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

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflict of interest.

ABSTRACT

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

Location: Europe

Taxon: *Bombina variegata* and its lineages

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

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

Main conclusions:

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

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

1. INTRODUCTION

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

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

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

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

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

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

2. MATERIALS AND METHODS

2.1. Model species

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

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

2.2. Occurrence data

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

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

2.3. Climate data

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

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

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

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

2.4. Niche similarity between lineages

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

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

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

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

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

3. RESULTS

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

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

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

3.2 Current distribution models

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

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

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

3.3. Projections under past climates

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

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

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

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

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

3.4. Projections under future climate change

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

Species level

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

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

Lineage level

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

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

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

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

4. DISCUSSION

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

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

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

4.1. Intraspecific level strongly impacts forecasts

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

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

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

4.2. Improving models' relevance with dispersal limitation

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

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

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

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

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

5. CONCLUSION

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

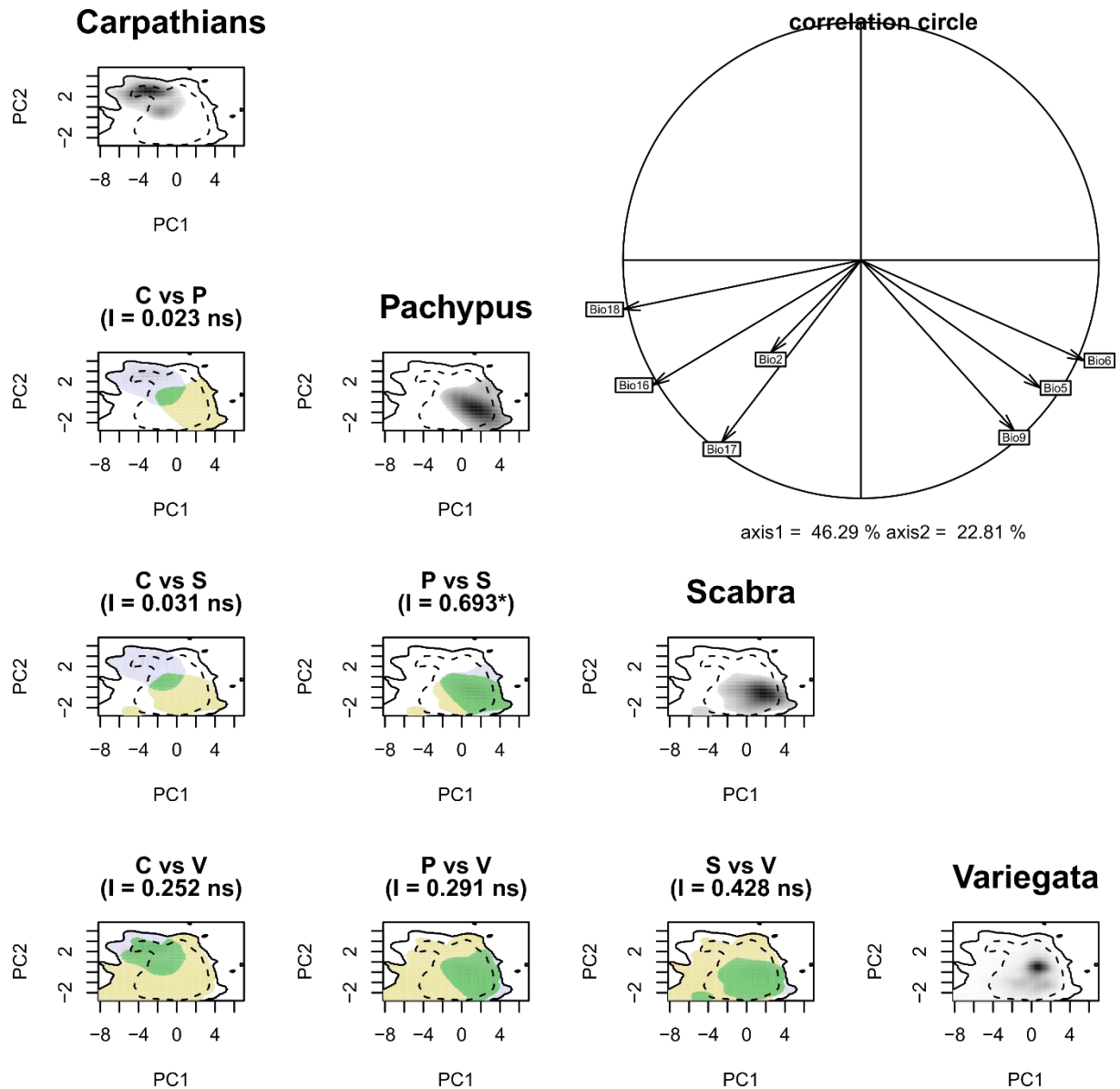


FIGURE 1 Bioclimatic niche similarities amongst the four *Bombina variegata* lineages. The horizontal axis in the correlation circle represents the first component (explaining 46.29% of the total variation), whereas the vertical axis represents the second component (22.81% of the total variation). Bio2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

