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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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Abstract

Interspecific interactions are crucial in determining species occurrence and community assembly. Understanding these interactions is thus essential for correctly predicting species' responses to climate change. We focussed on an avian forest guild of four hole-nesting species with differing sensitivities to climate that show a range of well-understood reciprocal interactions, including facilitation, competition and predation. We modelled the potential distributions of black woodpecker and boreal, tawny and Ural owl, and tested whether the spatial patterns of the more widespread species (excluding Ural owl) were shaped by interspecific interactions. We then modelled the potential future distributions of all four species, evaluating how the predicted changes will alter the overlap between the species' ranges, and hence the spatial outcomes of interactions. Forest cover/type and climate were important determinants of habitat suitability for all species. Field data analysed with N-mixture models revealed effects of interspecific interactions on current species abundance, especially in boreal owl (positive effects of black woodpecker, negative effects of tawny owl). Climate change will impact the assemblage both at species and guild levels, as the potential area of range overlap, relevant for species interactions, will change in both proportion and extent in the future. Boreal owl, the most climate-sensitive species in the guild, will retreat, and the range overlap with its main predator, tawny owl, will increase in the remaining suitable area: climate change will thus impact on boreal owl both directly and indirectly. Climate change will cause the geographical alteration or disruption of species interaction networks, with different consequences for the species belonging to the guild and a likely spatial increase of competition and/or intraguild predation. Our work shows significant interactions and important potential changes in the overlap of areas suitable for the interacting species, which reinforce the importance of including relevant biotic interactions in predictive climate change models for increasing forecast accuracy.

KEYWORDS

biotic interactions, citizen science, global warming, owls, SDM, woodpeckers

Mattia Brambilla and Davide Scridel should be considered joint first author.

1 | INTRODUCTION

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

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

Facilitation (a positive interaction whereby one species promotes the occurrence of another) and intraguild predation are two particular biotic interactions that have been found to be very important for predicting the occurrence of several species (Heikkinen et al., 2007; Holt & Huxel, 2007), but have received little attention in terms of how they could be altered by the influence of climate change (but see Bateman, Vanderwal, Williams, & Johnson, 2012). In fact, variation in climatic conditions may impact on facilitation relationships as well as on intraguild predation (e.g. Rogers, Gouhier, & Kimbro, 2018), with potentially cascading effects over the entire system (Barton & Schmitz, 2009).

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

2 | MATERIALS AND METHODS

2.1 | Study system

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

Black woodpecker, the only diurnal taxon among the modelled species, is tied to mature forests, with large stems and availability of dead wood and ant-rich habitats (Brambilla & Saporetti, 2014; Karimi, Moradi, Rezaei, Brambilla, & Ghadimi, 2018; Pirovano & Zecca, 2014) over a wide elevation gradient, from sea level to c. 2,000 m a.s.l. This species has shown a dramatic increase in the Alps, and colonization of previously unoccupied lowland forests (Nardelli et al., 2015). This expansion is most likely due to an increase in forest quality and extent (Nardelli et al., 2015; see also Mikusiński, 1995), yet no study has investigated the potential impact of climate change on this species, with the exception of a paper suggesting future retraction in central Europe (Vos et al., 2008).

The Alps are a climate *refugium* for boreal owl, representing a relict portion of the former range that the species occupied in a colder past (Brambilla, Bergero, Bassi, & Falco, 2015). According to this, climate change will likely impact on boreal owl by reducing the suitability of most of its current range as a consequence of increasing
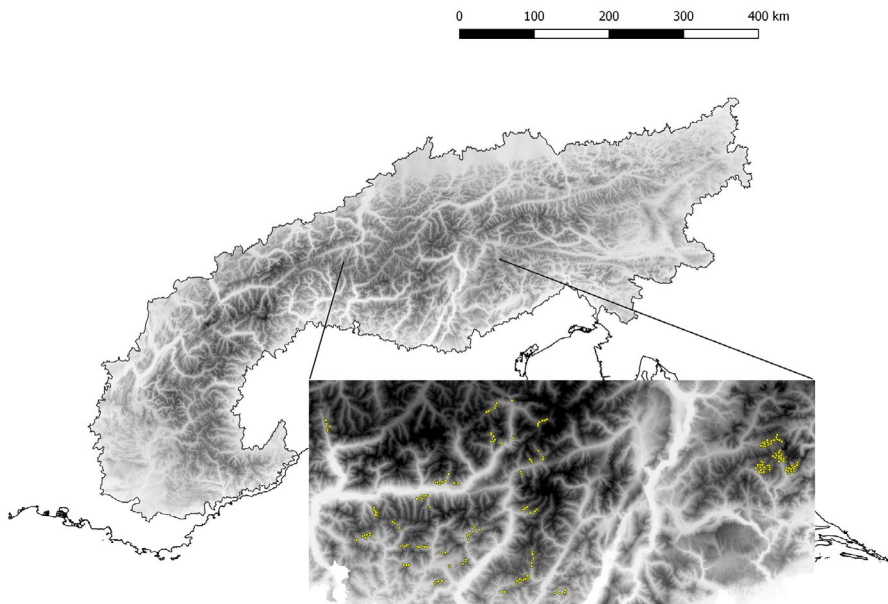
FIGURE 1 Study area. The darker the colour, the higher the elevation. The inset shows the location of the point counts (yellow dots) used to test the interspecific effects on current distribution patterns for boreal and tawny owl [Colour figure can be viewed at wileyonlinelibrary.com]

