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Modelling distribution of habitats required for different uses by the same species: implications for conservation at the regional scale

Mattia Brambilla^{1,2} & Fabio Saporetti³

¹ Fondazione Lombardia per l'Ambiente, Settore Biodiversità e Aree protette, Largo 10 luglio 1976 1, I-20822 Seveso (MB), Italy;

² Museo delle Scienze, Sezione Zoologia dei Vertebrati, Corso del Lavoro e della Scienza 3, I-38123 Trento, Italy;

³ Gruppo Insubrico di Ornitologia, Civico Museo Insubrico di Storia Naturale di Clivio e Induno Olona, Via Manzoni 21, 21050 Clivio (VA)

Corresponding author:

M. Brambilla

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

1, I-20822 Seveso (MB), Italy. Phone +39-02-80616123

brambilla.mattia@gmail.com

20 **ABSTRACT**

21 Most modelling exercises use generic occurrence points of a species, but the distribution of habitats
22 used for different purposes may differ. Modelling separately the availability of functionally
23 different habitats may allow for the identification of the habitats mostly affecting/limiting
24 distribution, with important implications for conservation. We analysed the regional distribution of
25 the black woodpecker in N Italy. We separately modelled the availability of feeding and nesting
26 habitats at the fine scale (20 m x 20 m), and compared the outputs with a more conventional
27 distribution modelling procedure, which included all records and was developed at the territory
28 scale (1 km x 1 km). Both the conventional and feeding habitat models performed well (although
29 they tended to under- and overestimated occurrence, respectively), whereas the nesting habitat
30 model had a lower discriminatory ability. Nesting and feeding habitats show different relationships
31 between woodpecker occurrence and habitat variables, this resulting in a weak overlap of the
32 respective niches and in quite different distributions. The conventional model provided less
33 information for management, being mainly affected by elevation and urbanized areas; the two
34 specific models instead showed effects of habitat variables on occurrence of feeding and nesting
35 sites. The availability of feeding habitat is likely the most important factor limiting distribution in
36 the area and could be the focus of possible habitat management, which should include the
37 preservation of grassland patches interspersed within woodlands, especially on S-facing, gently
38 sloping mountainsides. Modelling separately the availability of functionally different habitats may
39 provide useful information for conservation and management.

40

41 **Keywords:** distribution models; *Dryocopus martius*; functional habitats; habitat management;
42 habitat use; MaxEnt; spatial scales

43 **1. Introduction**

44 Modelling habitat suitability and species' distribution are increasingly important subjects in ecology
45 and conservation biology, and have become one of the main tasks for those scientific disciplines
46 (Rushton et al., 2004). The importance of knowing the spatial distribution of a species and the
47 spatial configuration of its preferred habitats, coupled with the ever increasing availability of data
48 layers with habitat information and of high-performance methods and programs, has resulted in a
49 huge production of distribution models for plant and animal species (Elith et al., 2006). Such
50 models have been used to predict the current distribution, but also to forecast the future and to
51 estimate the past distribution of target species (Fouquet et al, 2010; Louzao et al., 2013). The
52 commonest of those models are correlative species distribution models (SDMs), which assess
53 relationships between species distribution data and environmental features, to evaluate the
54 suitability of a given area for a species of interest. Models provide a measure of the probability of
55 presence or an estimate of the environmental suitability, which can be used to define species' spatial
56 occurrence (Graham et al., 2004a; Brambilla et al., 2009; Báez et al., 2012), inform surveys
57 (Raxworthy et al., 2003; Bourg et al., 2005), evaluate impacts of climate and habitat change
58 (Thuiller et al., 2005a; Brambilla et al., 2010; Fouquet et al., 2010; Elith et al., 2011; Chamberlain
59 et al., 2013; Temunović et al., 2013; Brambilla and Gobbi, 2014), test evolutionary hypotheses
60 (Peterson et al., 1999; Graham et al., 2004b), predict species invasions (Roura-Pascual et al., 2004;
61 Thuiller et al., 2005b; Rödder and Lötters, 2009; Ficetola et al., 2010; Stiels et al., 2011; Barbet-
62 Massin et al., 2013) and inform conservation planning (Araújo and Williams, 2000; Ferrier et al.,
63 2002; Rödder et al., 2010). In recent years, SDMs have become one of the most frequent tasks in
64 conservation, and presence-only and presence-background SDMs are becoming prevalent because
65 they do not require absence data (Jiménez-Valverde et al., 2008). Their use has been progressively
66 extended beyond the description of the crude species' distribution, and recently SDMs have been
67 adopted also to estimate maximum abundance (VanDerWal et al., 2009), population density

68 (Oliver et al., 2012) or reproductive parameters, such as productivity and territory size (Brambilla
69 and Ficetola, 2012).

