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1 Improving biological relevance of model projections in response to climate change  
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3

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### 33 CONFLICT OF INTEREST STATEMENT

34 The authors declare they have no conflict of interest.

35

36

### 37 ABSTRACT

38 **Aim:** When modelling future or past geographic distributions of a species, attention should be  
39 paid to the possible differentiated responses to climate changes between lineages. Dispersal also  
40 plays an important role in the capacity of species to track suitable climate, which is particularly  
41 relevant for amphibians with limited dispersal ability. In this study, we included different lineages  
42 and dispersal distances into species distribution models to make them more biologically relevant  
43 in face of climate change scenarios.

44 **Location:** Europe

45 **Taxon:** *Bombina variegata* and its lineages

46 **Methods:** Using MaxEnt, we fitted correlative niche models for *B. variegata* lineages and also for  
47 the species level (*B. variegata sensu lato*) that we projected under Last Glacial Maximum (LGM)  
48 and future climate scenarios (RCP2.6, RCP8.5). A comparison of projections was conducted  
49 considering both unlimited and limited dispersal abilities.

50 **Results:** We found that the *B. variegata* lineages differed in their bioclimatic niches. In general,  
51 models run without discriminating the lineages showed reduced suitable areas compared to  
52 models run at each lineage, especially those for *Bombina variegata pachypus* and *Bombina*  
53 *variegata scabra* (southern lineages). Suitable areas identified for the LGM match with the climatic  
54 refugia identified in phylogeographic studies. Projections for the mid-Holocene showed the  
55 increase of suitable areas for the lineages *B. variegata variegata* "Carpathians" and "Western"  
56 while they decreased for the southern lineages. In the future (2040-2080), only models under  
57 limited dispersal predict the extinction of the Carpathian lineage and a reduction in suitable areas  
58 for the other lineages, regardless of periods and scenarios.

### 59 **Main conclusions:**

60 We demonstrated important shifts in habitat suitability in Europe suggesting range-shifts about  
61 hundreds of kilometres in response to past climate changes. However, rapid and unprecedented  
62 changes in suitability are expected in the future due to the accelerated climate warming during  
63 the 21st. According to their limited dispersal abilities, the persistence of all *B. variegata* lineages  
64 over time appears uncertain. We further recommend to integrate the intraspecific levels, when  
65 available, in modelling process to catch local variations and obtain more accurate results.

66 KW: *Bombina variegata*, climate refugia, ecological niche modelling, Europe, intraspecific levels,  
67 niche differentiation, range-shift

## 68 1. INTRODUCTION

69 Climate change caused by human activities is one of the main drivers of biodiversity decline  
70 worldwide (Parmesan, 2006). One of the main effects of climate change is the shift of thermal  
71 isoclines upward and poleward, leading to the redistribution of climate conditions on a global  
72 scale (Loarie et al., 2009). Species may respond to those changes through phenotypic plasticity  
73 and local adaptation (Urban et al., 2014) or may shift their distribution range to track favourable  
74 climate conditions (Lenoir et al., 2020). Possibilities and magnitudes of range shifts are  
75 determined by the species' propensity and ability to disperse (Travis et al., 2013). Climate-  
76 induced dispersal has been reported in many species (Blaustein et al., 2010) and likely contributes  
77 to the unprecedented biodiversity redistribution reported in recent studies (Lenoir et al., 2020).  
78 However, the evolvability of thermal performances as well as dispersal potential strongly varies  
79 at both interspecific and intraspecific levels (Bestion et al., 2015), therefore making accurate  
80 prediction of species response to climate change a challenging task.

81 Niche-based models (also called 'ecological niche models' or 'species distribution models'), relying  
82 on correlative relationships between observed species distributions and environmental factors,  
83 are powerful tools to predict range shifts driven by future or past climate variations (Araújo et al.,  
84 2006). However, those models have historically suffered from conceptual and technical  
85 limitations that critically affected the reliability of their predictions (Hernandez et al., 2006). First,  
86 relatively few studies explicitly considered species dispersal ability when modelling past and  
87 future range shifts, despite the fact that running models with unlimited dispersal overestimates  
88 the potential future range, especially for species with moderate to low dispersal ability (Urban et  
89 al., 2016). Second, most studies did not consider the intraspecific levels in climate-related  
90 phenotypic performances.

91 Recent studies suggest that populations of the same species may differ in their responses to  
92 climate variation (see, for instance, Bestion et al., 2015 and Trochet et al., 2018). Differences in  
93 population sensitivity to climate fluctuations likely rely on population-specific reaction norms to  
94 thermal and hydric conditions and/or adaptation to local climatic conditions (Gienapp et al., 2007;  
95 Urban et al., 2014). Those population-specific responses are expected to be particularly broad in  
96 ectotherms whose physiology and fitness components (i.e., survival, reproduction and growth)  
97 strongly depend on local/regional thermic and hygrometric variation (Beebee, 1995; Blaustein et  
98 al., 2010). Such variation in population responses to climatic conditions could have a genetic base  
99 (Wilson, 2001) depending on population evolutionary history. This is especially true for  
100 ectotherm vertebrates from temperate areas that experienced broad climate variation and  
101 complex demographic/evolutionary processes during the Pleistocene period (Hewitt, 2000;  
102 Zeisset & Beebee, 2008). In many of those species, the occupancy of multiple glacial refuges led to  
103 the emergence of glacial lineages that have experienced repeated periods of allopatry, often  
104 punctuated by secondary contacts with more or less intense gene flow (Rowe et al., 2006). Those

105 lineages often display partially overlapping climatic niches and contrasted thermal preferences  
106 resulting from the effect of climate-driven selection on their respective glacial refugia (Gilbert &  
107 Miles, 2017).

108 Therefore, considering dispersal ability and bioclimatic preferences at the intraspecific or lineage  
109 level in niche-based models seems a promising way to produce more accurate projections of  
110 species distribution in response to past or future climate changes and to guide conservation  
111 actions (Fong G. et al., 2015). In this study, we focus on a western Palearctic amphibian – the  
112 yellow-bellied toad - *B. variegata* (*sensu lato*), which appears to be an excellent candidate on  
113 which to test this assumption since it has a relatively limited dispersal ability (most of its dispersal  
114 movements have distances of less than 500 m; see Cayuela et al., 2018) and can be separated into  
115 different lineages. Indeed, as a result of *B. variegata*'s complex evolutionary history during  
116 Pleistocene glaciations, four distinct lineages occupy regions with contrasted climatic conditions  
117 (Hofman et al., 2007; Pabijan et al., 2013). Moreover, rainwater fluctuations are known to impact  
118 the survival of *Bombina variegata* and because of its dependency to temporary ponds for its  
119 reproduction, extreme drought events increased by global warming are expected to particularly  
120 threaten the development of this toad (Cayuela et al., 2014). Therefore, we asked the following  
121 nested questions: how meaningful is it to run the models while considering intraspecific levels?  
122 How has each lineage responded, and how will it respond, to climate change when we consider  
123 the dispersal ability of the species? What lineage could suffer the most in the face of future climate  
124 change?

125 First, we fitted correlative niche models for each *B. variegata* lineage using MaxEnt (Phillips *et al.*,  
126 2017) and projected both past (LGM and Mid-Holocene) and future climate change scenarios.  
127 Second, we compared model projections that had limited and unlimited dispersal abilities.

128

## 129 2. MATERIALS AND METHODS

### 130 2.1. Model species

131

132 *Bombina variegata* is a pond-breeding amphibian with a widespread distribution in Europe. Over  
133 the last century, the species suffered from a sharp decline, especially in Western Europe (Lescure  
134 et al., 2011), and is registered in Appendix II of the Bern Convention and in Appendices II and IV  
135 of the EU Habitat Directive. This species occupies various habitats, such as forests and meadows,  
136 and reproduces mainly in temporary waterbodies filled by rainfall that could result from human  
137 activities (Cayuela et al., 2014; Scheele et al., 2014). Temperature and precipitation are important  
138 determinants of post-metamorphic survival and reproduction (Cayuela et al., 2016).

