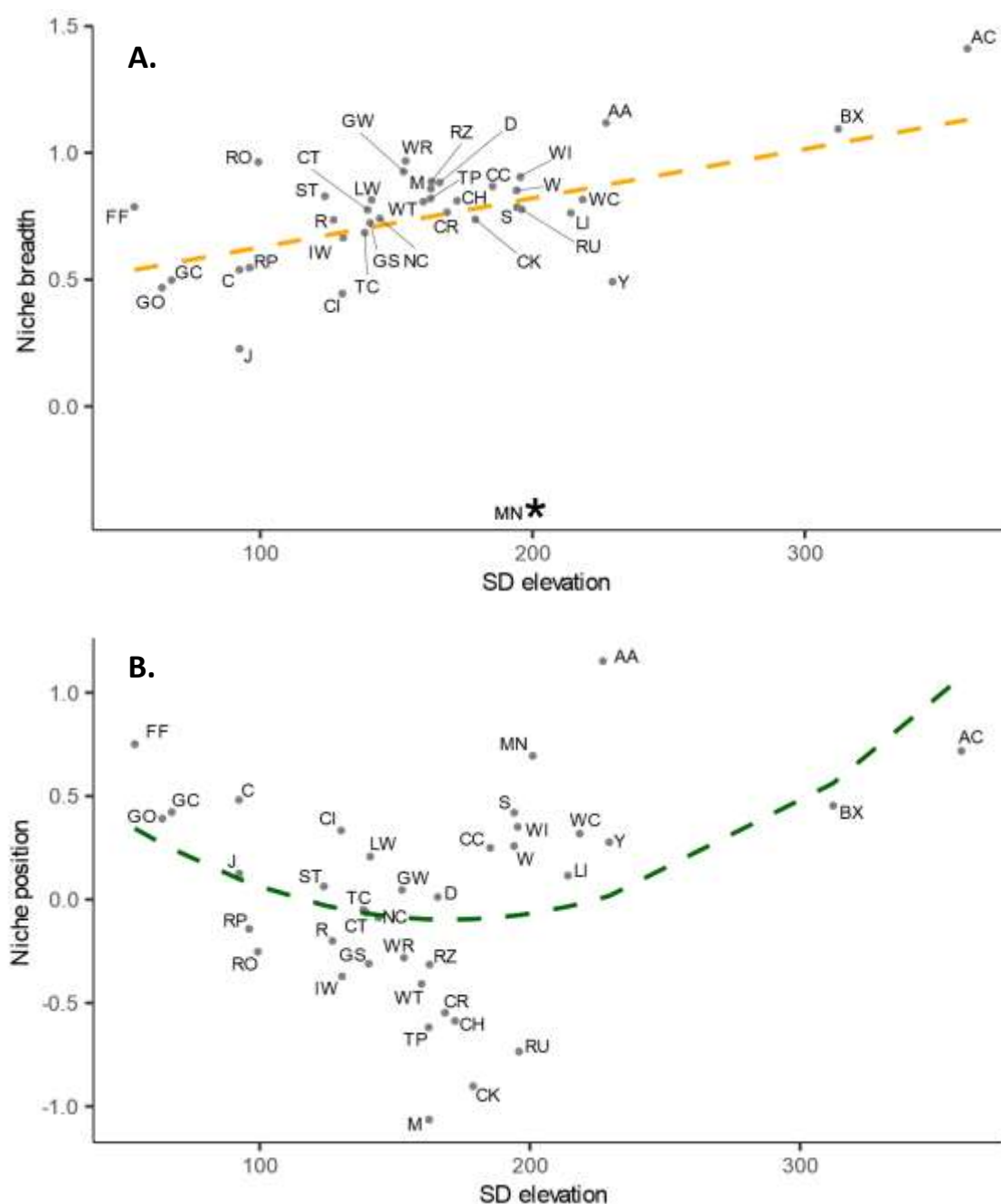(Snowfinch). See Table 1 for species codes.

Fig. 2 Standard deviation of elevation in relation to habitat niche breadth (A) and niche position (B). Influential outlier is represented by a bold black star with code in bold (Snowfinch). The orange line represents the prediction of the linear model (with all the species; Table S2). The green line represents the prediction of the quadratic model (with all the species; Table S2). See Table 1 for species codes.

Table 1 Number of records for each species contacted during the surveys (Count, given as all records/breeding records). Species with less than 3 records were removed from the data sets for analyses.

Code	Species		Count	Code	Species		Count
AA	Alpine Accentor	*Prunella collaris*	21/10	LI	Linnet	*Linaria cannabina*	10/4
AC	Alpine Chough	*Pyrrhocorax graculus*	6/0	LW	Lesser Whitethroat	*Sylvia curruca*	38/32
B	Blackbird	*Turdus merula*	1/1	M	Mistle Thrush	*Turdus viscivorus*	45/23
BF	Bullfinch	*Pyrrhula pyrrhula*	1/0	MN	Snowfinch	*Montifringilla nivalis*	3/0
BK	Black Grouse	*Lyrurus tetrix*	1/0	NC	Nutcracker	*Nucifraga caryocatactes*	9/0
BT	Blue Tit	*Cyanistes caeruleus*	1/0	PM	Rock Ptarmigan	*Lagopus muta*	1/0
BX	Black Redstart	*Phoenicurus ochruros*	72/54	Q	Common Quail	*Coturnix coturnix*	1/1
C	Carrion Crow	*Corvus corone*	4/0	R	Robin	*Erithacus rubecula*	29/29
CC	Chiffchaff	*Phylloscopus collybita*	44/43	RO	Rock Thrush	*Monticola saxatilis*	3/0
CF	Citril Finch	*Carduelis citronella*	2/1	RP	Rock Partridge	*Alectoris graeca*	4/0
CG	Red-billed Chough	*Pyrrhocorax pyrrhocorax*	1/0	RU	Rock Bunting	*Emberiza cia*	37/17
CH	Chaffinch	*Fringilla coelebs*	184/172	RZ	Ring Ouzel	*Turdus torquatus*	32/10
CI	Crested Tit	*Lophophanes cristatus*	11/4	S	Skylark	*Alauda arvensis*	63/56
CK	Cuckoo	*Cuculus canorus*	19/16	SK	Siskin	*Spinus spinus*	1/1
CR	Red Crossbill	*Loxia curvirostra*	30/0	ST	Song Thrush	*Turdus philomelos*	10/9
CT	Coal Tit	*Periparus ater*	66/58	TC	Treecreeper	*Certhia familiaris*	29/13
D	Dunnock	*Prunella modularis*	48/47	TP	Tree Pipit	*Anthus trivialis*	80/79
FF	Fieldfare	*Turdus pilaris*	4/2	W	Northern Wheatear	*Oenanthe oenanthe*	83/59
GC	Goldcrest	*Regulus regulus*	6/6	WC	Whinchat	*Saxicola rubetra*	10/7
GO	Goldfinch	*Carduelis carduelis*	4/3	WI	Water Pipit	*Anthus spinoletta*	99/81
GS	Great Spotted Woodpecker	*Dendrocopos major*	20/4	WR	Wren	*Troglodytes troglodytes*	69/69
GW	Garden Warbler	*Sylvia borin*	7/7	WT	Willow Tit	*Poecile montanus*	91/50
IW	Bonelli's Warbler	*Phylloscopus bonelli*	35/35	Y	Yellowhammer	*Emberiza citrinella*	13/9
J	Eurasian Jay	*Garrulus glandarius*	4/0				

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