temperatures (Brambilla et al., 2017; Scridel et al., 2017) and/or by altering its preferred breeding habitat type (coniferous or mixed forests; Brambilla et al., 2015; Hartl-Meier et al., 2014).

Tawny owl is a generalist species with a wide niche and distribution, occurring over most of Europe in forest, farmland and also urban habitats, and occupying a broad climatic gradient (Francis & Saurola, 2004; Marchesi, Sergio, & Pedrini, 2006; Vrezec & Tome, 2004a). In the Alps, the species is currently expanding its distribution towards higher elevation, most likely due to milder climates (P. Pedrini and others, over the last two decades, personal observation) similar to the northwards expansion observed at higher latitudes, a response to warmer winters and reduced snow cover (Francis & Saurola, 2004).

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

These four species represent an ideal set of interspecific interactions (Figure 2) for testing the potential disrupting effect of climate change. Black woodpecker facilitates the occurrence of tawny and, especially, boreal owl, providing the great majority of nest cavities for the latter and potential nesting sites for the former (Brambilla et al., 2013; Gustin, Brambilla, & Celada, 2010). Tawny owl is one of the main predators of boreal owl (Konig et al., 1999; Mikkola, 1976).
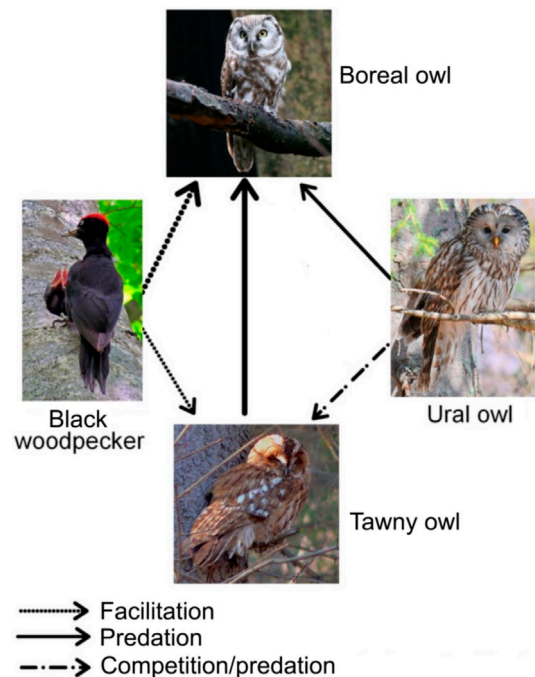

FIGURE 2 Schematic representation of the interspecific interactions characterizing the study guild of forest birds. Larger arrows indicate stronger effects. The negative effect of Ural owl on tawny owl, in combination with the negative effect of tawny owl on boreal owl, appears as facilitation for boreal owl when viewed in isolation [Colour figure can be viewed at wileyonlinelibrary.com]

Ural owl can predate both tawny and boreal owls (Mikkola, 1983); competitive exclusion of tawny owls from areas occupied by Ural owls has been reported from northern (Korpimaki, 1986), southern (Vrezec & Tome, 2004a) and eastern Europe (Kajtoch, Żmihorski, & Wieczorek, 2015). Even if Ural owl have been reported to negatively affect breeding density and reproductive success of boreal owl in northern Europe (Hakkarainen & Korpimaki, 1996), the competitive

exclusion exerted by Ural on tawny owl in the eastern Alps benefits the smaller boreal owl. Ural owl exerts a much lower predation pressure on boreal owl than on tawny owl, and the sites free of tawny owl created by Ural owl occurrence are regularly occupied by boreal owl (Vrezec & Tome, 2004b).

