

1 **Abstract**

2 The selection of relevant factors and appropriate spatial scale(s) is fundamental when modelling  
3 species response to climate change. We evaluated whether the effects of climate factors on species  
4 distribution/occurrence are consistently modelled over different spatial scales in birds, and used a  
5 two-scale approach to identify species-climate correlations unlikely to represent causal effects.  
6 We used passerine birds inhabiting mountain grassland in the Apennines (Italy) as a model. We  
7 surveyed four grassland species at 400 sampling points, and built habitat selection models (territory  
8 scale) and distribution models (7 algorithms, landscape scale). We compared the effect of climatic  
9 predictors on occurrence/distribution highlighted by models over to the two spatial scales, and with  
10 the effects supposed a priori based on the climatic niche of each species.  
11 Models at the territory level included at least one climatic predictor for three species; the observed  
12 effect of climatic predictors was seldom consistent with supposed effects. At the broadest scale,  
13 distribution models for all species included climatic predictors, with varying consistence with  
14 supposed effects and findings at the finer scale.  
15 Despite the importance of climate for species distribution, occurrence could be more directly related  
16 to other factors, with important implications for understanding/predicting the impacts of  
17 climate/environmental changes. Our approach revealed key variables for grassland birds, and  
18 highlighted the scale-dependent perceived importance of climate. At the local scale, climate effects  
19 were weak or hard to interpret. We found a general lack of consistence between supposed and  
20 observed effects at the territory level, and between landscape and territory models. Our results show  
21 the importance of predicting the potential effect of climatic factors prior to the analyses, carefully  
22 selecting ecologically meaningful variables and scales, and evaluating the nature and scale of  
23 climate-species links. We call for caution when predicting under future climates, especially when  
24 mechanistic effects and consistency across scales lack.

25

26 **Keywords**

27 Climate change; distribution; habitat selection; Passeriformes; SDM; territory scale

28

29

## 30 **Introduction**

31 Anthropogenic climate change is one of the main threats to biodiversity and ecosystems and will  
32 continue to impact on Earth's environments in the next decades (Sala et al. 2000). Several studies in  
33 the recent literature evaluated and predicted the impacts of climate change on species and  
34 ecosystems; such studies are essential for conservation as they allow to propose adaptation and  
35 mitigation strategies (Bellard et al. 2012). However, the evaluation of climate change impacts on  
36 living species suffers because of several sources of uncertainty (Bagchi et al. 2013, Engler et al.  
37 2017). Uncertainties include those linked to distribution modelling (such as data appropriateness  
38 and resolution, extrapolation, modelling algorithm(s), biases in geographical/environmental  
39 sampling; e.g. Virkkala et al., 2010; Braunisch et al., 2013; Fourcade et al., 2014; Pacifici et al.,  
40 2015; Mitchell et al., 2017; Quillfeldt et al., 2017; Titeux et al., 2017a), those tied to species  
41 characteristics (e.g. dispersal limitations, local adaptation, interactions with other species; e.g.  
42 Zurell, 2017), as well as the uncertainties due to heterogeneity and variability in predictions of  
43 future climate and to the frequent need to project distribution patterns on non-analogous climates  
44 (Kujala et al. 2013, Stoklosa et al. 2015). In addition, ignoring land-use and land-cover impacts  
45 could result in partial understanding of climate effects and in inaccurate predictions (Titeux et al.  
46 2017b). A particular case in point is represented by spatial scale. In fact, climate is likely to be  
47 particularly relevant when modelling species distribution over broad extent, i.e. regional to global  
48 (Pearson and Dawson 2003), even if fine-scale models have been reported to reduce uncertainties in  
49 predicting distribution (Jiménez-Alfaro et al. 2012). Studies comparing predictions in range shifts  
50 obtained over different spatial scales have shown contrasting results for plant species across scales  
51 (Franklin et al. 2013), with evidence for both under- (Trivedi et al. 2008) and over-estimation  
52 (Randin et al. 2009) of impacts at broad scales. In fact, there is increasing evidence of the  
53 importance of spatial scale at which the relationships between species and their environment are  
54 analysed (Mertes and Jetz 2018). In animals, considering that habitat selection is often a multi-scale

55 process (Jedlikowski et al. 2016), it is very likely that climate may also have different importance at  
56 different spatial scales, and that its effect on species distribution could appear different across  
57 different spatial levels. In any case, a proper evaluation of such effects requires that the climate  
58 gradient sampled within a study is representative of the broad climate gradient occupied by the  
59 target species (Titeux et al. 2017a, Brambilla et al. 2017b).

60 All these challenges result in uncertainty in understanding and predicting species distribution in  
61 relation to present and future climate, and are particularly relevant when dealing with birds: being  
62 endotherm species, they are less strictly affected by a direct effect of climatic predictors as is often  
63 the case for ectotherm species. In addition, they display great mobility (Engler et al. 2017) and  
64 frequent seasonal variation in habitat association (Engler et al. 2014), respond at different  
65 environmental drivers at different spatial scales (Jedlikowski and Brambilla 2017) and can use  
66 different habitats for different purposes (Brambilla and Saporetto 2014). Studies sampling species  
67 occurrence along elevation gradients in mountain areas revealed important effects of both habitat  
68 characteristics and climate, with relative importance depending on species (Chamberlain et al. 2013,  
69 2016).

70 Given the sensitivity of birds to climate (Stephens et al. 2016), and the common importance of  
71 multi-scale and different determinants of species occurrence and habitat selection (Brambilla 2015,  
72 Jedlikowski et al. 2016), avian species are an ideal model to test whether the effect of climate on  
73 species distribution is constant or vary across spatial scales. Previous studies of the relationships  
74 between bird occurrence and climate have provided rather different outcomes; whereas their  
75 distribution had been reported to be substantially in equilibrium with climate in Europe (Araújo and  
76 Pearson 2005), in 19 passerine species in Northern America, occurrence was found to be more  
77 related to spatial coordinates and neighbourhood occupancy, rather than to climate (Rich and Currie  
78 2018).

79 With this study, we investigate the determinants of avian species occurrence in grassland-dominated  
80 areas in a mountain region at two different spatial scales, namely territory and landscape, evaluating  
81 the effects of climate and of other environmental variables describing land-use/land-cover,  
82 vegetation structure and management. We aim at specifically evaluating the importance of climate  
83 over different spatial scales and considering different predictors, according to two frequently  
84 adopted approaches in studies dealing with bird ecology and conservation, i.e. i) habitat selection at  
85 territory scale and ii) species distribution modelling (SDM) at landscape scale. We expect a stronger  
86 effect of climate at the broadest scale (assessed by using distribution models), whereas climate  
87 could have a secondary importance when fine-scale descriptors of habitat characteristics are also  
88 considered (within habitat selection models), at least for some species likely to be more affected by  
89 other environmental factors. We also postulate that for major effects of climate, coherent patterns of  
90 species-climate relationships should be found across scales. Recently, this has been the case of a  
91 high-elevation specialist of alpine grassland in European mountains, the white-winged snowfinch  
92 *Montifringilla nivalis*, across landscape (Maggini et al. 2014, Brambilla et al. 2017b), meso-  
93 (Brambilla et al. 2017a) and micro-habitat scales (Brambilla et al. 2018). On the opposite,  
94 potentially different patterns could suggest indirect associations between a species and climate  
95 (Rich and Currie 2018), and call for careful extrapolations of the species-climate relationships over  
96 e.g. different areas or future scenarios.