70 Until now, modelling exercises mostly used presence data collected in multiple ways,
71 including all occurrence points in a unique dataset, without distinguishing among 'functionally
72 different' records of the model species (e.g. breeding, foraging, etc.), or among records of
73 individuals of different sexes or ages, which also can use different habitats and sites (e.g. Singh et
74 al., 2010; Ficetola et al., 2013). However, such records tied to different type of individuals or
75 animal activities are likely to occur in mobile animal species with complex habitat requirements
76 (González-Solís et al., 2008; Ficetola et al., 2009). The overall distribution of an animal species
77 may result from the combination of factors acting at different spatial scales (Brambilla et al., 2010;
78 Hortal et al., 2010), and may be affected by species interactions (e.g. Giannini et al., 2013). At the
79 regional scale, species distribution may theoretically be driven by the combination of the relative
80 distributions/availability of habitats used for different purposes or by different individuals. This is
81 the reason why various type of habitat should be included within cells used as units for such
82 species; some alternative approaches have been proposed to address this task (Guisan and Thuiller,
83 2005): (i) larger modelling cells accounting for larger portions of the landscape, to ensure that all
84 habitat types can be included (Jaberg and Guisan, 2001); (ii) focal predictors that summarize
85 information on the neighbouring landscape within the focal cell; or (iii) fitting a separate model for
86 each type of habitat use or for various types of individuals. Due to several reasons including this
87 neighbourhood influence (information in a given point relate also to the adjacent habitat patches),
88 valid absences are hard to obtain for these species (Boyce et al., 2002), and in most cases specific
89 presence-only models should be fitted (Guisan and Thuiller, 2005). The use of large modelling cells
90 (including several habitat types) is likely to be the approach currently most used for wide-ranging,
91 large species. Here, we explore the results of building a model with large cells, to ensure that all
92 habitat types can be included (Jaberg and Guisan, 2001), and the results of fitting models separately
93 for each type of habitat used (cfr. the third approach described above), considering focal predictors

that summarize information on the neighbouring landscape within the focal cell (cfr. the second approach described above). In all cases, we used presence-background models.

In this study, we analyze at the regional scale the breeding distribution of the largest Eurasian woodpecker species, the black woodpecker *Dryocopus martius*. We model the species distribution using all species records at a large scale, and the fine-scaled distribution of habitats used for different activities (feeding and nesting/resting, respectively) by the species, which uses nests also as resting sites (Cramp, 1985). Then, we compare the outputs of the different modelling procedures (cfr. Estrada and Arroyo, 2012) to evaluate the similarity of the predicted distributions and estimate niche overlap (Warren et al., 2008) between feeding and nesting habitat suitabilities.

We believe that such a kind of assessment is potentially relevant to both modelling ability and conservation planning. If modelling separately the availability of habitats with different functions provides more accurate models than traditional methods, adequate data are available such an approach can be adopted for wide-ranging species with complex requirements to allow finer predictions of their distribution. On the other hand, and more importantly, pointing out what kind of functional habitat is currently lacking or under-represented for a species in a given area could allow conservationists to implement the most suitable management for the target species, without unnecessary efforts. If functional habitats differ in their features, and just one or a few are affecting a species in a portion of its range, focussing on the relevant functional habitat(s) would promote species occurrence/abundance and avoid wasting resources to promote the availability of already existing habitats.

114 2. Materials and methods

115

116 2.1. Model species

117 The black woodpecker *Dryocopus martius* inhabits a wide variety of forest habitats, especially
118 coniferous, mixed and beech *Fagus sylvatica* woodlands (Cramp, 1985). The home-ranges of the
119 species are usually comprised between one and a few hundreds of hectares (Cramp, 1985), and a
120 radio-tracking study in the Italian Alps suggested that home-ranges average 316 ha, whereas the
121 area most exploited (core area) during breeding period averages 92.4 ± 10.9 ha (Bocca et al., 2007).
122 This species generally prefers woodland with large trees, favouring tall trunks of climax and mature
123 forest, preferably well spaced, to which it is tied for nesting; on the other hand, it often feeds on
124 ants, thus relying also on more or less open ground for foraging (Cramp, 1985), or on young
125 plantations (Rolstad et al., 1998).

126 We believe that black woodpecker in the study area could be a good model species to
127 investigate the fine-scaled distribution of habitats required for different uses, because of the
128 following reasons: i) all the area we investigated is within the dispersal distance (cfr. Merow et al.,
129 2013) shown by the species (Cramp, 1985), which actually had been observed outside the breeding
130 season in all the geographical sectors of the area (Saporetti et al., unpubl. data); ii) interactions with
131 other species are unlikely to affect the distribution of that species at that scale, as the black
132 woodpecker has a very few predators and competitors in this part of its range (cfr. Cramp, 1985).

133 In the study area, the black woodpecker is still expanding its breeding range, from the
134 mountain portion in the north, the first to be occupied, toward the lowland areas in the south-
135 western areas (Saporetti 2010).

136

137 2.2. Study area and fieldwork

138 Our work took place in the province of Varese, Lombardy, N Italy. The province of Varese
139 encompasses c. 1200 km² of mainly hilly and low-mountain areas (elevation 140–1650 m a.s.l.),

140 with a gradient of increasing elevation from south to north. The landscape is dominated by
141 woodland in the north, whereas in the south urbanized areas alternate with intensive cultivations
142 and woodlands especially along river valleys (C.C.I.A.A., 1988). The climate of the area (pre-
143 Alpine wet climate, without arid seasons) is characterized by relatively abundant precipitation
144 (1100–2300 mm/year over the study area) with two maxima (in spring and autumn) and relatively
145 small temperature variability. Climate is rather uniform over the whole study area, with temperature
146 variations mostly due to differences in elevation (C.C.I.A.A., 1988).

147 We searched for nests between 2008 and 2012, within all the territories identified in the
148 province during previous surveys dedicated to the local atlas (Gagliardi et al., 2007) and during a
149 work investigating woodpecker distribution (Saporetto, 2010). A total of 18 nests within 11 different
150 territories were found. Feeding sites were searched for and mapped in the northern portion of the
151 province (in the northernmost SCI - Site of Community Importance, Val Veddasca, about 50 km²;
152 see Fig. 1). Feeding sites (N = 140) were identified on the basis of the typical traces left by foraging
153 black woodpeckers, especially on snags, logs and stumps (Saporetto, 2010). All the exact positions
154 of nests and feeding sites were recorded by means of a portable GPS.