2.2 | Data collection

Two different data sets were used for this study. For distribution modelling, we gathered already existing, georeferenced occurrence data, fulfilling the following requirements: spatial accuracy equal or higher than 2 km, period 2000–2017, records within the breeding season of the target species (March–June) or data with an associated atlas code indicating breeding or territorial behaviour. Data were collected both via research projects and citizen science initiatives: (a) during previous surveys carried out within the framework of different projects (e.g. Brambilla et al., 2015; Brambilla et al., 2017; Mihelič et al., 2019; Vrezec & Mihelič, 2013; Vrezec & Tome, 2004a, 2004b); (b) via online platforms (www.ornitho.ch, www.ornitho.at, www.ornitho.it), after official requests specifying the aims of the study. Data were from the study area and from neighbouring sites (i.e. areas surrounding the study region, within the countries investigated; see Supporting Information). A few occurrence points of black woodpecker, located at high elevations (>2000 m a.s.l.) outside the breeding habitat of the species, were discarded as non-representative of the environmental contexts used by the species for reproduction. The final data set used for modelling comprised 41,911 records and included the following sample sizes (number of 2 km × 2 km cells occupied by each species): 9,323 for black woodpecker, 1,207 for boreal owl, 5,791 for tawny owl, and 436 for Ural owl.

The second data set was used for testing the current effects of interspecific interactions on the presence of three of the species, boreal owl, tawny owl and black woodpecker, given the simultaneous effects of environmental suitability and species co-occurrence. These data were collected by means of dedicated surveys, carried out in northern Italy (in Lombardy region and Trento province), during March–June 2017. Surveys consisted of point counts carried out in the morning (for black woodpecker) and on the same day at dusk/night (for owls). Points were located along several different valleys (see Figure 1), at an average nearest neighbour distance of ~1,100 m (with a minimum of ~450 m in the case of different sides of the same relief), set according to local morphology to avoid double counting of the same individuals as well as to avoid large, unsurveyed tracts of valley. However, there were some general differences in the spacing of points because of the variable geomorphology of the study sites. In Lombardy, the 122 survey sites had an average distance between neighbouring points of c. 1.3 km, and most points were separated by at least 1 km, except when placed on different sides of the same mountain massifs. Within the Trento province study sites, neighbouring points were sometimes located at closer distances (average distance ~850 m, minimum ~450), because of the complex valley morphology in the survey sites. At each point, after 10 min

of listening to spontaneous vocalizations, if the target species was/were not recorded, we broadcast territorial calls (taken from Roché & Chevereau, 2001) of males (owls; playback order: boreal, tawny) and drumming (woodpecker) for one minute (stopping immediately after any contacts), and listened again for 4 min. 218 points were surveyed for black woodpecker (68 once, 99 twice, 51 three times). Of these, 192 points were also surveyed for owls (57 once, 91 twice, 44 three times). The estimated position of all individuals of target species was recorded on aerial photographs or other detailed maps to avoid double counting from the same or neighbouring points. Ural owl does not occur within the test area, but there is a strong evidence base from intensive fieldwork in the eastern Alps of its interactions with the other species of the guild (Vrezec, 2019; Vrezec & Tome, 2004b, 2004a).

2.3 | Modelling current and future distributions

To model the current and likely future distribution of the target species, we used ENMs, which combine the occurrence data of a species with a set of environmental predictors (including e.g. climatic, land use/land cover and topographical variables) to estimate the suitability of a given area for the study species. We considered a grid composed of 2 km × 2 km cells, covering the entire Alpine region. For each cell, we estimated the proportional cover of the most representative land use/land cover types (from CORINE CLC; European Environment Agency, 2016), tree density according to Moreno, Neumann, and Hasenauer (2017) and the average value for global solar radiation in May (derived from a 30 m digital elevation model and calculated in GRASS 7.04; Neteler, Bowman, Landa, & Metz, 2012) and climatic variables (from CHELSA database; Karger et al., 2017). We then removed from the environmental predictors those occurring only rarely within the study area (identified by means of visual plotting of each predictor), and the most intercorrelated ones based on the generalized variance inflation factors <16 (Zuur, Ieno, Walker, Saveliev, & Smith, 2009); the resulting set of variables is summarized in Table S1.