97

98

## 99 **Material and Methods**

100

### 101 **Study area**

102 Our study was carried out in the Central Apennines (central Italy), a mountain area where traditional  
103 land-uses have created large extents of grassland along broad elevation gradients. Such grassland  
104 extents, mostly used as seasonal pastures, occur from relatively low (below 1000m asl) to much  
105 higher elevation (>2000m). In the study area, the forest limit is usually around 1400-1600m  
106 (Piermattei et al. 2016), whereas the treeline would naturally occur mostly between 1700 and  
107 1800m (according to the elevation limit of beech *Fagus sylvatica*, cf. Magnani, 2007; Pezzi et al.,  
108 2007), whereas, above this elevation, low shrubland and grassland represent the climax vegetation  
109 because of climatic constraints.

110 We investigated five main different areas corresponding to different mountain systems included in  
111 National or Regional Parks: Sibillini, Laga, Gran Sasso, Velino-Sirente, Marsica, Majella (Fig. 1).  
112 We sampled sites at an elevation of 752-2129 m asl (mean  $1528 \pm 232$  SD).

113

### 114 **Model species**

115 We investigated passerine birds breeding in mountain grassland, because species tied to this habitat  
116 are among the most threatened ones because of ongoing climate and habitat changes (Chamberlain  
117 et al. 2013, Brambilla et al. 2017b, Scridel et al. 2018, Lehtikoinen et al. 2018) and thus both require  
118 urgent research and qualify as an ideal model for our aims. We selected four species likely to show  
119 different relationships with climate and land-cover: water pipit *Anthus spinoletta*, tawny pipit  
120 *Anthus campestris*, northern wheatear *Oenanthe oenanthe* and linnet *Linaria cannabina*. Water  
121 pipit is a mainly insectivorous species restricted to open habitats in the main mountain areas of  
122 central and southern Europe and western Asia. Water pipit breeds only at relatively high elevation,  
123 often performing elevational movements in winter or short migration, and has been considered as

124 threatened by climate change on European mountains (Chamberlain et al. 2013, Brambilla et al.  
125 2016, 2017b). Tawny pipit is an insectivorous species, long-distance migrant, tied to relatively  
126 warm and dry areas, where it occupies open habitats with low and sparse vegetation, usually in  
127 sunny and flat or gentle sloping areas (Cramp 1998). Northern wheatear is a long-distance migrant,  
128 insectivorous species, tied to areas with low vegetation (usually grassland), sandy or rocky soil and  
129 bare ground or sparse herbaceous vegetation, occupying a broad spectrum of climatic conditions  
130 (Cramp 1998). Linnet feeds predominantly on seeds, and is a resident or short-distance migrant; it  
131 occurs over very broad environmental and elevational gradients, being found e.g. in Italy both in  
132 fruit orchards in very warm areas (e.g. Sicily, Lo Valvo and Lo Valvo 1987) as well as in high-  
133 elevation habitats with sparse shrubs (e.g. sites above 2000m asl in the Alps and the Apennines)  
134 (Gustin et al. 2010). Therefore, we expected to find a stronger importance of climate for water pipit,  
135 coherent across scales. On the other side, we did not expect such a strong importance of climate for  
136 northern wheatear and linnet, as the latter two species inhabit wide areas and elevational gradients,  
137 including all (or almost so) the climatic conditions found within our study areas. Finally, for tawny  
138 pipit we expected a potentially limiting effect of most extreme climates (especially of coldest and  
139 wettest conditions). All these four species have a concerning conservation status (“inadequate”,  
140 sensu Brambilla et al., 2013) in Italy (Gustin et al. 2016).

141

## 142 **Fieldwork**

143 We recorded birds during the breeding period at 400 points (Fig. S1), in spring 2016 (June-July).  
144 All points were surveyed in the morning (from dawn to 11:00) by the authors, and each survey  
145 lasted 10 minutes. All points were surveyed once in the period 9-29 June, and then 172 points were  
146 surveyed a second time (30 June-10 July). At each point, we measured topographic (derived from  
147 an European DEM-Digital Elevation Model:  
148 <https://www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-eu-dem>) and

149 climatic factors obtained via the CHELSA (<http://chelsa-climate.org/>) database (Karger et al.  
150 2017) in a GIS environment, whereas we recorded in the field detailed habitat variables, including  
151 land-cover parameters (several types of natural, semi-natural and anthropogenic habitats), and  
152 management-related parameters (mowing, grazing, sward height). Habitat variables recorded at  
153 survey points are described in Table 1. Both birds and variables were recorded within a 100m radius  
154 from the point.

155

### 156 **Supposed effect of climatic predictors**

157 To refine the expectation about the effect of the climatic variables tested in the models, we  
158 compared the values of such predictors in our study site vs. the values recorded all over the range of  
159 the target species in Italy, to hypothesize the likely direction of the climate effect on species  
160 occurrence (see Fig. 2 for a graphical summary). In fact, if the climatic niche of a species for a  
161 given parameter at the national level (hereafter, climatic niche) encompasses the values recorded for  
162 the same parameter within our study area, we supposed that such a climate parameter would not  
163 affect (at least, directly) the occurrence of that species within the study area, because the local range  
164 of values falls within the values at which the species occurs at a broader scale. Otherwise, if the  
165 range of values of a climatic parameter within the study area are larger than or are only partially  
166 overlapping with the species climatic niche, an effect (for that parameter on that species) could be  
167 supposed based on the relationship between climate in the study area and climatic niche (Fig. 2). As  
168 an example, if the values of a certain parameter in the study area are generally higher than the  
169 climatic niche of a species, we suppose that the occurrence probability of such a species in the study  
170 area should be negatively affected by the parameter value. Given the broad latitudinal and  
171 elevational gradients that characterize Italy, the species distribution within the country could be  
172 considered as representative for the purposes of our work (Brambilla et al. 2016). We calculated  
173 mean  $\pm$  SE for each climate predictor considered in models for the range (given as occurrence cells)



174 of each species as recently defined by Nardelli et al. (2015), who provided the most update  
175 summary of species distribution in Italy. To be conservative in the identification of the potential  
176 effects, and to take into account the broad range units (10 km x 10 km cells) used by Nardelli et al.  
177 (2015), we opted to use mean  $\pm$  SE to define the ‘typical’ climatic niche of a species in Italy. The  
178 comparison between the climatic values found in our study area and the climatic niche of each  
179 species at the national range, as well as the supposed effects at both scales, are displayed in Table 2.

180

### 181 **Habitat suitability models**

182 We excluded from the samples 12 points at which no bird was recorded within the fixed radius; the  
183 final sample size of the dataset used in the analyses was thus equal to 388 points. We built models  
184 to evaluate the factors potentially affecting habitat suitability for grassland passerine species at two  
185 different spatial scales: territory and landscape. We adopted different methods at the two scales i) to  
186 match different approaches currently adopted in distribution studies, ii) to correctly deal with  
187 different kind of data (presence-absence at territory level, vs. presence-background at the landscape  
188 scale).

189

### 190 ***Territory models***

191 Models at the territory level were based on bird occurrence and a dataset of variables integrating  
192 predictors measured in the field within 100m from survey points, and others calculated via GIS  
193 (Table 1). Before analyses, we checked variable distribution and excluded a few factors, which had  
194 value zero in most cases (snow cover, water cover, bare soil, buildings, wetland). We then  
195 standardized all variables (centred around mean and scaled by standard deviation), a procedure  
196 recommended to evaluate multicollinearity and relative effect (Schielzeth 2010, Cade 2015), and  
197 checked for the occurrence of outliers within the dataset so obtained.