139 *Bombina variegata* has a complex biogeography: distinct glacial lineages were previously  
140 identified based on mitochondrial DNA (Hofman et al., 2007), including *B. v. variegata* in western  
141 Europe, *B. v. variegata* in the Carpathian Mountains, *B. v. pachypus* in Italy and *B. v. scabra* in the  
142 Balkan Peninsula.

143

## 144 2.2. Occurrence data

145

146 Occurrence data were obtained from several sources for the period 1979–2016. We gathered data  
147 of the different *Bombina* lineages across Europe, including southern, western and part of eastern  
148 Europe (Fijarczyk et al., 2011; Hofman et al., 2007). Occurrence data of *B. v. variegata*  
149 ‘Carpathians’, *B. v. scabra* and *B. v. pachypus* were all obtained from GBIF.org (accessed May 2019)  
150 GBIF Occurrence Download (DOI: <https://doi.org/10.15468/dl.ndtync> for *B. v. pachypus*;  
151 DOI: <https://doi.org/10.15468/dl.86wc6h> for the other lineages). The data set for the western  
152 lineage of *B. v. variegata*, which has the largest distribution area, was completed by occurrence  
153 data from the association Faune-France, the Écrins National Park, Montagne de Reims Regional  
154 Natural Park, naturalistic associations in the region of Centre-Val de Loire, the Swiss Wildlife  
155 Mapping Center and some additional data from the northeast of France (Cayuela et al., 2020).  
156 Occurrence data were upscaled to correspond at the centroid of a 10 x 10 km grid. This  
157 transformation allows us to reduce sample bias by removing over-sampled locations and thus  
158 increases the predictive abilities of the model by reducing spatial autocorrelation (Boria et al.,  
159 2014). Because *B. v. scabra* and the two lineages of *B. v. variegata* were not distinguished in the  
160 GBIF and International Union for Conservation of Nature (IUCN), we separated them according to  
161 the genetic clusters identified by Fijarczyk et al. (2011) and Hofman et al. (2007).

162 After removing suspicious occurrences (i.e., older occurrences and data outside the current  
163 species range), the sample size used for modelling was as follows: 1956 occurrence data for *B. v.*  
164 *variegata* ‘western lineage’ (V), 123 for *B. v. variegata* ‘Carpathians’ (C), 26 for *B. v. scabra* (S) and  
165 28 for *B. v. pachypus* (P). These final two lineages occupy the smallest distribution areas, restricted  
166 to the Balkan region and to the main part of Italy, whereas the first has the widest distribution  
167 area (see Supporting Information Appendix S1).

168

## 169 2.3. Climate data

170

171 We selected nine bioclimatic variables (representing temperature and precipitation conditions)  
172 known to influence the different development stages of the *Bombina* toads (see Supporting  
173 Information Appendix S2 for a complete description of variables), from egg to adulthood (Cayuela  
174 et al., 2014; Kaplan & Phillips, 2006; Reyer & Barandun, 1997). These variables were obtained  
175 from ‘Climatologies at high resolution for the Earth’s land surface area’ (CHELSA, (Karger et al.,  
176 2017), <http://www.chelsa-climate.org/>) for the period 1979–2013 (30 arcsec resolution, ~1 km).  
177 Climatic layers were averaged at a 10 x 10 km spatial resolution to match the species occurrence  
178 grid. Climate data were extracted at the location of lineage occurrences and used to fit the niche-  
179 based model.

180 We calculated the Pearson correlation coefficient among each of the bioclimatic variables, as well  
181 as their variance inflation factor (VIF) in the niche-based model, using the R packages ‘usdm’ and  
182 ‘ecospat’ (Broennimann et al., 2012; Naimi et al., 2014). Only variables with a correlation  
183 coefficient lower than 0.75 and a VIF of less than 10 were retained (Naimi et al., 2014). This  
184 method allowed us to avoid collinearity that could bias forecasts made by the niche-based model.  
185 Thus, we retained seven variables that were used throughout this study (see Appendix S2).

186 For past climatic conditions, we used CCSM4 and MIROC-ESM models according to the reviews of  
187 Svenning et al. (2011) and Varela et al. (2011). Indeed, these climate models are the most widely  
188 used in Europe and show less bias compared to other global circulation models (GCMs) for the  
189 LGM (Harrison et al., 2014). Both model outputs were extracted from the CHELSA database  
190 (Karger et al., 2017) for the LGM (i.e., 21 000 years ago) and from the WorldClim database (v1.4;  
191 Fick & Hijmans, 2017) for the mid-Holocene (i.e., 6000 years ago).

192 We used two other GCMs for future climate conditions expected during the 21st century: CSIRO-  
193 Mk3.6.0 and HadGEM2-ES (Collier et al., 2011; Collins et al., 2008), which we extracted from the  
194 CHELSA and WorldClim databases, respectively. These widely used GCMs were selected because  
195 they generate robust predictions (Buisson et al., 2010; Farzaneh et al., 2012) and have been  
196 recognized for generating divergent predictions (Mitchell et al., 2004). These two GCMs were used  
197 to model two future periods, 2041–2060 and 2061–2080, under two Representative  
198 Concentration Pathway (RCP) scenarios: RCP2.6 and RCP8.5, which are optimistic and pessimistic  
199 scenarios that respectively predict a global increase in mean temperature of 0.9–2.3°C to 3.2–  
200 5.4°C and changes in global mean precipitation correlated with changes in global mean  
201 temperature (Baek et al., 2013; Riahi et al., 2011; van Vuuren et al., 2011). Species redistribution  
202 forecasts on several GCMs and climate change scenarios account for future climate condition  
203 uncertainties in our work (Buisson et al., 2010).

204

#### 205 2.4. Niche similarity between lineages

206

207 Prior to modelling, we analysed the bioclimatic niches of the different lineages identified by  
208 Fijarczyk et al. (2011) and their possible overlap using the R package ‘ecospat’. A similarity test  
209 was performed to estimate the climate niche similarity between two lineages by comparing  
210 climate conditions (defined by the first two components of a principal component analysis (PCA))  
211 where lineages occur (with replications  $n = 1000$ ). We calculated the similarity measure  $I$  based  
212 on the Hellinger distance to assess niche overlaps (Schoener, 1968; Warren et al., 2008). The  $I$   
213 metric ranges from 0 (no overlap) to 1 (perfect overlap), has no biological assumptions  
214 concerning the distribution of the two tested species and only considers them as probability  
215 distributions (Warren et al., 2008).

216

#### 217 2.5. Niche-based modelling and forecasts

218

219 General modelling. We used MaxEnt v3.4.1, one of the most used and robust models (Elith et al.,  
220 2011), which also demonstrated good performance in situations with few occurrence data (Elith  
221 et al., 2006; Hernandez et al., 2006). Our models were calibrated according to current bioclimatic  
222 conditions from all of Europe (see above), which is the best way to encompass a large range of  
223 conditions, limit model extrapolation and identify the overall global niche of the species (Pearson  
224 et al., 2002).

225 We ran 50 replicates with 25% of test data (random seed, bootstrap) and set the other parameters  
226 by defaults. Because MaxEnt uses an exponential model and extrapolates projections when  
227 environmental data used are outside their present range, we used the clamping method. This  
228 method considers variables outside their range as if they were at the limit of their training range  
229 and thereby limits extrapolation (Phillips, 2017).