155 Finally, we estimated the current species distribution by means of data collected from local
156 amateur ornithologists and birdwatchers, in the framework of the new Italian Breeding Bird Atlas
157 (2010-2014; accessed on 03 February 2014; www.ornitho.it). The approximate current species
158 range was defined as the extent obtained by considering the municipalities including at least one
159 record (with atlas codes suggesting breeding or territorial behaviour) of the species during the
160 breeding season in the period 2010-2013 (Fig. 1). Such records did not have the required spatial
161 precision to be used for model building; anyway, being associated with municipalities, they can be
162 used to define the current species range in the area.

163

164 *2.3. Modelling distributions and niche overlap between habitats required for different uses*

165 We modelled distribution at two different spatial scale: at the fine-scale (cells 20 m x 20 m), we
166 worked out two different models, one for feeding and one for nesting habitat, respectively, whereas
167 at the territory-scale (cells 1 km x1 km) we worked out a single model considering together all
168 observations. We modelled distributions by using Maximum Entropy Modelling (MaxEnt) to build
169 SDMs, relating woodpecker presence to environmental features (Phillips et al., 2006). MaxEnt
170 assesses the environmental suitability in a given cell on the basis of environmental features in that
171 cell; it is considered one of the most efficient approaches to SDM using presence-only data (Elith et
172 al., 2006; Elith et al., 2011), and can significantly predict species distribution even with low sample
173 size (Pearson et al., 2007; Wisz et al., 2008; Baldwin, 2009).

174 To model nesting and feeding habitat, presence data were the exact positions of nests and of
175 feeding sites, respectively. As environmental variables, we used land cover variables, treated as
176 raster cells of 20 m x 20 m derived from a detailed land-use and hedgerow map (DUSAF 2.1; date
177 2007; Regione Lombardia & Ersaf; www.cartografia.regione.lombardia.it; resolution 20 m). Cell
178 size corresponds to the resolution of the DUSAF data. For each 20 m x 20 m cell, we measured land
179 cover variables as the cover of some selected habitat types in a 100-m radius from the cell centre.
180 We also included three topographic variables (elevation, slope, aspect) derived from a Digital
181 Terrain Model (DTM; resolution 20 m; source Regione Lombardia;
182 www.cartografia.regione.lombardia.it) of the regional surface. Aspect is a circular variable and was
183 therefore transformed into a categorical predictor before analyses (8 classes corresponding to 45°-
184 intervals). We did not include climatic data because in the whole study area the climate is suitable
185 for woodpeckers (Cramp, 1985), and the limited variations are mostly due to elevation; notably, in
186 neighbouring parts of Lombardy, black woodpecker occurs both at higher and lower elevation. For
187 details on characteristics of the data layers used for modelling, see also Brambilla et al. (2012,
188 2013a) and Brambilla and Ficetola (2012). From the several land cover variables, we selected the
189 ones potentially relevant for the species, according also to the available sample size for the different
190 models. Variables included in models were the following one: nesting habitat model: slope

191 (degrees), elevation (m a.s.l.), aspect (8 categories), cover of broadleaved woodland, coniferous
192 woodland, mixed woodland, arable land; feeding habitat model: slope, aspect, cover of broadleaved
193 woodland, coniferous woodland, mixed woodland, arable land, alpine grassland, permanent
194 grassland, permanent grassland with scattered trees and shrubs, urbanized areas. Background was
195 created using 10 000 random points, automatically generated by MaxEnt. Given that feeding sites
196 were mapped only within Val Veddasca, we entered a bias file in MaxEnt analysis, which defined
197 exactly the sampled area, to correct for the limited sampling. In that way, background was derived
198 from the area actually sampled, and then the outcome of the model was projected to the rest of the
199 study area.

200 Then, we built another SDM after combining all records, and working with a different cell
201 size, i.e. with a 1 km x1 km grid (37 cells with records; 11 including the 18 nests, and 26 including
202 all the feeding sites). 1327 random points (background) were generated by the program. The 1 km
203 x1 km cell size better matches the actual territory size of the species, and corresponding to core
204 areas of the home-ranges of the species (Bocca et al., 2007); this cell size should be the most
205 appropriate scale for modelling 'general' distribution according to conventional approaches, which
206 do not consider the modelling of functionally different habitats. Habitat variables were mean
207 elevation within the cell, mean slope and cover within the cell of broadleaved woodland, coniferous
208 woodland, mixed woodland, permanent grassland, tree crops, wetlands, and urbanized areas.

209 For all MaxEnt models, we selected the following features: linear, quadratic, hinge
210 (Brambilla et al., 2013a; Merow et al.; 2013); after some attempts, regularization coefficient values
211 were set to avoid overfitting, looking at the species-habitat relationships modelled in the 10-fold
212 cross-validated models. We used a beta multiplier equal to 1.5 for the nesting habitat and for the
213 complete model, and equal to 2 for the feeding habitat model. We performed a 10-fold cross-
214 validation, and calculated the area under the curve (AUC) of the the receiver operating
215 characteristic (ROC) plot (Phillips et al., 2006; Elith et al., 2011) and its standard deviation over the
216 cross-validated models, given the lack of alternative methods to estimate model discriminatory

217 ability (Lobo et al., 2008; Merow et al., 2013). Anyway, it is important to note that AUC values of
218 different models are not directly comparable; together with the relative standard deviation, AUC
219 values may give an idea of the discriminatory power of the model and of its stability over the 10
220 replicates. All models were worked out as raw output (Phillips et al., 2006; Merow et al., 2013).

