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1 Improving biological relevance of model projections in response to climate change
2 by considering dispersal amongst lineages in an amphibian

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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

4.2. Improving models' relevance with dispersal limitation

440

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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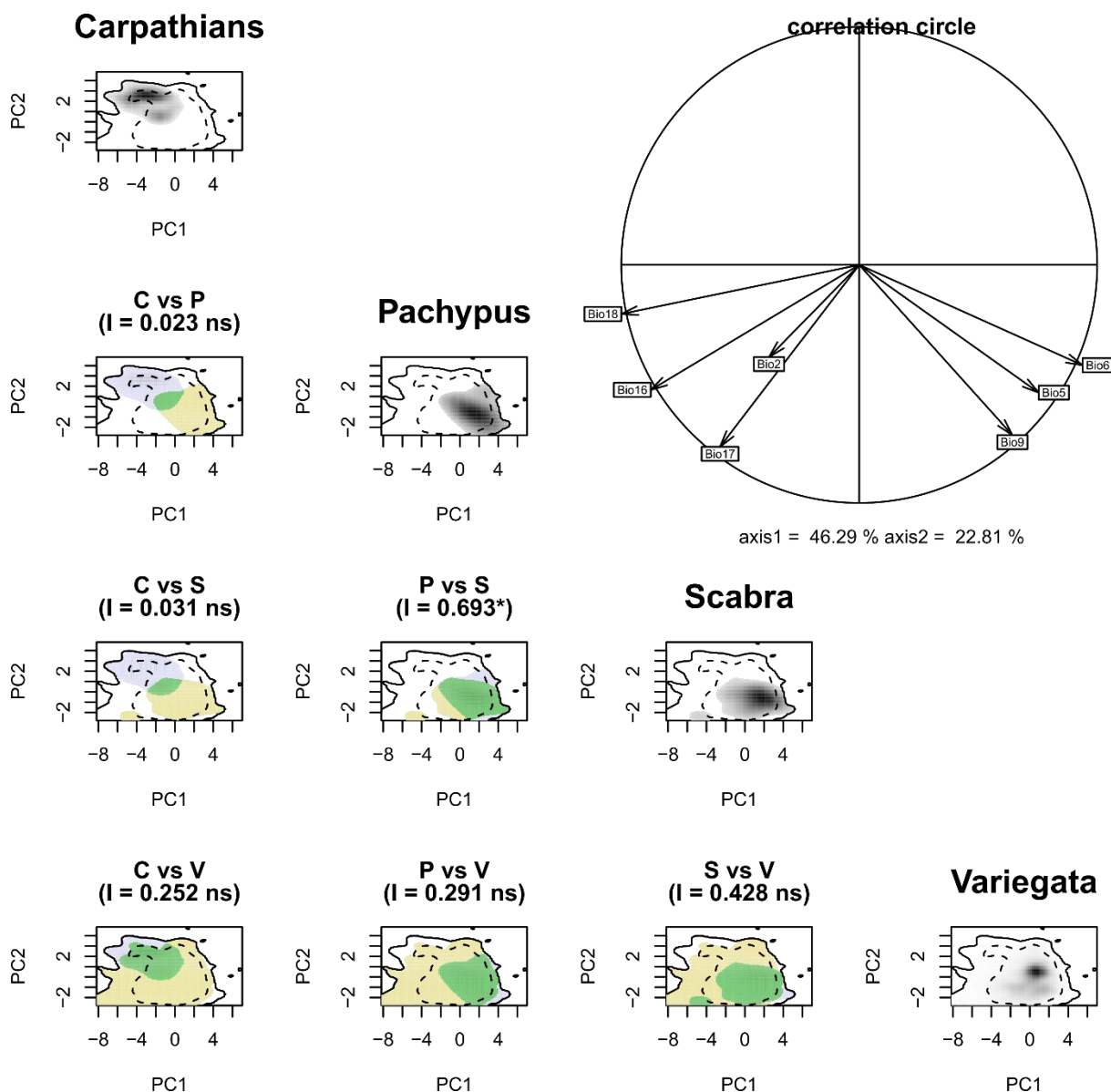