230 The model performance was assessed with the area under the receiver operating characteristic  
231 curve (AUC), the true skill statistic (TSS; usdm package) and the kappa statistic (Araújo et al.,  
232 2019). The AUC ranges between 0 and 1, where 0.5 and below indicate that the model has no  
233 predictive ability better than random (Hanley & McNeil, 1982). The kappa statistic and TSS range  
234 from -1 to 1, where 1 indicates a perfect model and values of less than 0 indicate a performance  
235 no better than random predictions (Allouche et al., 2006; Cohen, 1960). We explored models'  
236 extrapolations by identifying areas where predictors are outside of their training range with the  
237 multivariate environmental similarity surface (MESS) option.

238 After binarization based on the 'maximum training sensitivity plus specificity' threshold rule (Liu  
239 et al., 2013), we calculated the percentage of loss and gain of suitable habitats and projected these  
240 results on maps. Changes in areas of suitable habitats of each lineage were combined in one map  
241 by model and period.

242

243 *Species and intraspecific level.* We ran separate models following the methods described above for  
244 each lineage and also without considering the intraspecific level (*B. variegata sensu lato*).  
245 Moreover, we ran the models with the most adapted value of regularization multiplier and feature  
246 class, according to the AICc, calculated under the R package "ENMeval" (Muscarella et al., 2014).  
247 The best regularization multipliers and feature classes were 0.5HP (Hinge plus Product features),  
248 1T (Threshold features), 0.5LQ (Linear plus Quadratic features), 0.5HP (Hinge plus Product  
249 features) and 0.5HPQ (Hinge plus Product plus Quadratic features) respectively for *B. v. variegata*  
250 'Carpathian', *B. v. pachypus*, *B. v. scabra*, *B. v. variegata* 'western lineage' and *B. variegata* (i.e.,  
251 species level).

252

253 *Limited vs. unlimited dispersal scenarios.* We considered the dispersal capacity based on the study  
254 from Cayuela et al. (2018), who assessed the dispersal abilities of the yellow-bellied toad at  
255 different life stages in a forest environment located in eastern France. The median dispersal event



256 distance comprised between 444 and 695 m per year, depending on the age class (Cayuela,  
257 Bonnaire, et al., 2018). Based on these results, we considered in this study that *B. variegata* was  
258 able to disperse at a rate of 500 m per year, which corresponds to the distance covered by most  
259 of the individuals within a population in a favourable environment.

260 We took into account the dispersal ability by adding a buffer zone around the current distribution  
261 area (obtained from the IUCN) of the considered lineage. The buffer width was calculated by  
262 multiplying the number of years that separates the current period from the past or future studied  
263 period by 500 m. For each lineage at the species level, future projections were conducted in the  
264 current distribution areas with additional buffers of 15 and 30 km for the periods 2041–2060 and  
265 2061–2080, respectively. We also ran models under unlimited dispersal for these periods.

266 Considering the time scale for past projections, the buffer areas were as large as Europe  
267 (equivalent to unlimited dispersal). Nevertheless, for LGM projections, the continental area has  
268 been modified by taking into account the large continental glaciers and changes in emerged land  
269 surface due to sea levels' temporal variations (Ehlers & Gibbard, 2007; Lambeck, 2001). We  
270 considered continental glaciers to be unsuitable areas. Also, we considered islands to be  
271 unreachable and therefore unlikely to be colonized.

272

### 273 3. RESULTS

#### 274 3.1 Divergence of bioclimatic niches among the *Bombina* glacial lineages

275

276 The first two components of the PCA explained 69% of the total variance (Figure 1). The first  
277 component represented a water balance gradient ranging from humid/fresh to dry/hot  
278 conditions. The second component described specific climate conditions in summer,  
279 distinguishing cold/dry and hot/humid locations.

280 We detected a significant niche similarity between the Italian (*B. v. pachypus*) and the Balkan (*B.*  
281 *v. scabra*) lineages, suggesting they occur in similar climate conditions ( $I = 0.693$ ; see Supporting  
282 Information Appendix S3). Other climate niche comparisons among lineages were not significant,  
283 showing a high level of intraspecific niche differentiation within the *B. variegata* species. The  
284 Carpathian lineage had the smallest bioclimatic niche and always presented the lowest scores of  
285 niche similarity with the other three lineages (Figure 1). The maximal niche similarity for this  
286 lineage was observed with its sister lineage, western *B. v. variegata* ( $I = 0.252$ ). Whereas the  
287 western lineage of *B. v. variegata* had the largest niche, which overlapped greatly with the other  
288 lineages, niche similarity was low ( $I_{\min/\max} = 0.252/0.428$ ) as a large part of the climate niche  
289 of the western lineage is not shared with any other lineages.

290

#### 291 3.2 Current distribution models

292

293 Models at both the species and lineage levels performed well according to the mean values of the  
294 AUC, TSS and kappa, which ranged from 0.937 ( $\pm$  0.036) to 0.961 ( $\pm$  0.044), 0.760 ( $\pm$  0.016) to  
295 0.923 ( $\pm$  0.076) and 0.412 ( $\pm$  0.101) to 0.781 ( $\pm$  0.015), respectively (see Supporting Information  
296 Appendix S4).

297 According to the models' outputs, the most suitable areas were located in the central Carpathian  
298 Mountains for the Carpathian lineage of *B. v. variegata*, in the Balkan Mountains for *B. v. scabra*, in  
299 southern Italy for *B. v. pachypus* and in western Europe for the western lineage of *B. v. variegata*  
300 (Figure 2a). Models at the species level identified suitable areas that correspond almost  
301 exclusively to those identified for the western lineages (i.e., in western Europe) (Figure 2b).

302 The bioclimatic variables that contributed the most to the models were 'Precipitation of the  
303 Wettest Quarter' (Bio16: 33.4% and 39.8%) for the Carpathian and Italian lineages, 'Mean  
304 Temperature of the Driest Quarter' (Bio9: 36.5%) for *B. v. scabra* and 'Precipitation of the Driest  
305 Quarter' (Bio17) for the western lineage of *B. v. variegata* and also for the species-level model  
306 (53.1% and 52.4%, respectively) (see Supporting Information Appendix S5).

307

### 308 3.3. Projections under past climates

309

310 Due to the large range of the time period (6000 to 21000), past projections were made without  
311 any dispersal limitation (see Materials and Methods).

312 For models conducted at the species level, the location and percentage of suitable areas were  
313 similar to the western lineage (-93.1% to -88.2% for the LGM and -45.1% to -37.8% for the mid-  
314 Holocene).

315 Considering the western lineage of *B. v. variegata*, only the southwest of France was suitable 21  
316 000 years ago (Figure 3; Table 1). CCSM4-based projections indicated that the west coast of  
317 France, a part of the Apennine Mountains in Italy and a small area of the Balkan Peninsula were  
318 also suitable, while MIROC-ESM-based projections showed additional suitable areas in the north  
319 of Italy and in the Dinaric Alps (see Supporting Information Appendix S6). As a result, suitable  
320 areas were smaller than they are today, with an average of -91% to -68.2%. During the mid-  
321 Holocene, suitable areas appeared toward the north, but these areas were smaller compared to  
322 current areas, ranging from -43% to -31.3%. For the Carpathian lineage, models' outputs showed  
323 much smaller suitable areas than the current situation, between -100% to -84.2% smaller on  
324 average. Those suitable areas were potentially located in the Pannonian Basin and in Germany 21  
325 000 years ago (see Appendix S1). Later, 6000 years ago, suitable areas were less restricted, with  
326 a mean percentage ranging from -80% to -20% in comparison to the current distribution.  
327 Therefore, the model showed that this lineage shifted its range toward the centre and the south  
328 of the Carpathians (Figure 3; Table 1).

329 The *B. v. pachypus* lineage model projections for 21 000 years ago identified larger suitable areas  
330 than the lineage's current range, mostly in the Balkan Peninsula, western France and Spain.  
331 Models made with the CCSM4 climate scenario resulted in suitable areas 50% larger than the  
332 current distribution (Figure 3; Table 1; see Appendix S6). During the mid-Holocene, models  
333 showed a reduction in suitable areas restricted to the south of Italy, resulting in a climatic suitable  
334 area of -44.1% to -26.5% compared to current areas.