We adopted a maximum entropy approach by developing MaxEnt models (Elith et al., 2011; Phillips, Anderson, & Schapire, 2006) in R (R Development Core Team, 2016), using the package ENMeval (Muscarella et al., 2014). We discarded all duplicates, that is, records occurring within a 2 km × 2 km cell already having a given species' record. We built models considering the effectively sampled area, by restricting background points (N = 10,000) to cells with at least one record of any of the target species. In this way, the background corresponded to the visited areas and corresponding environmental characteristics. We built models limiting the type of species–habitat relationships to linear and quadratic, to avoid overfitting; simpler models have to be preferred when it is necessary to expand model outcomes over different areas or temporal scenarios (Brambilla, Pedrini, Rolando, & Chamberlain, 2016). However, for black woodpecker, we also included hinge relationships as the simpler model was not precise enough in terms of correspondence between predicted distribution and current

knowledge about real occurrence within the study region. For each species, occurrence data were partitioned into two groups, according to a checkerboard scheme ('checkerboard1' in ENMeval) with each of the units aggregating four original (2 km × 2 km) cells. This allowed testing model validity over independent data sets, assessing model robustness and enhancing generalizability. Model validity was checked by evaluating variations in discriminatory power (area under the curve of the receiver operating characteristic plot) over the two different data partitions (bins), and by checking omission rates on test data, which had been reclassified using two threshold-dependent metrics, that is, 10% training omission rates, and training omission for minimum training presence (i.e. lowest suitability at occurrence sites used for training the model); omission rates larger than the expected values suggest overfitting (Muscarella et al., 2014).

We tested different values of the regularization multiplier: each model was trained with eight different values (from 0.5 to 4), and then the one with the lowest Akaike's information criterion (AIC) was selected. Successively, all variables unlikely to be important for species' distribution (i.e. with both permutation importance and percentage contribution <1) were discarded, and the model was run again with different values of the regularization multiplier, until we obtained a most supported model with no variables showing both permutation importance and percentage contribution <1. The raw model outcome was reclassified by means of a logistic transformation to allow an easier interpretation (Elith et al., 2011). The final logistic output of the model was then reclassified into three-class maps of suitability: unsuitable, partly suitable and suitable. This reclassification was made on the basis of some widely adopted thresholds, generally used for binary reclassification of MaxEnt models, that is, the 10th percentile and the *maximum training sensitivity plus specificity threshold* (Engler, Rödder, Stiels, & Förschler, 2014; Liu, Berry, Dawson, & Person, 2005; Liu, White, & Newell, 2013). Values between 0 and the lowest of such thresholds were considered as unsuitable, values between the thresholds as partly suitable and values above the highest one, as definitely suitable. To calculate potential range overlap between species and changes in range extent between current and future conditions for each species, we considered all sites with suitability higher than the lower threshold as potentially occupied by a species (thus, both partly suitable and definitely suitable were treated as potentially occupied). Finally, for all species, we removed all those locations at an elevation higher than 2,200 m a.s.l. from suitable and partly suitable areas. In fact, even if some cells around that elevation could be predicted as suitable for the target species, the occurrence of the mature forests required by them is very unlikely at such an elevation in the Alps, and will be rather unlikely to reach it in the near future.

Distribution models were then projected over future scenarios of climate change, derived from the HADGEM model, under the worst scenario (representative concentration pathway RCP 8.5; IPCC, 2013), with future climate conditions (for 2050) taken from the Worldclim database (www.worldclim.org; Fick & Hijmans, 2017).

We selected a single, pessimistic, scenario because (a) we were interested in exploring the potential effect of climate change on a guild of interacting species rather than in obtaining several alternative predictions, for example, for planning or conservation purposes and (b) scenarios with larger changes are becoming unfortunately increasingly probable (Peters et al., 2013).

2.4 | Testing the effects of interspecific interactions

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

We tested for the effect of tawny owl abundance on the number of boreal owls at survey points, and of the effect of black woodpecker occurrence on the local abundance of both tawny and boreal owl. N-mixture models, developed using the package 'unmarked' (Fiske & Chandler, 2011) in R (R Development Core Team, 2016), were employed for evaluating the effect of species co-occurrence and environmental suitability on the latent abundance of the target species, while taking into account the potential variation in detectability and hence imperfect detection. Under this approach, repeated counts in a set of sites are used to estimate simultaneously the detectability and the abundance of individuals at survey sites (Ficetola et al., 2018; Royle, 2004). We evaluated the factors that can affect the species' local density by modelling the latent abundance of each species. We assumed population closure because we focused on a single breeding season.