198 To appropriately take into account the effect of double counts performed in one half of sites, we  
199 added a species-specific weight to the models. In fact, the observed absence of a species is less  
200 reliable for (absence) sites surveyed only once, than for sites surveyed twice. All sites surveyed  
201 twice and all occurrence sites were weighted one, and the absence sites surveyed only once were  
202 weighted 0.5.

203 At the territory level, we related species occurrence to fine-scale environmental predictors, after  
204 omitting a few factors which inflated multicollinearity according to the generalized variance  
205 inflation factors (gVIFs; (Zuur et al. 2009): the variables finally used for modelling were thus  
206 broadleaved forest, shrubland, transitional shrubland, grassland, shrubs, trees, arable land, rock,  
207 hedges, height of the grassland sward, occurrence of ski piste with modification on ground  
208 vegetation, grazing occurrence, slope, solar radiation, bio1 (maximum temperature of the warmest  
209 month), bio4 (temperature seasonality expressed as standard deviation multiplied by 100), bio18  
210 (precipitation of warmest quarter), bio19 (precipitation of coldest quarter). Most variables had a  
211 gVIF value <3; two predictors had a slightly higher value (bio4 and grassland cover, value ~5); we  
212 retained such variables to allow a proper comparison with landscape models (see below).

213 Considering that the effects of parameters in single-variable models and in final ones were fully  
214 coherent, we are confident that collinearity did not affect models. We used generalized additive  
215 models with binomial error distribution, and progressively simplified models according to a step-  
216 down procedure (Zuur et al. 2009, Calvi et al. 2018), , using  $P = 0.01$  as threshold for variable  
217 removal. Environmental variables were tested as smooth terms, whereas a tensor term (full tensor  
218 product smooth; Wood 2017) of longitude and latitude was added to control for spatial  
219 autocorrelation. This analysis was performed in R (R Development Core Team 2016), by means of  
220 the package ‘mgcv’ (Wood 2019).

221

222 ***Landscape models***

223 At the landscape level, models were built using the same species' occurrence data (plus a few  
224 occurrence record collected while moving between different survey points – 3 for water pipit, 4 for  
225 tawny pipit, 3 for northern wheatear, 2 for linnet). For water pipit, to increase the limited sample  
226 size, we considered the precise location of all the single individuals we were able to record with  
227 good spatial accuracy (a few meters/tens of meters, in any case < 50 m). Bird data were coupled  
228 with environmental variables (topographical, climatic and relative to land-use and land-cover)  
229 derived from GIS layers, at a 1km-resolution (1km x 1km cells). We calculated average values per  
230 cell of climatic factors (derived from the CHELSA database) and topographic factors (derived from  
231 the DEM; see above); for land-use/land-cover factors, we calculated the percentage cover within the  
232 cell of each cover categories comprised in the CORINE database (European Environment Agency  
233 2016). As a study area, we used the polygon resulting from the creation of a 4km buffer around all  
234 point counts with at least one species recorded (132 433 ha; eight polygons of size varying between  
235 7087 and 41 639 ha). This area (Fig. 1) was used for model development. Occurrence data were  
236 filtered as to have one record per each cell, apart from water pipit, for which this procedure resulted  
237 in a very small sample size: for the latter, we kept all records (note that a qualitative comparison  
238 with models built using the filtered occurrence records led to comparable effects for the most  
239 important variables). Environmental predictors adopted in this analysis were the following ones:  
240 continuous urban fabric, discontinuous urban fabric, non-irrigated arable land, permanently  
241 irrigated land, vineyards, pastures, annual crops associated with permanent crops, complex  
242 cultivation patterns, land principally occupied by agriculture with significant areas of natural  
243 vegetation, broad-leaved forest, coniferous forest, mixed forest, natural grassland, moors and  
244 heathland, transitional woodland-shrub, bare rocks, sparsely vegetated areas, water bodies, bio1  
245 (annual mean temperature), bio4 (temperature seasonality expressed as standard deviation  
246 multiplied by 100), bio18 (precipitation of warmest quarter), bio19 (precipitation of coldest  
247 quarter), slope, solar radiation. Landscape models were created using a Maximum Entropy

248 (MaxEnt) approach, by means of the package ENMeval (Muscarella et al. 2014) in R. MaxEnt is  
249 the most suited method for our purposes, i.e. to investigate the effect of climatic parameters on  
250 species distribution over the regional scale, without the use of absence data. Background points  
251 were constrained within 4 km from point counts, as to match background with actually sampled  
252 environmental conditions. MaxEnt models were based on an AICc-model selection among eight  
253 different values of the regularization parameter (ranging between 0.5 and 4); all variables with both  
254 percentage contribution and permutation importance lower than 0.5% were excluded from the  
255 model in an iterative way (for water pipit, level was increased to 1% to limit the number of  
256 predictors in the model, given the smaller sample size). Models were developed partitioning  
257 occurrence data into two spatially independent bins, via a checkerboard scheme (method  
258 *checkerboard1* in ENMeval). Effects were evaluated on models run with all selected predictors.  
259 Given that the choice of a specific algorithm over other ones may affect modelling results (Hijmans  
260 et al. 2016, Quillfeldt et al. 2017), even if MaxEnt is considered as the most suited method to deal  
261 with dataset lacking absence data, we developed models using also different approaches to compare  
262 the modelled species-environment relationships, namely Generalized Linear Models (GLM),  
263 Generalized Boosted Models (GBM), Random Forests (RF), Classification Tree Analysis (CTA),  
264 Artificial Neural Networks (ANN), Multiple Adaptive Regression Splines (MARS), Flexible  
265 Discriminant Analysis (FDA). These additional models, based on the same variables and occurrence  
266 data, were also developed in R, via biomod2 package (Thuiller et al., 2013). As pseudoabsence  
267 locations, we selected all available cells within 4 km from the point counts. We partitioned  
268 occurrence data in two dataset, one comprising 70% of the data for calibration, and 30% for testing  
269 (except for water pipit, 85% vs. 15%, due to the smaller sample size). Even if most studies carried  
270 out using biomod2 use the recommended default settings (Thuiller et al. 2013), we adopted specific  
271 values for some algorithm-species combination, because for the latter a visual inspection of the  
272 response curves clearly suggested overfitting with default settings. Therefore, every time we found

273 a biologically unsupported relationship putatively due to overfitting, we decreased model  
274 complexity by progressively adjusting model settings (Table S2). For all species, MARS and GBM  
275 models were fitted without interactions. To assess concordance between supposed and observed  
276 species-climate relationships, we considered the environment-species relationships modelled by the  
277 top four (out of six) models in terms of AUC of the ROC plot (hereafter, best performing models).  
278 We evaluated as “coherent” identical or very similar effects (see Table S3 for criteria). We  
279 considered concordance “high” when all models provided relationships coherent with supposed  
280 effects; “good” when at least three models were coherent with supposed effects; “moderate” when  
281 two models were coherent with supposed effects; and “weak” when only one or no model was  
282 coherent with the supposed effects.

## 283 **Results**

284

285 Water pipit was detected at 32 points, tawny pipit at 101, northern wheatear at 159 and linnet at 162.

286 At 111 points, none of the target species was detected. The distribution of species records is shown

287 in Figs. S2 and S3.

