1

Past and future impact of climate change on foraging habitat suitability in a

high-alpine bird species: management options to buffer against global warming

effects

5

6 **Running head:** *Climate change and snowfinch foraging habitat*

7

8 Mattia Brambilla*[a,b], Jaime Resano-Mayor*[c], Davide Scridel*[a,d,e], Matteo Anderle[a,], Giuseppe

9 Bogliani[d], Veronika Braunisch[c], Federico Capelli[a,f], Matteo Cortesi[a,f], Nathan Horrenberger[c], Paolo

10 Pedrini[a], Beatrice Sangalli[f], Dan Chamberlain[g], Raphaël Arlettaz[c], Diego Rubolini[f]

11

12 *shared first-authors

13 [a] Museo delle Scienze, Sezione Zoologia dei Vertebrati, Corso della Scienza e del Lavoro 3, I-38123

14 Trento, Italy

15 [b] Fondazione Lombardia per l'Ambiente, Settore Biodiversità e Aree protette, Largo 10 luglio 1976

16 1, I-20822 Seveso, MB, Italy

17 [c] University of Bern, Institute of Ecology and Evolution, Division of Conservation Biology,

18 Baltzerstrasse 6, CH-3012 Bern, Switzerland

19 [d] Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, Pavia, Italy

20 [e] Parco Naturale Paneveggio Pale di San Martino,

21 [f] Dipartimento di Bioscienze, Università degli Studi di Milano, Via Celoria 26, 20133 Milan, Italy

22 [g] Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia

23 Albertina 13, 10123, Turin, Italy

24

25 Corresponding author: Mattia Brambilla, email: brambilla.mattia@gmail.com; phone: +39 02

26 80616123

Abstract

The majority of predictions about the impacts of climate change on wildlife have relied either on the study of species' physiological tolerance or on broad-scale distribution models. In comparison, little attention has been paid to species' mechanistic responses to fine-grained, climate-induced modifications of habitat suitability. However, such studies would be pivotal to the understanding of species' ecological requirements (and hence their adaptive potential to environmental change) and the designing of management strategies. We investigated foraging microhabitat selection in a climate-change endangered species, the white-winged snowfinch *Montifringilla nivalis*, during the breeding season in the Alps. Our microhabitat selection model considered topographical, ground-cover variables and sward height within a 5-m radius at foraging and control locations. Habitat selection was positively affected by grassland cover, negatively by sward height and quadratically by snow cover (optimum around 40%); birds avoided anthropized (urban areas, roads) sites. We estimated past (1976) and future (2066) climate-driven changes in foraging microhabitat suitability, assuming a progressively earlier date of snowmelt due to increasing temperatures over this entire time span. We then modelled the potential impact of snow-melt (and related sward height) on habitat suitability under two scenarios: maintaining the current situation (i.e. irregular seasonal grazing) and implementing targeted management in an attempt to mitigate impacts of earlier snowmelt. Predicted foraging habitat suitability (estimated as the fraction of suitable plots) significantly declined over time (-23% between 1976 and 2016, further 32% loss by 2066). However, model outputs demonstrated that maintaining sward height below 6 cm on breeding grounds (e.g. by regular grazing) would significantly decrease the predicted loss of suitable foraging habitat. Detailed information about patterns of resource exploitation allows the identification of mechanistic, functional responses of species to environmental change, and enables an evaluation of habitat management options that can buffer against the detrimental effects of global warming.

Introduction

55

56   Anthropogenic climate change is increasingly threatening ecosystems and species worldwide

57 (IPCC, 2013; Rosenzweig et al., 2008). Evidence from a wide range of taxa and ecological systems

58 suggests that climate change has already started to affect biodiversity at a global scale (e.g.

59 Carnaval and Moritz, 2008), for instance by modifying species distributions, altering their habitats

60 or increasing extinction risk due to rapid shifts in abiotic conditions (Chen et al., 2011; Parmesan

61 and Yohe, 2003). Based on forecast climatic scenarios, several studies have furthermore attempted

62 to predict future climatic impacts on biodiversity (e.g. Bellard et al., 2012; Thomas et al., 2004).

63   The potential effects of climate, and hence of climate change, on animal species have been

64 mostly assessed either by experimental approaches evaluating physiological tolerance to climate

65 variations (e.g. temperature) at the individual level (Johnson, 1968) and under controlled

66 environments (Chapin et al., 1995), or via large-scale distribution models, the latter representing

67 one of the commonest ways to explore potential changes in species distributions owing to climate

68 change (Fitzpatrick and Hargrove, 2009; Hijmans and Graham, 2006). Eco-physiological

69 investigations usually include field observations and laboratory measurements that aim to detect

70 how alterations of environmental constraints influence species' physiological responses and hence

71 population processes (Arlettaz et al., 2000; Pörtner and Knust, 2007). In contrast, correlative models

72 of species distribution (Guisan and Thuiller, 2005) rely on environmental factors such as climate,

73 land-cover and topographical variables, which are usually linked with species occurrence at a broad

74 scale, and thus can help identifying ~~what~~ those species that are most likely to be affected by climate

75 or environmental change in a given area. They can, to ~~a certain~~ some extent, be downscaled to the

76 territory/home-range size of a target species (Brambilla et al., 2015; Braunisch et al., 2013), but

77 often remain fairly ~~crude~~limited in their predictive power as they may miss essential mechanistic

78 components (Williams and Jackson, 2007) linked to patterns of resources exploitation, such as food

79 acquisition. ~~, i.e. they~~ Hence, species distribution models may not embrace species' niche

80 complexity as a whole (Braunisch et al., 2013) and may both over- and underestimate extinction

81 risk due to climate change (Bellard et al., 2012). ~~Despite this serious caveat, s~~Although species

82 distribution models ~~remain~~ are indeed the most widely used (and scalable) ~~and widespread~~ approach

83 to assess species' spatio-temporal responses to climate change (Engler et al., 2017; Moritz and

84 Agudo, 2013), ~~Correlative in essence, such models may both over- and underestimate extinction~~

85 ~~risk due to climate change T~~there is ~~therefore~~ a need for complementary approaches that integrate

86 finer-scale ecological information for, on the one hand, improving our mechanistic understanding of

87 the tolerance and resilience, i.e. the adaptive potential of target organisms to shifting environmental

88 conditions (e.g. Baudier et al., 2015; Bennett et al., 2015), and, on the other hand, modelling

89 appropriately the consequences of environmental changes upon population dynamics (Fedy and

90 Martin, 2011; Fordham et al., 2017). This could be addressed by considering the impacts of climate

91 change upon fine-scale habitat structure and availability (henceforth, microhabitat), which

92 eventually drives habitat suitability. However, this aspect has received comparatively ~~very~~ little

93 attention so far, despite its crucial importance in understanding mechanistic responses of species to

94 environmental change~~, in particular their adaptive potential, for more accurate forecasts~~ (Fordham

95 et al., 2017; Kearney and Porter, 2009). Fine-grained species-habitat associations are essential to

96 understand how changes in microhabitat due to climate change will affect species' habitat suitability

97 at local and broader scales, which will ultimately influence a species' ability to respond to climate-

98 induced environmental changes (Scheffers et al., 2014).

99 Studies of the effects of microhabitat alteration due to changing climatic conditions have

100 mostly focused on small-sized organisms (e.g. invertebrates) that are ~~very~~highly sensitive to local

101 climatic/habitat variation, especially due to their strong temperature-dependent life-cycles (Davies

102 et al., 2006). Pincebourde et al. (2016) have shown that microhabitat properties shape species

103 responses to climate change. Research has generally focused on species with limited mobility (e.g.

104 plants (Pradervand et al., 2014), benthic invertebrates (Schiel et al., 2004)). In contrast, studies on

105 the distribution of terrestrial and highly-mobile species usually deal with broad spatial scales,

106 despite the fact that habitat selection in these species operates at multiple scales. In birds for

107 instance, this concerns the selection of breeding sites (Jedlikowski et al., 2016; Rauter et al., 2002),

108 foraging grounds (Brambilla et al., 2017c; Martínez-Miranzo et al., 2016; Schaub et al., 2010), and

109 even shelters to avoid unsuitable climate (Visinoni et al., 2015). An absence of information about

110 microhabitat preferences can lead to serious biases in predictions of climate change effects on

111 species distributions (cf. Bellard et al., 2012). As a matter of fact, microhabitat characteristics may

112 allow species persistence when the general climate of the region appears to have become unsuitable,

113 and vice versa. Studies of microhabitat suitability are thus pivotal to our basic understanding of

114 species' ecological requirements and to efficient conservation management of climate-sensitive

115 biodiversity. Several such studies have emerged recently (Suggitt et al., 2011; Turlure et al., 2010),

116 which have established the importance of both microhabitat and microclimate to understand the

117 sensitivity of species to environmental shifts and, ultimately, their population dynamics and

118 distribution patterns (Fedy and Martin, 2011; Frey et al., 2016). The basic question here is to which

119 extent can microhabitat characteristics and potential management thereof buffer against any

120 detrimental effects of overall climate change (e.g. Braunisch et al., 2014)?

