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2 **Species interactions and climate change: how the disruption of species co-occurrence will**
3 **impact on an avian forest guild**

4

5 **Running Head:** Climate change and interactions in birds

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35 **Abstract:**

36 Interspecific interactions are crucial in determining species occurrence and community assembly.

37 Understanding these interactions is thus essential for correctly predicting species' responses to

38 climate change. We focussed on an avian forest guild of four hole-nesting species with differing

39 sensitivities to climate, that show a range of well-understood reciprocal interactions, including

40 facilitation, competition and predation. We modelled the potential distributions of black

41 woodpecker and boreal, tawny and Ural owl, and tested whether the spatial patterns of the more

42 widespread species (excluding Ural owl) were shaped by interspecific interactions. We then

43 modelled the potential future distributions of all four species, evaluating how the predicted changes

44 will alter the overlap between the species' ranges, and hence the spatial outcomes of interactions.

45 Forest cover/type and climate were important determinants of habitat suitability for all species.

46 Field data analysed with N-mixture models revealed effects of interspecific interactions on current

47 species abundance, especially in boreal owl (positive effects of black woodpecker, negative effects

48 of tawny owl). Climate change will impact the assemblage both at species and guild-levels, as the

49 potential area of range-overlap, relevant for species interactions, will change in both proportion and

50 extent in the future. Boreal owl, the most climate-sensitive species in the guild, will retreat, and the

51 range-overlap with its main predator, tawny owl, will increase in the remaining suitable area:

52 climate change will thus impact on boreal owl both directly and indirectly. Climate change will

53 cause the geographical alteration or disruption of species interaction networks, with different
54 consequences for the species belonging to the guild and a likely spatial increase of competition
55 and/or intraguild predation. Our work shows significant interactions and important potential
56 changes in the overlap of areas suitable for the interacting species, which reinforce the importance
57 of including relevant biotic interactions in predictive climate change models for increasing forecast
58 accuracy.

59

60 **Keywords:** biotic interactions, citizen science, global warming, SDM, Strigidae, woodpeckers

61 **Introduction**

62 The importance of environmental factors such as climate, topography and land-cover in dictating
63 species distributions is well recognized in the literature (e.g. Hawkins et al., 2003; Elith &
64 Leathwick, 2009) and it is the basis of correlative species distribution models (SDMs). These
65 models, also known as environmental niche models (ENMs), have represented one of the most
66 frequent applications in ecology, biogeography and conservation over recent decades (see e.g.
67 Engler et al., 2017). In addition to the above-mentioned environmental factors, interspecific
68 interactions can also be crucial in determining species occurrence over different spatial scales (Wisz
69 et al., 2013), as well as in structuring biological communities (Bertness & Callaway, 1994). This
70 underlies the growing interest in macroecological models that include or evaluate biotic interactions
71 (Dormann et al., 2018). In fact, biotic interactions have been hypothesized from macroecological
72 patterns (Pollock et al., 2014), as well as used to improve distribution predictions for interacting
73 species (Araújo & Luoto, 2007; Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007).

74 One of the greatest recent challenges for ecologists is to predict the likely consequences of
75 climate change on species, communities and ecosystems (Valiente-Banuet et al., 2015): proper
76 forecasting is essential for species conservation and the maintenance of functioning ecosystems.
77 (Groves et al., 2012). A crucial point that severely complicates the assessment of the potential
78 impacts of climate change on wildlife is represented by its indirect effects via changes in biotic
79 interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008), to the point that considering biotic
80 interactions is essential to correctly predict species' responses to climate change (Van der Putten,
81 Macel, & Visser, 2010). Climate change may disrupt trophic webs by altering the distribution of
82 species acting as key resources, competitors and predators, or by shifting phenologies of interacting
83 organisms, ultimately causing important changes in the nature of relationships between species
84 (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Kubelka et al., 2018; Van der Putten et al., 2010).

85 Facilitation (a positive interaction whereby one species promotes the occurrence of another) and
86 intraguild predation are two particular biotic interactions that have been found to be very important

87 for predicting the occurrence of several species (Heikkinen et al., 2007; Holt & Huxel, 2007), but
88 have received little attention in terms of how they could be altered by the influence of climate
89 change (but see (Bateman, Vanderwal, Williams, & Johnson, 2012). In fact, variation in climatic
90 conditions may impact on facilitation relationships as well as on intraguild predation (e.g. Rogers et
91 al., 2018), with potentially cascading effects over the entire system (Barton & Schmitz, 2009).

92 In this study, we focus on an avian forest guild of four hole-nesting species with different types
93 of reciprocal interactions, ranging from facilitation to competition and predation. The distribution of
94 the model species we considered is partially limited by climate, and in particular by temperature.
95 On this basis, our study system offers an unprecedented opportunity to evaluate the potential effect
96 of climate change on species distributions and, in particular, on different types of interaction among
97 species in the studied guild. On the basis of well-established interspecific relationships, we
98 formulated an *a priori* interaction scenario, that accounts for the effects of co-occurrence in this
99 guild. Then, using a large sample size and relevant environmental predictors, measured at a
100 biologically meaningful spatial scale, we modelled potential species distributions. Successively, we
101 evaluated whether the co-occurrence patterns that could be hypothesized on the basis of both
102 environmental suitability (according to species-specific SDMs), and whether potential biotic
103 interactions of the three more widespread species within the Alpine region were consistent with real
104 occurrence data (under current climatic conditions) gathered through dedicated fieldwork. Finally,
105 we modelled the potential future distribution of the study species according to the forecast future
106 climate, to provide an estimate of the potential impact of climate change on (co)occurrence and
107 hence on likely interspecific interactions.

