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

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# UNIVERSITÀ DEGLI STUDI DI TORINO

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

16

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

18

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46

47 **Abstract:**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

65 cause the geographical alteration or disruption of species interaction networks, with different

66 consequences for the species belonging to the guild and a likely spatial increase of competition  
67 and/or intraguild predation. Our work shows significant interactions and important potential  
68 changes in the overlap of areas suitable for the interacting species, which reinforce the importance  
69 of including relevant biotic interactions in predictive climate change models for increasing forecast  
70 accuracy.

71

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

## 73 **Introduction**

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

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

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

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

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

120

121

122 **Material and methods**

123 **Study system**

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

131

132 [Figure 1 approximately here]

133

134 Black woodpecker, the only diurnal taxon among the modelled species, is tied to mature forests,  
135 with large stems and availability of dead wood and ant-rich habitats (Brambilla & Saporetti, 2014;  
136 Karimi, Moradi, Rezaei, Brambilla, & Ghadimi, 2018; Pirovano & Zecca, 2014) over a wide  
137 elevation gradient, from sea level to c.2000 m asl. This species has shown a dramatic increase in the  
138 Alps, and colonization of previously unoccupied lowland forests (Nardelli et al., 2015). This  
139 expansion is most likely due to an increase in forest quality and extent (Nardelli et al., 2015; see  
140 also Mikusiński, 1995), yet no study has investigated the potential impact of climate change on this  
141 species, with the exception of a paper suggesting future retraction in central Europe (Vos et al.,  
142 2008).

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



148 Hartl-Meier et al., 2014).

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

155 Ural owl, the largest of the owls studied here, is widely distributed in northern Eurasia (Konig,  
156 Weick, & Becking, 1999). Towards the south it occurs mostly in mountain areas, inhabiting  
157 intermediate elevations in the eastern Alps, particularly in mixed forests with mature trees and  
158 clearings (Benussi & Genero, 2008; Rassati, 2006; Vrezec & Mihelič, 2013; Vrezec & Tome,  
159 2004a). However, this pattern might be due to the lack of mature forest stands in the lowlands  
160 because of intensive logging, since the Ural owl is relatively abundant in preserved mature forest  
161 stand fragments in lowlands (Vrezec & Mihelič, 2013). Recent observations indicate that this  
162 species is expanding in montane as well as in lowland forest areas in different parts of its southern  
163 range in Europe (Bashta, 2009; Vrezec, 2019). So far, only a single study (Huntley, Green,  
164 Collingham, & Willis, 2007) has evaluated the potential effect of climate change on its distribution  
165 in central-southern Europe.

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

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

179

180 [Figure 2 approximately here]

181

182

### 183 **Data collection**

184 Two different datasets were used for this study. For distribution modelling, we gathered already  
185 existing, georeferenced occurrence data, fulfilling the following requirements: spatial accuracy  
186 equal or higher than 2 km, period 2000-2017, records within the breeding season of the target  
187 species (March-June), or data with an associated atlas code indicating breeding or territorial  
188 behaviour. Data were collected both via research projects and citizen science initiatives: i) during  
189 previous surveys carried out within the framework of different projects (e.g. (Brambilla et al., 2015,  
190 2017; Mihelič et al., 2019; Vrezec & Mihelič, 2013; Vrezec & Tome, 2004a, 2004b), ii) via online  
191 platforms (www.ornitho.ch, www.ornitho.at, www.ornitho.it), after official requests specifying the  
192 aims of the study. Data were from the study area and from neighbouring sites (i.e., areas  
193 surrounding the study region, within the countries investigated; see Suppl. Mat.). A few occurrence  
194 points of black woodpecker, located at high elevations (>2000m asl) outside the breeding habitat of  
195 the species, were discarded as non representative of the environmental contexts used by the species  
196 for reproduction. The final dataset used for modelling comprised 41911 records and included the  
197 following sample sizes (number of 2km x 2km cells occupied by each species): 9323 for black  
198 woodpecker, 1207 for boreal owl, 5791 for tawny owl, and 436 for Ural owl.