121   Among terrestrial organisms, high-elevation cold-adapted species seem to be particularly

122 vulnerable to climate change (Dirnböck et al., 2011; Lagerholm et al., 2017), with their future

123 distribution being either expected to contract towards higher elevations due to ambient temperature

124 warming (La Sorte and Jetz, 2010; Braunisch et al., 2013; Chamberlain et al., 2013; Pernollet et al.,

125 2015; Sekercioglu et al., 2008), or to vary in a complex way in response to shifts in precipitation

126 regimes that remain difficult to forecast (e.g. Tingley et al., 2012). Mountain areas are indeed

127 subject to higher rates of warming compared to the global average (e.g. Böhm et al., 2001; Brunetti

128 et al., 2009), yet at the same time, they are also experiencing strong changes in landscape and land

129 use (e.g. forest encroachment in abandoned pastures, upward treeline shift or loss of areas

130 permanently covered by snow). High-elevation ecosystems thus represent an ideal setting to

131 investigate the fine-grained impact of environmental change on habitat and biocenoses, especially

132 due to the complex topography, including steep altitudinal gradients, that generates a large range of

133 microhabitats and microclimates (hereafter topoclimates) and offers numerous refugia opportunities

134 (Körner and Ohsawa, 2006). Such heterogeneity may *per se* represent a chance to maintain

135 biodiversity, either naturally (Brambilla et al., 2016a) or through informed conservation

136 management (Braunisch et al., 2014). However, to the best of our knowledge, mitigation strategies

137 to maintain niche opportunities for high-alpine biodiversity facing climatic risks have never been

138 investigated so far (Shoo et al., 2011; Turlure et al., 2010).

139   In this study, we investigated the foraging microhabitat selection in a high-elevation, cold-

140 adapted and snow-exploiting passerine bird, the white-winged snowfinch *Montifringilla nivalis*

141 (Aves: Passeridae; henceforth: snowfinch), during the nestling rearing period, a crucial phase of the

142 life-cycle – especially for short-lived species such as the snowfinch – which is likely to drive

143 overall population dynamics (Hanssen et al., 2005). The snowfinch is a mountain specialist

144 ~~bird~~species breeding at high elevations above the treeline (in the European Alps mostly between

145 1800 and 3000 m asl; (Cramp and Perrins, 1994). Nests are usually located in rock crevices or

146 human-built infrastructure such as mountain buildings or ski-lift pylons (Cramp and Perrins, 1994).~~,~~

147 Females lay ~~snowfincheswhere at the end of May-early June~~ first clutches of 4-5 eggs at the end of

148 May-early June, ~~. After two weeks of incubation performed exclusively by the female, hatching~~

149 ~~occurs~~and nestlings fledge at ca.18-22 days of age (del Hoyo et al. 2009). During the nestling

150 rearing period, adults collect multiple invertebrate prey in the ~~proximity~~surroundings of nest sites,

151 usually within 300 m of the nest, frequently on or at the margin of melting snow patches and in

152 alpine grasslands (Antor, 1995; Brambilla et al., 2017c; Catzeflis, 1975; Cramp and Perrins, 1994;

153 Strinella et al., 2007).

154   A recent study of foraging habitat selection by breeding snowfinches in the Italian Alps

155 highlighted the importance of habitat factors that are largely climate-dependent, such as snow cover

156 (positively selected), height of the grass sward (lower sward preferred), and solar radiation (lower

157 values favoured, especially late in the season, indicating avoidance of warmer sites). This previous

158 study~~at study~~ was based on 314 m^2 plots (i.e. at meso-scale) and did not explicitly address the key

159 question of climate change effects on habitat suitability (Brambilla et al., 2017c). Based on the

160 outcome of correlative distribution models which accounted for climatic, topographic and land-

161 cover variables, both at the landscape (Maggini et al., 2014) and the territory level (Brambilla et al.,

162 2016b), the snowfinch is expected to undergo a marked range contraction in the Alps because of

163 climate change, ~~and~~ especially due to increases in ambient temperature and habitat loss, snow cover

164 being a key component in the species' ecology (Brambilla et al., 2017c). ~~Our objectives~~ In this

165 study, we focus on ~~were to quantifying~~ assessing the magnitude of climate change effects on the

166 ~~foraging habitat loss~~suitability of foraging habitats, and to identify habitat management measures at

167 the territory-level scale that might help mitigate some detrimental effects of climate change. ~~We~~

168 ~~first identified key habitat characteristics that influence site selection for food collection by parents~~

169 ~~and current habitat suitability in the Central Alps. As snow cover appears~~ More specifically, our

170 aims were: 1) to identify key habitat factors driving foraging microhabitat selection during food

171 provisioning to ~~chicks~~nestlings by parents in a wide area of the Central Alps; 2) to evaluate past and

172 forecast future changes in foraging microhabitat suitability by building ~~past and future~~ models of

173 microhabitat suitability, based on longitudinal data (both historical and projected) on ~~in relation to~~

174 changing climatic conditions (snowmelt date; Klein et al., 2016), which has been progressively

175 anticipating in recent decades by c. 6 days per decade); and, 3) to assess whether habitat

176 management operations could maintain microhabitat suitability in the face of climate change. To the

177 best of our knowledge, this is the first study to explicitly model the potential impact of climate

178 change on foraging microhabitat suitability in a terrestrial vertebrate. Our study ~~which~~, paves the

179 way for better forecasts of wildlife responses to climate-induced alterations of habitat, and provides

180 targeted conservation guidance for maintaining suitable foraging grounds in the face of climate

181 change.

182

Methods

~~Study species~~

~~A recent study of foraging habitat selection by breeding snowfinches in the Italian Alps highlighted the importance of habitat factors that are largely climate-dependent, such as snow cover (positively selected), height of the grass sward (lower sward preferred), and solar radiation (lower values favoured, especially late in the season, indicating avoidance of warmer sites). That study was based on 314 m² plots (i.e. at meso-scale) and did not explicitly address the key question of climate change effects on habitat suitability~~

Study area and data collection

We investigated foraging microhabitat selection by 22 snowfinch~~es~~ breeding ~~at 12 breeding sites~~ pairs ~~in~~from 8 different regions (Sorebois, Zermatt, Furka Pass, Valle Spluga, Stelvio, Gavia, Passo Sella, Rosetta) of~~in~~ the Swiss and Italian Alps (Fig. 1). The elevation of the study sites ranged ~~from~~between 1880 ~~to~~and 2840 m a.s.l., adequately covering the altitudinal and macroclimatic gradient of snowfinch distribution in the Alps. All surveys were carried out between 14th June and 26th July 2016, focusing exclusively on snowfinches collecting food for nestlings (nestling-rearing period). First, by means of direct observations, we located snowfinch breeding pairs and active nests. Once an occupied nest was located, we adopted the following field protocols in order to record foraging and random non-foraging points (hereafter, foraging and control plots).

In Switzerland, we mist-netted at least one parent from each monitored breeding pair to attach a radio-transmitter (Holohil Systems Ldt., model BD-2, weight: 1.4 g – corresponding to 3.2-3.9% of our birds' body mass, life span: 9 weeks) to its back using a leg-loop harness (Naef-Daenzer et al., 2001; Rappole and Tipton, 1991). Studies of the effects of radio-transmitters on passerines have shown no negative impact on physiology, behaviour or survival (Naef-Daenzer et al., 2001; Townsend et al., 2012) as long as tag weight is less than 5% of bird body mass. As soon as tagged birds were provisioning food to the nestlings, foraging events were monitored over 2-6 days (spread along the nestling rearing period) with the aid of a hand-held three-element foldable Yagi antenna

209 wired to a radio-receiver (Australis 26k, Lawnton, Australia). Radio-tagged birds were first located

210 from a distance from the radio signal and, once the foraging bird was visually located, the exact site

211 of a successful prey capture was located with the aid of binoculars and marked with a labelled stick.

212 Then, a control plot was generated by selecting a random angle (0-359º) and a random distance

213 (between 26-100 m) from the actual foraging plot.