108

109

110 **Material and methods**

111 **Study system**

112 The forest guild we investigated included four avian hole-nesting species, black woodpecker
113 *Dryocopus martius*, boreal owl *Aegolius funereus*, tawny owl *Strix aluco* and Ural owl *Strix*
114 *uralensis*. The study area encompassed the Alpine region, i.e. the Alps and the surrounding areas
115 across seven European countries (Fig. 1). This iconic mountain system harbours all the model
116 species, although they display rather different breeding distribution patterns. The Ural owl is limited
117 to the eastern portion of the study area, whereas the other three species occur over most of the Alps,
118 showing different associations with elevation belts and with forest types.

119

120 [Figure 1 approximately here]

121

122 Black woodpecker, the only diurnal taxon among the modelled species, is tied to mature forests,
123 with large stems and availability of dead wood and ant-rich habitats (Brambilla & Saporetti, 2014;
124 Karimi, Moradi, Rezaei, Brambilla, & Ghadimi, 2018; Pirovano & Zecca, 2014) over a wide
125 elevation gradient, from sea level to c.2000 m asl. This species has shown a dramatic increase in the
126 Alps, and colonization of previously unoccupied lowland forests (Nardelli et al., 2015). This
127 expansion is most likely due to an increase in forest quality and extent (Nardelli et al., 2015; see
128 also Mikusiński, 1995), yet no study has investigated the potential impact of climate change on this
129 species, with the exception of a paper suggesting future retraction in central Europe (Vos et al.,
130 2008).

131 The Alps are a climate *refugium* for boreal owl, representing a relict portion of the former range
132 that the species occupied in a colder past (Brambilla et al., 2015). According to this, climate change
133 will likely impact on boreal owl by reducing the suitability of most of its current range as a
134 consequence of increasing temperatures (Brambilla et al., 2017; Scridel et al., 2017) and/or by
135 altering its preferred breeding habitat type (coniferous or mixed forests) (Brambilla et al., 2015;

136 Hartl-Meier et al., 2014).

137 Tawny owl is a generalist species with a wide niche and distribution, occurring over most of
138 Europe in forest, farmland and also urban habitats, and occupying a broad climatic gradient (Francis
139 & Saurola, 2004; Vrezec & Tome, 2004a; Marchesi et al., 2006). In the Alps, the species is currently
140 expanding its distribution towards higher elevation, most likely due to milder climates (pers. obs.)
141 similar to the northwards expansion observed at higher latitudes, a response to warmer winters and
142 reduced snow cover (Francis & Saurola, 2004).

143 Ural owl, the largest of the owls studied here, is widely distributed in northern Eurasia (Konig,
144 Weick, & Becking, 1999). Towards the south it occurs mostly in mountain areas, inhabiting
145 intermediate elevations in the eastern Alps, particularly in mixed forests with mature trees and
146 clearings (Benussi & Genero, 2008; Rassati, 2006; Vrezec & Mihelič, 2013; Vrezec & Tome,
147 2004a). However, this pattern might be due to the lack of mature forest stands in the lowlands
148 because of intensive logging, since the Ural owl is relatively abundant in preserved mature forest
149 stand fragments in lowlands (Vrezec & Mihelič, 2013). Recent observations indicate that this
150 species is expanding in montane as well as in lowland forest areas in different parts of its southern
151 range in Europe (Bashta, 2009; Vrezec, 2019). So far, only a single study (Huntley, Green,
152 Collingham, & Willis, 2007) has evaluated the potential effect of climate change on its distribution
153 in central-southern Europe.

154 These four species represent an ideal set of interspecific interactions (Fig. 2) for testing the
155 potential disrupting effect of climate change. Black woodpecker facilitates the occurrence of tawny
156 and, especially, boreal owl, providing the great majority of nest cavities for the latter and potential
157 nesting sites for the former (Brambilla et al., 2013; Gustin, Brambilla, & Celada, 2010). Tawny owl
158 is one of the main predators of boreal owl (Konig et al., 1999; Mikkola, 1976). Ural owl can predate
159 both tawny and boreal owls (Mikkola, 1983); competitive exclusion of tawny owls from areas
160 occupied by Ural owls has been reported from northern (Korpimaki, 1986), southern (Vrezec &
161 Tome, 2004a) and eastern Europe (Kajtoch, Źmihorski, & Wieczorek, 2015). Even if Ural owl have

162 been reported to negatively affect breeding density and reproductive success of boreal owl in
163 northern Europe (Hakkarainen & Korpimäki, 1996), the competitive exclusion exerted by Ural owl on
164 tawny owl in the eastern Alps benefits the smaller boreal owl. Ural owl exerts a much lower
165 predation pressure on boreal owl than on tawny owl, and the sites free of tawny owl created by Ural
166 owl occurrence are regularly occupied by boreal owl (Vrezec & Tome, 2004b).