288

### 289 **Territory level**

290 Models worked out at the territory level show medium-low to high explanatory power for all

291 species, with  $R^2$  ranging from 0.13 to 0.56 (Table 3). They included at least one climatic predictor

292 for all species except tawny pipit, which occurrence was dictated only by grassland cover, and

293 which had the lowest explanatory power (Table 3). The observed effect of climatic predictors was

294 seldom consistent with the supposed effects (Table 4). The effect of other predictors (and especially,

295 but not exclusively, of land-cover variables) was often important, and the spatial tensor was

296 included in the final model in three out of four species, indicating some sort of spatial patterns in

297 species occurrence (Table 3).

298

### 299 **Landscape scale**

300 Sample size at the landscape scale was equal to 54 for water pipit (after the inclusion of all

301 individual records), 65 for tawny pipit, 82 for northern wheatear and 94 for linnet. The distribution

302 of the occurrence records used for landscape models is shown in Fig. S3. At the broadest scale,

303 MaxEnt distribution models showed an explanatory power generally consistent over the two bins in

304 which the occurrence dataset was partitioned, with the only partial exception of water pipit, the

305 species with the lowest sample size (Table S2). Climatic predictors were included in the models of

306 all species (although with varying importance; Fig. 2). The supposed effect of climate variables and

307 the species-climate relationships modelled at the landscape scale were substantially coherent for the

308 two pipit species, whereas the concordance was lower for linnet and, especially northern wheatear  
309 (Table 5).

310

311 **Data deposition**

312 Data available from the Dryad Digital Repository: <http>

## 313 **Discussion**

314

315 The importance of climate on species distribution (including for avian taxa) is beyond any doubt  
316 (Stephens et al. 2016). However, regional to continental distribution could be to some extent more  
317 directly related to other spatially structured factors (Rich and Currie 2018). This has critical  
318 implications for understanding and predicting the potential impacts of climate and environmental  
319 changes. Our approach helps reveal the relative importance of key variables affecting grassland bird  
320 occurrence; in particular, the use of different spatial scales and modelling approaches (reflecting  
321 common ways used to investigate the link between environment and species) highlights important  
322 issues related to the perceived importance of climate on species distribution, confirming the  
323 importance of scales, grain, variables and approaches in distribution modelling (Quillfeldt et al.  
324 2017, Mertes and Jetz 2018, Fourcade et al. 2018).

325 Even if our analysis of concordance between the supposed effects and the relationships depicted by  
326 distribution models is qualitative in nature (see Tab. S3), and includes also models that perform  
327 better with ‘true’ absence (Elith and Graham 2009), it could provide the basis for an informed  
328 comparison of the coherence between expectations and modelling output. Whereas we found an  
329 acceptable concordance between the supposed effect of climate variables and the species-climate  
330 relationships modelled at the landscape scale for the two pipits (but with the important exceptions  
331 of bio1 for tawny pipit and bio18 for water pipit), consistent with a distribution largely in  
332 equilibrium with climate (Araújo and Pearson 2005) and with expectations at a large scale (Pearson  
333 and Dawson 2003), the concordance was lower for linnet and, especially northern wheatear (Table  
334 5). For the latter, almost all the effects of climate factors suggested by distribution models were  
335 different from the supposed ones, according to all or most modelling algorithms. When moving to  
336 the local scale, the interpretation of climate effects become even harder. We found indeed a  
337 common lack of consistence between supposed and modelled effects of climate on species



338 occurrence at the territory level (Table 4). In addition, there was also a lack of congruence in terms  
339 of different effects suggested by landscape and territory models. Indeed, it could be expected that, at  
340 a finer level, species occurrence is primarily driven by other characteristics, which are more likely  
341 to have a direct importance at such a scale, as e.g. suitable land-cover, prey availability, vegetation  
342 composition or structure, or biotic interactions (Pearson and Dawson 2003). The only instance for  
343 which a relatively consistent pattern of response to climate variables was recorded across both  
344 scales was temperature for water pipit, i.e. the species most expected to be directly affected by  
345 climate (Chamberlain et al. 2013) and especially by temperature (Brambilla et al. 2016): the latter  
346 factor was identified as the most important variable affecting the species occurrence over both  
347 scales, coherently with evidence from other areas (Brambilla et al. 2017b). Tawny pipit was  
348 apparently not affected by climate at the local scale (Table 4), but climatic predictors turned out to  
349 be important when evaluated at the landscape scale (Table 5). Apparently even more surprising, we  
350 found contrasting effects of the same predictor over the two spatial scales, as was the case for  
351 average temperature (bio1) for linnet: this variable had a U-shaped quadratic effect at the territory  
352 scale, but a hump-shaped effect (thus, the exact opposite) according to landscape models, within the  
353 same range of values (cf. Figs. 3 and 4; Fig. S4). The hump-shaped effect found at the landscape  
354 level is coherent with the supposed effect of average temperature on the species, according to its  
355 climatic niche. On the other side, the U-shaped effect found at the territory level is very likely to  
356 reflect the distribution of key resources for the species, or local adaptation to individual habitats not  
357 occurring at 'intermediate' temperatures within the study area. Consequently, it would be unreliable  
358 to project changes in occurrence because of temperature variation on the basis of such a  
359 relationship. Whatever the specific reason of such diverging patterns, this finding confirms the  
360 importance of predicting the potential effect of climatic factors prior to the analyses, on the basis of  
361 the species' realized distribution over broader scales; such a task, which we implemented in a

362 largely descriptive manner, could be potentially developed also from a quantitative point of view in  
363 future applications.

364 Some of the effects suggested by the models in fact contrast with the ones supposed to occur on the  
365 basis of the comparison between the range of climate experienced by the species at the national  
366 level (the climatic niche) vs. the climate found in the study area. The negative effects of average  
367 temperature (bio1) on the occurrence of tawny pipit (at landscape scale) and wheatear (at territory  
368 level), when the expected effects were quadratic and null, respectively, serve as examples of likely  
369 indirect effects, mediated by other environmental processes. Specifically, for tawny pipit the study  
370 area includes some of the coldest sites of known occurrence, and comparing the temperature  
371 experienced by the species over its broad national range and within the study area, revealed a weak  
372 overlap between temperature values (bio1) at the territory scale, which would lead to a positive  
373 effect of bio1 (Table 2). At the landscape scale, a quadratic effect could be supposed as the values  
374 defining the climatic niche of the species (for bio1) fall well within the range recorded at the  
375 broader scale within the study area. This suggests that the negative effect of temperature at the  
376 landscape level is likely due to other factors, such as higher predator density at warmer sites (the  
377 abundance of foxes, martens, corvids and snakes is definitely higher towards lower elevation in  
378 Central Apennines; our pers. obs.), or vegetation structure/density (e.g. the composition and  
379 structure of the grass sward could be more suitable in colder sites within the study area). Notably, at  
380 the territory level temperature had no effect on species' occurrence, this indirectly confirming that  
381 the temperature effect is due to other factors (spatial, environmental, or biotic; see above), which  
382 could have a spatial pattern somewhat mirroring the spatial variation of temperature (Brambilla et  
383 al. 2016, Rich and Currie 2018). Modelling future distribution according to forecast warmer  
384 climates would result in a substantial loss of suitability/distribution for this species according to the  
385 relationships modelled within our study, something that is hard to envision when the warm climates

386 to which the species is associated are considered (Cramp 1998), or when the full range of the  
387 species is taken into account (cf. Barbet-Massin et al., 2010).