214   In Italy, breeding individuals were visually tracked when flying from the nest to foraging sites,

215 with the help of binoculars (Brambilla et al., 2017c). Once a foraging event was encountered, the

216 exact location was recorded with a GPS device or by mapping the point on a detailed aerial

217 photograph. The foraging location was established as the first position where a food item was

218 collected (or as the last location of the bird before returning to the nest, when we could not directly

219 assess prey capture, since snowfinches usually provision food to the nest immediately after prey

220 capture; Brambilla et al., 2017b). After the collection of 10 foraging locations per study pair, an

221 equal number of control plots (with the only constraint ~~of~~that they should not overlap with foraging

222 plots) were randomly selected within a radius of 300 m around the nest (Brambilla et al., 2017c;

223 Grangé, 2008; Strinella et al., 2007) so as to map habitat characteristics.

224   The difference in the method used for the selection of control plots between Switzerland and

225 Italy did not affect the results, as control plots showed ~~comparable~~similar suitability values across

226 the two approaches (as revealed by a mixed model analysing habitat suitability of control plots

227 ~~using~~in response to the method used, including site identity as a random factor and methods of

228 control plot selection as fixed effect, where the AIC value was larger than the null model; details not

229 shown for brevity).

230   Habitat cover and structure were recorded within a 5 m-radius around each foraging location

231 and control plot. Habitat variables described vegetation and other ground cover, as well as sward

232 height and the occurrence of grazing (Table 1). In addition, topographical features (slope, solar

233 radiation) were calculated in a geographic information system (GRASS 7.04) using detailed Digital

234 Elevation Models (resolution between 1 and 5 m) made publicly available by regional/provincial

235 authorities in Italy and by SwissTopo maps for 2013 (Swiss Federal Office of Topography). Solar

236 radiation was calculated as global radiation on 21st June, taking into account the shadowing effect of

237 the relief.

238 Sward height ~~was~~could not be ~~not obviously~~ recorded where grass was absent (N = 16

239 locations out of a total of 470). ~~Due to this absence~~Because of this, in exploratory analyses we

240 compared the modelled relationships between foraging occurrence and sward height by setting

241 sward height to zero at these 16 locations ~~against~~or by omitting ~~them~~these locations from the

242 analysis. Given that the coefficients for sward height were very similar between models with ~~and~~or

243 without 'filled gaps' (-1.02 and -1.03, respectively), we ~~considered appropriate to apply the~~decided

244 to apply the former option.

245

246 **Statistical analyses**

247 **Foraging habitat selection**

248 Habitat variables were recorded at 470 locations (235 foraging and 235 control plots) obtained

249 from 22 breeding pairs. All variables were standardized (i.e. centred on their mean value and scaled

250 by their standard deviation ~~SD~~) ~~prior to~~before analyses. After checking for outliers and zero-

251 inflated variables, sand and mud cover were discarded, and human-altered habitats (two types of

252 roads and urbanized areas) were joined into a single variable (anthropized areas).

253 We modelled foraging habitat selection by means of conditional logistic regression (Hosmer

254 and Lemeshow 1989), which accounts for the intrinsically paired nature of the sampling protocol

255 and resulting dataset. According to this approach, each set of foraging plots of a given breeding pair

256 was matched to the respective control plots, henceforth taking into account the pair-based sampling

257 design. Pair identity was thus specified as a so-called "stratum" variable. Study region was also

258 tested as a random factor, but was subsequently discarded as no regional effect was found (P ~ 1).

259 Conditional logistic regressions were run by using the 'clogit' function of the 'survival' package in

260 R (R Development Core Team, 2016).

261   Model selection was performed using an information-theoretic approach, based on the

262 Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson,

263 2002). First, to reduce the risk of model overfitting and to limit the potential effects of

264 multicollinearity, the explanatory variables were divided in two groups (Assandri et al., 2018).

265 These groups were "vegetation" and "other variables" (Table 1). We tested for within-group

266 collinearity by calculating the variance inflation factor (VIF) using the package *car* in R (R

267 Development Core Team, 2016). For all variables within a given group, there were no collinearity

268 issues (VIF < 3 for all variables in both groups). Within each group, models with all possible

269 variable combinations were constructed, and models were ranked according to their AICc value

270 using the MuMIn package (Bartoń, 2016). The difference in AICc between each model and the top-

271 ranking model (ΔAICc) was calculated. Based on previous studies, we hypothesised that

272 snowfinches would preferentially forage in sites with high grass cover but low sward height

273 (Brambilla et al., 2017c). Therefore, we added a potential interaction term to the "vegetation" group

274 (grassland cover × sward height). Moreover, in order to test for selection of melting

275 snow patch margins (see e.g. Antor, 1995) and according to preliminary data

276 exploration (which suggested a potential curvilinear relationship for snow cover), we also

277 included a quadratic term for snow cover (in the "other variables" group). Then, for each group we

278 selected all the variables (and interactions) included in the most supported models (ΔAICc < 2)

279 after the exclusion of 'uninformative parameters' (i.e. variables which inclusion resulted in a higher

280 AICc value of the model, but with an increase in AICc lesser than 2; Arnold, 2010; Jedlikowski et

281 al., 2016). We finally combined the retained variables of both groups and carried out a further

282 model selection using the same procedure (see e.g. Assandri et al., 2016; Brambilla et al., 2016a). In

283 the latter process, given that snowfinches could preferentially forage in fine-scaled mosaics of snow

284 and grass (Brambilla et al., 2017c), we added an interaction term (snow × grassland cover).

285   **Past, current and future habitat suitability**

286   To predict climate-driven changes in foraging habitat suitability, we modelled snow cover and

287 sward height as a function of season progression and environmental characteristics, selected on the

288 basis of a potential effect of climate on those two variables according to literature and general

289 knowledge. We built models based on the control plots, which were randomly selected and thus

290 ensured unbiased sampling (snowfinches may select ~~for~~ patches where micro-topography or other

291 local conditions can result in values of snow cover or sward height deviating from the

292 ~~averagely~~average values of each territory ~~expected ones~~). First, we built a model relating snow

293 cover to Julian date, solar radiation, elevation and slope. Then, we modelled sward height as a

294 function of solar radiation, elevation, slope, snow cover and grazing occurrence, excluding the few

295 sites without grass cover. In both cases, we used linear mixed models (LMM)~~and fitted by means of~~

296 ~~maximum likelihood~~ considering breeding pair as a random factor to take into account the spatial

297 dependency of control plots within areas frequented by the same breeding pair. Effect size for

298 variables in the mixed models was calculated according to the semi-partial R^2 statistic proposed by

299 (Jaeger et al., 2017) using the r2glmm package in R.

300   We estimated past and simulated future conditions based on the observed rate of change in the

301 date of snow melt: research from the Swiss Alps reported a linear pattern of advance in snow melt

302 timing by c. 6 days per decade (5.8 days/decade; Klein et al., 2016). To hindcast past conditions (40

303 years ago), we therefore decreased the sampling date by 24 days. To model conditions 50 years into

304 the future (at year 2066), we added 30 days, assuming the trend in melting pattern will remain

305 unaltered. We then recalculated predicted snow cover and grassland height for each of the three

306 time steps (in the following termed 'past', 'current' and 'future').

307   Finally, we calculated for each plot (foraging or control, n = 470) the potential suitability under

308 past, current and future conditions, by means of the final habitat selection model obtained in the

309 previous analysis, and averaged predicted habitat suitability for all plots related to each breeding

310 pair. We used modelled snow cover and sward height (predicted values from snow cover and sward

311 height models), instead of the values actually recorded in the field~~)~~, also for the current conditions,

312 in order to eliminate the effect of the site- and time- specific conditions associated with the

313 sampling period and to obtain habitat suitability estimates that were comparable with past and

314 future conditions. In this estimation of habitat suitability in different periods, we used the original

315 values for the two other variables (cover of grassland and of anthropized areas) included in the

316 habitat selection model.

317 **Mitigation scenarios**

318 To simulate and evaluate any potential benefits of targeted management actions to maintain

319 foraging microhabitat suitability, we also modelled current and future suitability under two

320 scenarios, with and without mitigation management. The 'non-mitigation' scenarios (without

321 management) corresponded to the modelled habitat suitability as described above. For the

322 mitigation scenarios (via habitat management), we assumed that sward height would be managed

323 according to snowfinch optimal requirements by keeping grass height below 6 cm (see Fig. 2 and

324 Brambilla et al., 2017b). We assumed that such optimal sward height could be achieved by mowing

325 or controlled grazing. We therefore used the predicted sward height under current and future climate

326 conditions, respectively, both adjusted by truncating the highest values at 6 cm. Finally, to evaluate

327 whether habitat suitability significantly changed from past to current and from current to future

328 conditions under both scenarios (with vs without management), we performed a Wilcoxon matched-

329 pairs test on the mean plot suitability for each pair. For descriptive purposes, we also counted the

330 number of plots with average plot suitability above 0.5 (suitable plots) for each time step (past,

331 current, and future).