167
168 [Figure 2 approximately here]
169

171 **Data collection**

172 Two different datasets were used for this study. For distribution modelling, we gathered already
173 existing, georeferenced occurrence data, fulfilling the following requirements: spatial accuracy
174 equal or higher than 2 km, period 2000-2017, records within the breeding season of the target
175 species (March-June), or data with an associated atlas code indicating breeding or territorial
176 behaviour. Data were collected both via research projects and citizen science initiatives: i) during
177 previous surveys carried out within the framework of different projects (e.g. (Brambilla et al., 2015,
178 2017; Mihelič et al., 2019; Vrezec & Mihelič, 2013; Vrezec & Tome, 2004a, 2004b), ii) via online
179 platforms (www.ornitho.ch, www.ornitho.at, www.ornitho.it), after official requests specifying the
180 aims of the study. Data were from the study area and from neighbouring sites (i.e., areas
181 surrounding the study region, within the countries investigated; see Suppl. Mat.). A few occurrence
182 points of black woodpecker, located at high elevations (>2000m asl) outside the breeding habitat of
183 the species, were discarded as non representative of the environmental contexts used by the species
184 for reproduction. The final dataset used for modelling comprised 41911 records and included the
185 following sample sizes (number of 2km x 2km cells occupied by each species): 9323 for black
186 woodpecker, 1207 for boreal owl, 5791 for tawny owl, and 436 for Ural owl.

187 The second dataset was used for testing the current effects of interspecific interactions on the

188 presence of three of the species, boreal owl, tawny owl and black woodpecker, given the
189 simultaneous effects of environmental suitability and species co-occurrence. These data were
190 collected by means of dedicated surveys, carried out in northern Italy (in Lombardy region and
191 Trento province), during March-June 2017. Surveys consisted of point counts carried out in the
192 morning (for black woodpecker) and on the same day at dusk/night (for owls). Points were located
193 along several different valleys (see Fig. 1), at an average nearest neighbour distance of ~1100 m
194 (with a minimum of ~450 m in the case of different sides of the same relief), set according to local
195 morphology to avoid double counting of the same individuals as well as to avoid large, unsurveyed
196 tracts of valley. However, there were some general differences in the spacing of points because of
197 the variable geomorphology of the study sites. In Lombardy, the 122 survey sites had an average
198 distance between neighbouring points of c. 1.3 km, and most points were separated by at least 1 km,
199 except when placed on different sides of the same mountain massifs. Within the Trento province
200 study sites, neighbouring points were sometimes located at closer distances (average distance ~850
201 m, minimum ~450), because of the complex valley morphology in the survey sites. At each point,
202 after 10 min of listening to spontaneous vocalizations, if the target species was/were not recorded,
203 we broadcast territorial calls (taken from Roché & Chevereau (2000) of males (owls; playback
204 order: boreal, tawny) and drumming (woodpecker) for one minute (stopping immediately after any
205 contacts), and listened again for four minutes. 218 points were surveyed for black woodpecker (58
206 once, 99 twice, 51 three times). Of these, 192 points were also surveyed for owls (57 once, 91
207 twice, 44 three times). The estimated position of all individuals of target species was recorded on
208 aerial photographs or other detailed maps to avoid double counting from the same or neighbouring
209 points. Ural owl does not occur within the test area, but there is a strong evidence base from
210 intensive fieldwork in the eastern Alps of its interactions with the other species of the guild (Vrezec,
211 2019; Vrezec & Tome, 2004b, 2004a).

212

213 **Modelling current and future distributions**

214 To model the current and likely future distribution of the target species, we used environmental
215 niche models, which combine the occurrence data of a species with a set of environmental
216 predictors (including e.g. climatic, land-use/land-cover and topographical variables) to estimate the
217 suitability of a given area for the study species. We considered a grid composed of 2 km x 2 km
218 cells, covering the entire Alpine region. For each cell, we estimated the proportional cover of the
219 most representative land-use/land-cover types (from CORINE CLC; European Environment
220 Agency, 2016), tree density according to (Moreno, Neumann, & Hasenauer, 2017), and the average
221 value for global solar radiation in May (derived from a 30-m DEM and calculated in GRASS 7.04;
222 Neteler et al., 2012) and climatic variables (from CHELSA database; Karger et al., 2017). We then
223 removed from the environmental predictors those occurring only rarely within the study area
224 (identified by means of visual plotting of each predictor), and the most intercorrelated ones based
225 on CORVIF ($GVI\bar{F} < 16$) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009); the resulting set of
226 variables is summarised in Table S1.

227 We adopted a maximum entropy approach by developing MaxEnt models (Jane Elith et al., 2011;
228 Phillips, Anderson, & Schapire, 2006) in R (R Development Core Team, 2016), using the package
229 ENMeval (Muscarella et al., 2014). We discarded all duplicates, i.e. records occurring within a 2km
230 x 2km cell already having a given species' record. We built models considering the effectively
231 sampled area, by restricting background points ($N = 10\ 000$) to cells with at least one record of any
232 of the target species. In this way, the background corresponded to the visited areas and
233 corresponding environmental characteristics. We built models limiting the type of species-habitat
234 relationships to linear and quadratic, to avoid overfitting; simpler models have to be preferred when
235 it is necessary to expand model outcomes over different areas or temporal scenarios (Brambilla,
236 Pedrini, Rolando, & Chamberlain, 2016). However, for black woodpecker, we also included hinge
237 relationships as the simpler model was not precise enough in terms of correspondence between
238 predicted distribution and current knowledge about real occurrence within the study region. For
239 each species, occurrence data were partitioned into two groups, according to a checkerboard scheme

240 (“checkerboard1” in ENMeval) with each of the units aggregating four original (2km x 2km) cells.
241 This allowed testing model validity over independent datasets, assessing model robustness and
242 enhancing generalizability. Model validity was checked by evaluating variations in discriminatory
243 power (AUC – Area Under the Curve of the receiver operating characteristic (ROC) plot) over the
244 two different data partitions (bins), and by checking omission rates on test data, which had been
245 reclassified using two threshold-dependent metrics, i.e. 10% training omission rates, and training
246 omission for minimum training presence (i.e. lowest suitability at occurrence sites used for training
247 the model); omission rates larger than the expected values suggest overfitting (Muscarella et al.,
248 2014).