335 For the Balkan lineage, *B. v. scabra*, a large part of the Balkans appeared suitable, including the  
336 Dinaric Alps and Rhodope Mountains during the LGM (Figure 3, see Appendix S1). Results based  
337 on climate conditions inferred from the CCSM4 model are more restricted than those based on the  
338 MIROC-ESM model (see Appendix S6). Thus, suitable areas were about 12.3% to 253% larger than  
339 current areas. During the mid-Holocene, suitable areas were generally smaller than their current  
340 distribution by -93.8% to 33.1% (Table 1). Models identified suitable areas mainly in high  
341 elevation areas such as the Rhodope but also in Ukraine (see Appendix S6).

342

#### 343 3.4. Projections under future climate change

344

345 Results correspond to models run at species or lineage level by considering either unlimited or  
346 limited dispersal.

347

##### 348 Species level

349 According to species distribution models (SDMs) made at the species level, *B. variegata* is  
350 expected to undergo a reduction in suitable areas similar to the western lineage of *B. v. variegata*,  
351 ranging from -99.6% to -54.1% in 2061–2080 under dispersal limitation. Thus, percentages of  
352 predicted suitable areas under dispersal limitation are lower than those obtained for the southern  
353 lineages (*B. v. pachypus* and *B. v. scabra*).

354 Under unlimited dispersal, forecasts indicated that *B. variegata* will likely not expend its range,  
355 and whereas the western lineage of *B. v. variegata* could gain 37.6% more suitable areas in 2061–  
356 2080 according to the HadGEM2-ES GCM coupled with the RCP2.6, *B. variegata (sensu lato)* could  
357 only gain 5.5% more suitable areas. Nevertheless, losses in suitable areas are less significant  
358 under unlimited dispersal, ranging from -93.3% to 5.5% (Table 2; see Supporting Information  
359 Appendix S7).

360

##### 361 Lineage level

362 The models showed that the two lineages of *B. v. variegata* had the lowest increase of suitable  
363 areas, with a mean percentage increase of -99.6% to 170.2% and -39.1% to 37.6%, compared to  
364 current areas, in 2061–2080 for the Carpathians and western lineage under unlimited dispersal,

365 respectively (all scenarios and periods). Under dispersal limitations, forecasts were pessimistic,  
366 with suitable areas ranging from -100% to 44.5% compared to current areas (all scenarios,  
367 periods and lineages).

368 According to projections based on the RCP8.5 under unlimited dispersal, potential suitable areas  
369 were expected to be 2.3 to more than 20 times larger than current areas for *B. v. pachypus* and *B.*  
370 *v. scabra* (Table 2; see Supporting Information Appendix S8, S9). Even if suitable areas were  
371 expected to increase for these lineages according to this scenario under unlimited dispersal, the  
372 two lineages of *B. v. variegata* should undergo reduction in suitable areas from -97.7% to -59% in  
373 2061–2080. Under dispersal limitations, forecasts obtained for the RCP8.5 were always  
374 pessimistic compared to those obtained under unlimited dispersal, even for *B. v. pachypus* and *B.*  
375 *v. scabra*, with a mean percentage of suitable areas between -63.2% and 1.5% in 2061–2080.

376 Thus, SDMs often predicted less loss of suitable areas under unlimited dispersal even if some  
377 predictions still indicated an almost complete disappearance of suitable areas (Table 2). Finally,  
378 the Carpathian lineage appears to be the most threatened, and only a few areas remain suitable in  
379 altitude according to the optimistic climate scenario, while the other models project an almost  
380 complete loss of suitable habitat in 2061–2080 under dispersal limitations (Figure 4, 5). In the  
381 same way, the western lineage of *B. v. variegata* will also suffer from a drastic reduction in suitable  
382 habitat, and the remaining suitable areas are located in the north or altitude (Figure 5).

383

384

#### 385 4. DISCUSSION

386 For this paper, we developed models that simulated the changes in suitable areas for *B. variegata*  
387 in response to past and future climate changes by testing the different lineages independently and  
388 taking into account the dispersal capacity. This study is the first forecast of the future geographic  
389 distribution of bioclimatic suitable areas for this vulnerable amphibian. This is also the first that  
390 explored the animal's potential distribution during the LGM and mid-Holocene period.

391 The results of all the models are supported by good performances of the metrics that are broadly  
392 used in modelling studies. In addition, as expected, MESS analysis indicated that reachable areas  
393 have a low degree of extrapolation, which is due to our calibration with current bioclimatic data  
394 from all of Europe (Supporting Information Appendix S10).

395 Our study revealed that considering dispersal limitation by expanding the distribution area has a  
396 broad influence on model projections of future and past distribution of *B. variegata*. Indeed,  
397 whereas suitable areas will endure in Europe over time, many of them will not be reachable for  
398 the yellow-bellied toad.

399

##### 400 4.1. Intraspecific level strongly impacts forecasts

401

402 The analysis of the bioclimatic niches of the lineages commonly identified in the scientific  
403 literature showed enough discrepancies to treat each lineage independently in the models, also  
404 suggesting contrasted thermal and hydric preferences between lineages. According to the niche  
405 similarity measures, each lineage had relatively little overlap, and we distinguished two main  
406 groups: the southern group including *B. v. pachypus* and *B. v. scabra* and the northern group  
407 including the other lineages. With the smallest overlap scores, the Carpathian lineage appears to  
408 be the most different, with populations living in a particular climatic environment. Our results are  
409 consistent with genetic studies (Fijarczyk et al., 2011) that showed this lineage to be the most  
410 genetically divergent. The Italian lineage, sometimes considered a distinct species, *Bombina*  
411 *pachypus* (Canestrelli et al., 2006), had a significantly similar bioclimatic niche than the Balkan  
412 lineage. Populations of these two lineages are geographically separated, apparently with a quasi-  
413 absence of populations between their current range areas. Thus, the proximity of these two niches  
414 is likely due to similarities in the bioclimatic conditions of the Balkan and Italian peninsulas.

415 Models' outputs were different if we considered the species or the lineage level, and simulations  
416 for the LGM gave contrasting results, depending on the lineages. According to species models for  
417 past projections, no suitable area was present near the Carpathians or in the Balkan Peninsula,  
418 even if these areas had served as climatic refugia during the LGM (Hofman et al., 2007). For the  
419 Carpathian's lineage, models have identified suitable areas in lowland regions, in the Pannonian  
420 Basin. The localization of these suitable areas is consistent with phylogeographic studies and  
421 supports the fact that this region served as a climatic refuge for ectotherms during the LGM  
422 (Fijarczyk et al., 2011; Horreo & Fitze, 2018). For *B. v. pachypus*, suitable areas were located in  
423 lowlands between the Tyrrhenian Sea and the Apennine Mountains and in southern Italy, as  
424 suggested by genetic studies during the LGM (Canestrelli et al., 2006).

425 Current models at species level indicated that Carpathians and the Balkan and Italian Peninsulas  
426 were not suitable to host *B. variegata* populations. By contrast, when we considered the  
427 intraspecific level, we showed that the suitability of these areas was higher than expected  
428 according to the species model. These results support the fact that distinct populations of the same  
429 species may react differently to climate and habitat changes (Gotelli & Stanton-Geddes, 2015),  
430 highlighting the importance of integrating intraspecific levels when data are available. Dowell and  
431 Hekkala (2016) have shown that the predicted suitable areas differed depending on the lineages  
432 of *Varanus niloticus* and therefore should not face the same future threats. In our case, forecasts  
433 for the species models were similar to those obtained for the western lineage of *B. v. variegata*  
434 (see Appendix S10). One plausible explanation is that the western lineage of *B. v. variegata*, which  
435 has the largest distribution and accounts for 91.7% of the occurrences in Europe, largely  
436 influenced the model, hiding the diversity within the species models. Consequently, the suitable  
437 areas identified in the Italian and Balkan Peninsulas for the southern lineages have been  
438 considerably reduced, leading to pessimistic predictions.