332

333

334   **Results**

335   **Foraging habitat selection**

336   We obtained ~~a~~one single most supported synthetic model, as all other candidate models (after

337   the exclusion of uninformative parameters) had a ΔAICc > 2 (Table A2). According to this model

338   (R^2=0.35), ~~foraging habitat selection by breeding snowfinches was driven~~ the most suitable foraging

339   habitats were characterized by ~~negative effects of both~~ low sward height and cover of anthropized

340   areas, ~~a quadratic effect of~~ intermediate snow cover and ~~a positive effect~~ high ~~of~~ grassland cover~~, all~~

341   ~~terms being statistically significant~~ (Table 2). Effect sizes for these variables ranged between 0.17

342   and 0.34, with snow cover and sward height having the largest effects (Table 2). The influence of

343   these predictors on the probability of occurrence of foraging snowfinches is shown graphically in

344   Fig. 2.

345   **Past, current and future habitat suitability**

346   The model for snow cover (intercept: -0.19±0.10~~; coefficients for standardized predictors~~)

347   suggested, as expected, a positive effect of elevation (0.24±0.11, effect size: r = 0.28) and negative

348   effects of Julian date (-0.13±0.07, r = 0.17), slope (-0.05±0.09, r = 0.04) and solar radiation (-

349   0.08±0.09, r = 0.07), and had a conditional R^2 equal to 0.23. The model for sward height ~~(intercept:~~

350   ~~0.35±0.14; coefficients for standardized predictors)~~ revealed a positive effect of solar radiation

351   (0.26±0.09, r = 0.23) and slope (0.47±0.09, r = 0.41): well exposed steep slopes are likely those

352   where snow disappears earlier and where the plant growing season may be earlier, leading to higher

353   swards. As expected, a negative effect on sward height was found for grazing (grazing occurrence:

354   -0.08±0.15, r = 0.05), elevation (-0.60±0.14, r = 0.61) and snow cover (-0.14±0.08, r = 0.15), likely

355   due to both different grass species at different elevations and to the delay in growing season caused

356   by elevation and snow cover. The model for sward height had a conditional R^2 equal to 0.53.

357   Foraging habitat suitability was predicted to have declined from 1976 to 2016, and to continue

358   declining from 2016 to 2066 at all breeding sites (Fig. 3). The predicted average site-level plot

359   suitability had strongly~~significantly~~ declined from 1976 to 2016 (Wilcoxon matched pairs test, Z =

360   -4.11, ~~p < 0.001~~effect size: r = 0.71, n = 22 breeding sites), and is expected to ~~significantly~~greatly

361   decline further by 2066 (Z = -4.11, ~~p < 0.001~~r = 0.71). The overall number of suitable plots (plots

362   with habitat suitability higher than 0.5; n = 470) declined from 364 (77%) to 281 (60%) from 1976

363   to 2016 (-23% in the number of suitable plots), and was predicted to further decline to 191 (41%)

364   by 2066 (i.e. a further change of -32% in the number of suitable plots relative to the current

365   situation).

366   **Mitigation scenarios**

367   The mitigation scenarios yielded higher current and future habitat suitability values than the

368   estimates obtained without any intervention targeted at limiting sward height, especially for sites

369   with most or some plots located at the lower end of the altitudinal range exploited by the species

370   (Fig. 3). Under current conditions, if appropriate management actions were implemented, the

371   number of suitable plots would be 359 (76%; which roughly corresponds to the figure back-

372   projected to 1976 without management), while the average territory-level plot suitability would be

373   significantly higher (+0.07; Wilcoxon matched pairs test; Z = -3.52, effect size: ~~p < 0.001~~r = 0.62, n

374   = 22 breeding sites) compared to a scenario without management. The future number of suitable

375   plots under an active mitigation scenario would be 268 (57%; very close to the number of currently

376   suitable plots). Compared to a scenario with no management implemented in the future, average

377   habitat suitability could thus be increased by 0.07 (Wilcoxon matched pairs test; Z = -3.52, ~~p <~~

378   ~~0.001~~r = 0.62, n = 22 breeding sites) via mitigation measures.

379

380

Discussion

Our retrospective and prospective modelling show~~ed~~eds that a climate-sensitive species of high-Alpine ecosystems, the white-winged snowfinch, is ~~put~~ at risk ~~by~~from microhabitat loss induced by climate warming, confirming at a fine-scale level ~~what had been already suggested~~ previous suggestions derived by large-scale modelling (Brambilla et al., 2017a, 2016a). Not only has it seemingly already lost a substantial fraction (-17% of plots, or -23% of suitable plots, from 1976) of its structurally suitable foraging habitat ~~area~~ in the Central European Alps over the past decades, but the unabated habitat alterations induced by climate change w~~ill~~ould also continue to reduce habitat suitability in the decades to come (-19%, or -32% of suitable plots, by 2066). To the best of our knowledge, this is the first study that has quantified species' fine-grained microhabitat requirements for reconstructing past, and ~~constructing~~predicting future, foraging habitat suitability in a high-elevation species, i.e. a species occurring in an ecosystem that is more affected by climate change than the global average (see Moritz and Agudo, 2013 and references therein). Indeed, most research on the impact of climate change on biodiversity has so far dealt with modelling macro-ecological relationships between climate and species' biological attributes (Bellard et al., 2012). Even if such broad-scale correlative models could identify the pool of species in a given area that are likely to be mostly impacted by climate change, more detailed approaches (like the one we have adopted here) are required to produce accurate projections of changes in fine-scale habitat suitability and to assess the potential effectiveness of habitat management as a mitigation measure ~~like the one we adopted are required , more detailed approaches .~~ This study is also one of the first to illustrate that mitigation measures (targeted sward management by grazing) could be implemented to maintain habitat suitability and thus buffer against the detrimental effects of climate change, in line with what Braunisch et al. (2014) have proposed for montane and subalpine forest bird species, and with what Regos et al. (2017) suggested for birds in wildfire-prone ecosystems. This lack of fine-grained mechanistic studies of habitat selection is surprising as understanding species' ecological requirements is a prerequisite both for sound modelling of species-habitat relationships and for

designing adequate mitigation strategies for conservation. In particular, microhabitat selection studies carried out during the main bottlenecks of a species' life cycle, notably the critical and intense phase of food provisioning to offspring ~~chicks~~(nestlings), are key as breeding output depends on parental investment into progeny, which, in short-lived species such as the snowfinch, drives demographic trajectories (Hanssen et al., 2005). The mechanical links evidenced in our field surveys between environmental characteristics favouring foraging activity (snow cover and sward height) and the alterations of these characteristics induced by climate warming exemplifies how meaningful forecasting of future species distributions via spatial modelling should operate to gain predictive power. On the other side, the lack of fine-grained studies is probably linked to the intensive and time-consuming data collection required, and such studies are unlikely to be feasible for a large number of species at the same time. Additionally, the high-precision information required for the study we carried out prevented similar modelling over broad scales (e.g. at the regional or continental level), even if the increasing availability of high-resolution data will likely allow new steps in that direction in the near future.

~~H~~Microhabitat suitability for foraging snowfinches is affected by climate-related habitat variables and anthropization

Breeding snowfinches collected food for nestlings in microhabitats characterized by ~~the~~ intermediate snow cover intermixed with short grassland, while avoiding human-altered areas, notably roads and buildings. These results are in line with ~~former~~previous findings obtained at a much coarser scale in a largely overlapping study area, where snowfinches were also found to primarily select short grassland and snow-covered areas (Brambilla et al., 2017c). In addition, at a coarser scale snowfinches were found to be associated ~~also~~ to sites with lower solar radiation (especially later in the season, when those sites are the ones most likely to be still covered by snow and with short vegetation), bare ground and some boulders (Brambilla et al., 2017c), which were no longer important at the fine scale we considered. The preference for an intermediate snow cover (optimum at c.~~a~~ 40%) reflects the species' foraging tactics: snowfinches either collect invertebrate

433 ~~prey trapped~~ fallout on the snow surface (Antor, 1995), or exploit the melting margins of ~~melting~~

434 snow fields where they can find abundant tipulid larvae ~~abound~~, one of their favourite and most

435 profitable prey items ~~(authors' personal observations)~~ (Cramp and Perrins, 1994). Sward height

436 constrains foraging opportunities: short grass is likely to boost prey availability, which is prey

437 abundance modified by its accessibility (Schaub et al., 2010). Yet, to further refine our mechanistic

438 understanding of microhabitat-species associations, future work should also investigate how prey

439 abundance varies in~~with~~ respect to snow cover and the melting front of the snow field in particular,

440 and throughout the breeding season in relation to the different habitat types in general.