249 We tested different values of the regularization multiplier: each model was trained with eight
250 different values (from 0.5 to 4), and then the one with the lowest AIC was selected. Successively, all
251 variables unlikely to be important for species’ distribution (i.e. with both permutation importance
252 and percentage contribution < 1) were discarded, and the model was run again with different values
253 of the regularization multiplier, until we obtained a most supported model with no variables
254 showing both permutation importance and percentage contribution < 1. The raw model outcome
255 was reclassified by means of a logistic transformation to allow an easier interpretation (Elith et al.,
256 2011). The final logistic output of the model was then reclassified into three-class maps of
257 suitability: unsuitable, partly suitable, and suitable. This reclassification was made on the basis of
258 some widely adopted thresholds, generally used for binary reclassification of MaxEnt models, i.e.
259 the 10th percentile and the *maximum training sensitivity plus specificity threshold* (Engler, Rödder,
260 Stiels, & Förschler, 2014; Liu, Berry, Dawson, & Person, 2005; Liu, White, & Newell, 2013).
261 Values between 0 and the lowest of such thresholds were considered as unsuitable, values between
262 the thresholds as partly suitable, and values above the highest one, as definitely suitable. To
263 calculate potential range overlap between species and changes in range extent between current and
264 future conditions for each species, we considered all sites with suitability higher than the lower
265 threshold as potentially occupied by a species (thus both partly suitable and definitely suitable were

266 treated as potentially occupied). Finally, for all species, we removed all those locations at an
267 elevation higher than 2200m asl from suitable and partly suitable areas. In fact, even if some cells
268 around that elevation could be predicted as suitable for the target species, the occurrence of the
269 mature forests required by them is very unlikely at such an elevation in the Alps, and will be rather
270 unlikely to reach it in the near future.

271 Distribution models were then projected over future scenarios of climate change, derived from
272 the HADGEM model, under the worst scenario (representative concentration pathway RCP 8.5,
273 IPCC, 2013), with future climate conditions (for 2050) taken from the Worldclim database
274 (www.worldclim.org; Fick & Hijmans, 2017). We selected a single, pessimistic, scenario because i)
275 we were interested in exploring the potential effect of climate change on a guild of interacting
276 species rather than in obtaining several alternative predictions, e.g. for planning or conservation
277 purposes, and ii) scenarios with larger changes are becoming unfortunately increasingly probable
278 (Peters et al., 2013).

279

280 **Testing the effects of interspecific interactions**

281 To check whether interspecific interactions have the potential to affect the model species, we carried
282 out a field test considering current patterns of co-occurrence of three of our species in a sample of
283 sites in the Italian Alps.

284 We tested for the effect of tawny owl abundance on the number of boreal owls at survey points,
285 and of the effect of black woodpecker occurrence on the local abundance of both tawny and boreal
286 owl. N-mixture models, developed using the package ‘unmarked’ (Fiske & Chandler, 2011) in R (R
287 Development Core Team, 2016), were employed for evaluating the effect of species co-occurrence
288 and environmental suitability on the latent abundance of the target species, while taking into
289 account the potential variation in detectability and hence imperfect detection. Under this approach,
290 repeated counts in a set of sites are used to estimate simultaneously the detectability and the
291 abundance of individuals at survey sites (Ficetola et al., 2018; Royle, 2004). We evaluated the

292 factors that can affect the species' local density by modelling the latent abundance of each species.
293 We assumed population closure because we focused on a single breeding season.

294 As factors potentially affecting the observation process (and hence detection), we tested time of
295 day, survey date, disturbance as a three-level categorical factor (absent; weak – some far or faint
296 noises; strong – close noise or human activities potentially affecting species detection by the
297 observer or even species behaviour), and wind, a three-level categorical factor (calm - Beaufort
298 scale 0-1; weak - Beaufort scale 2-3; moderate - Beaufort scale 4-5). For boreal owl, the number of
299 calling tawny owls was also considered as a variable potentially affecting detection. Instead of
300 entering several abiotic and habitat factors potentially determining species' abundance into the
301 model, we used the environmental suitability produced by the respective MaxEnt models for each
302 species (taking the value of the model cell including the surveyed point), and the maximum
303 abundance of tawny owl recorded at a site for boreal owl. We also tested for a positive effect of
304 occurrence of black woodpecker at a survey point as a proxy for nest-site availability for both owl
305 species. All continuous variables were standardized before the analyses for a better comparison of
306 their relative effects (Cade, 2015; Schielzeth, 2010). For each species, we then developed models
307 based on all possible variable combinations, and ranked them based on the AICc (Akaike's
308 Information Criterion for small sample size), using the package 'MuMIn' (Bartoń, 2016), and
309 checked whether the co-occurrence factors were selected in the most supported models. We
310 repeated the analysis excluding the points surveyed in the Trento province, which often were closer
311 to each other, considering only the points surveyed in Lombardy (see under "Data collection") to
312 check for consistency in the model results when only well-spaced points were included.