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

200 presence of three of the species, boreal owl, tawny owl and black woodpecker, given the  
201 simultaneous effects of environmental suitability and species co-occurrence. These data were  
202 collected by means of dedicated surveys, carried out in northern Italy (in Lombardy region and  
203 Trento province), during March-June 2017. Surveys consisted of point counts carried out in the  
204 morning (for black woodpecker) and on the same day at dusk/night (for owls). Points were located  
205 along several different valleys (see Fig. 1), at an average nearest neighbour distance of ~1100 m  
206 (with a minimum of ~450 m in the case of different sides of the same relief), set according to local  
207 morphology to avoid double counting of the same individuals as well as to avoid large, unsurveyed  
208 tracts of valley. However, there were some general differences in the spacing of points because of  
209 the variable geomorphology of the study sites. In Lombardy, the 122 survey sites had an average  
210 distance between neighbouring points of c. 1.3 km, and most points were separated by at least 1 km,  
211 except when placed on different sides of the same mountain massifs. Within the Trento province  
212 study sites, neighbouring points were sometimes located at closer distances (average distance ~850  
213 m, minimum ~450), because of the complex valley morphology in the survey sites. At each point,  
214 after 10 min of listening to spontaneous vocalizations, if the target species was/were not recorded,  
215 we broadcast territorial calls (taken from Roché & Chevereau (2000) of males (owls; playback  
216 order: boreal, tawny) and drumming (woodpecker) for one minute (stopping immediately after any  
217 contacts), and listened again for four minutes. 218 points were surveyed for black woodpecker (58  
218 once, 99 twice, 51 three times). Of these, 192 points were also surveyed for owls (57 once, 91  
219 twice, 44 three times). The estimated position of all individuals of target species was recorded on  
220 aerial photographs or other detailed maps to avoid double counting from the same or neighbouring  
221 points. Ural owl does not occur within the test area, but there is a strong evidence base from  
222 intensive fieldwork in the eastern Alps of its interactions with the other species of the guild (Vrezec,  
223 2019; Vrezec & Tome, 2004b, 2004a).

224

225 **Modelling current and future distributions**

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

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

252 (“checkerboard1” in ENMeval) with each of the units aggregating four original (2km x 2km) cells.  
253 This allowed testing model validity over independent datasets, assessing model robustness and  
254 enhancing generalizability. Model validity was checked by evaluating variations in discriminatory  
255 power (AUC – Area Under the Curve of the receiver operating characteristic (ROC) plot) over the  
256 two different data partitions (bins), and by checking omission rates on test data, which had been  
257 reclassified using two threshold-dependent metrics, i.e. 10% training omission rates, and training  
258 omission for minimum training presence (i.e. lowest suitability at occurrence sites used for training  
259 the model); omission rates larger than the expected values suggest overfitting (Muscarella et al.,  
260 2014).

261 We tested different values of the regularization multiplier: each model was trained with eight  
262 different values (from 0.5 to 4), and then the one with the lowest AIC was selected. Successively, all  
263 variables unlikely to be important for species’ distribution (i.e. with both permutation importance  
264 and percentage contribution < 1) were discarded, and the model was run again with different values  
265 of the regularization multiplier, until we obtained a most supported model with no variables  
266 showing both permutation importance and percentage contribution < 1. The raw model outcome  
267 was reclassified by means of a logistic transformation to allow an easier interpretation (Elith et al.,  
268 2011). The final logistic output of the model was then reclassified into three-class maps of  
269 suitability: unsuitable, partly suitable, and suitable. This reclassification was made on the basis of  
270 some widely adopted thresholds, generally used for binary reclassification of MaxEnt models, i.e.  
271 the 10<sup>th</sup> percentile and the *maximum training sensitivity plus specificity threshold* (Engler, Rödder,  
272 Stiels, & Förchler, 2014; Liu, Berry, Dawson, & Person, 2005; Liu, White, & Newell, 2013).  
273 Values between 0 and the lowest of such thresholds were considered as unsuitable, values between  
274 the thresholds as partly suitable, and values above the highest one, as definitely suitable. To  
275 calculate potential range overlap between species and changes in range extent between current and  
276 future conditions for each species, we considered all sites with suitability higher than the lower  
277 threshold as potentially occupied by a species (thus both partly suitable and definitely suitable were

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

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

291

## 292 **Testing the effects of interspecific interactions**

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

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

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

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

325  
326

327 **Results**

328

329 **Current distribution and overlap**

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

338

339 [Figure 3 approximately here]

340

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



353

354

[Table 1 approximately here]

355

356 The overlap in current modelled distributions was highest for boreal owl and black woodpecker  
357 (99% of the former species' range overlapping with the latter), followed by tawny and boreal owls  
358 (25%), tawny and Ural owls (15%), boreal and Ural owls (12%), boreal-tawny-Ural owls (6%).

359

### 360 **Effect of interactions**

361 The N-mixture models revealed important effects of observation covariates on owl detection (see  
362 Tables S3 and S4) and, most importantly, a positive effect of environmental suitability (as  
363 calculated by MaxEnt models) on species abundance for both owl species considered in the field  
364 surveys, with a particularly strong effect for tawny owl (for boreal owl, the variable ranking was  
365 slightly different according to the dataset used; Tables S3 and S4). A positive effect of black  
366 woodpecker occurrence was found for boreal owl, but not for tawny owl. A negative effect of the  
367 abundance of tawny owl on that of boreal owl was also suggested by the models; for boreal owl, the  
368 effect of variables describing interspecific interactions was particularly important (Table S3).  
369 Notably, all boreal owls occurring in sites where black woodpecker was not detected during the  
370 2017 survey, occupied sites predicted to be suitable for the woodpecker by the MaxEnt model, thus  
371 potentially offering nest-sites excavated by the woodpecker in previous seasons. The test of  
372 interaction effects therefore strongly supported the importance of interspecific interactions for  
373 boreal owl, but not for tawny owl.