388 In northern wheatear, a quadratic effect of temperature was expected at the landscape scale, as the  
389 temperature range generally occupied by the species at the national scale falls well within the  
390 thermal range recorded within the study area, whereas at the territory level no effect was supposed,  
391 as the climatic niche of the species largely coincided with the range of values recorded at such a  
392 scale within the study area (Tab. 2). The effects we found were negative (and highly significant) at  
393 territory level and quadratic/negative at the landscape scale. Again, it is likely that the broadly  
394 negative effect of temperature on wheatear occurrence could be due to indirect effects, possibly the  
395 same ones mentioned above for tawny pipit.

396 Well-built ecological niche models may identify truly important factors affecting species' ecology,  
397 to the point that, in addition to distribution (Engler et al., 2017), they can sometimes predict even  
398 annual recruitment (Searcy and Shaffer 2016) or breeding success and territory size (Brambilla and  
399 Ficetola 2012), whereas the habitat suitability measure they provide is frequently associated with  
400 local abundance (VanDerWal et al. 2009, Brambilla et al. 2009, Oliver et al. 2012). Sometimes  
401 ecological niche models, which are correlative in nature, may be based on non-causal relationships;  
402 the correlation between climate and distribution may be the outcome of the effect of non-climate  
403 variables (Chapman 2010, Rich and Currie 2018). In the case of tawny pipit, the lack of effect at the  
404 territory scale enabled us to discard a causal relationship between tawny pipit occurrence and  
405 climate. This calls for extreme caution when predicting distribution under future climates, in the  
406 lack of evidence of consistent effects across spatial scales. For northern wheatear, however, the  
407 largely negative relationship with temperature unexpectedly found at the landscape scale was  
408 reinforced by the negative effect found at the territory scale, when also fine-scale determinants are  
409 considered: this suggests an underlying mechanism acting with a spatial pattern matching that of  
410 temperature, resulting in a proxy effect of the latter. It is possible that future changes in temperature

411 will induce changes in the ultimate factor(s) driving the distribution pattern of the species (e.g.  
412 predation). Under that circumstance, the potential effect of climate change on the species will be  
413 similar to those forecast in the case of a direct ('mechanistic') link with climate. However, further  
414 insights into local species' ecology are definitely needed to understand mechanisms and  
415 consequences of climate factors and their change. In conclusion, careful evaluation of the nature  
416 and scale of the link between climate and species is required for safe projections of the potential  
417 outcomes of climate change on species occurrence; the selection of biologically meaningful  
418 predictors is a key issue in distribution modelling indeed (Rich and Currie 2018, Fourcade et al.  
419 2018), as well as the proper selection of spatial scale (Mertes and Jetz 2018). As a consequence, the  
420 choice of the right factors and scales is of basic importance for meaningful conservation planning,  
421 being irreplaceable for the definition of protected sites or management plans targeted at preserving  
422 key habitats or areas in the face of climate change.

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424

## 425 **Declarations**

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431 *Author contributions* – X planned fieldwork; X carried out fieldwork; X led the analyses and wrote  
432 the first draft of the ms; all authors contributed to analysis interpretation and to the writing of the  
433 final version of the ms.

434 *Conflict of interest* – There were no conflicts of interest.

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439 **Table 1.** Habitat variables recorded at each point count, within a 100-m radius, and used for  
 440 building models at the territory scale. Not all variables were tested in the models, because of scarce  
 441 occurrence of a given habitat or because of multicollinearity issues (see text).

442

Variable	Description
<b>Climate and topography</b>	average values within the 100m radius (measured in GIS)
slope	average value (°)
solar radiation	global value for 21 <sup>st</sup> June(kWh/m <sup>2</sup> )
bio1	average annual temperature
bio4	temperature seasonality expressed as standard deviation multiplied by 100
bio18	precipitation of warmest quarter
bio19	precipitation of coldest quarter
<b>Land use/land cover</b>	percentage cover estimated within the 100m radius (~5%; measured on the field)
Broadleaved forest	forest and woodland composed by broadleaved trees
Coniferous forest	forest and woodland composed by coniferous trees (pines)
Mixed forest	forest and woodland composed by broadleaved and coniferous trees
Shrubs	woody plants taller than 4m
Transitional shrubland	shrubs and young trees (evolving into forest)
Grassland	natural or semi-natural grassland
Isolated shrubs	number of isolated shrubs (height 1-4m)
Isolated trees	number of isolated trees (height >4 m)
Arable land	arable land (ploughed and seeded)
Bare soil	bare ground (compact)
Rock	rocky substrate
Sand, scree	bare ground with sandy or scree soil
Building	buildings of different kind
Paved roads	paved (tarmac) roads
Tracks	unpaved roads, tracks
Hedgerows and tree rows	length (m) of hedgerows and tree rows
Waterbodies	lakes, ponds, rivers
Wetland vegetation	wetland and marsh plants
Snow/ice	snow-covered surfaces
<b>Habitat structure/management</b>	categorical predictors describing grassland management (measured on the field)
Height of grassland sward	categorical measure of the height of the grassland sward: low 0-10

Ski-pistes	cm; medium: 10-40 cm; high: >40 cm categorical (binary): ski-pistes with original grassland or similar plant communities
Ski-pistes with altered vegetation	categorical (binary): ski-pistes with degraded/altered vegetation
Grazing	categorical (binary): active or recent grazing (grazing occurring or recent dung)
Mowing	categorical (binary): recent mowing

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443

444 **Table 2.** Values of climatic predictors used in the models: range of values defining the climatic  
445 niche of each species in Italy (expressed as mean  $\pm$  SE), minimum and maximum values recorded at  
446 sampling units at both scales, and supposed effect on each species (supposed effects have been  
447 derived from a comparison between climatic niche at national scale and climate within the study  
448 area; see Fig. 2 and text for details). Legend of abbreviation used for the supposed effect: T:  
449 territory; L: landscape; 0: no effect; +/-: quadratic effect (higher occurrence probability for  
450 intermediate values); +: positive effect; -: negative effect; +/-: quadratic or negative; +/-:  
451 quadratic or positive; 0/-: null or slightly negative; 0/+ null or slightly positive.  
452

species	bio1	supposed effect	bio14	supposed effect	bio18	supposed effect	bio19	supposed effect
water pipit	29.48-76.94	T: -	5779.82-	T: 0/-	243.03-	T: +	170.22-	T: +
		L: -	6317.87	L: 0	357.30	L: +	274.93	L: +
tawny pipit	116.57-	T: +	5717.52-	T: 0/-	84.33-	T: -	188.08-	T: 0/+
	144.57	L: +/-	6201.54	L: 0/-	145.70	L: -	236.52	L: +/-
northern		T: 0	5795.75-	T: 0/-	155.59-	T: 0/+	172.86-	T: 0/+
	59.38-112.5							
wheatear		L: +/-	6345.48	L: 0	285.66	L: +/-	258.52	L: +/-
	95.24-	T: +	5718.14-	T: 0/-	103.47-	T: -	176.61-	T: +/-
linnet								
	140.44	L: +/-	6286.74	L:0/-	210.77	L: +/-	241.57	L: +/-
Study area:	70.16-		5927.00-		151.00-		154.00-	
Territory	115.00		6472.00		215.00		219.00	
Study area:			5756.87-		91.00-		106.00-	
Landscape	0.80-167.00		6699.22		298.20		435.00	

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459 **Table 3.** Summary of the habitat suitability models obtained at the territory level for each target  
 460 species; + means positive effect, - negative effect, +/- quadratic effect (suitability higher at  
 461 intermediate values, unless specified otherwise). The percentage of deviance explained and the R<sup>2</sup>  
 462 of each model are reported as calculated by ‘mgcv’ package in R. Legend for P-value: \*: 0.1 < P <  
 463 0.05; \*\*: 0.05 < P < 0.01; \*\*\* 0.01 < P < 0.001; \*\*\*\* P < 0.001.