As factors potentially affecting the observation process (and hence detection), we tested time of day, survey date, disturbance as a three-level categorical factor (absent; weak—some far or faint noises; strong—close noise or human activities potentially affecting species detection by the observer or even species behaviour) and wind, a three-level categorical factor (calm—Beaufort scale 0–1; weak—Beaufort scale 2–3; moderate—Beaufort scale 4–5). For boreal owl, the number of calling tawny owls was also considered as a variable potentially affecting detection. Instead of entering several abiotic and habitat factors potentially determining species' abundance into the model, we used the environmental suitability produced by the respective MaxEnt models for each species (taking the value of the model cell including the surveyed point), and the maximum abundance of tawny owl recorded at a site for boreal owl. We also tested for a positive effect of occurrence of black woodpecker at a survey point as a proxy for nest site availability for both owl species. All continuous variables were standardized before the analyses for a better comparison of their relative effects (Cade, 2015; Schielzeth, 2010). For each species, we then developed models based on all possible variable combinations, and ranked them based on the AIC_c (AIC_c for small sample size), using the package 'MuMIn' (Bartoń, 2016), and checked whether the co-occurrence factors were selected in the

most supported models. We repeated the analysis excluding the points surveyed in the Trento province, which often were closer to each other, considering only the points surveyed in Lombardy (see under Section 2.2) to check for consistency in the model results when only well-spaced points were included.

3 | RESULTS

3.1 | Current distribution and overlap

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

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

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

3.2 | Effect of interactions

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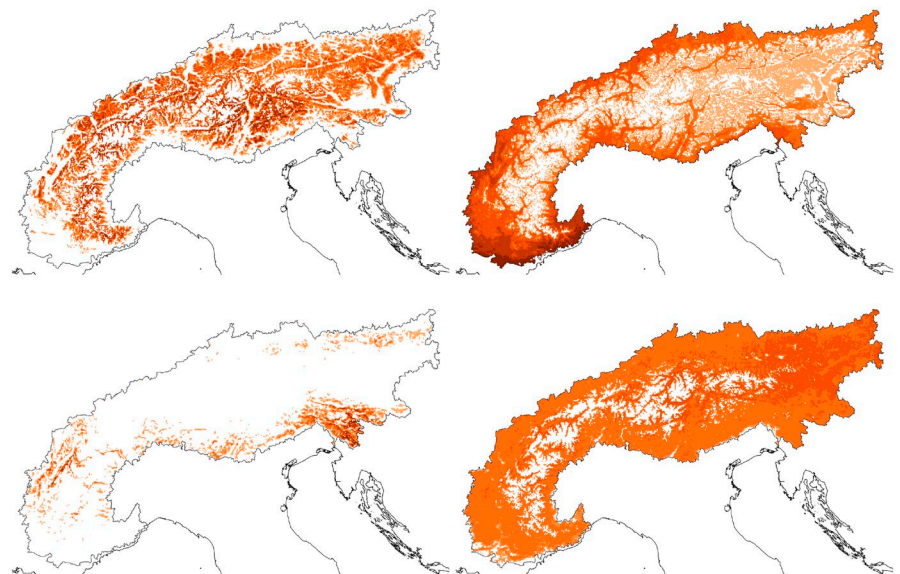

FIGURE 3 Modelled current environmental suitability or boreal owl (upper left), tawny owl (upper right), Ural owl (lower left) and black woodpecker (lower right). The darker the colour, the higher the environmental suitability [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Environmental factors used to model species distributions that were selected in at least one model (see Table S1 for full list), the relative importance of each factor (percentage contribution/permutation importance) and short description of the effect (within brackets; relative to the model including all the selected predictors) according to final models for each species

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 (+)

Note: Numerical codes for land cover variables represent CORINE categories. Symbols used for effects: +: positive, −: negative, +/−: quadratic (hump-shaped), −/+: quadratic (U-shaped), +/−−: quadratic (hump-shaped)/negative, 0: nearly null (very weak positive effect).

3.3 | Future distributions

Predicted future environmental suitability for the target species is displayed in Figure S2 and changes are summarized in Table 2. The distribution of boreal owl will be substantially affected by climate change, with a range reduction and especially a contraction towards higher elevation. Ural owl is predicted to gain suitable areas in Austria and in the central and western Alps, where it is currently absent. Tawny owl will likely show a range expansion towards higher elevations, especially in the central Alps. Black woodpecker distribution will likely undergo only minor changes, even under the rather 'extreme' climate change scenario considered.