439

## 440 4.2. Improving models' relevance with dispersal limitation

441

442 Dispersal is one of the keys that allows species to migrate and to modify their range in response  
443 to environmental changes. Several studies have discussed modelling species distributions using  
444 different dispersal scenarios. Two 'dispersal assumptions' are particularly widespread in  
445 modelling studies: unlimited dispersal and no dispersal. In the case of unlimited dispersal, it is  
446 recognized that forecasts tend to over-predict suitable areas and are unrealistic because the areas  
447 predicted as suitable are, in general, unreachable by the species (Araújo et al., 2006). With regard  
448 to the no dispersal scenario, forecasts often under-predict suitable areas because they are limited  
449 by the current distribution area of the species studied. Even if this latter dispersal assumption  
450 appears more realistic than that of unlimited dispersal, it suffers from severe limitations, mainly  
451 because many species have the ability to track their bioclimatic niches to some extent,  
452 emphasizing the importance of integrating a biologically relevant dispersal distance (Araújo et al.,  
453 2006).

454 Under unlimited dispersal, our models often predicted an increase in new suitable areas for all  
455 lineages, mainly predicted to be located in north or at altitude, out of the lineages' current range.  
456 However, under limited dispersal scenarios, despite predicted new suitable areas, results showed  
457 a global reduction of suitable areas and sometimes an almost total disappearance of them.  
458 Consequently, three of the four lineages (*B. v. scabra*, Carpathians and western *B. v. variegata*) are  
459 predicted to lose all of their suitable areas in the future, according to at least one model. The  
460 discrepancy between the results under limited and unlimited dispersal could be explained by the  
461 dispersal abilities of the yellow-bellied toad. Indeed, even if suitable areas remain in Europe over  
462 time, many of them will likely be unreachable, according to our dispersal buffer. Thus, only a  
463 fraction of these suitable areas will likely be reached, mainly in altitude or to the north of the  
464 lineages' current range.

465 The integration of a coherent dispersal distance is still a major issue in modelling studies because  
466 of the lack of data, but studies that rely on demographic or genetic approaches could help  
467 (Cayuela, Rougemont, et al., 2018). Indeed, dispersal distance can be inferred through genetic  
468 differentiation between two distinguished populations. Genetic differentiation depends on  
469 genetic drift and gene flow, and thus individuals that colonize another distant population could  
470 modify its allele frequencies and therefore its genetic differentiation (Broquet & Petit, 2009).  
471 However, because genetic differentiation also depends on genetic drift, its use as a dispersal proxy  
472 could lead to misleading results. Thus, we recommend jointly the use of genetic and demographic  
473 approaches (Cayuela, Rougemont, et al., 2018). For instance, Cayuela et al. (2020) used a  
474 combined demographic and genetic approach to study and compare two populations of *B. v.*  
475 *variegata*, one of which exhibited dispersal syndromes. Using this method, they identified that the  
476 costs and benefits of dispersal drive the behaviour of spatially structured populations in logging  
477 environments, and they were able to distinguish the effect of genetic drift from gene flow. These  
478 results bring us to a new point: populations could differ in terms of dispersal behaviour, and those  
479 with lower dispersal abilities and weaker genetic structure are expected to be particularly

480 vulnerable to environmental changes (Cayuela et al., 2020). The integration of the intraspecific  
481 differences in dispersal abilities using dispersal kernels would therefore pose a future challenge  
482 in obtaining more accurate and realistic SDMs. Nonetheless, integration of intraspecific  
483 differences would require precise knowledge of the dispersal behaviour of populations across the  
484 range extent of the species studied.

485 In our study, we considered a dispersal distance of 500 m per year. Even though this distance is  
486 biologically relevant, it was assessed in a homogenous landscape, while human infrastructures  
487 are known to limit dispersal events (Cayuela, Bonnaire, et al., 2018; Trochet et al., 2019). Thus, at  
488 a smaller scale, the integration of the landscape resistance could also allow us to obtain more  
489 biologically relevant predictions. According to the negative impact of human infrastructure on  
490 animal movements, the width of the dispersal buffers may be too large in some regions.  
491 Nevertheless, while human infrastructures have negative effects on dispersal events, logging  
492 activities could generate waterbodies (for instance ruts) used for reproduction (Cayuela et al.,  
493 2014). Thus, landscape management could counterbalance human impacts in harvested forest  
494 that were supposed to provide high quality habitat especially during drought (Scheele et al., 2014)

495

## 496 5. CONCLUSION

497 We demonstrated that incorporating intraspecific levels into niche-based models is a valuable  
498 approach to obtaining more biologically relevant projections in response to environmental  
499 changes, especially when the species has lineages with divergent bioclimatic niches across its  
500 distribution. Predictions at the intraspecific level were generally more optimistic than those made  
501 at the species level, notably by their limited decline in response to future climate change. Taking  
502 into account each lineage separately reflected adaptations to 'regional' climates and allowed us to  
503 observe specific responses rather than an average global response. However, when dispersal  
504 ability was considered, future projections of the two sister lineages of *B. v. variegata*, particularly  
505 the one from the Carpathians, showed a drastic reduction in suitable areas, which could lead to  
506 extinction in less than 70 years. In the face of unprecedentedly high current climate velocity,  
507 further studies should focus on obtaining better knowledge about species dispersal. Finally, our  
508 approach is particularly valuable for species such as European amphibians that exhibit a complex  
509 biogeography inherited by isolation and recolonization events that occurred during Pleistocene  
510 glaciation and that resulted in distinct lineages.