221 To describe what were the main habitat factors responsible for the modelled distributions,
222 we evaluated the relative importance of habitat variables according to percentage contribution,
223 permutation importance and jackknife tests of variable importance. Variables with the highest
224 percentage contribution were invariably also the ones with the highest jackknife importance, both
225 on training and on test datasets, and almost invariably coincided with the ones with the highest
226 permutation importance, the only exception being the complete model (elevation had the highest
227 percentage contribution and the third permutation importance, urbanization had the third percentage
228 contribution and the highest permutation importance). Main results are summarised in Table 1.

229 To evaluate the degree of similarity between the nesting and feeding habitat, we performed
230 niche overlap analyses (Warren et al., 2008; Warren & Seifert, 2011) in ENMTools (Warren et al.,
231 2010), by measuring similarity between predictions of habitat suitability between the two functional
232 habitats. We worked with the average suitabilities obtained from the 10-fold cross-validated
233 models. ENMTools provides estimates of niche overlap using three different statistics: the
234 Schoener's D (Schoener, 1968), the I statistic (Warren et al. 2008), and relative rank (RR, Warren
235 and Seifert 2011). All those metrics may vary from 0 (completely discordant niches) to 1 (identical
236 niches). The D and I statistics are based on the difference in environmental suitability score at each
237 grid cell (after that suitabilities are standardized), whereas RR is based on the probability that the
238 relative ranking of any two cells is the same for the two models being compared, irrespective of the
239 quantitative difference in suitability estimates (Warren et al, 2010; Warren and Seifert, 2011).

240

241 *2.4. Comparing the accuracy of the three models*

242 To evaluate the difference in the accuracy of predictions made by the different models, we
243 calculated the respective discriminatory ability over the study area, considering 36 occupied cells
244 (the same used for the 1 km x 1 km model) and 36 cells randomly selected outside the approximate
245 current species' range in the study area (see above). With this approach, we were able to identify
246 some cells likely to be unoccupied by the species. We compared the AUC of ROC plot of the
247 different models on this dataset comprising 36 occupied and 36 unoccupied cells of 1 km x 1 km.
248 We calculated the suitability per each cell, according to the original suitability (1 km x 1km model)
249 or to the average suitability of the respective 10-fold cross-validated models (20 m x 20 m models).
250 It should be noted that for the individual models of single functional habitats, such an evaluation of
251 model discriminatory ability is carried out at a spatial scale different from the original one at which
252 such models were worked out. The average AUC of the ROC plot was calculated (\pm its standard
253 error) on 1,000 bootstraps, based on a non-parametric assumption.

254

255

256 **3. Results**

257

258 *3.1. Conventional distribution model*

259 Results of the complete model at the 1 km x 1 km scale are shown in Fig. 2. The AUC of the ROC
260 plot of the 10-fold cross-validated model was 0.87 ± 0.10 . The habitat factors most importantly
261 affecting woodpecker occurrence were mean elevation (positive effect), urbanized areas (negative),
262 slope (positive). Moreover, a less important effect was found for broadleaved woodland (positive
263 effect except for the highest cover values, which have strongly negative effect), alpine grassland
264 (negative), arable land (negative), coniferous woodland (positive effect for low values, then
265 negative), mixed forest (roughly quadratic), permanent grasslands, wetlands, tree crops (the latter
266 three variables all with mainly negative effects).

267

268 *3.2. Availability of nesting and feeding habitat and relative overlap*

269 The map of nesting habitat suitability is shown in Fig. 3. The AUC of the ROC plot of the 10-fold
270 cross-validated model was 0.81 ± 0.15 , and the larger SD revealed a lower model stability when
271 compared with the feeding and the complete models, due to the lower sample size. The variables
272 most importantly affecting the occurrence of woodpecker nesting habitat were slope (positive effect
273 for low values, then negative), mixed woodland (roughly positive effect), broadleaved woodland
274 (positive effect apart from very high cover values, which result in a sudden drop in suitability),
275 aspect (rather weak pattern; SE, SW, W aspects unpreferred). The other and less important variables
276 in the model were arable land (negative effect), elevation (weak positive effect) and conifer
277 woodlands (negative effect).

278 Map of habitat suitability for feeding woodpeckers is shown in Fig. 4. The AUC of the ROC
279 plot of the 10-fold cross-validated model was 0.82 ± 0.05 , and the small SD revealed high model
280 stability. The variables most importantly affecting the occurrence of woodpecker feeding habitat
281 were aspect (strong pattern; southern faces preferred, and especially S and SW), mixed coniferous

282 and broadleaved woodland (roughly quadratic effect), broadleaved woodland (roughly quadratic
283 effect); other variables with less important contribution to the model were permanent grasslands
284 with scattered trees (positive effect), slope (roughly quadratic effect), coniferous woodlands
285 (quadratic effect), urbanized areas (negative effect), alpine grassland (roughly quadratic effect),
286 permanent grasslands (roughly quadratic effect).

287 The analyses of the overlap between the two use-specific niches gave the following values
288 for the three statistics considered: Schoener's D: 0.61, I statistic: 0.78, Relative Rank: 0.48.