313
314

315 **Results**

316

317 **Current distribution and overlap**

318 For all modelled species, the discriminatory power over the two data partitions was nearly identical
319 (all differences < 0.013), omission rates at test sites according to the 10% training threshold showed
320 values invariably close (0.09-0.12) to the expected one (0.10) on both bins (data partitions), and
321 similarly omission values on both bins were always close to zero, as expected (< 0.005); most
322 importantly, the predicted distribution matched well the known breeding range. Summary statistics
323 for models are shown in Table S2. For Ural owl, suitable sites were predicted to occur not only
324 within the current range of the species in the eastern Alps, but also in the central and western part of
325 the Alpine region, although much more sparsely (Fig. 3).

326

327 [Figure 3 approximately here]

328

329 All species were associated with higher forest cover, although for boreal owl, this positive
330 association was relevant only for coniferous forest, and for tawny owl, only deciduous forest (Table
331 1). Furthermore, tawny owl was negatively associated with coniferous forest. Both Ural owl and
332 tawny owl also showed evidence of greater habitat suitability at intermediate cover of variables that
333 can be considered as proxies for open or semi-open habitats within forests (grassland, sparsely
334 vegetated areas, complex cultivation patterns, discontinuous urban fabric). In terms of climatic
335 variables, there was a clearer distinction in the response of the four species. Black woodpecker
336 exhibited a wide thermal niche, with average annual temperature from a few degrees below zero up
337 to 15°C, whilst boreal owl inhabited a cooler part of the temperature gradient, preferring values
338 between -2° and 5°C. Tawny owl was the only species showing a positive linear effect of average
339 temperature on habitat suitability. Habitat suitability for Ural owl was positively affected by annual
340 temperature range and annual precipitation, but negatively by precipitation seasonality (Table 1).

341

342

[Table 1 approximately here]

343

344 The overlap in current modelled distributions was highest for boreal owl and black woodpecker
345 (99% of the former species' range overlappig with the latter), followed by tawny and boreal owls
346 (25%), tawny and Ural owls (15%), boreal and Ural owls (12%), boreal-tawny-Ural owls (6%).

347

348 **Effect of interactions**

349 The N-mixture models revealed important effects of observation covariates on owl detection (see
350 Tables S3 and S4) and, most importantly, a positive effect of environmental suitability (as
351 calculated by MaxEnt models) on species abundance for both owl species considered in the field
352 surveys, with a particularly strong effect for tawny owl (for boreal owl, the variable ranking was
353 slightly different according to the dataset used; Tables S3 and S4). A positive effect of black
354 woodpecker occurrence was found for boreal owl, but not for tawny owl. A negative effect of the
355 abundance of tawny owl on that of boreal owl was also suggested by the models; for boreal owl, the
356 effect of variables describing interspecific interactions was particularly important (Table S3).
357 Notably, all boreal owls occurring in sites where black woodpecker was not detected during the
358 2017 survey, occupied sites predicted to be suitable for the woodpecker by the MaxEnt model, thus
359 potentially offering nest-sites excavated by the woodpecker in previous seasons. The test of
360 interaction effects therefore strongly supported the importance of interspecific interactions for
361 boreal owl, but not for tawny owl.

362

363 **Future distributions**

364 Predicted future environmental suitability for the target species is displayed in Fig. S2 and changes
365 are summarized in Table 2. The distribution of boreal owl will be substantially affected by climate
366 change, with a range reduction and especially a contraction towards higher elevation. Ural owl is

367 predicted to gain suitable areas in Austria and in the central and western Alps, where it is currently
368 absent. Tawny owl will likely show a range expansion towards higher elevations, especially in the
369 central Alps. Black woodpecker distribution will likely undergo only minor changes, even under the
370 rather 'extreme' climate change scenario considered.

371

372 [Table 2 approximately here]

373

374 The potential overlap between the interacting species will change in the future (Fig. 4; see Table
375 S5 for absolute variation). Almost the entire range of boreal owl is predicted to be suitable for black
376 woodpecker both in current and future conditions (Fig. 5); the decrease in extent of potential
377 overlap, due to owl contraction (Fig. 4 and Table S5) will not impact on the potential interactions.
378 The predicted overlap between boreal owl and its main intraguild predator, tawny owl, will show a
379 marked (proportional) increase (from 25% to 54% of boreal owl potential range) and, importantly,
380 will increase in the central Alps (one of the strongholds for boreal owl under a changing climate),
381 because milder climates will enable tawny owl to expand its potential distribution in Alpine valleys.
382 The likely overlap between boreal and Ural owls will decrease in absolute terms, but will keep
383 nearly stable in relative share over the boreal owl range. The areas where Ural owl occurrence could
384 benefit boreal owl (i.e. those with potential occurrence of tawny owl) will decrease (from 6% to 2%
385 of boreal owl range). Finally, the overlap between tawny owl and its competitor/intra-guild
386 predator, the Ural owl, will probably increase over most of the Alps.