441 Overall, our findings confirm that properly predicting mountain birds' responses to global

442 change necessitates the consideration of both climate and habitat factors simultaneously

443 (Chamberlain et al., 2016), as habitat traits could be extremely important and interact with climate

444 change itself (Sirami et al., 2017; Titeux et al., 2017, 2016). High-elevation species spend a large

445 part of their life-cycle in extreme habitats. They have thus evolved specific adaptations to cope with

446 harsh environmental conditions (Cheviron and Brumfield, 2012). However, climate change is

447 accompanied by increased weather variability and an acceleration of extreme events, which

448 represents a new evolutionary challenge for biodiversity in general (Di Marco and Santini, 2015)

449 and high-alpine biodiversity in particular (Lu et al., 2009). The effects of the increased weather

450 variability and frequency of extreme events on the suitability of foraging habitats also deserve

451 further investigation. Moreover, direct anthropogenic impacts on Alpine ecosystems are increasing:

452 the tourism industry modifies high-altitude landscapes and biodiversity via the creation of new

453 infrastructures (e.g. Rolando et al., 2007), recreational disturbance (e.g. Arlettaz et al., 2015, 2013,

454 2007) and other anthropogenic stressors (Chamberlain et al., 2016). Although ~~the snowfinch, a~~

455 ~~partly synanthropic bird, can benefit~~the snowfinch is considered a synanthropic species benefiting

456 from human infrastructures both for nesting (mountain buildings, skilift-pylons and even nest-

457 boxes) and winter foraging (seed-feeding stations at ski resorts or mountain chalets) (Cramp and

458 Perrins, 1994), our results show that roads, paths, buildings and other man-made structures decrease

foraging microhabitat quality during the reproductive period. It would thus be particularly

interesting to estimate the year-round costs and benefits of breeding in anthropized ~~vs~~ in contrast to

natural ~~conditions for snowfinche~~habitats.

Climate change can threaten Alpine species to such an extent that the large-scale distribution of

species like the snowfinch could shrink considerably (Brambilla et al., 2017b; Maggini et al., 2014).

Our study demonstrates a high sensitivity of ~~the~~ snowfinch towards climate-induced alteration of

microhabitat conditions, notably in snow cover and sward, shedding light on the possible

mechanistic causes behind the ongoing range contraction of this and other cold-adapted~~loving~~

species (Scridel et al., 2017). Warming climate induces both an anticipation of the seasonal timing

of snowmelt (Klein et al., 2016) and an earlier and faster grass growth at high elevations (Theurillat

and Guisan, 2001), which affects the snowfinch as well as other elements of Alpine biocenoses

(Pettorelli et al., 2007).

A note of caution should be made about our models for snow cover and sward height. ~~On one

hand, t~~The snow cover model had a rather low explanatory power, suggesting that local conditions

may be very important in driving seasonal patterns of snow cover changes. In particular, winter

precipitation and spring temperature are crucial in determining how long snowfields can last during

the snowfinch breeding season. Therefore, improving the modelling of snow melting patterns at a

high spatial resolution would be an important future task for a better assessment of changes in

foraging habitat suitability for alpine birds. On the other ~~side~~hand, sward height may also depend on

the pool of locally occurring grassland species ~~locally occurring~~. Despite this, ~~our~~ the sward height

model performed very well, suggesting that common patterns in the study area can be detected even

without considering ~~the~~grassland ~~species'~~ compositions. ~~In short~~Hence, our results can be

considered as representative of the general patterns of snow cover and sward height variation

experienced by snowfinches in the Alps.

Buffering climate change impacts via habitat management

While slowing down climate warming requires long-term global measures to drastically reduce

485 society's reliance on fossil energy sources, sward management through targeted grazing is amenable

486 to local action. Our model outcomes suggest that the management ~~option to maintain~~ of sward

487 height ~~below ca 6 cm~~ might offer some room to buffer the negative impacts of climate warming on

488 foraging microhabitat configuration, especially for sites located at relatively low elevation, where

489 grassland cover and sward height play a crucial role in determining habitat suitability for

490 snowfinches (for sites located at higher elevation or with low grassland cover, this would ~~not~~hardly

491 provide any tangible benefit – see e.g. the first plots on the left side of ~~in~~ Fig. 2). According to our

492 ~~various~~ proposed scenario~~s~~, a systematic implementation of sward height~~that~~ management ~~option~~ at

493 our study sites would have compensated for the decline in structural microhabitat suitability that has

494 occurred from the 1970s and could also strongly reduce the predicted reduction of foraging habitat

495 suitability over the next 50 years. However, it remains to be seen ~~i)~~ whether: 1) other effects of

496 climate change may turn into unsuitable also the sites where foraging habitat can be kept

497 structurally suitable by means of management,~~,~~ and 2~~ii)~~ ~~whether~~implementing this measure would

498 be suffici~~ent~~e to compensate for the effect of the snowpack reduction and earlier snowmelt, which

499 may directly or indirectly impact on the invertebrate community upon which alpine birds

500 feed~~diminution of the area of suitable foraging habitat due to a thinner and earlier retreating snow~~

501 ~~pack~~. If the dependence on accessible foraging grounds is the main factor, then ~~this~~management

502 might effectively increase habitat suitability~~work~~. However, if the conditions prevailing along the

503 melting snow front dictate not only prey accessibility, but also prey abundance and phenology, this

504 measure will likely not suffice, unless the ~~species~~snowfinches can alter ~~its~~ their breeding phenology

505 towards earlier nesting. This emphasizes the need to better understand, first, how invertebrate prey

506 availability (which is, again, abundance modified by accessibility) drives foraging microhabitat

507 selection (Vickery and Arlettaz, 2012); and, second, what is the adaptive potential of the species to

508 environmental change, notably in terms of plasticity in reproductive phenology. From that

509 viewpoint, the results of our retrospective habitat suitability model suggest that the snowfinch might

510 have a limited capacity to cope with environmental change, notably with the ongoing major

511 alterations in snow cover conditions. Investigations of its long-term breeding phenology are also

512 needed to further appraise its adaptive potential. Finally, preventing the construction of new

513 infrastructures at high elevation, converting disused tracks at construction sites into grassland, as

514 well as ski-piste revegetation (Caprio et al., 2016), may limit or reduce further losses of suitable

515 habitats due to human activities.

516 ~~Further research is needed to~~ Future studies should evaluate whether a generalization of our

517 recommendations is possible, both from a spatial and a taxonomic point of view. Indeed, ~~it is~~

518 ~~possible that~~ keeping a low sward height could favour prey capture by breeding snowfinches also in

519 the other parts of the species' breeding range. Similarly, this management regime could favour other

520 insectivorous birds, ~~which require~~ requiring low swards (Vickery and Arlettaz, 2012) ~~that~~and dwell

521 in alpine grassland, such as water pipit *Anthus spinoletta*, ring ouzel *Turdus torquatus*, alpine

522 accentor *Prunella collaris* or northern wheatear *Oenanthe oenanthe*~~, but the effects should be~~

523 ~~assessed by means of dedicated investigations~~. More in general, the potential consequences of

524 grassland management on plant species (for which grazing or mowing could be both beneficial or

525 counter-indicated, Pierce et al., 2007) and habitats should also be evaluated locally.

526 The present study highlights the importance of considering microhabitat selection for revealing

527 fine-scale, functional and interacting effects of climate and land-use changes on climate-sensitive

528 species and for identifying compensatory habitat management strategies that could to some extent

529 allow buffering the negative effects of climate warming on high-~~Alpine~~elevation biodiversity.

530

531

542 **Table 1.** List of habitat variables measured within a 5-m radius at foraging and control plots, with

543 information about methods, metrics and descriptor category. Ground cover variables sum up to

544 100%. ~~For the statistical analyses, The first three variables~~Ssward height, grassland cover, shrubs

545 cover were assigned~~belong~~ to the "vegetation" group, whereas all the others~~following ones~~ were

546 assigned to the "other variables" group.