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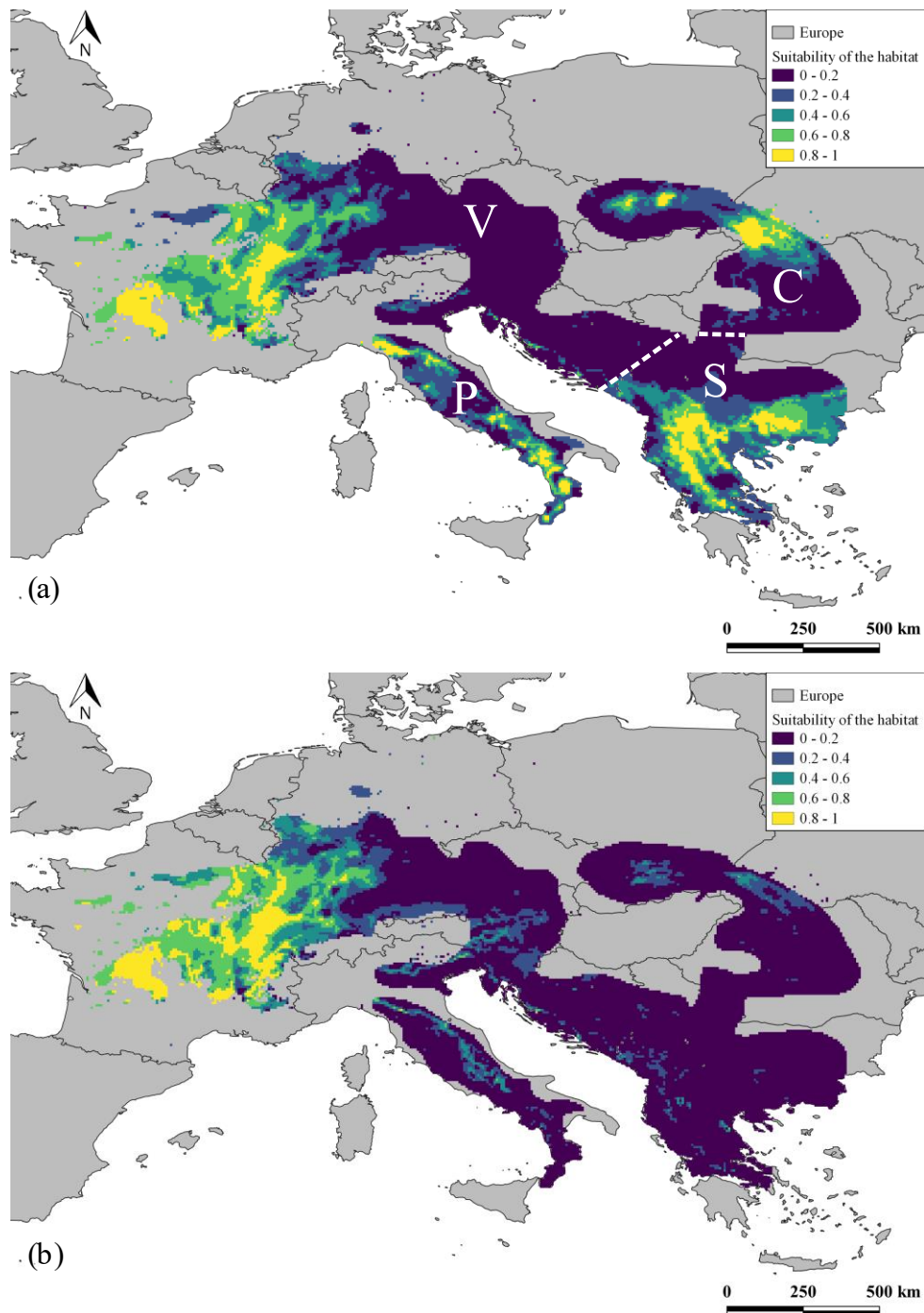
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518 FIGURE 1 Bioclimatic niche similarities amongst the four *Bombina variegata* lineages. The
 519 horizontal axis in the correlation circle represents the first component (explaining 46.29% of the
 520 total variation), whereas the vertical axis 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.