387

388

389 [Figure 4 approximately here]

390 [Figure 5 approximately here]

391

392

393 **Discussion**

394 Modification of species interactions in terms of spatial or functional patterns is a potentially crucial,
395 but usually overlooked, consequence of climate change on biological communities. To our
396 knowledge, this is one of the few studies that has investigated patterns of co-occurrence for an
397 interacting guild of birds in response to climate change. We have demonstrated the importance of
398 these interactions on the current distribution of the focal species based on field surveys (boreal owl,
399 tawny, black woodpecker) and empirical evidence (Ural owl). Our combined analyses indicated that
400 both environmental variables (habitat and climate) and interactions with other species were
401 important predictors of species occurrence. The models predicted the current species distribution
402 well and therefore were used to evaluate the potential disruption of the interaction network (via
403 changes in spatial co-occurrence) in this guild in response to future climatic alterations. We have
404 shown that changes to the interaction network are likely to have highly variable effects depending
405 on the particular species, but for boreal owl at least, a spatial increase in areas with negative
406 interactions (without compensatory increases in areas with positive interactions) is very likely to
407 have net negative effects in the future.

408

409 **Large-scale environmental predictors of species occurrence**

410 Environmental correlates of habitat suitability for all model species were coherent with the
411 biological and ecological requirements found in the literature (e.g. Lundberg, 1980; Vrezec &
412 Bertoneclj, 2018; Vrezec & Tome, 2004b). Considering the link with climate, black woodpecker
413 and tawny owl showed the broadest thermal niche, consistent with their wider distribution over the
414 Palearctic. Habitat suitability for tawny owl in the Alps is linearly and positively affected by
415 temperature and thus a positive outcome of the temperature increase could be expected for that
416 species. The recent increase of tawny owl at higher elevations observed in several sites in the Alps
417 (all authors, pers. obs.) confirms this pattern. While temperature changes in the Alpine region are
418 unlikely to severely impact black woodpecker and Ural owl, a strong effect could be expected for

419 boreal owl. For the woodpecker, a possible minor shift towards upper elevations could be expected
420 under extreme scenarios, which is consistent with the broader distribution of the species, which is
421 much more abundant in mountain areas in southern Europe. Boreal owl has already been reported as
422 a climate-sensitive species in the Alps (Brambilla et al., 2015), its distribution at the European scale
423 appears strictly related to temperature (Brambilla et al., 2017), and it is among the cold-adapted
424 species undergoing population decline and range contraction in Europe (Korpimaki & Hakkarainen,
425 2012) and Italy (Scridel et al., 2017).

426

427 **Interspecific interactions, climate change and its consequences**

428 The relative abundance of boreal owl at sampling sites revealed the potential importance of co-
429 occurrence patterns on the species' distribution. Black woodpecker occurrence and abundance of
430 tawny owl were indeed even more important than environmental suitability *per se* for boreal owl in
431 the Central Italian Alps (see under 'Modelling issues' for further discussion), and likely also in the
432 wider Alpine region (Vrezec & Tome, 2004b). This means that, within this largely suitable belt,
433 interspecific dynamics play an important role in driving the occurrence of boreal owl, the species
434 most sensitive to interactions of those investigated. For tawny owl, the presence of black
435 woodpecker is less relevant as the former species has a greater flexibility in selecting suitable
436 cavities for breeding, which include woodpecker holes, but also a variety of old nests, rotten tree
437 trunks, other holes, ledges in rock cliffs and even buildings (Mikkola, 1983). For tawny owl, the
438 environmental suitability derived from MaxEnt models was a better predictor of abundance.

439

440 **Changes in the predicted 'room for interactions'**

441 According to our analysis, climate change will strongly impact on the investigated species both at
442 species level and in the form of community changes in interacting species resulting from
443 distribution shifts, as the area where species interactions are likely to occur is predicted to vary in
444 extent in the future. In most cases, the potential overlap between species range will decline, but it

445 will likely increase for tawny owl and Ural owl, potentially increasing the frequency of competitive
446 interactions between the species. The spatial relevance of the facilitator role of black woodpecker in
447 favour of boreal owl will probably remain unchanged.

448 Boreal owl was the most climate-sensitive species, and will retreat further into the mountains.
449 For this reason alone, the species will lose 65% of its habitat. Therefore, it is not surprising that,
450 while the absolute overlap with the tawny owl will decrease (-26%), the overlap will increase in the
451 area remaining suitable for boreal owl (from 25% to 54%). Since the potential overlap with the
452 black woodpecker and the Ural owl will remain roughly the same, climate change will have a
453 negative effect on the boreal owl both directly (via contraction of suitable areas) and indirectly, via
454 a likely increase in the overlap with tawny owl.

455 Interestingly, our modelling outcomes suggested a potential westwards expansion of Ural owl.
456 This species was until recently confined to the very eastern side of the Alps and eastern Europe
457 (Vrezec, 2009), but was more westerly distributed in historical times (Goffette, Denis, Pöllath, &
458 van Neer, 2016) and in recent decades it has colonized new areas, expanding its range towards the
459 central portion of the Alpine chain (Benussi & Genero, 2008, 2017; Nardelli et al., 2015; Rassati,
460 2006, 2017). Therefore, the modelled increase in suitability in the central and western Alps is fully
461 coherent with the current pattern of range expansion. Successful reintroduction projects recently
462 carried out in Lower Austria (Zink & Walter, 2018) further confirm environmental suitability of the
463 central-eastern Alps for the species, where the provisioning of nest-boxes, which compensates for
464 the widespread lack of nesting sites due to forest harvesting, could further favour the species'
465 westward expansion. The ongoing expansion of Ural owl, coupled with that of tawny owl, implies
466 an increasing potential overlap and thus likely increasing interactions between these two competing
467 species (Figs. 4 and 5).