547

Variable type / variable name	Description	Unit
Vegetation structure		
Sward height	5 measurements of grass height at the plot centre and at 2.5 m along each of the four cardinal directions (or at the closest point with grassland cover, respectively)	cm
Ground cover		
Grassland	cover of grassy vegetation	%
Shrubs	dwarf-woody vegetation (e.g. *Rhododendron*, *Juniperus*, *Salix*…)	%
Snow	snow-covered areas	%
Boulders	rocks detached from the substrate	%
Bare ground	bare soil (compact soil)	%
Rocks	emerging rocky substrate (bedrock)	%
Scree	small rocky material (a few cm in diameter)	%
Gravel roads	unpaved roads, large footpaths	%
Paved roads	roads, paved parking	%
Sand	sandy soil (not compact)	%
Urbanized	buildings, walls, pylons	%
Water	lakes, ponds, watercourses	%
Other	other uncovered categories	%
Pasture and/or presence of dung	dung of current or previous year or active grazing	yes / no
Topography		
Slope	angle in degrees (°) calculated at the plot center using a digital elevation model (resolution: 1-5 m)	degree
Solar radiation	calculated as global radiation for 21st June based on a digital elevation model, incorporating the shadowing effect of the surrounding relief	kWh/m^2

548

549 **Table 2.** Best-fitting conditional logistic regression model for foraging habitat selection by breeding

550 snowfinches during the nestling rearing period. Effect size (Pearson's r) was computed considering

551 a sample size equal to 235 dyads.

552

Variable	Estimate (SE)	Z	P	r
Grassland cover	0.57 (0.14)	4.14	< 0.001	0.26
Sward height	-0.85 (0.16)	5.37	< 0.001	0.34
Snow cover	2.00 (0.32)	6.18	< 0.001	-
Snow cover ^{2}	-0.72 (0.13)	5.32	0.003	0.34
Anthropized	-1.21 (0.45)	2.65	0.008	0.17

553

554

555

556

557 **Fig. 1.** Map of the study area showing the 12 study sites monitored in the Swiss and Italian Alps.

558 The location of some major towns (Bern, Chur, Milano and Trento) is also given for a better

559 interpretation of the geographical extent of the study area. The inset shows the location of the study

560 area (rectangle) within the European Alps (grey).

561

562

563 | **Fig. 2.** ~~Effects of~~ <u>H</u>~~h~~abitat variables ~~significantly (all P < 0.008; see Table 2)~~ affecting the

564 | probability that a bird foraged in a given habitat patch according to the best-fitting conditional

565 | logistic regression model reported in Table 2. In each panel, the variable's effect~~s~~ on predicted

566   probability of habitat use (mean and 95% confidence interval) are shown while all other predictors

567   included in the models are kept at their mean value.

568

569

570

571   **Fig. 3.** Upper half: boxplots of past, current and future habitat suitability of all sampled plots

572   (n=470) within each study area (n = 8 areas), according to the best-fitting model of microhabitat

573   selection and the simulated scenarios of managed vs. unmanaged grassland sward height (in the

574   managed scenario, grassland sward was kept at a maximum height of 6 cm; see Methods for details

575   of the procedure). For each area, boxes show from left to right habitat suitability for different time

576   steps and scenarios: past (black), current – unmanaged (white), current – management scenario

577   (grey), future – unmanaged (white), future – management (grey). Plots show median, upper quartile,

578   lower quartile, maximum and minimum values excluding outliers, i.e. value above 1.5 the upper

579   quartile or below 1.5 the lower quartile.

580   Lower half: boxplot of plot (foraging and control) elevation within each study area.

581

582 **References**

583 Antor, R.J., 1995. The Importance of Arthropod Fallout on Snow Patches for the Foraging of High-
584   Alpine Birds. J. Avian Biol. 26, 81–85. doi:10.2307/3677216

585 Arlettaz, R., Nusslé, S., Baltic, M., Vogel, P., Palme, R., Jenni-Eiermann, S., Patthey, P., Genoud,
586   M., 2015. Disturbance of wildlife by outdoor winter recreation: Allostatic stress response and
587   altered activity-energy budgets. Ecol. Appl. 25, 1197–1212. doi:10.1890/14-1141.1.sm

588 Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., Jenni-Eiermann, S., 2007.
589   Spreading free-riding snow sports represent a novel serious threat for wildlife. Proc. Biol. Sci.
590   274, 1219–24. doi:10.1098/rspb.2006.0434

591 Arlettaz, R., Patthey, P., Braunisch, V., 2013. Impacts of outdoor winter recreation on alpine wildlife
592   and mitigation approaches: a case study of the black grouse. impact Ski. Mt. Environnements
593   137, 137–154.

594 Arlettaz, R., Ruchet, C., Aeschimann, J., Brun, E., Genoud, M., Vogel, P., 2000. Physiological traits
595   affecting the distribution and wintering strategy of the bat Tadarida teniotis. Ecology 81, 1004–
596   1014. doi:10.1890/0012-9658(2000)081[1004:PTATDA]2.0.CO;2

597 Arnold, T.W., 2010. Uninformative Parameters and Model Selection Using Akaike's Information
598   Criterion. J. Wildl. Manage. 74, 1175–1178. doi:10.1111/j.1937-2817.2010.tb01236.x

599 Assandri, G., Bernardi, A., Schmoliner, A., Bogliani, G., Pedrini, P., Brambilla, M., 2018. A matter
600   of pipes: Wryneck Jynx torquilla habitat selection and breeding performance in an intensive
601   agroecosystem. J. Ornithol. 159, 103–114. doi:10.1007/s10336-017-1479-y

602 Assandri, G., Bogliani, G., Pedrini, P., Brambilla, M., 2016. Diversity in the monotony? Habitat
603   traits and management practices shape avian communities in intensive vineyards. Agric.
604   Ecosyst. Environ. 223, 250–260. doi:10.1016/j.agee.2016.03.014

605 Bartoń, K., 2016. MuMIn: Multi-Model Inference. R package version 1.15.6.

606 Baudier, K.M., Mudd, A.E., Erickson, S.C., O'Donnell, S., 2015. Microhabitat and body size effects
607   on heat tolerance: implications for responses to climate change (army ants: Formicidae,
608   Ecitoninae). J. Anim. Ecol. 84, 1322–1330. doi:10.1111/1365-2656.12388

609 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate
610   change on the future of biodiversity. Ecol. Lett. 15, 365–377. doi:10.1111/j.1461-
611   0248.2011.01736.x

612 Bennett, N.L., Severns, P.M., Parmesan, C., Singer, M.C., 2015. Geographic mosaics of phenology,
613   host preference, adult size and microhabitat choice predict butterfly resilience to climate
614   warming. Oikos 124, 41–53. doi:10.1111/oik.01490

615 Böhm, R., Auer, I., Brunetti, M., Maugeri, M., Nanni, T., Schöner, W., 2001. Regional temperature
616   variability in the European Alps: 1760-1998 from homogenized instrumental time series. Int. J.
617   Climatol. 21, 1779–1801. doi:10.1002/joc.689

618 Brambilla, M., Bergero, V., Bassi, E., Falco, R., 2015. Current and future effectiveness of Natura
619   2000 network in the central Alps for the conservation of mountain forest owl species in a

620   warming climate. Eur. J. Wildl. Res. 61, 35–44. doi:10.1007/s10344-014-0864-6

621   Brambilla, M., Caprio, E., Assandri, G., Scridel, D., Bassi, E., Bionda, R., Celada, C., Falco, R.,
622   Bogliani, G., Pedrini, P., Rolando, A., Chamberlain, D., 2017a. A spatially explicit definition of
623   conservation priorities according to population resistance and resilience, species importance
624   and level of threat in a changing climate. Divers. Distrib. 23, 727–738. doi:10.1111/ddi.12572

625   Brambilla, M., Caprio, E., Assandri, G., Scridel, D., Bassi, E., Bionda, R., Celada, C., Falco, R.,
626   Bogliani, G., Pedrini, P., Rolando, A., Chamberlain, D., 2017b. A spatially explicit definition
627   of conservation priorities according to population resistance and resilience, species importance
628   and level of threat in a changing climate. Divers. Distrib. 23, 727–738. doi:10.1111/ddi.12572

629   Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P., Rubolini, D., 2017c. Foraging
630   habitat selection by Alpine White-winged Snowfinches Montifringilla nivalis during the
631   nestling rearing period. J. Ornithol. 158, 277–286. doi:10.1007/s10336-016-1392-9

632   Brambilla, M., Gustin, M., Fulco, E., Sorace, A., Celada, C., 2017d. Coarse landscape features
633   predict occurrence, but habitat selection is driven by specific habitat traits: implications for the
634   conservation of the threatened Woodchat Shrike Lanius senator. Bird Conserv. Int. 27, 58–70.
635   doi:10.1017/S0959270916000034

636   Brambilla, M., Pedrini, P., Rolando, A., Chamberlain, D., 2016a. Climate change will increase the
637   potential conflict between skiing and high-elevation bird species in the Alps. J. Biogeogr. 43,
638   2299–2309. doi:10.1111/jbi.12796

639   Brambilla, M., Pedrini, P., Rolando, A., Chamberlain, D.E., 2016b. Climate change will increase the
640   potential conflict between skiing and high-elevation bird species in the Alps. J. Biogeogr.
641   doi:10.1111/jbi.12796