464

Species	% dev. explained	variables included
water pipit	58.9%; R <sup>2</sup> 0.56	bio1 (-)****, grazing occurrence (+)*, spatial tensor**
tawny pipit	11.6%, R <sup>2</sup> 0.13	grassland (+)*, spatial tensor***
northern wheatear	21.9%, R <sup>2</sup> 0.25	broadleaved woodland (-)***, shrubland (-)***, trees (-)**, ski-pistes with altered vegetation (-)***, grazing occurrence (-)*, slope (+/-)**, solar radiation**, bio1 (-)****, bio4 (-)*
linnet	27.1%, R <sup>2</sup> 0.28	transitional shrubland (-)**, rock (+)***, height of grassland sward (- for high grass)**, slope (+/-)**, bio1 (inverse +/-)****. spatial tensor**

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469 **Table 4.** Comparison of supposed (derived from a comparison between climatic niche at national  
470 scale and climate within the study area) and modelled effects (see text) of climatic factors on  
471 species occurrence at the local scale, according to the models obtained at the territory level.  
472 Legend of abbreviation used for the supposed effect: T: territory; L: landscape; 0: no effect; +/-:  
473 quadratic effect (higher occurrence probability for intermediate values); +: positive effect; -:  
474 negative effect; +/-: quadratic or negative; ++/-: quadratic or positive; 0/-: null or slightly negative;  
475 0/+ null or slightly positive.  
476

<b>Species</b>	<b>variable</b>	<b>Supposed effect</b>	<b>observed</b>
water pipit	bio1	-	-
	bio4	0/-	0
	bio18	+	0
	bio19	+	0
tawny pipit	bio1	+	0
	bio4	0/-	0
	bio18	-	0
	bio19	0/+	0
northern wheatear	bio1	0	-
	bio4	0/-	-
	bio18	0/+	0
	bio19	0/+	0
linnet	bio1	+	inverse +/-
	bio4	0/-	0
	bio18	-	0
	bio19	++/-	0

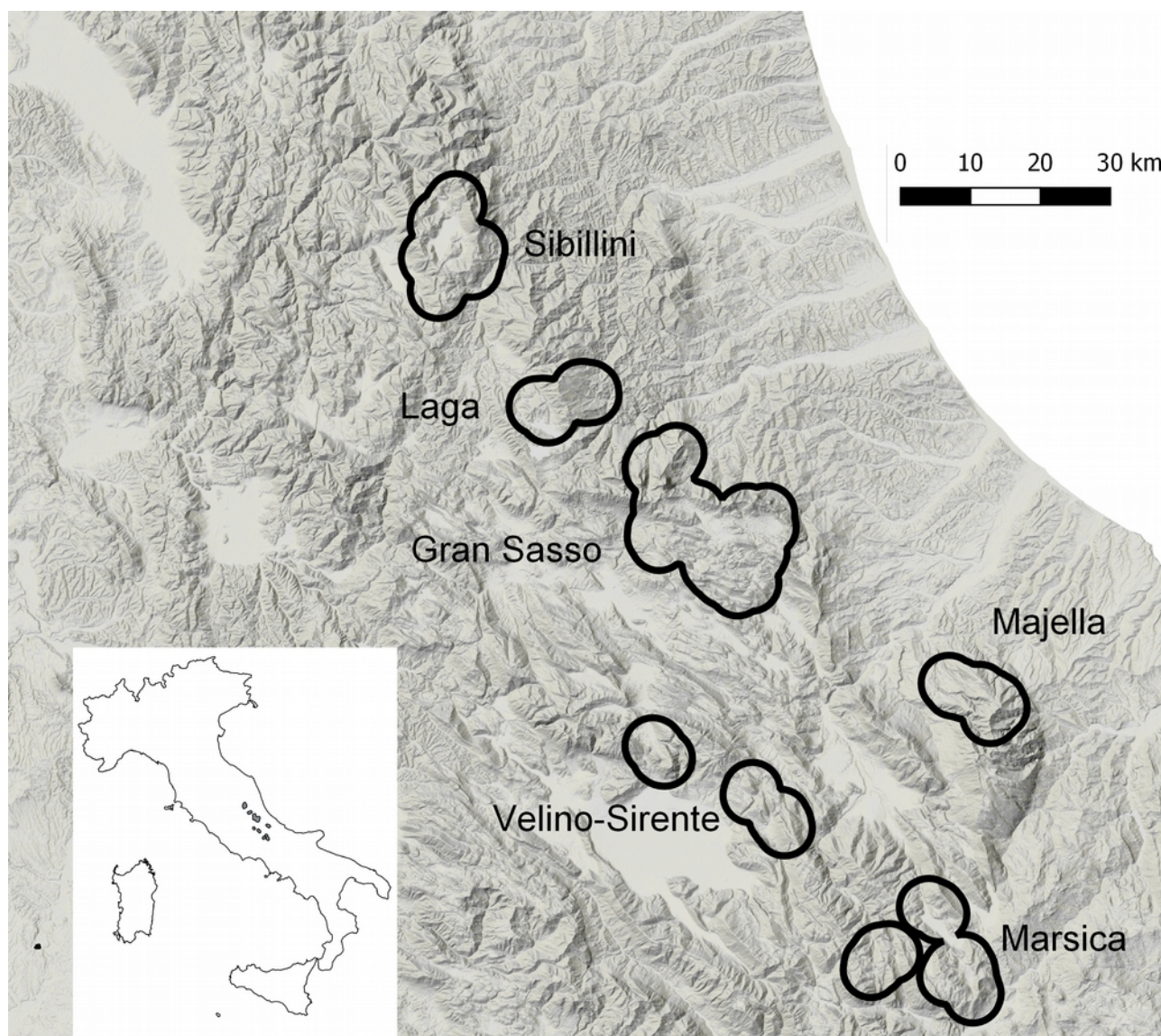
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478 **Table 5.** Comparison of supposed (derived from a comparison between climatic niche at national  
479 scale and climate within the study area) and modelled effects (see text) of climatic factors on  
480 species occurrence at the broad scale, according to the models obtained at the landscape level. For  
481 alternative models obtained via biomod2, only the effects of the four best performing models per  
482 each species are considered (see text). Legend of variable effects: + positive; (+) slightly positive; -  
483 negative; (-) slightly negative; +/- quadratic; +/- quadratic/negative; 0: null. Legend for  
484 “concordance” (see Table S3) categories: high: all models coherent with expectations; good: at least  
485 three models coherent with expectations; moderate: two models coherent with expectations; weak:  
486 one or no model coherent with expectations.  
487