468

469 **Modelling issues**

470 The distribution models we obtained (at a spatial scale highly representative of the territory

471 size/home range of the species) appeared rather robust for all species, with a high level of
472 consistency in discriminatory power over the two partitions of the dataset (Table S2). The resulting
473 predicted distributions were in line with the current range of target species in the Alps. Similarly,
474 the species-habitat relationships underlying the models were coherent with the knowledge of
475 species' ecology.

476 Other species interact with the target ones. These basically include prey, and especially voles
477 (Brommer, Pietiäinen, & Kolunen, 2002; Korpimäki & Hakkarainen, 2012; Vrežec, Saurola,
478 Avotins, Kocijančič, & Sulkava, 2018), as well as other predators, like goshawk *Accipiter gentilis*
479 and eagle owl *Bubo bubo* (Byholm, Burgas, Virtanen, & Valkama, 2012; Hakkarainen &
480 Korpimäki, 1996; Lõhmus, 2003; Mikkola, 1976, 1983; Sergio, Marchesi, Pedrini, & Penteriani,
481 2007). Such additional factors might further modulate the effect of competition and coexistence at a
482 finer scale (Ciach, 2008; Ciach & Czyżowicz, 2014).

483 Finally, local forest characteristics, potentially sensitive to human management and climate
484 change (Braunisch et al., 2014), can be important, especially for black woodpecker (Karimi et al.,
485 2018; Pirovano & Zecca, 2014). However, at broader scales they are unlikely to be relevant (see e.g.
486 Tjernberg, Johnsson, & Nilsson, 1993; Brambilla & Saporetti, 2014), as the ongoing range
487 expansion in a large part of the study area suggests (Gustin, Brambilla, & Celada, 2019). In
488 addition, we cannot completely exclude the possibility that the effect of black woodpecker and
489 tawny owl (positive and negative, respectively) on boreal owl occurrence, highlighted by N-mixture
490 models, could be due to an influence of some unmeasured habitat variable which has an effect on
491 both interacting species of a given species pair. However, we are confident that these effects are
492 likely mirroring true interaction effects. Black woodpeckers provide almost all boreal owl nest-sites
493 in the study area (Pedrini, Caldonazzi, & Zanghellini, 2005), and hence a potential unmeasured
494 habitat variable could also be represented by a better-than-average availability of cavities. On the
495 other side, tawny owls have been shown to significantly impact on boreal owl occurrence (Vrežec &
496 Tome, 2004b), and we are aware of several cases of local replacement in recent years (our pers. obs.

497 from Italy, Austria and Slovenia). Nevertheless, long-term studies that include more detailed habitat
498 descriptions would better elucidate whether the positive and negative relationships are consistent
499 with regard to temporal variation in the same habitat, and therefore some caution is needed in
500 interpreting the observed patterns.

501

502 **Conclusions**

503 Climate change will result in the disruption or alteration of species interaction networks (Blois et
504 al., 2013; Tylianakis et al., 2008). Several studies have investigated the potential impacts of
505 variations in climate on animal-plant networks (insects and host species, plants and their pollinators;
506 e.g. Schweiger et al., 2008; Gorostiague et al., 2018). However, fewer studies have dealt with
507 changes in interspecific relationships among vertebrates, with the main exception represented by
508 carnivorous mammals (e.g. Zielinski et al., 2017; Pandey & Papeş, 2018; Scully et al., 2018). Here,
509 we have shown how climate change will result in changes in the distribution overlap in a guild of
510 interacting species, with different consequences for the species belonging to this guild. The process
511 will likely result in an increase in areas where the target species will experience competition and/or
512 intraguild predation rates, due to a higher proportional range overlap between subordinate (boreal
513 and tawny owl) and dominant (tawny and Ural owl, respectively) species. In turn, these changes
514 will probably enhance the importance of interaction effects for those species at the regional scale.
515 The facilitation provided by black woodpecker to boreal owl (nest provision) would instead remain
516 substantially unchanged, but the latter species will likely be the most negatively affected by climate
517 change.

518 Our work modelled the potential effects of climate change on the distribution of an interacting
519 owl guild and of its main nest facilitator, the black woodpecker, and showed potential important
520 changes in the overlap of suitable areas for those interacting species. The analysis of current
521 patterns of abundance at the local scale confirmed the likely importance of interspecific
522 interactions. Taken together, our findings suggest that future predictions of species distribution

523 under climate change should include relevant biotic interactions to achieve higher forecast
524 accuracy; in particular, testing the relevance of interspecific interactions will facilitate the
525 interpretation of distribution models and the more reliable estimation of predicted range changes.