The potential overlap between the interacting species will change in the future (Figure 4; see Table S5 for absolute variation).

Almost the entire range of boreal owl is predicted to be suitable for black woodpecker both in current and future conditions (Figure 5); the decrease in extent of potential overlap, due to owl contraction (Figure 4; Table S5), will not impact on the potential interactions. The predicted overlap between boreal owl and its main intraguild predator, tawny owl, will show a marked (proportional) increase (from 25% to 54% of boreal owl potential range) and, importantly, will increase in the central Alps (one of the strongholds for boreal owl under a changing climate), because milder climates will enable tawny owl to expand its potential distribution in Alpine valleys. The likely overlap between boreal and Ural owls will decrease in absolute terms, but will keep nearly stable in relative share over the boreal owl range. The areas where Ural owl occurrence could benefit boreal owl (i.e. those with potential occurrence of tawny owl) will decrease (from

TABLE 2 Predicted extent of suitable habitats in current and future conditions (RCP 8.5 scenario for 2050) for the target species

Species	Current extent of suitable area (km^2)	Future extent of suitable area (km^2)	Change (%)
Boreal owl	85,644	29,988	−65
Tawny owl	95,200	120,928	+27
Ural owl	20,012	67,200	+236
Black woodpecker	160,452	151,564	−6

FIGURE 4 Predicted range overlap under current (yellow) and future climatic conditions (blue; in green, areas with predicted overlap under both scenarios), between boreal owl and black woodpecker (upper left), boreal owl and tawny owl (upper right), tawny owl and Ural owl (lower left), boreal owl and Ural owl (lower right) [Colour figure can be viewed at wileyonlinelibrary.com]
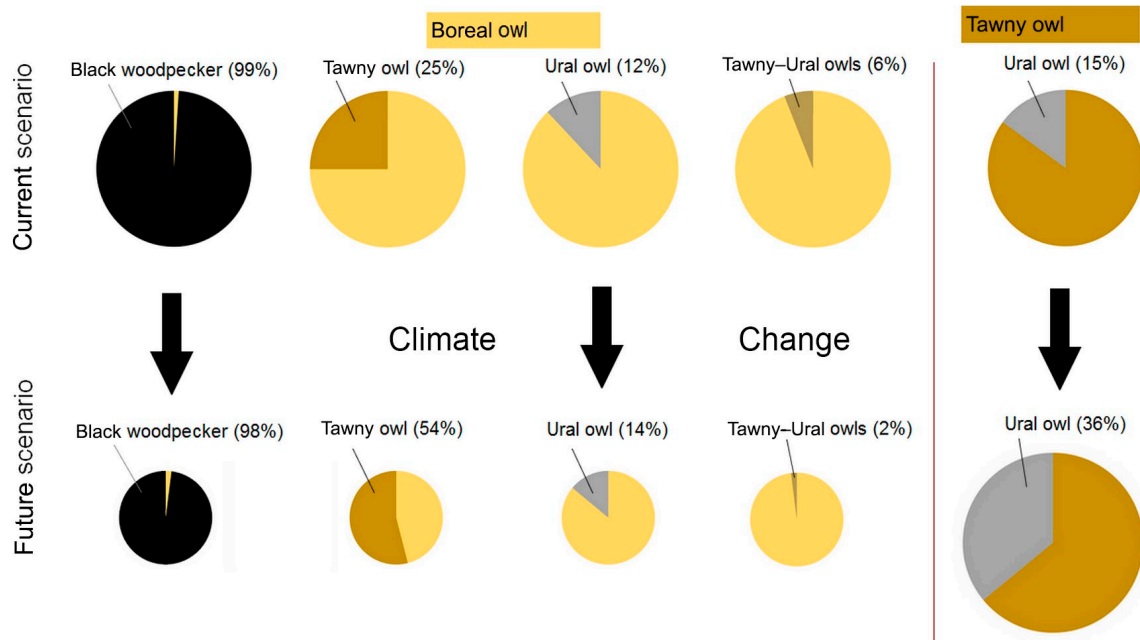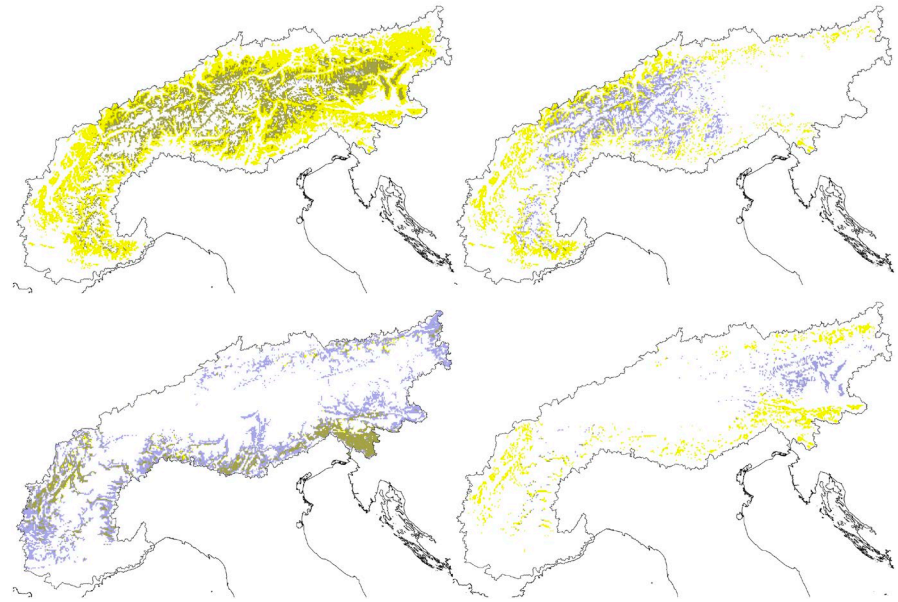
FIGURE 5 Graphical representation of predicted extent of overlap between species and relative variation due to climate change. For each scenario (current and future), boreal owl range is depicted in beige, and tawny owl range in brown. The proportional overlap with other species is shown in each pie chart, in black (black woodpecker for boreal owl), brown (tawny owl for boreal owl), grey (Ural owl for both species). For boreal owl, the overlap with both tawny and Ural owl is shown in grey-brown. Pie chart size is proportional to the relative value of current (100%) and future species range (35% for boreal owl, 127% for tawny owl) [Colour figure can be viewed at wileyonlinelibrary.com]