374

### 375 **Future distributions**

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

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

383

384 [Table 2 approximately here]

385

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

399

400

401 [Figure 4 approximately here]

402 [Figure 5 approximately here]

403

404

## 405 **Discussion**

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

420

## 421 **Large-scale environmental predictors of species occurrence**

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

431 boreal owl. For the woodpecker, a possible minor shift towards upper elevations could be expected  
432 under extreme scenarios, which is consistent with the broader distribution of the species, which is  
433 much more abundant in mountain areas in southern Europe. Boreal owl has already been reported as  
434 a climate-sensitive species in the Alps (Brambilla et al., 2015), its distribution at the European scale  
435 appears strictly related to temperature (Brambilla et al., 2017), and it is among the cold-adapted  
436 species undergoing population decline and range contraction in Europe (Korpimaki & Hakkarainen,  
437 2012) and Italy (Scridel et al., 2017).

438

### 439 **Interspecific interactions, climate change and its consequences**

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

451

### 452 **Changes in the predicted 'room for interactions'**

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

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

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

467 Interestingly, our modelling outcomes suggested a potential westwards expansion of Ural owl.  
468 This species was until recently confined to the very eastern side of the Alps and eastern Europe  
469 (Vrezec, 2009), but was more westerly distributed in historical times (Goffette, Denis, Pöllath, &  
470 van Neer, 2016) and in recent decades it has colonized new areas, expanding its range towards the  
471 central portion of the Alpine chain (Benussi & Genero, 2008, 2017; Nardelli et al., 2015; Rassati,  
472 2006, 2017). Therefore, the modelled increase in suitability in the central and western Alps is fully  
473 coherent with the current pattern of range expansion. Successful reintroduction projects recently  
474 carried out in Lower Austria (Zink & Walter, 2018) further confirm environmental suitability of the  
475 central-eastern Alps for the species, where the provisioning of nest-boxes, which compensates for  
476 the widespread lack of nesting sites due to forest harvesting, could further favour the species'  
477 westward expansion. The ongoing expansion of Ural owl, coupled with that of tawny owl, implies  
478 an increasing potential overlap and thus likely increasing interactions between these two competing  
479 species (Figs. 4 and 5).

480

#### 481 **Modelling issues**

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

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

488 Other species interact with the target ones. These basically include prey, and especially voles  
489 (Brommer, Pietiäinen, & Kolunen, 2002; Korpimäki & Hakkarainen, 2012; Vrezec, Saurola,  
490 Avotins, Kocijančič, & Sulkava, 2018), as well as other predators, like goshawk *Accipiter gentilis*  
491 and eagle owl *Bubo bubo* (Byholm, Burgas, Virtanen, & Valkama, 2012; Hakkarainen &  
492 Korpimäki, 1996; Lõhmus, 2003; Mikkola, 1976, 1983; Sergio, Marchesi, Pedrini, & Penteriani,  
493 2007). Such additional factors might further modulate the effect of competition and coexistence at a  
494 finer scale (Ciach, 2008; Ciach & Czyżowicz, 2014).

495 Finally, local forest characteristics, potentially sensitive to human management and climate  
496 change (Braunisch et al., 2014), can be important, especially for black woodpecker (Karimi et al.,  
497 2018; Pirovano & Zecca, 2014). However, at broader scales they are unlikely to be relevant (see e.g.  
498 Tjernberg, Johnsson, & Nilsson, 1993; Brambilla & Saporetto, 2014), as the ongoing range  
499 expansion in a large part of the study area suggests (Gustin, Brambilla, & Celada, 2019). In  
500 addition, we cannot completely exclude the possibility that the effect of black woodpecker and  
501 tawny owl (positive and negative, respectively) on boreal owl occurrence, highlighted by N-mixture  
502 models, could be due to an influence of some unmeasured habitat variable which has an effect on  
503 both interacting species of a given species pair. However, we are confident that these effects are  
504 likely mirroring true interaction effects. Black woodpeckers provide almost all boreal owl nest-sites  
505 in the study area (Pedrini, Caldonazzi, & Zanghellini, 2005), and hence a potential unmeasured  
506 habitat variable could also be represented by a better-than-average availability of cavities. On the  
507 other side, tawny owls have been shown to significantly impact on boreal owl occurrence (Vrezec &  
508 Tome, 2004b), and we are aware of several cases of local replacement in recent years (our pers. obs.

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

513

## 514 **Conclusions**

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

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

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

538

539

540

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558

#### 559 **Author contributions**

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



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

566

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

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 (+)

575

576 **Table 2.** Predicted extent of suitable habitats in current and future conditions (RCP 8.5 scenario for  
577 2050) for the target species.

578

<b>Species</b>	<b>current extent of suitable area (km<sup>2</sup>)</b>	<b>future extent of suitable area (km<sup>2</sup>)</b>	<b>change (%)</b>
boreal owl	85644	29988	-65
tawny owl	95200	120928	+27
Ural owl	20012	67200	+236
black woodpecker	160452	151564	-6

579

580

581

582

583 **Figure captions**

584

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

588

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

593

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

597

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

602

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

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

610



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