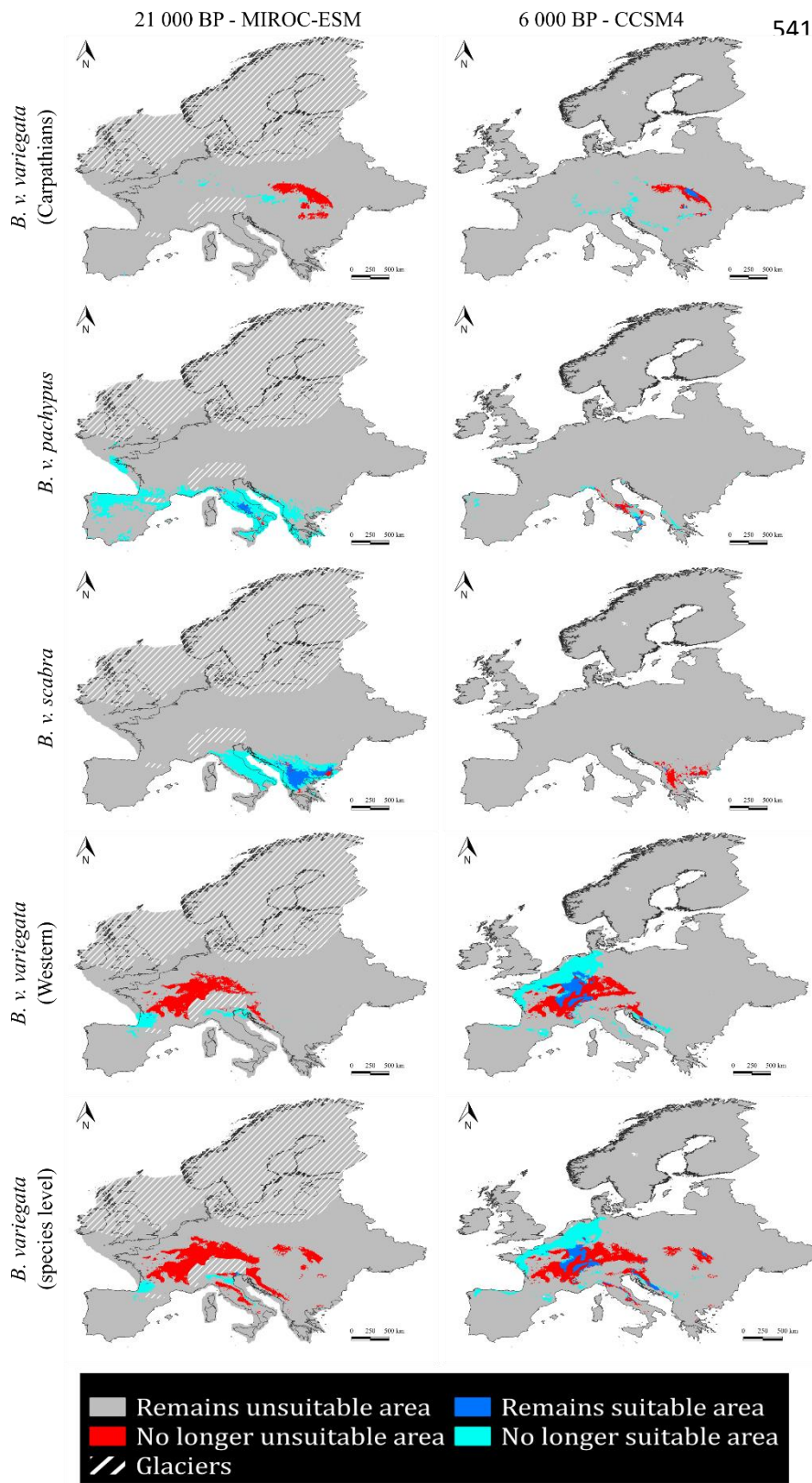
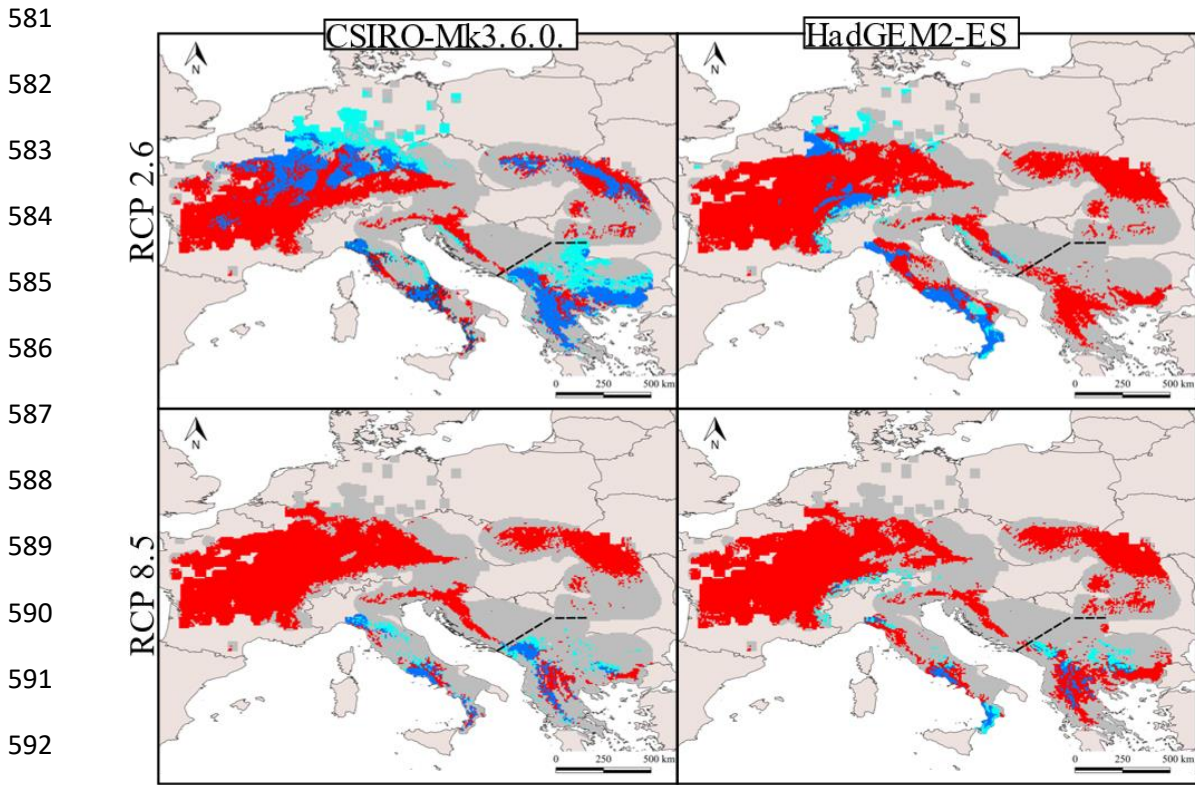