642   Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H., Bollmann, K., 2013. Selecting from
643   correlated climate variables: A major source of uncertainty for predicting species distributions
644   under climate change. Ecography (Cop.). 36, 971–983. doi:10.1111/j.1600-0587.2013.00138.x

645   Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F., Bollmann, K., 2014. Temperate
646   Mountain Forest Biodiversity under Climate Change: Compensating Negative Effects by
647   Increasing Structural Complexity. PLoS One 9, e97718. doi:10.1371/journal.pone.0097718

648   Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R., Schöner, W., 2009. Climate
649   variability and change in the greater alpine region over the last two centuries based on multi-
650   variable analysis. Int. J. Climatol. 29, 2197–2225. doi:10.1002/joc.1857

651   Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference, Book. Springer,
652   New York, NY. doi:10.1007/978-3-319-02868-2_3

653   Caprio, E., Chamberlain, D., Rolando, A., 2016. Ski-piste revegetation promotes partial bird
654   community recovery in the European Alps. Bird Study 63, 470–478.
655   doi:10.1080/00063657.2016.1216520

656   Carnaval, A.C., Moritz, C., 2008. Historical climate modelling predicts patterns of current
657   biodiversity in the Brazilian Atlantic forest. J. Biogeogr. 35, 1187–1201. doi:10.1111/j.1365-
658   2699.2007.01870.x

659   Catzeflis, F., 1975. Remarques sur la nidification rupestre de la Niverolle. Nos Oiseaux 33, 64–65.

660   Chamberlain, D., Brambilla, M., Caprio, E., Pedrini, P., Rolando, A., 2016a. Alpine bird
661   distributions along elevation gradients: the consistency of climate and habitat effects across
662   geographic regions. Oecologia 181, 1139–1150. doi:10.1007/s00442-016-3637-y

663   Chamberlain, D., Pedrini, P., Brambilla, M., Rolando, A., Girardello, M., 2016b. Identifying key
664   conservation threats to Alpine birds through expert knowledge. PeerJ 4, e1723.
665   doi:10.7717/peerj.1723

666   Chamberlain, D.E., Negro, M., Caprio, E., Rolando, A., 2013. Assessing the sensitivity of alpine
667   birds to potential future changes in habitat and climate to inform management strategies. Biol.
668   Conserv. 167, 127–135. doi:10.1016/j.biocon.2013.07.036

669   Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Laundre, J.A., 1995. Responses of
670   Arctic Tundra to Experimental and Observed Changes in Climate. Ecology 76, 694–711.
671   doi:10.2307/1939337

672   Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species of
673   climate warming. Science (80-.). 333, 1024–1026. doi:10.1126/science.1206432

674   Cheviron, Z.A., Brumfield, R.T., 2012. Genomic insights into adaptation to high-altitude
675   environments. Heredity (Edinb). doi:10.1038/hdy.2011.85

676   Cramp, S., Perrins, C.M., 1994. The birds of the Western Palearctic, vol VIII. Oxford University
677   Press, Oxford.

678   Davies, Z.G., Wilson, R.J., Coles, S., Thomas, C.D., 2006. Changing habitat associations of a
679   thermally constrained species, the silver-spotted skipper butterfly, in response to climate
680   warming. J. Anim. Ecol. 75, 247–256. doi:10.1111/j.1365-2656.2006.01044.x

681   Di Marco, M., Santini, L., 2015. Human pressures predict species' geographic range size better than
682   biological traits. Glob. Chang. Biol. 21. doi:10.1111/gcb.12834

683   Dirnböck, T., Essl, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude
684   endemic species under climate change. Glob. Chang. Biol. 17, 990–996. doi:10.1111/j.1365-
685   2486.2010.02266.x

686   Engler, J.O., Stiels, D., Schidelko, K., Strubbe, D., Quillfeldt, P., Brambilla, M., 2017. Avian SDMs:
687   current state, challenges, and opportunities. J. Avian Biol. 1483–1504. doi:10.1111/jav.01248

688   Fedy, B., Martin, K., 2011. The Influence of Fine-Scale Habitat Features on Regional Variation in
689   Population Performance of Alpine White-Tailed Ptarmigan. Condor 113, 306–315.
690   doi:10.1525/cond.2011.100070

691   Fitzpatrick, M.C., Hargrove, W.W., 2009. The projection of species distribution models and the
692   problem of non-analog climate. Biodivers. Conserv. 18, 2255–2261. doi:10.1007/s10531-009-
693   9584-8

694   Fordham, D.A., Bertelsmeier, C., Brook, B.W., Early, R., Neto, D., Brown, S.C., Ollier, S., Araújo,
695   M.B., 2017. How complex should models be? Comparing correlative and mechanistic range
696   dynamics models. Glob. Chang. Biol. doi:10.1111/gcb.13935

697 Frey, S.J.K., Hadley, A.S., Betts, M.G., Robertson, M., 2016. Microclimate predicts within-season
698   distribution dynamics of montane forest birds. Divers. Distrib. 22. doi:10.1111/ddi.12456

699 Grangé, J.-L., 2008. Biologie de reproduction de la Niverolle Alpine Montifringilla nivalis dans le
700   Pyrénées occidentales. Nos Oiseaux 55, 67–82.

701 Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat
702   models. Ecol. Lett. 8, 993–1009. doi:10.1111/j.1461-0248.2005.00792.x

703 Hanssen, S.A., Hasselquist, D., Folstad, I., Erikstad, K.E., 2005. Cost of reproduction in a long-
704   lived bird: incubation effort reduces immune function and future reproduction. Proceedings.
705   Biol. Sci. 272, 1039–46. doi:10.1098/rspb.2005.3057

706 Hijmans, R.J., Graham, C.H., 2006. The ability of climate envelope models to predict the effect of
707   climate change on species distributions. Glob. Chang. Biol. 12, 2272–2281.
708   doi:10.1111/j.1365-2486.2006.01256.x

709 IPCC, 2013. Working Group I Contribution to the IPCC Fifth Assessment Report, Climate Change
710   2013: The Physical Science Basis, Ipcc. doi:10.1017/CBO9781107415324.Summary

711 Jaeger, B.C., Edwards, L.J., Das, K., Sen, P.K., 2017. An R^2 statistic for fixed effects in the
712   generalized linear mixed model. J. Appl. Stat. 44, 1086–1105.
713   doi:10.1080/02664763.2016.1193725

714 Jedlikowski, J., Chibowski, P., Karasek, T., Brambilla, M., 2016. Multi-scale habitat selection in
715   highly territorial bird species: Exploring the contribution of nest, territory and landscape levels
716   to site choice in breeding rallids (Aves: Rallidae). Acta Oecologica 73, 10–20.
717   doi:10.1016/j.actao.2016.02.003

718 Johnson, R.E., 1968. Temperature regulation in the white-tailed ptarmigan, Lagopus leucurus.
719   Comp. Biochem. Physiol. 24, 1003–1014. doi:10.1016/0010-406X(68)90813-X

720 Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial
721   data to predict species' ranges. Ecol. Lett. 12, 334–350. doi:10.1111/j.1461-0248.2008.01277.x

722 Klein, G., Vitasse, Y., Rixen, C., Marty, C., Rebetez, M., 2016. Shorter snow cover duration since
723   1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. Clim. Change
724   139, 637–649. doi:10.1007/s10584-016-1806-y

725 Körner, C., Ohsawa, M., 2006. Mountain systems, in: Hassan, R., Scholes, R., Ash, N. (Eds.),
726   Ecosystem and Human Well-Being: Current State and Trends. Island Press, Washington, pp.
727   681–716.

728 La Sorte, F.A., Jetz, W., 2010. Projected range contractions of montane biodiversity under global
729   warming. Proc. Biol. Sci. 277. doi:10.1098/rspb.2010.0612

730 Lagerholm, V.K., Sandoval-Castellanos, E., Vaniscotte, A., Potapova, O.R., Tomek, T., Bochenski,
731   Z.M., Shepherd, P., Barton, N., Van Dyck, M.C., Miller, R., Höglund, J., Yoccoz, N.G., Dalén,
732   L., Stewart, J.R., 2017. Range shifts or extinction? Ancient DNA and distribution modelling
733   reveal past and future responses to climate warming in cold-adapted birds. Glob. Chang. Biol.
734   23, 1425–1435. doi:10.1111/gcb.13522

735 Lu, X., Ke, D.H., Zeng, X.H., Yu, T.L., 2009. Reproductive ecology of two sympatric Tibetan
736   snowfinch species at the edge of their altitudinal range: Response to more stressful
737   environments. J. Arid Environ. 73, 1103–1108. doi:10.1016/j.jaridenv.2009.06.011

738 Maggini, R., Lehmann, A., Zbinden, N., Zimmermann, N.E., Bolliger, J., Schröder, B., Foppen, R.,
739   Schmid, H., Beniston, M., Jenni, L., 2014. Assessing species vulnerability to climate and land
740   use change: the case of the Swiss breeding birds. Divers. Distrib. 20, 708–719.
741   doi:10.1111/ddi.12207

742 Martínez-Miranzo, B., Banda, E.I., Aguirre, J.I., 2016. Multiscale analysis of habitat selection by
743   Bonelli's eagle (Aquila fasciata) in NE Spain. Eur. J. Wildl. Res. 62, 673–679.
744   doi:10.1007/s10344-016-1041-x

745 Moritz, C., Agudo, R., 2013. The Future of Species Under Climate Change: Resilience or Decline?
746   Science (80-.). 341, 504–508. doi:10.1126/science.1237190

747 Naef-Daenzer, B., Widmer, F., Nuber, M., 2001. A test for effects of radio-tagging on survival and
748   movements of small birds. Avian Sci. 1, 15–23.