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292 *3.3. Comparison of model predictions with the observed distribution*

293 Records during the breeding period were available for 45 municipalities in the study area (see Fig.
294 1). Of those municipalities, all hosted patches of both suitable feeding habitats and suitable nesting
295 habitats, but four completely missed suitable 1 km x 1 km patches and two others were only
296 marginally interested by extremely small portions of 1 km x 1 km suitable cells (Figs. S4 and S7).
297 On the other hand, many sites located outside the occupied municipalities host suitable patches of
298 feeding or nesting habitat (see Figs. S5-S6 and S8-S9).

299 The AUC of the ROC plot of the three models over the 72 grid cells revealed very high
300 model discriminatory power for both the complete and the feeding habitat models, whereas the
301 AUC value of the nesting habitat model was fairly lower (Table 2).

302 4. Discussion

303

304 Distribution models are allowing deeper insight into species' ecology and distribution (Guisan &
305 Thuiller, 2005; Elith & Leathwick, 2009), and provide increasingly finer tools for potential
306 estimates of population parameters (VanDerWal et al., 2009; Brambilla and Ficetola, 2012). The
307 never ending increase in model performance and in their potential applications makes SDMs one of
308 the most intensively exploited research areas (Elith et al., 2006). Our findings suggest that
309 modelling different habitat uses according to specific activities or individual traits (Guisan and
310 Thuiller, 2005; Ficetola et al., 2013) can increase model usefulness for planning habitat
311 management for species with complex ecological requirements.

312 Many species and groups of species use different habitats during different parts of their life
313 cycle (e.g. amphibians breeding in water but living in woodlands, several migratory birds), but
314 many others may show different pattern of habitat use during the same phase of the life cycle (as the
315 breeding period in our study), according to specific activities or individual traits. In general, the
316 distribution of an animal species may result from the combination of factors acting at different
317 spatial scales (Hortal et al., 2010; Santangeli et al., 2013). At the regional scale, the availability of
318 habitats used for different purposes (e.g. Väänänen et al., 2011) or by different individuals (e.g.
319 González-Solís et al., 2008) may shape distribution, and thus separate models for each type of
320 habitat use can be fitted (Guisan and Thuiller, 2005). In our study case, we separately modelled
321 habitat suitability for nesting and foraging black woodpeckers. The niche overlap statistics (which
322 in that case evaluate the overlap between the use-specific niches), as well as the effect of variables
323 included in the models (Table 1) and the maps of predicted suitabilities (Figs. 2-4), suggest that
324 feeding and nesting suitability do not coincide, but are somewhat alternative to each other. Niche
325 overlap between nesting and feeding habitat was rather weak, with three different statistics
326 indicating that the two niches are far from being identical (cfr. Warren et al., 2008, 2010). The same
327 habitat factors have different effects on environmental suitability when considering nesting and

328 feeding habitats. Southern aspects are strongly associated with high suitability of foraging habitat,
329 whereas for the nesting habitat, the pattern of association with aspect is much weaker and different,
330 with most southern and western aspects associated with lower suitability. Nesting habitat suitability
331 is positively affected by cover of broadleaved and mixed woodlands (almost linearly), whereas the
332 same forest covers have a markedly quadratic effect on feeding habitat suitability; that means that
333 areas mostly covered by forest may be suitable for nesting, but not for foraging. Feeding habitat
334 suitability is positively associated with the cover of permanent grasslands with scattered trees, and
335 shows a quadratic relationship with alpine grassland and permanent grasslands, this suggesting that
336 patches of open habitats may increase foraging opportunities (e.g. by providing more ants and other
337 insect preys; Anonymous 2005); the species is known to forage frequently in open ground (Cramp,
338 1985) and in small clearings, which can provide rich invertebrate preys (Brooks, 1985). The rather
339 marked differences existing between the two functionally different habitats suggest that most
340 suitable conditions for the species represent a compromise between the availability of the two
341 habitats. Modelling the availability of habitats required for different functions separately (cfr.
342 Guisan & Thuiller, 2005) may produce finer assessments of species distribution, and, most
343 importantly, may point out what type of habitat is acting as a limiting resource for a target species
344 in a given area.

345 The discriminatory abilities of the models over the 72 cells used to assess their accuracy
346 revealed lower performances for the nesting habitat model. This finding suggests that the
347 woodpecker distribution cannot be explained by the fine-scaled distribution of just one of the two
348 functional habitats. On the other side, the AUC of the feeding habitat model was higher and
349 comparable to the one of the complete model (Table 2), this indicating that feeding habitat may be a
350 major driver of species distribution in the area. However, the distribution of suitable feeding habitat
351 exceeded the distribution of the species in the study area, showing suitable patches also e.g. in the
352 south-eastern corner where the species is absent (cfr. Figs. 1 and S9) and nesting suitable habitat
353 lacks (Fig. S8). In general, the two specific models (nesting and feeding habitats, respectively),

354 represent an overestimation of the current species distribution (especially the nesting habitat model;
355 see Figs. S5-S6 and S8-S9).

356 The use of larger modelling cells to account for larger portions of the landscape, to ensure
357 that all habitat types can be included (Jaberg and Guisan, 2001; Guisan and Thuiller, 2005), here
358 represented by the 1 km x 1 km model, provided with reliable results, but underestimated species
359 occurrence in the southern portion of the study area (Figs. S4 and S7) and did not provide any
360 evidence on what functional habitat can limit species' distribution in the different part of the study
361 area. Moreover, when considering the species-habitat relationships, the information provided by the
362 complete model are of limited use for conservation planning: the most influential variables were
363 related to topography (elevation and slope), and to urban areas (cover of urbanized areas), all
364 factors which cannot be subjected to e.g. management.