Species	variable	supposed effect	MaxEnt	GLM	GBM	CTA	ANN	FDA	MARS	RF	concordance
water pipit	bio1	-	-	-		(-)	-	-			high
	bio4	0	0	0		0	+/-	+			good
	bio18	+	(-)	-		0	+/-	(-)			weak
	bio19	+/-	(-)	-		-	-	0			good
AUC			0.991	0.990	0.909	0.936	0.947	0.943	0.798	0.789	
tawny pipit	bio1	+	-		(-)	0		+/-		(-)	weak
	bio4	0/-	0		0	0		0		(+)	good
	bio18	-	-		(-)	0		(-)		(-)	good
	bio19	+/-	-		(-)	-		+/-		(-)	high
AUC			0.894	0.645	0.794	0.764	0.677	0.717	0.715	0.749	
northern wheatear	bio1	+/-	+/-		(-)	-	-			-	weak
linnet	bio4	0	-		(-)	-	-			0	weak
	bio18	+/-	(-)		(-)	-	-			(-)	weak
	bio19	+/-	-		(-)	-	-			0	good
	AUC			0.881	0.810	0.828	0.825	0.829	0.802	0.818	0.834
linnet	bio1	+/-	+/-	+/-	0			0		-	moderate
	bio4	0/-	-	-	-			-		0	good
	bio18	+/-	+/-	(+)	(+)			0		(+)	weak
	bio19	+/-	-	-	(-)			0		0	good
AUC			0.853	0.825	0.826	0.767	0.702	0.829	0.821	0.870	

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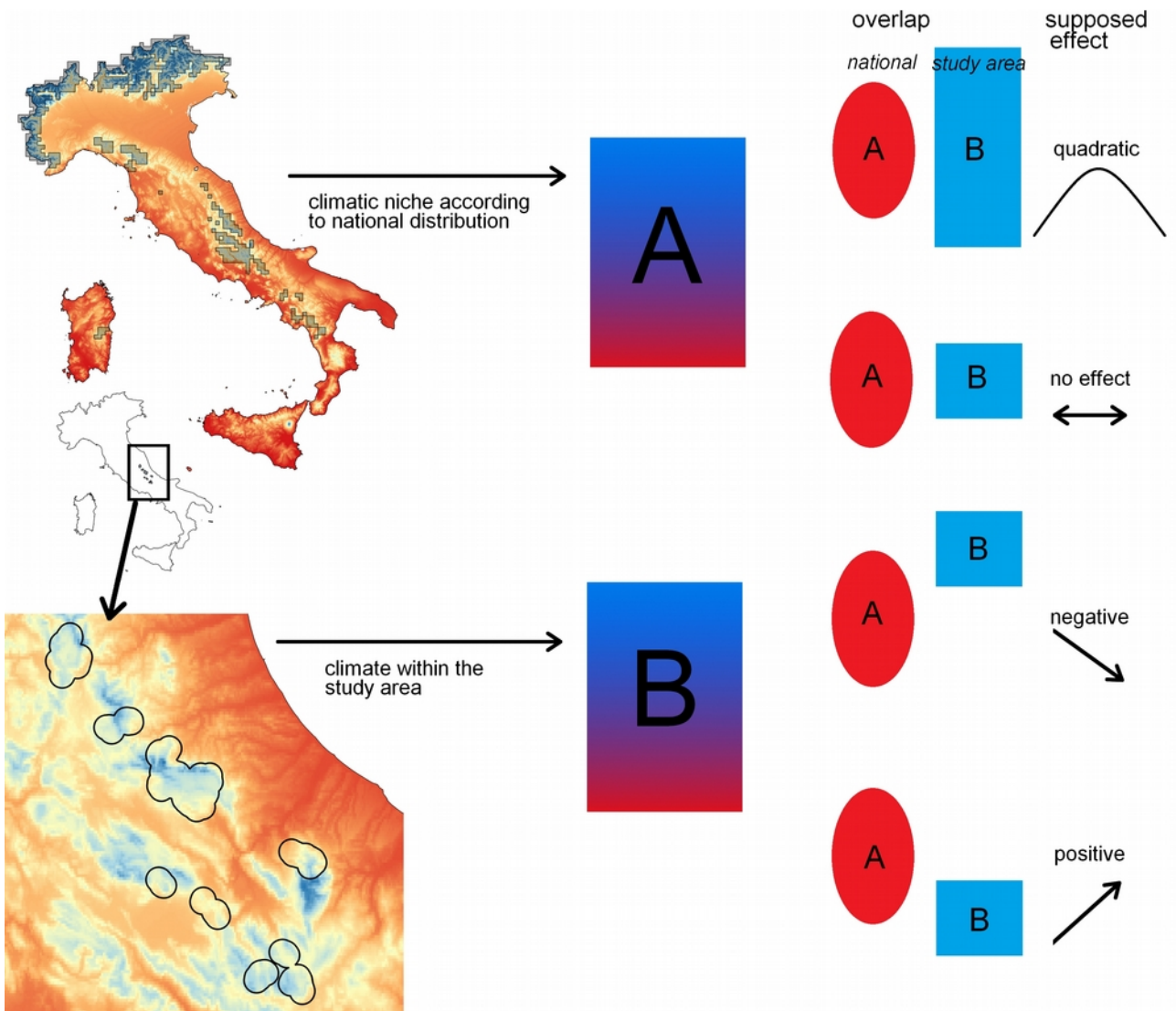
489 **Figure 1.** Study areas (plots with black margins) in Central Apennines (Italy); the bottom left inset  
490 shows the location of the study areas within Italy.  
491