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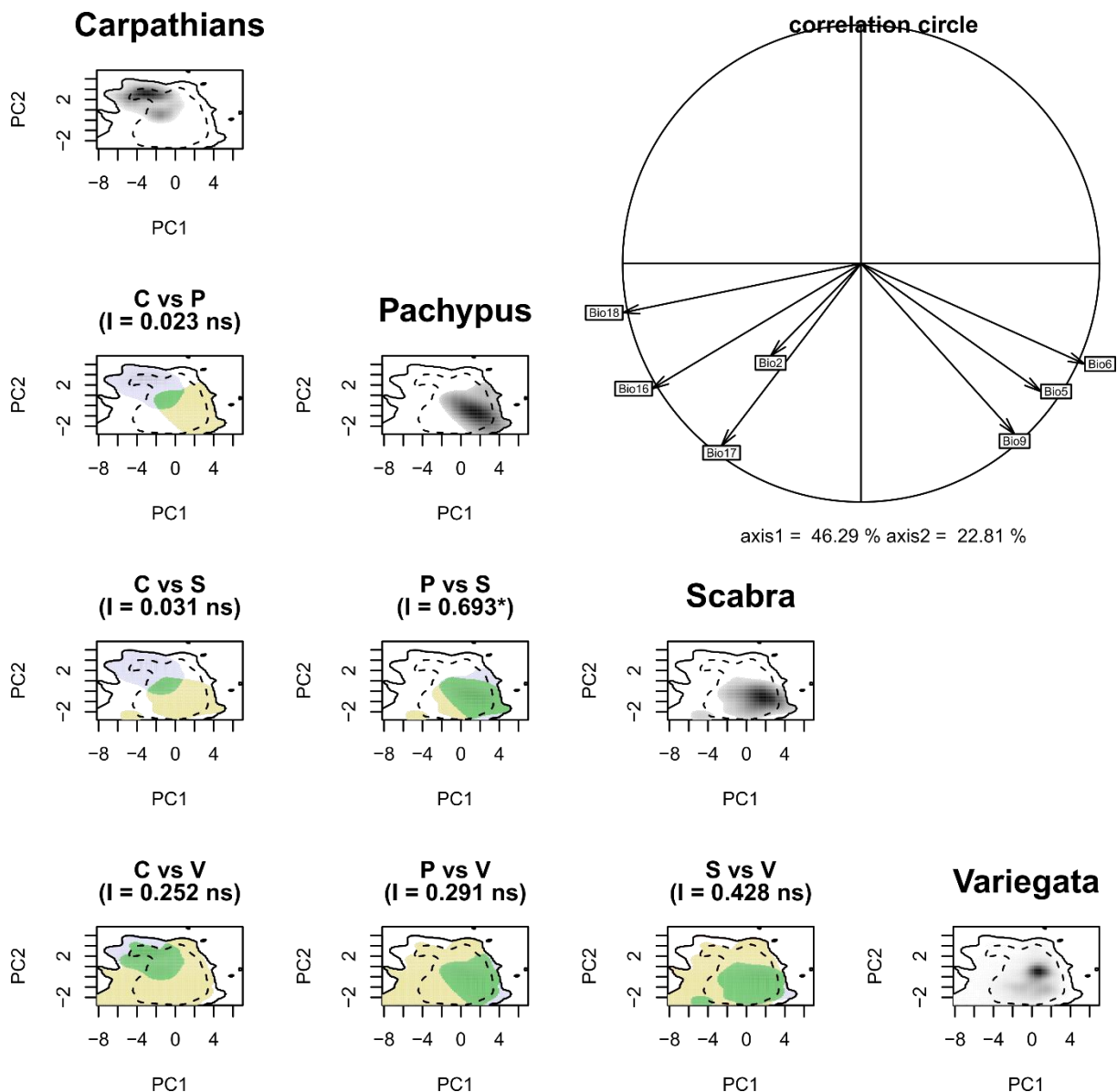
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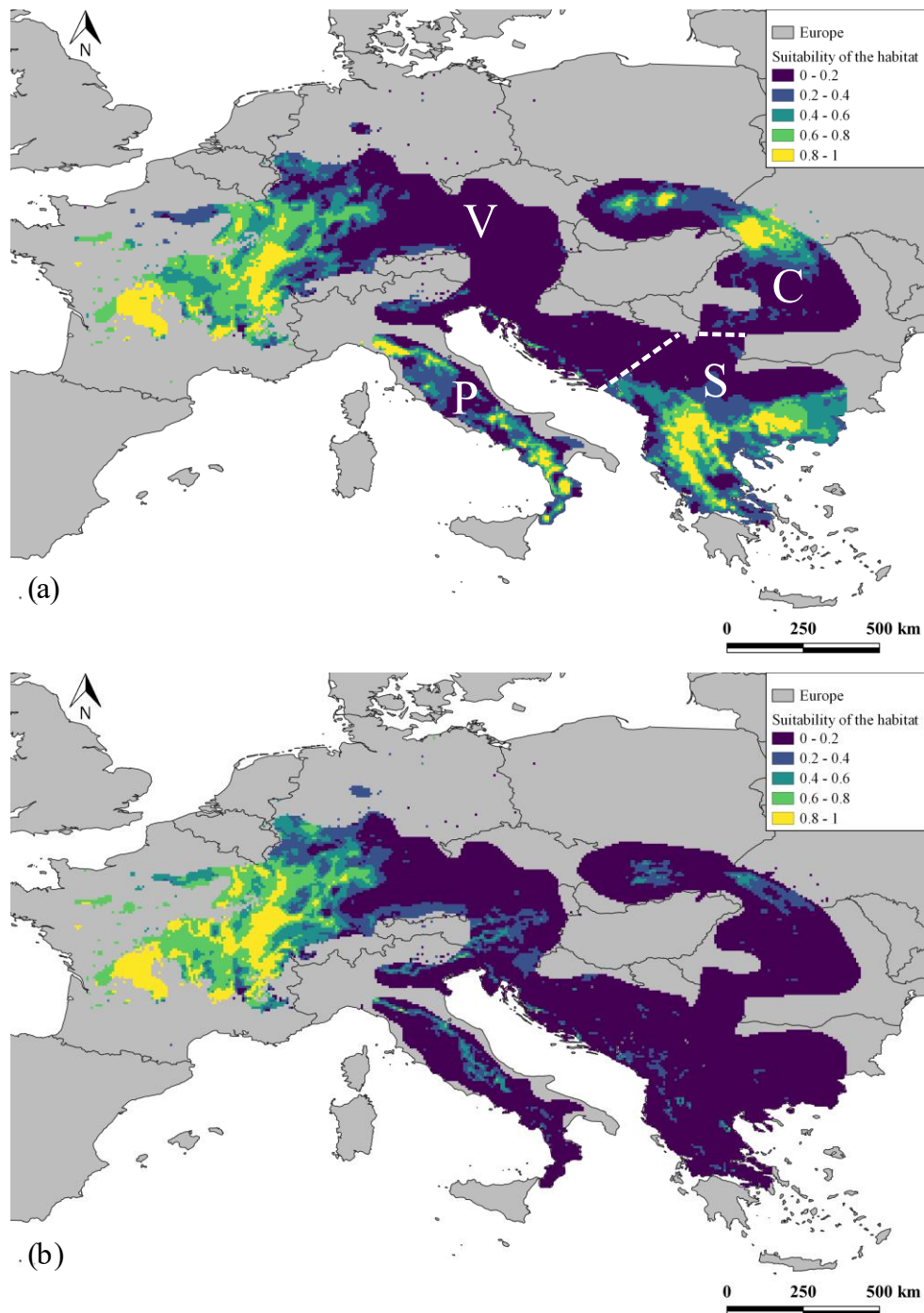


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518 FIGURE 1 Bioclimatic niche similarities amongst the four *Bombina variegata* lineages. The  
 519 horizontal axis in the correlation circle represents the first component (explaining 46.29% of the  
 520 total variation), whereas the vertical axis represents the second component (22.81% of the total  
 521 variation). Bio2 = Mean Diurnal Range, Bio5 = Maximum Temperature of Warmest Month, Bio6 =  
 522 Minimum Temperature of Coldest Month, Bio9 = Mean Temperature of Driest Quarter, Bio16 =  
 523 Precipitation of Wettest Quarter, Bio17 = Precipitation of Driest Quarter, Bio18 = Precipitation of  
 524 Warmest Quarter. Grey shading represents the density of the occurrences by cell, with darker  
 525 shading indicating higher density of occurrences. Solid and dashed contour lines represent 100%  
 526 and 50% of the available environment, respectively. Green colour represents niche overlap  
 527 between two lineages, whereas yellow and lavender represent non-overlapping niches. PC1 and  
 528 PC2 are the first two axes of principal component analysis (PCA). Similarity I indices between two  
 529 lineages are mentioned in parentheses above the representation of related bioclimatic niches. A  
 530 significant value denotes a pair of species that are ecologically similar (\*,  $p \leq 0.05$ ).

531





532

533 FIGURE 2 (a) Habitat suitability of each lineage of *Bombina variegata* in Europe, performed  
 534 separately, within their distribution areas. Models of each lineage were fitted separately, and their  
 535 outputs were clipped by the current distribution limits of each lineage and pooled in the same  
 536 map. The letters correspond to the lineages and locate their distribution areas: C = *Bombina*  
 537 *variegata variegata* 'Carpathians'; P = *Bombina variegata pachypus*; S = *Bombina variegata scabra*;  
 538 V = *Bombina variegata variegata* 'western'. The dotted white line separates the distribution areas  
 539 of B. v. scabra from the Carpathian and western lineages of B. v. variegata. (b) Habitat suitability  
 540 of *Bombina variegata* in Europe (species level). Maps were projected under the WGS84 system.