365 Modelling the availability of habitats required for different uses at a fine spatial scale
366 represent a challenging but fascinating task for the creation of species distribution models; such an
367 approach could offer further sound information for the definition and implementation of practical
368 management actions. Knowing what kind of habitat is required, and where, may lead to more
369 detailed, more efficient and more justifiable programs for habitat management targeted at species of
370 conservation concern (Chiatante et al., 2013). In our study case, it is quite evident that nesting
371 habitat is not a limiting resource for the species: suitable nesting sites are widespread throughout the
372 area, including many areas not occupied by the species (Fig. S8), and the nesting models had the
373 lowest accuracy in predicting cell occupancy by black woodpeckers (Table 2). Actually, we are
374 aware of nests in small woodlots close to urban areas or wetlands (Saporetti, 2010), or even within
375 gardens, this confirming that the black woodpecker in Alps and pre-Alps is a flexible species able to
376 adapt to a range of conditions (yet showing clear preferences for particular habitats, depending on
377 feeding and nesting requirements; Bocca et al., 2007), given that tall trunks in easy-to-access stands
378 are provided for nesting (Cramp, 1985). On the other hand, feeding habitat seems to be more
379 restricted, and somewhat limiting the potential distribution of the species, as suggested by its

380 distribution (Figs. 4, S6 and S9). Increasing nesting habitat availability would not provide real
381 benefits for the species (although the species needs tall trees to nest), whereas promoting feeding
382 habitats (favouring patches of mixed and broadleaved forests with patches of open or semi-open
383 habitats at intermediate elevations and on predominantly S-facing and gently sloping sites) would
384 probably increase the potential distribution and abundance of the species.

385

386

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392

393

394 **Supplementary material**

395 Supplementary data associated with this article can be found in the online version

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572

Table 1

Summary of MaxEnt models obtained with the different functional records, at the two spatial scales (20 m x 20 m and 1 km x 1 km, respectively). Variable importance is calculated on the 10-fold cross-validated models. Variables shown are the ones with percentage contribution or permutation importance higher than 5% in at least one model; other variables with less important contribution to the models are reported in the text.

Variable	models								
	effect			percentage contribution			permutation importance		
	nesting	feeding	complete	nesting	feeding	complete	nesting	feeding	complete
elevation	slightly positive	not tested	positive	1.3	not tested	53.4	8.7	not tested	27.0
aspect	SE, SW, W, NW unpreferred	southern aspects favoured	not tested	11.2	40.6	not tested	1.4	38.5	not tested
slope	positive for low value	quadratic	positive	32.6	4.7	24.4	37.9	7.1	4.4
broadleaved forest	positive	roughly quadratic	positive	19.0	8.7	1.2	28.4	15.1	0.5
mixed forest	slightly positive	roughly quadratic	positive	30.1	32.6	0.0	11.0	17.4	0.1
urbanized	not tested	negative	negative	not tested	3.0	13.4	not tested	7.4	44.1
alpine grassland	not tested	quadratic	negative	not tested	1.9	2.2	not tested	8.2	0.8
arable land	negative	null	negative	4.9	0.0	0.8	12.0	0.0	5.1

583 **Table 2**
 584 AUC of the ROC plot of the different models (suitability calculated according to the respective
 585 average values of the 10-fold cross-validated models) over 72 sample 1 km x 1 km cells (36
 586 occupied cells and 36 cells outside the municipalities with records of the species in the breeding
 587 period; see text). *P* is the probability that the observed value is different from the null hypothesis
 588 (AUC = 0.5 and discriminatory power no better than random).

589

Model	AUC ± SE	<i>P</i>	95% c.i.
complete model (1 km x 1 km)	0.93 ± 0.03	< 0.001	0.87-0.99
mean suitability (nesting habitat)	0.75 ± 0.06	< 0.001	0.63-0.86
mean suitability (feeding habitat)	0.91 ± 0.04	< 0.001	0.84-0.99