526

527

528

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546

547 **Author contributions**

548 MB conceived the idea, which was then developed by all authors. MB, DS, PP, GBa, LI, EB, RB,

549 LM, FG, NT, RP, AV, PK, TM, RP, GA, HS collected data on the field and/or through database
550 interrogation. DS processed bird data; DS and AI prepared environmental layers. MB ran the
551 analyses and all authors contributed to model checking/development and check final model
552 outcomes. MB with DS' help wrote a first draft of the ms. All authors critically contributed to the
553 final version.
554

555 **Table 1.** Environmental factors used to model species distributions that were selected in at least one
556 model (see Table S1 for full list), the relative importance of each factor (percentage
557 contribution/permutation importance) and short description of the effect (within brackets; relative to
558 the model including all the selected predictors) according to final models for each species.
559 Numerical codes for land cover variables represent CORINE categories. Symbols used for effects:
560 +: positive, -: negative, +/-: quadratic (hump-shaped), -/+: quadratic (U-shaped), +/--: quadratic
561 (hump-shaped)/negative, 0: nearly null (very weak positive effect).
562

Variable	Description	Boreal owl	Tawny owl	Ural owl	Black woodpecker
bio_1	Annual Mean Temperature	76.60/81.27 (+/--)	31.93/54.68 (+)		16.91/20.23 (+/--)
bio_12	Annual Precipitation		1.47/2.67 (+)	17.61/2.80 (+)	14.17/36.82 (-)
bio_15	Precipitation Seasonality (Coefficient of Variation)	2.96/4.21 (-)	5.93/0.00 (-)	12.47/22.94 (-)	
bio_19	Precipitation of Coldest Quarter	2.64/0.37 (-/+)		4.05/0.00 (0)	
bio_7	Temperature Annual Range (BIO5-BIO6)	2.23/5.66 (-)	24.01/35.13 (-)	15.99/14.94 (+)	
solarMay	Global solar radiation for May		1.66/4.49 (+)	0.86/0.78 (+)	8.24/13.22 (+/--)
X15	2.2.1 Vineyards				0.64/0.66 (-)
X18	2.3.1 Pastures		1.02/0.43 (+)	0.61/0.22 (-)	0.20/0.69 (-)
X1.1	1.1.2 Continuous urban fabric			0.38/0.94 (+)	0.90/0.25 (-)
X2.1	1.1.1 Discontinuous urban fabric	0.29/1.05 (-)	0.85/0.77 (+)	1.03/0.94 (+)	1.60/0.0 (-)
X20	2.4.2 Complex cultivation patterns		0.25/1.21 (+)		0.65/3.33 (-)
X21	2.4.3 Land principally occupied by agriculture, with significant areas of natural vegetation			0.62/0.42 (-)	
X25	3.1.3 Mixed forest			4.75/0.00 (+)	
X26	3.2.1 Natural grasslands		9.44/0.00 (-)		
X31	3.3.2 Bare rocks		2.79/0.44 (-)		
X32	3.3.3 Sparsely vegetated areas	0.75/0.48 (-)	6.03/0.00 (-)	1.55/1.50 (-)	
X35	4.1.1 Inland marshes				1.61/2.97 (+)
X4	1.2.2 Road and rail networks and associated land				0.49/2.31 (-)
X40	5.1.1 Water courses				1.03/3.43 (+)
x2632_TCD_TCD_20m	Tree cover density	0.72/1.63 (+)		25.89/0.22 (-)	18.07/11.02 (+/--)
X2.2	x2632_TCD_FTY_20m Coniferous forest	13.83/5.33 (+)	14.62/0.19 (-)	5.16/17.55 (+)	33.63/2.00 (+)
X1.2	x2632_TCD_FTY_20m Deciduous forest			9.14/36.75 (+)	1.84/3.07 (+)

564

565

566 **Table 2.** Predicted extent of suitable habitats in current and future conditions (RCP 8.5 scenario for
567 2050) for the target species.

568

Species	current extent of suitable area (km²)	future extent of suitable area (km²)	change (%)
boreal owl	85644	29988	-65
tawny owl	95200	120928	+27
Ural owl	20012	67200	+236
black woodpecker	160452	151564	-6

569

570

571

572

573 **Figure captions**

574

575 **Figure 1.** Study area. The darker the colour, the higher the elevation. The inset shows the location
576 of the point counts (yellow dots) used to test the interspecific effects on current distribution patterns
577 for boreal and tawny owl.

578

579 **Figure 2.** Schematic representation of the interspecific interactions characterizing the study guild of
580 forest birds. Larger arrows indicate stronger effects. The negative effect of Ural owl on tawny owl,
581 in combination with the negative effect of tawny owl on boreal owl, appears as facilitation for
582 boreal owl when viewed in isolation.

583

584 **Figure 3.** Modelled current distribution of boreal owl (upper left), tawny owl (upper right), Ural
585 owl (lower left) and black woodpecker (lower right). The darker the colour, the higher the
586 environmental suitability.

587

588 **Figure 4.** Predicted range overlap under current (yellow) and future climatic conditions (blue; in
589 green, areas with predicted overlap under both scenarios), between boreal owl and black
590 woodpecker (upper left), boreal owl and tawny owl (upper right), tawny owl and Ural owl (lower
591 left), boreal owl and Ural owl (lower right).

592

593 **Figure 5.** Graphical representation of predicted extent of overlap between species and relative
594 variation due to climate change. For each scenario (current and future), boreal owl range is depicted
595 in beige, and tawny owl range in brown. The proportional overlap with other species is shown in
596 each pie chart, in black (black woodpecker for boreal owl), brown (tawny owl for boreal owl), grey
597 (Ural owl for both species). For boreal owl, the overlap with both tawny and Ural owl is shown in
598 grey-brown. Pie chart size is proportional to the relative value of current (100%) and future species

599 range (35% for boreal owl, 127% for tawny owl).

600

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