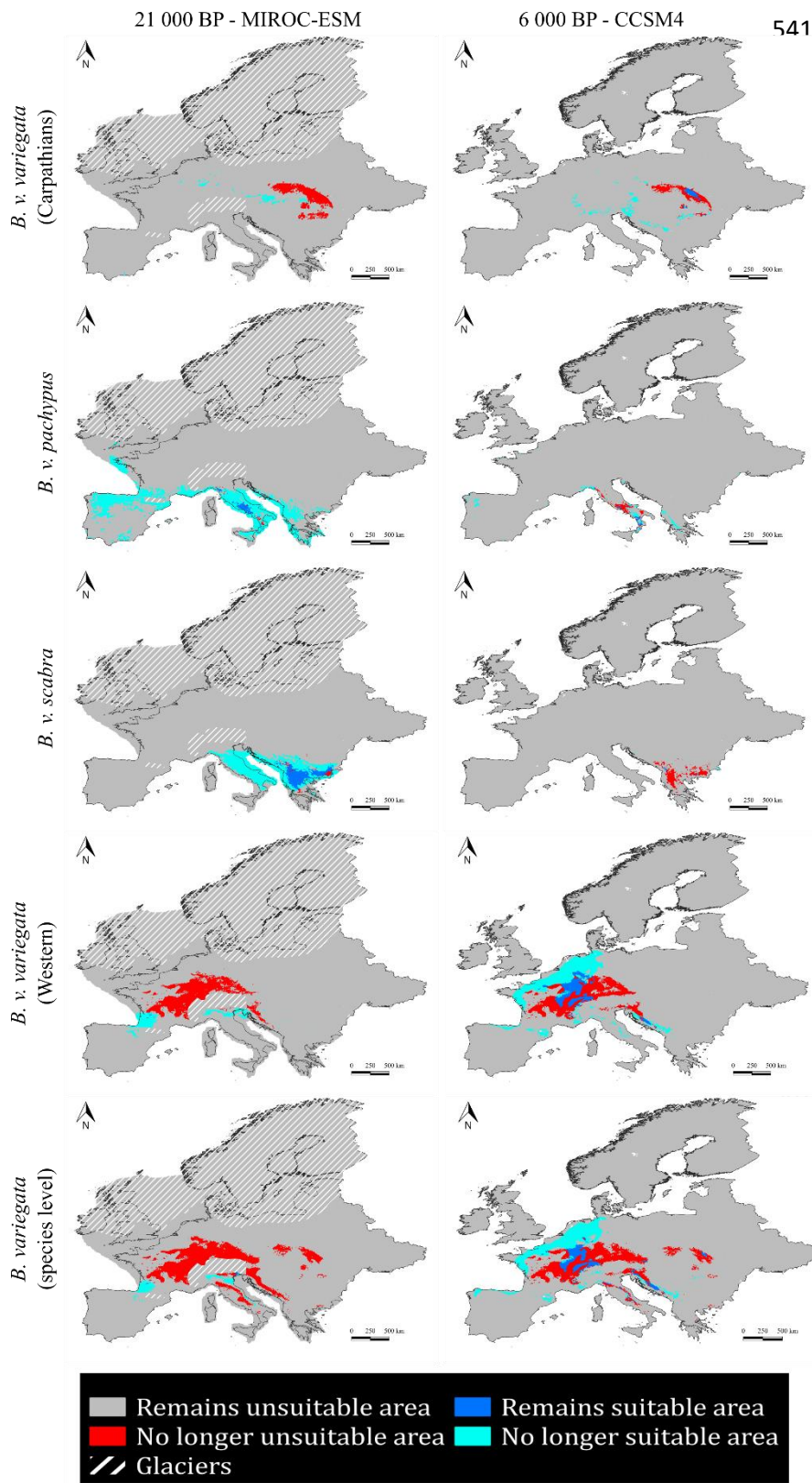
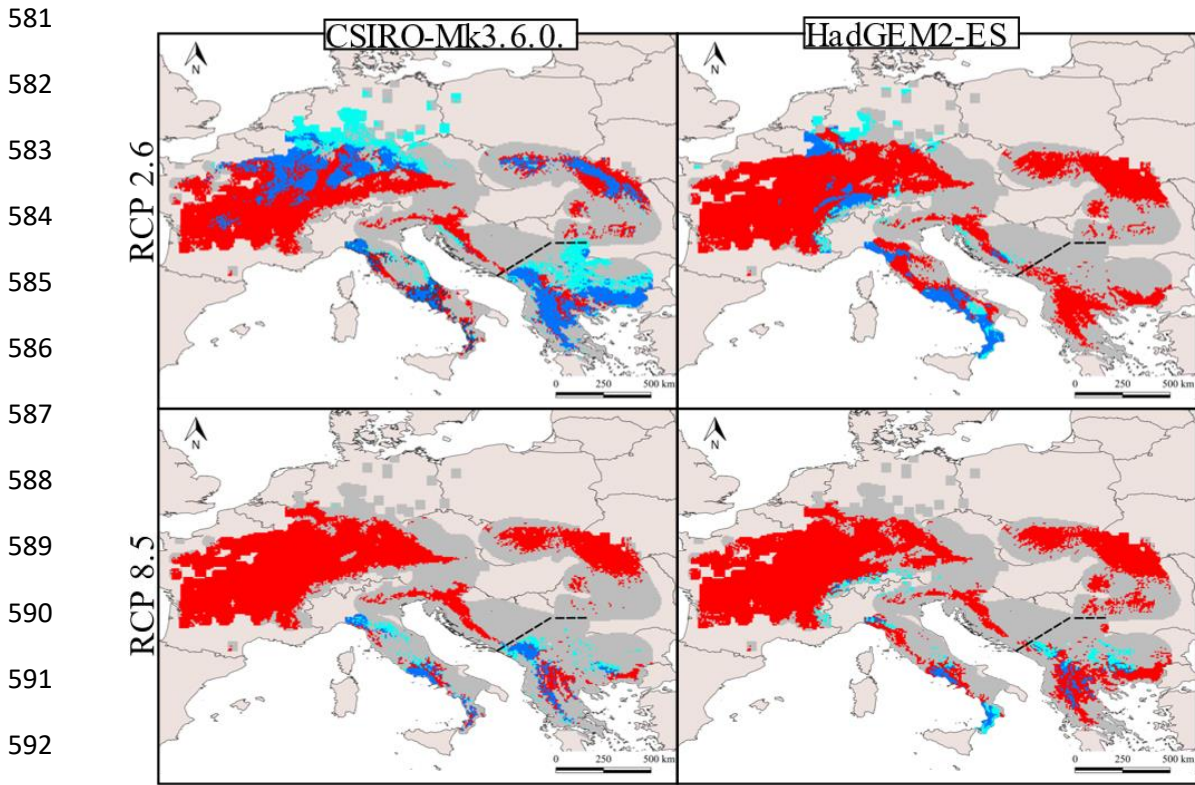


FIGURE 3 Predicted changes in habitat suitability for *Bombina variegata* lineages in Europe during 21,000 and 6,000 bp in comparison to the current period. Red indicates areas that were previously unsuitable but are currently suitable, dark blue indicates areas that have been suitable and are still currently suitable and light blue indicates areas that were previously suitable but are now unsuitable. Grey indicates areas that remain unsuitable, taking into account dispersal ability. Emerged land surface due to lower sea levels and major glaciers has been taken into account in the 21,000 bp models. Projections are valuable under both limited and unlimited dispersal scenarios. Maps were projected under the WGS84 system.

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593

594 FIGURE 4 Predicted changes in habitat suitability in Europe for *Bombina variegata* lineages by  
 595 2050 (period 2041–2060) under dispersal limitation. Because predictions for each lineage were  
 596 made in different areas, they were pooled in the same map. The colours show the differences from  
 597 the current distributions: red shows lost suitable areas (i.e., areas that will become unsuitable),  
 598 dark blue indicates suitable areas that are predicted to persist, light blue indicates new suitable  
 599 areas and grey indicates areas that remain unsuitable, taking into account dispersal ability. A  
 600 dashed line separates the predictions for *Bombina variegata scabra* (in the south) from those of  
 601 the Carpathian and western lineages of *Bombina variegata variegata*. Maps were projected under  
 602 the WGS84 system.