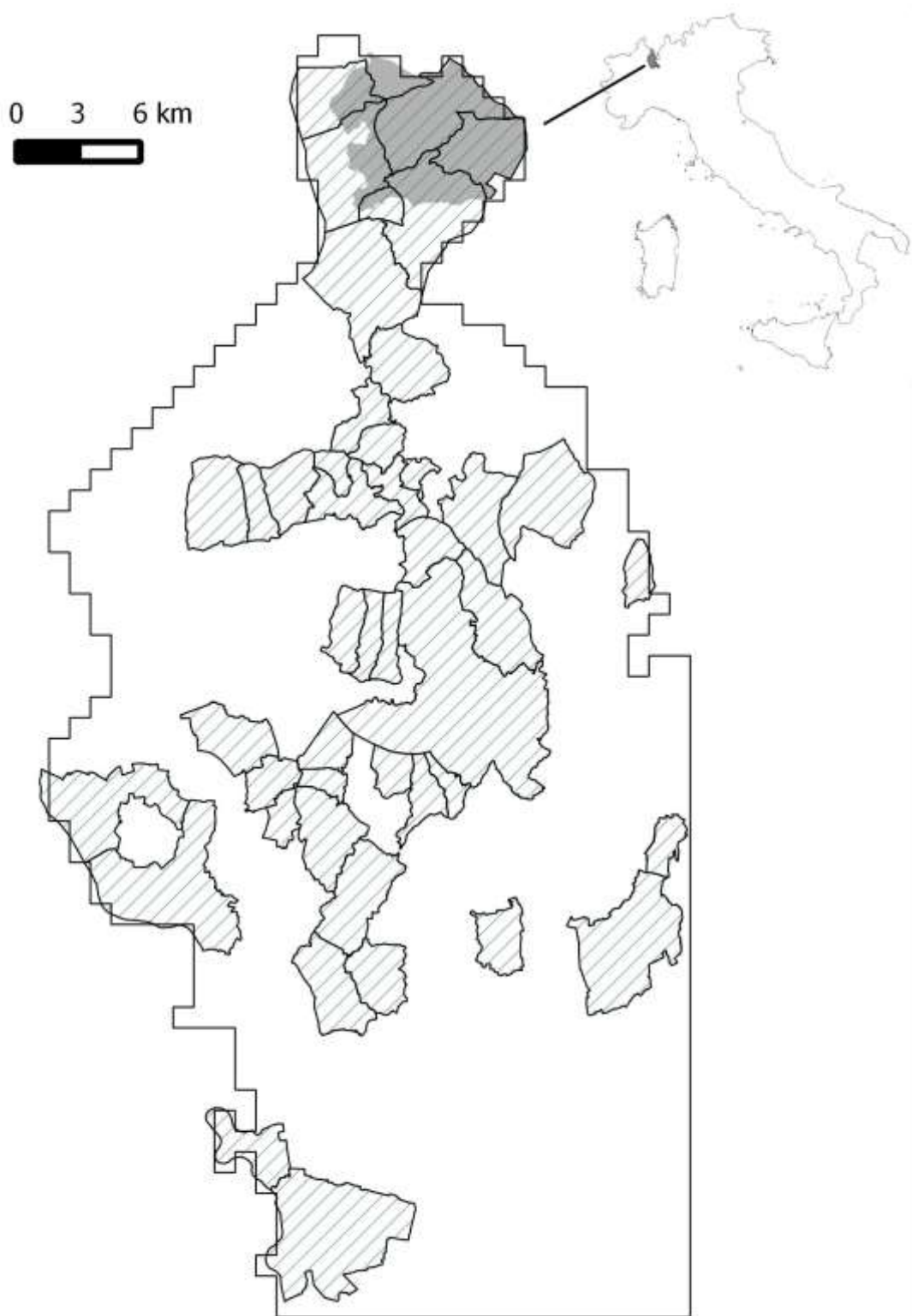
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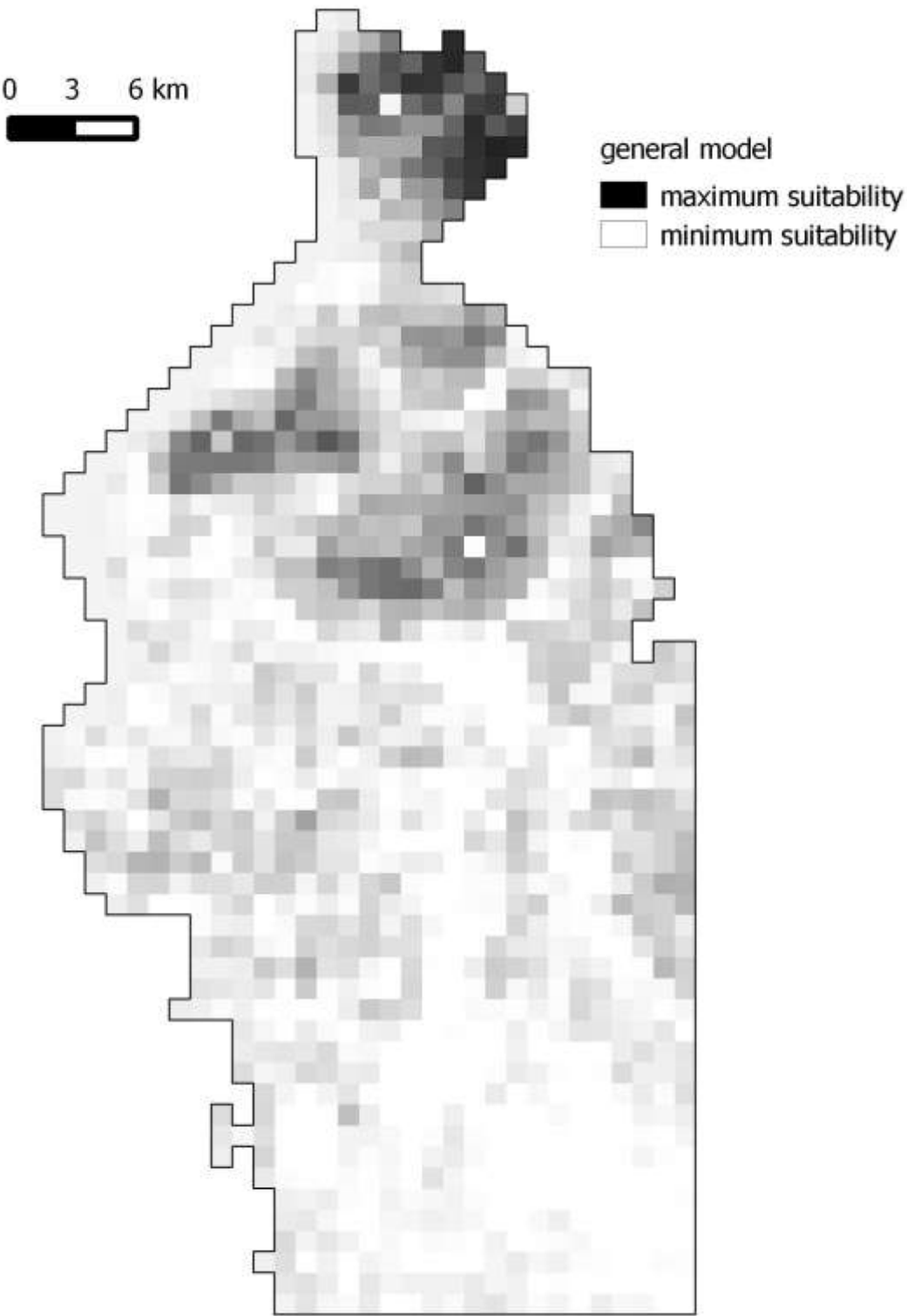
593 **Figure 1**