FIGURE 3 Predicted changes in habitat suitability for *Bombina variegata* lineages in Europe during 21,000 and 6,000 bp in comparison to the current period. Red indicates areas that were previously unsuitable but are currently suitable, dark blue indicates areas that have been suitable and are still 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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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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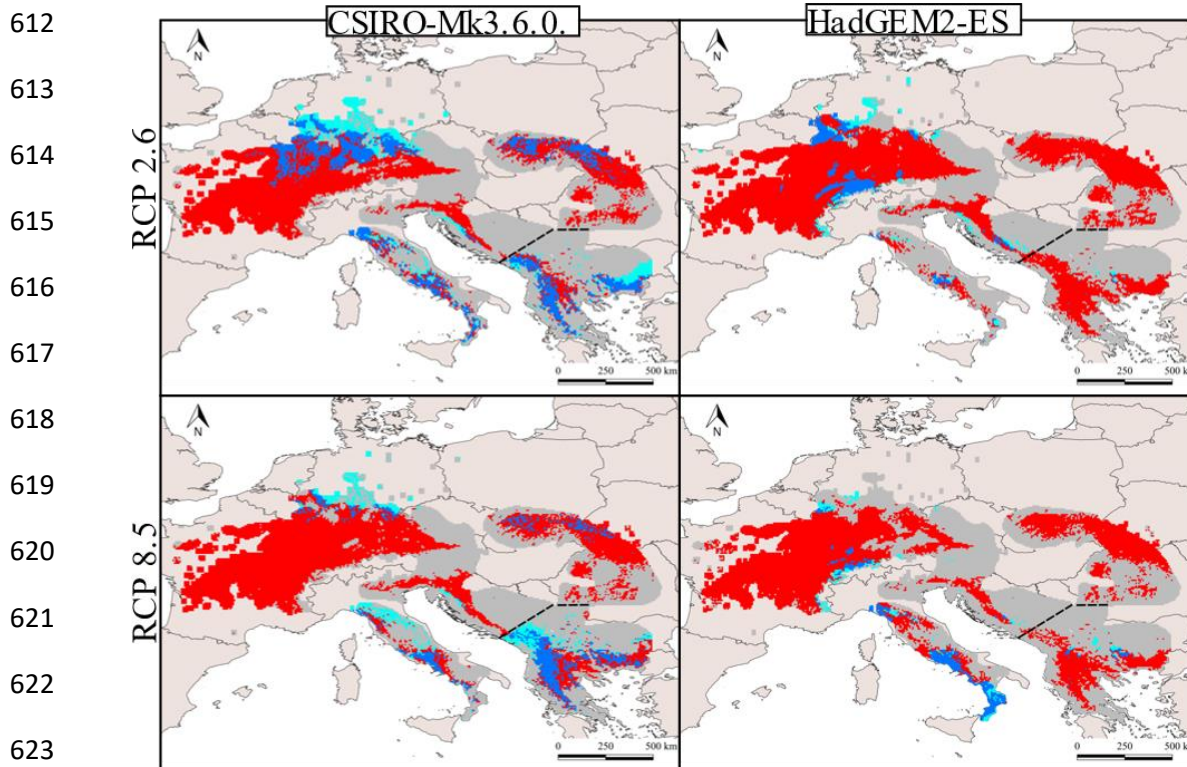
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624 FIGURE 5 Predicted distribution change in Europe by 2070 (period 2061–2080) for *Bombina*
 625 *variegata* lineages under dispersal limitation (see details in Figure 4).

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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854 managed the whole project.

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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>.