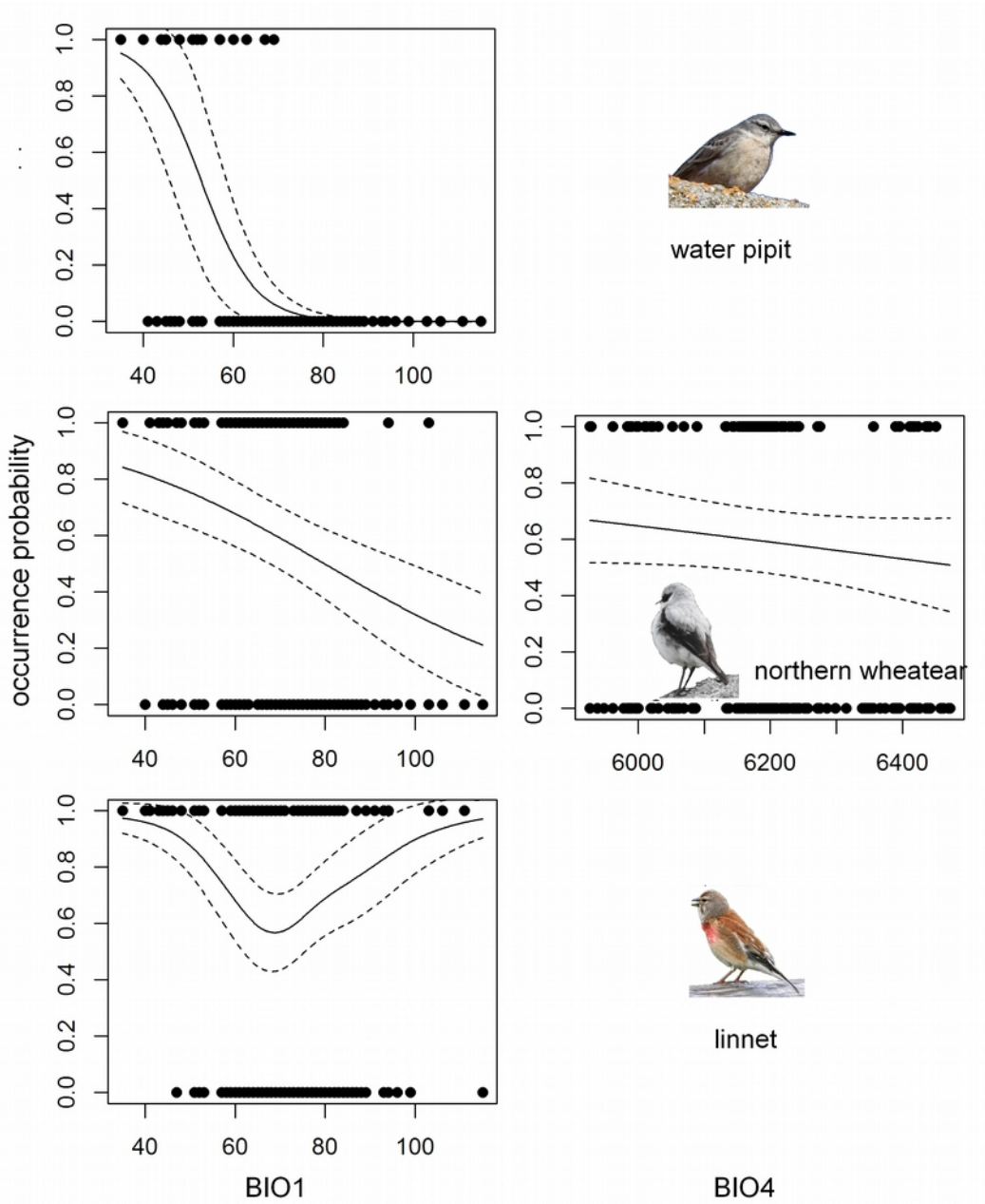
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495 **Figure 2.** A schematic representation of the approach adopted to define the supposed effect of  
 496 climatic predictor on species distribution within the study area, based on a comparison between the  
 497 climatic niche of the species at the national scale (here, water pipit and bio1; indicated with “A”)  
 498 and the values of the same climatic predictor recorded within the study area (indicated with “B”).  
 499 This approach was replicated for each scale, for each climatic variable and for each species.  
 500



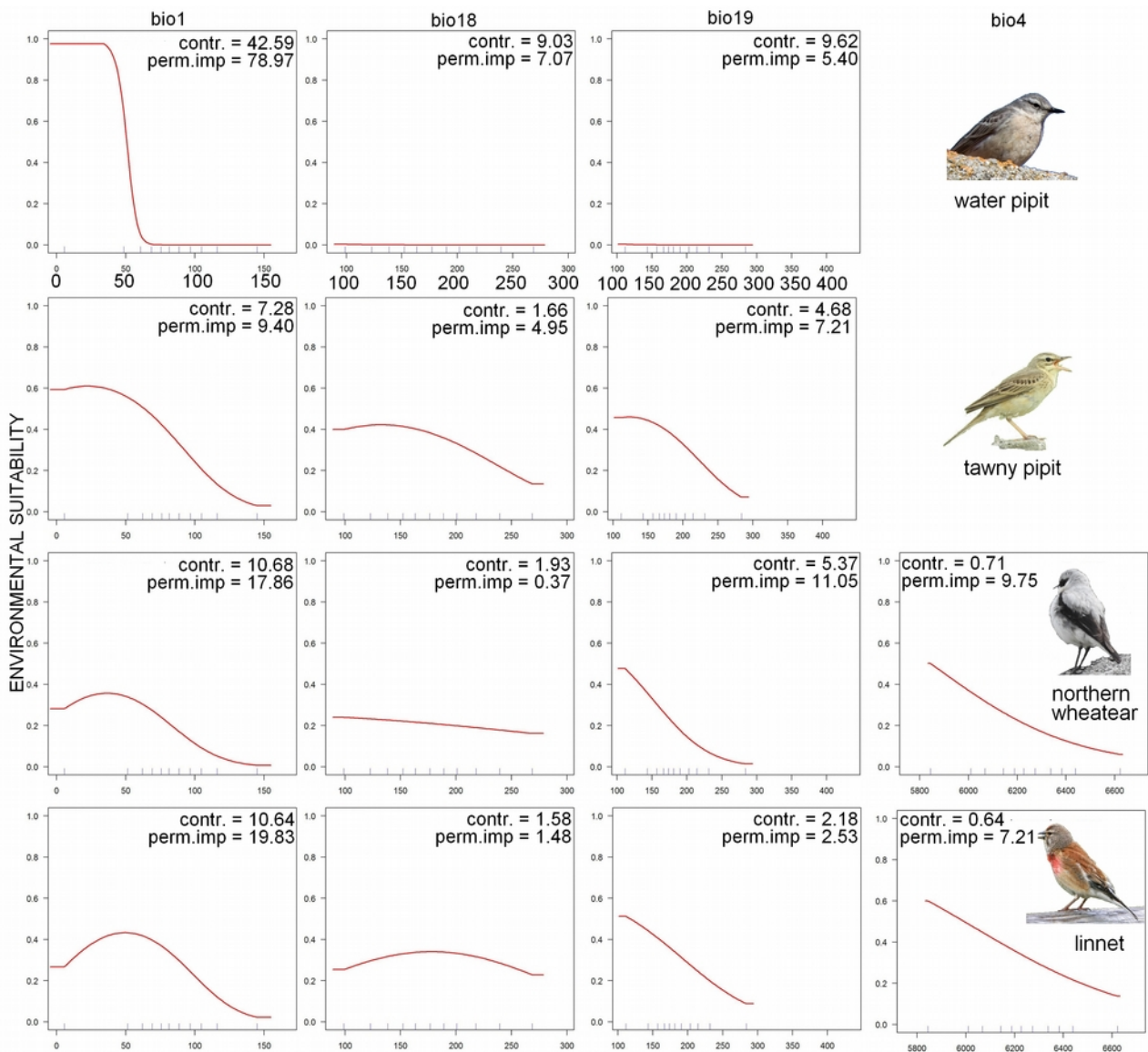
502 **Figure 3.** Modelled effects of climate variables on species occurrence at the territory scale,  
503 according to the GAM model. No climate variable was included in the model for tawny pipit.  
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508 **Figure 4.** Modelled effect of climate variables on species occurrence and relative variable  
 509 importance (percentage contribution, abbreviated “contr.,” and permutation importance, and  
 510 permutation importance, abbreviated “perm.imp.”; both given as percentages) at the landscape scale  
 511 according to the MaxEnt model (plotted effects: models run with all selected predictors).  
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517 **Supplementary material**

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520

521 **Table S1.** Manual setting of models' parameters in biomod2, adopted to prevent data overfitting  
522 based on a critical visual inspection of species-environment curves.

523 **Table S2.** Summary of MaxEnt model performances.

524 **Table S3.** Criteria adopted for the evaluation of coherence between supposed (derived from the  
525 comparison between climatic niche of a species and climate of the study area) effects and  
526 relationships depicted by the models.

527 **Table S4.** Variable importance (percentage contribution and permutation importance, both  
528 expressed as percentages) for predictors included in the final MaxEnt models.**Figure S1.**  
529 Distribution of point counts.

530 **Figure S2.** Distribution of occurrence records used for the analysis at the territory level.

531 **Figure S3.** Distribution of occurrence records used for the analysis at the landscape level.

532 **Figure S4.** Comparison of bio1 effect on linnet occurrence.

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