594 Study areas: Varese province, with Val Veddasca study area in dark grey. Barred polygons are the
595 municipalities within which black woodpecker was recorded during the breeding season in the
596 period 2010-2013. The inset shows the position of Varese province within Italy.

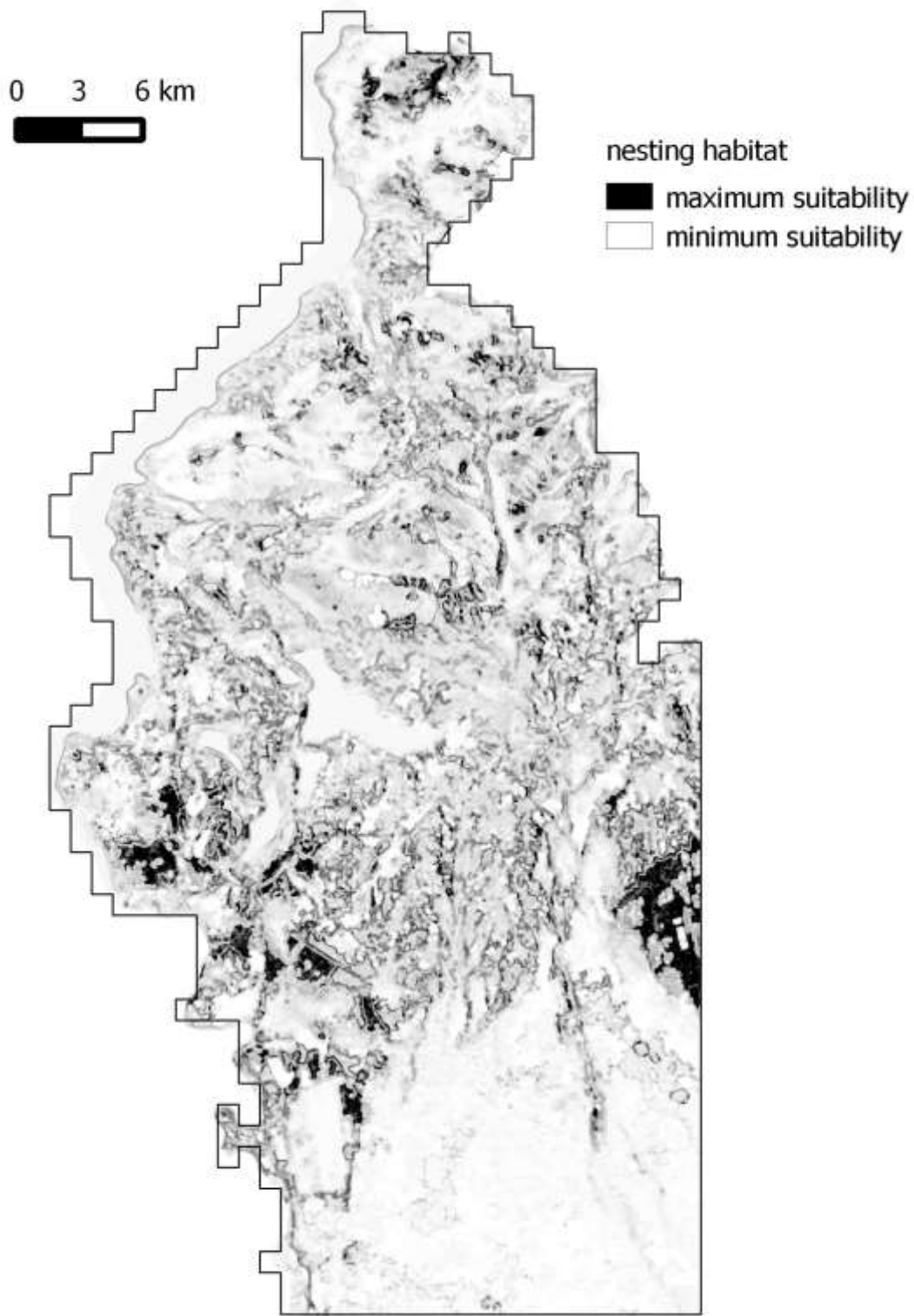


598 **Figure 2**

599 Black woodpecker distribution according to the complete model obtained at the 1 km x 1 km scale .



601 **Figure 3**
602 Distribution of suitable nesting habitats for black woodpecker.



604 **Figure 4**
605 Distribution of suitable feeding habitats for black woodpecker.