6% to 2% of boreal owl range). Finally, the overlap between tawny owl and its competitor/intraguild predator, the Ural owl, will probably increase over most of the Alps.

4 | DISCUSSION

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

4.1 | Large-scale environmental predictors of species occurrence

Environmental correlates of habitat suitability for all model species were coherent with the biological and ecological requirements found in the literature (e.g. Lundberg, 1980; Vrezec & Bertoncelj, 2018; Vrezec & Tome, 2004b). Considering the link with climate, black woodpecker and tawny owl showed the broadest thermal niche, consistent with their wider distribution over the Palaearctic. Habitat suitability for tawny owl in the Alps is linearly and positively affected by temperature, and thus, a positive outcome of the temperature increase could be expected for that species. The recent increase of tawny owl at higher elevations observed in several sites in the Alps (P. Pedrini and others, over the last two decades, personal observation) confirms this pattern. While temperature changes in the Alpine region are unlikely to severely impact black woodpecker and Ural owl, a strong effect could be expected for boreal owl. For the woodpecker, a possible minor shift towards upper elevations could be expected under extreme scenarios, which is consistent with the broader distribution of the species, which is much more abundant in mountain areas in southern Europe. Boreal owl has already been reported as a climate-sensitive species in the Alps (Brambilla et al., 2015), its distribution at the European scale appears strictly related to temperature (Brambilla et al., 2017) and it is among the cold-adapted species undergoing population decline and range contraction in Europe (Korpimaki & Hakkarainen, 2012) and Italy (Scridel et al., 2017).

4.2 | Interspecific interactions, climate change and its consequences

The relative abundance of boreal owl at sampling sites revealed the potential importance of co-occurrence patterns on the species' distribution. Black woodpecker occurrence and abundance of tawny owl were indeed even more important than environmental suitability per se for boreal owl in the Central Italian Alps (see under Section 4.4 for further discussion), and likely also in the wider Alpine region (Vrezec & Tome, 2004b). This means that, within this largely suitable belt, interspecific dynamics play an important role in driving the occurrence of boreal owl, the species most sensitive to interactions of those investigated. For tawny owl, the presence of black woodpecker is less relevant as the former species has a greater flexibility in selecting suitable cavities for breeding, which include woodpecker holes, but also a variety of old nests, rotten tree trunks, other holes, ledges in rock cliffs and even buildings (Mikkola, 1983). For tawny owl, the environmental suitability derived from MaxEnt models was a better predictor of abundance.