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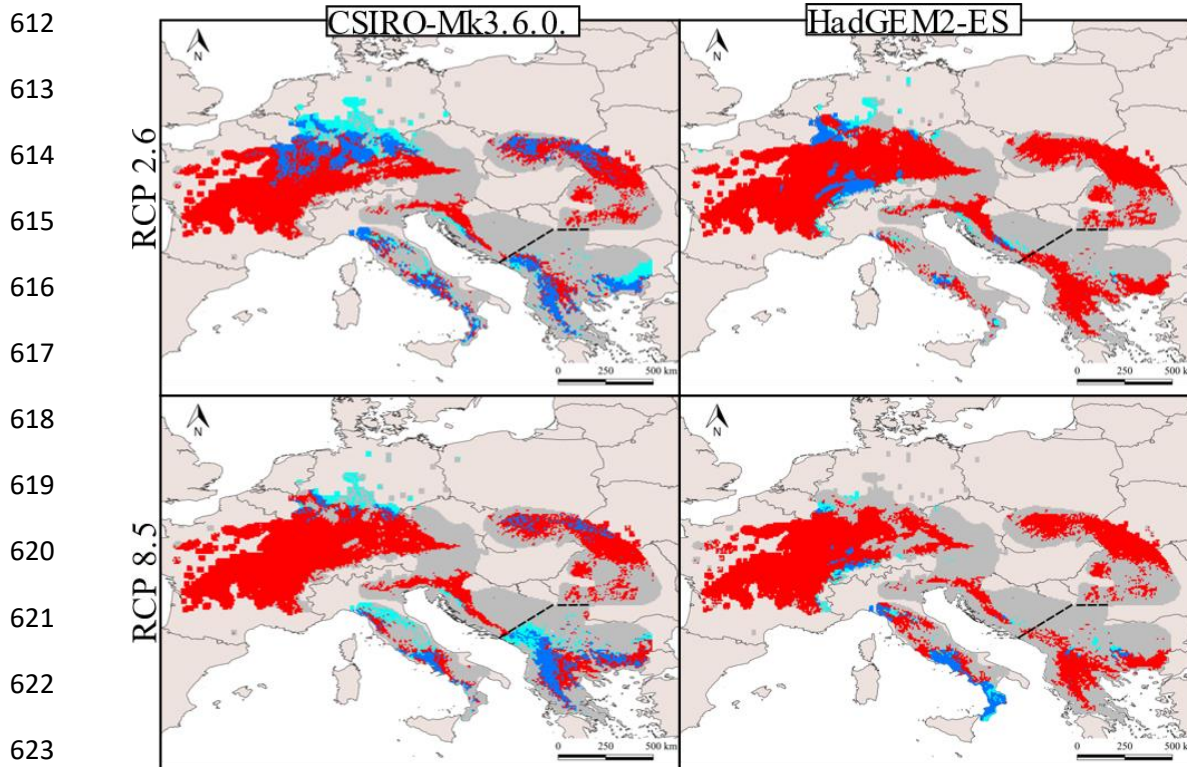
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624 FIGURE 5 Predicted distribution change in Europe by 2070 (period 2061–2080) for *Bombina*  
 625 *variegata* lineages under dispersal limitation (see details in Figure 4).

626 TABLE 1 Predicted change of suitable areas in the past compared to the current period under  
 627 unlimited dispersal. Species models did not take into account intraspecific diversity (i.e., *Bombina*  
 628 *variegata* sensu lato).

Lineages	Period	GCM	Percentage of suitable areas
<i>B. v. variegata</i> "Carpathians"	21000 BP	CCSM4	-100
		MIROC-ESM	-84.2
	6000 BP	CCSM4	-22.5
		MIROC-ESM	-80
<i>B. v. pachypus</i>	21000 BP	CCSM4	50
		MIROC-ESM	1792.4
	6000 BP	CCSM4	-26.5
		MIROC-ESM	-44.1
<i>B. v. scabra</i>	21000 BP	CCSM4	12.3
		MIROC-ESM	253.7
	6000 BP	CCSM4	-93.8
		MIROC-ESM	33.1
<i>B. v. variegata</i> "western"	21000 BP	CCSM4	-68.2
		MIROC-ESM	-91
	6000 BP	CCSM4	-31.3
		MIROC-ESM	-43
Species level ( <i>Bombina variegata</i> )	21000 BP	CCSM4	-88.2
		MIROC-ESM	-93.1
	6000 BP	CCSM4	-37.8
		MIROC-ESM	-45.1

629 TABLE 2 Predicted change of suitable areas in the future compared to the current period under  
 630 limited and unlimited dispersal. Species models did not take into account intraspecific diversity  
 631 (i.e., *Bombina variegata sensu lato*).

Lineages	Period	RCP	GCM	Percentage of suitable areas compared to current (%)	
				Limited dispersal	Unlimited dispersal
<i>B. v. variegata</i> "Carpathians"	2050	RCP2.6	CSIRO	-77.4	92.7
			HadGEM2-ES	-100	-99.6
	RCP8.5	CSIRO	-89.4	-50.7	
		HadGEM2-ES	-100	-99.2	
	2070	RCP2.6	CSIRO	-62.9	170.2
			HadGEM2-ES	-100	-97.5
RCP8.5	CSIRO	-100	-76.3		
	HadGEM2-ES	-100	-73		
<i>B. v. pachypus</i>	2050	RCP2.6	CSIRO	-16.4	543.2
			HadGEM2-ES	-65.8	257
	RCP8.5	CSIRO	-6.1	1688.6	
		HadGEM2-ES	-77.2	411.4	
	2070	RCP2.6	CSIRO	-28.7	1051.7
			HadGEM2-ES	-41.4	310.4
RCP8.5	CSIRO	1.5	2103		
	HadGEM2-ES	-43.8	1342.6		
<i>B. v. scabra</i>	2050	RCP2.6	CSIRO	-6.6	151.8
			HadGEM2-ES	-97.9	33
	RCP8.5	CSIRO	-19.7	234.8	
		HadGEM2-ES	-91.3	121	
	2070	RCP2.6	CSIRO	44.5	176.9
			HadGEM2-ES	-100	-58.8
RCP8.5	CSIRO	-14.5	535.5		
	HadGEM2-ES	-63.2	359.3		
<i>B. v. variegata</i> "western"	2050	RCP2.6	CSIRO	-68.9	-39.1
			HadGEM2-ES	-85	35.3
	RCP8.5	CSIRO	-92	-70.2	
		HadGEM2-ES	-93.9	-3.7	
	2070	RCP2.6	CSIRO	-56.7	6.9
			HadGEM2-ES	-84.4	37.6
RCP8.5	CSIRO	-100	-97.7		
	HadGEM2-ES	-97.3	-59		
Species level ( <i>Bombina variegata</i> )	2050	RCP2.6	CSIRO	-62.4	-15.1
			HadGEM2-ES	-86.8	1.7
	RCP8.5	CSIRO	-89.5	-51.2	
		HadGEM2-ES	-94.8	-30.5	
	2070	RCP2.6	CSIRO	-54.1	5.5
			HadGEM2-ES	-83.5	-0.9
RCP8.5	CSIRO	-99.6	-93.3		
	HadGEM2-ES	-96.8	-46.2		

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845 BIOSKETCH

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856 DATA AVAILABILITY STATEMENT

857 The data on which this paper is based are available in the Figshare digital repository available at  
858 <https://doi.org/10.6084/m9.figshare.12982016.v2>.