749 Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across
750   natural systems. Nature 421, 37–42. doi:10.1038/nature01286

751 Pernollet, C.A., Korner-Nievergelt, F., Jenni, L., 2015. Regional changes in the elevational
752   distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. Ibis (Lond.
753   1859). 157, 823–836. doi:10.1111/ibi.12298

754 Pettorelli, N., Pelletier, F., Von Hardenberg, A., Festa-Bianchet, M., Côté, S.D., 2007. Early onset of
755   vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates. Ecology 88,
756   381–390. doi:10.1890/06-0875

757 Pierce, S., Luzzaro, A., Caccianiga, M., Ceriani, R.M., Cerabolini, B., 2007. Disturbance is the
758   principal α-scale filter determining niche differentiation, coexistence and biodiversity in an
759   alpine community. J. Ecol. 95, 698–706. doi:10.1111/j.1365-2745.2007.01242.x

760 Pincebourde, S., Murdock, C.C., Vickers, M., Sears, M.W., 2016. Fine-scale microclimatic variation
761   can shape the responses of organisms to global change in both natural and urban environments,
762   in: Integrative and Comparative Biology. Oxford University Press, pp. 45–61.
763   doi:10.1093/icb/icw016

764 Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation
765   of thermal tolerance. Science (80-.). 315, 95–97. doi:10.1126/science.1135471

766 Pradervand, J.-N., Dubuis, A., Pellissier, L., Guisan, A., Randin, C., 2014. Very high resolution
767   environmental predictors in species distribution models: Moving beyond topography? Prog.
768   Phys. Geogr. 38, 79–96. doi:10.1177/0309133313512667

769 R Development Core Team, 2016. A Language and Environment for Statistical Computing.

770 Rappole, J.H., Tipton, A.R., 1991. New harness design for attachment of radio transmitters to small
771   passerines (Nuevo Diseño de Arnés para Atar Transmisores a Passeriformes Pequeños). J. F.
772   Ornithol. 62, 335–337.

773 Rauter, C.M., Reyer, H.-U., Bollmann, K., 2002. Selection through predation, snowfall and
774   microclimate on nest-site preferences in the Water Pipit Anthus spinoletta. Ibis (Lond. 1859).
775   144, 433–444. doi:10.1046/j.1474-919X.2002.00013.x

776 Regos, A., Clavero, M., D'Amen, M., Guisan, A., Brotons, L., 2017. Wildfire-vegetation dynamics
777   affect predictions of climate change impact on bird communities. Ecography (Cop.).
778   doi:10.1111/ecog.02990

779 Rolando, A., Caprio, E., Rinaldi, E., Ellena, I., 2007. The impact of high-altitude ski-runs on alpine
780   grassland bird communities. J. Appl. Ecol. 44, 210–219. doi:10.1111/j.1365-
781   2664.2006.01253.x

782 Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L.,
783   Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., Imeson, A., 2008. Attributing
784   physical and biological impacts to anthropogenic climate change. Nature 453, 353–357.
785   doi:10.1038/nature06937

786 Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi,
787   F., Zbinden, N., Jenni, L., Arlettaz, R., 2010. Patches of Bare Ground as a Staple Commodity
788   for Declining Ground-Foraging Insectivorous Farmland Birds. PLoS One 5, e13115.
789   doi:10.1371/journal.pone.0013115

790 Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.A., 2014. Microhabitats
791   reduce animal's exposure to climate extremes. Glob. Chang. Biol. 20, 495–503.
792   doi:10.1111/gcb.12439

793 Schiel, D.R., Steinbeck, J.R., Foster, M.S., 2004. Ten years of induced ocean warming causes
794   comprehensive changes in marine benthic communities. Ecology 85, 1833–1839.
795   doi:10.1890/03-3107

796 Scridel, D., Bogliani, G., Pedrini, P., Iemma, A., Von Hardenberg, A., Brambilla, M., 2017. Thermal
797   niche predicts recent changes in range size for bird species. Clim. Res. 73, 207–216.
798   doi:10.3354/cr01477

799 Sekercioglu, C.H., Schneider, S.H., Fay, J.P., Loarie, S.R., 2008. Climate change, elevational range
800   shifts, and bird extinctions. Conserv. Biol. 22, 140–150. doi:10.1111/j.1523-
801   1739.2007.00852.x

802 Shoo, L.P., Olson, D.H., McMenamin, S.K., Murray, K.A., Van Sluys, M., Donnelly, M.A.,
803   Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S.M., Bishop, P.J., Corn, P.S., Dovey, L.,
804   Griffiths, R.A., Lowe, K., Mahony, M., McCallum, H., Shuker, J.D., Simpkins, C., Skerratt,
805   L.F., Williams, S.E., Hero, J.-M., 2011. Engineering a future for amphibians under climate
806   change. J. Appl. Ecol. 48, 487–492. doi:10.1111/j.1365-2664.2010.01942.x

807 Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., Martin, J.L., 2017.
808   Impacts of global change on species distributions: obstacles and solutions to integrate climate
809   and land use. Glob. Ecol. Biogeogr. 26. doi:10.1111/geb.12555

810 Strinella, E., Ricci, F., Vianale, P., 2007. Uso dell'habitat nel Fringuello alpino (Montifringilla
811   nivalis) in periodo riproduttivo in un'area sub-antropizzata: Campo Imperatore (Gran Sasso-

812   Abruzzo). Alula 14, 107–114.

813 Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., Thomas, C.D., 2011.
814   Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos 120, 1–8.
815   doi:10.1111/j.1600-0706.2010.18270.x

816 Theurillat, J.-P., Guisan, A., 2001. Potential Impact of Climate Change on Vegetation in the
817   European Alps: A Review. Clim. Change 50, 77–109. doi:10.1023/A:1010632015572

818 Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C.,
819   Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van
820   Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L.,
821   Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–8.
822   doi:10.1038/nature02121

823 Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C., Beissinger, S.R., 2012. The push and pull of
824   climate change causes heterogeneous shifts in avian elevational ranges. Glob. Chang. Biol. 18,
825   3279–3290. doi:10.1111/j.1365-2486.2012.02784.x

826 Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H.,
827   Brotons, L., 2017. Global scenarios for biodiversity need to better integrate climate and land
828   use change. Divers. Distrib. doi:10.1111/ddi.12624

829 Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H.,
830   Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. Glob. Chang. Biol.
831   22. doi:10.1111/gcb.13272

832 Townsend, J.M., Rimmer, C.C., McFarland, K.P., 2012. Radio-transmitters do not affect seasonal
833   mass change or annual survival of wintering Bicknell's Thrushes. J. F. Ornithol. 83, 295–301.
834   doi:10.1111/j.1557-9263.2012.00378.x

835 Turlure, C., Choutt, J., Baguette, M., Van Dyck, H.A.N.S., 2010. Microclimatic buffering and
836   resource-based habitat in a glacial relict butterfly: Significance for conservation under climate
837   change. Glob. Chang. Biol. 16, 1883–1893. doi:10.1111/j.1365-2486.2009.02133.x

838 Vickery, J., Arlettaz, R., 2012. The importance of habitat heterogeneity at multiple scales for birds
839   in European agricultural landscapes, in: Birds and Habitat: Relationships in Changing
840   Landscapes. pp. 177–204.

841 Visinoni, L., Pernollet, C.A., Desmet, J.-F., Korner-Nievergelt, F., Jenni, L., 2015. Microclimate and
842   microhabitat selection by the Alpine Rock Ptarmigan (Lagopus muta helvetica) during
843   summer. J. Ornithol. 156, 407–417. doi:10.1007/s10336-014-1138-5

844 Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological
845 surprises. Front. Ecol. Environ. 5, 475–482. doi:10.1890/070037