4.3 | Changes in the predicted 'room for interactions'

According to our analysis, climate change will strongly impact on the investigated species both at species level and in the form of community changes in interacting species resulting from distribution shifts, as the area where species interactions are likely to occur is predicted to vary in extent in the future. In most cases, the potential overlap between species range will decline, but it will likely increase for tawny owl and Ural owl, potentially increasing the frequency of competitive interactions between the species. The spatial relevance of the facilitator role of black woodpecker in favour of boreal owl will probably remain unchanged.

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

Interestingly, our modelling outcomes suggested a potential westwards expansion of Ural owl. This species was until recently confined to the very eastern side of the Alps and eastern Europe (Vrezec, 2009), but was more westerly distributed in historical times (Goffette, Denis, Pöllath, & van Neer, 2016), and in recent decades, it has colonized new areas, expanding its range towards the central portion of the Alpine chain (Benussi & Genero, 2008, 2017; Nardelli et al., 2015; Rassati, 2006, 2017). Therefore, the modelled increase in suitability in the central and western Alps is fully coherent with the current pattern of range expansion.

Successful reintroduction projects recently carried out in Lower Austria (Zink & Walter, 2018) further confirm environmental suitability of the central-eastern Alps for the species, where the provisioning of nest boxes, which compensates for the widespread lack of nesting sites due to forest harvesting, could further favour the species' westward expansion. The ongoing expansion of Ural owl, coupled with that of tawny owl, implies an increasing potential overlap and thus likely increasing interactions between these two competing species (Figures 4 and 5).

4.4 | Modelling issues

The distribution models we obtained (at a spatial scale highly representative of the territory size/home range of the species) appeared rather robust for all species, with a high level of consistency in discriminatory power over the two partitions of the data set (Table S2). The resulting predicted distributions were in line with the current range of target species in the Alps. Similarly, the species–habitat relationships underlying the models were coherent with the knowledge of species' ecology.

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

Finally, local forest characteristics, potentially sensitive to human management and climate change (Braunisch et al., 2014), can be important, especially for black woodpecker (Karimi et al., 2018; Pirovano & Zecca, 2014). However, at broader scales, they are unlikely to be relevant (see e.g. Brambilla & Saporetti, 2014; Tjernberg, Johnsson, & Nilsson, 1993), as the ongoing range expansion in a large part of the study area suggests (Gustin, Brambilla, & Celada, 2019). In addition, we cannot completely exclude the possibility that the effect of black woodpecker and tawny owl (positive and negative respectively) on boreal owl occurrence, highlighted by N-mixture models, could be due to an influence of some unmeasured habitat variable which has an effect on both interacting species of a given species pair. However, we are confident that these effects are likely mirroring true interaction effects. Black woodpeckers provide almost all boreal owl nest sites in the study area (Pedrini, Caldonazzi, & Zanghellini, 2005), and hence, a potential unmeasured habitat variable could also be represented by a better-than-average availability of cavities. Tawny owls have been shown to significantly impact on boreal owl occurrence (Vrezec & Tome, 2004b), and we are aware of several cases of local replacement in recent years (our personal observation from Italy, Austria and Slovenia). Nevertheless, long-term studies that include more detailed habitat descriptions would better elucidate whether the positive and negative relationships are consistent with regard to temporal variation in the same habitat, and therefore, some caution is needed in interpreting the observed patterns.

5 | CONCLUSIONS

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

Our work modelled the potential effects of climate change on the distribution of an interacting owl guild and of its main nest facilitator, the black woodpecker, and showed potential important changes in the overlap of suitable areas for those interacting species. The analysis of current patterns of abundance at the local scale confirmed the likely importance of interspecific interactions. Taken together, our findings suggest that future predictions of species distribution under climate change should include relevant biotic interactions to achieve higher forecast accuracy; in particular, testing the relevance of interspecific interactions will facilitate the interpretation of distribution models and the more reliable estimation of predicted range changes.

AUTHOR CONTRIBUTIONS

MB conceived the idea, which was then developed by all authors. MB, DS, PP, GBa, LI, EB, RB, LM, FG, NT, RP, AV, PK, TM, RP, GA, HS collected data on the field and/or through database interrogation. DS processed bird data; DS and AI prepared environmental layers. MB ran the analyses and all authors contributed to model checking/development and check final model outcomes. MB with DS' help wrote a first draft of the manuscript. All authors critically contributed to the final version.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.