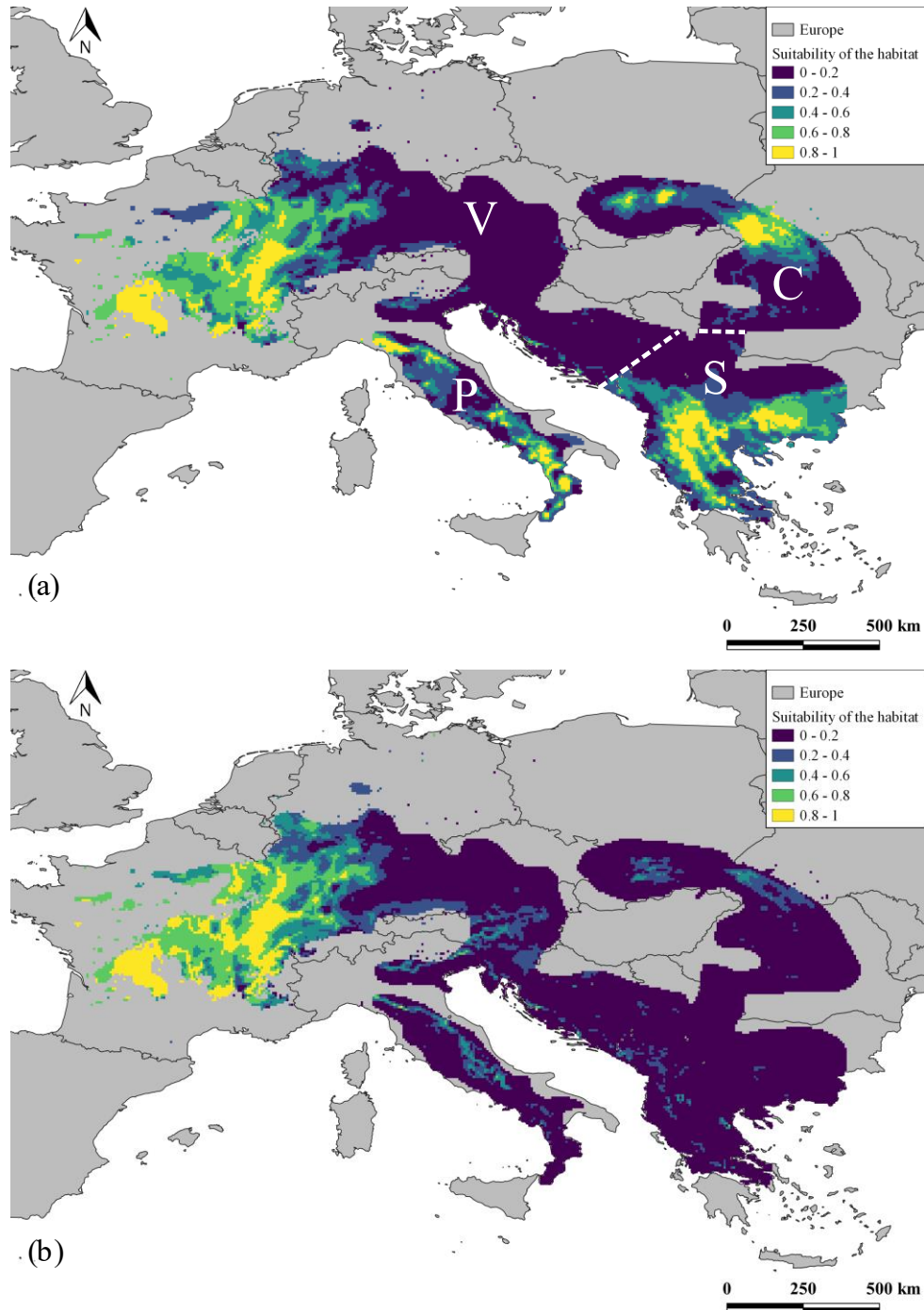


FIGURE 2 (a) Habitat suitability of each lineage of *Bombina variegata* in Europe, performed separately, within their distribution areas. Models of each lineage were fitted separately, and their outputs were clipped by the current distribution limits of each lineage and pooled in the same map. The letters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

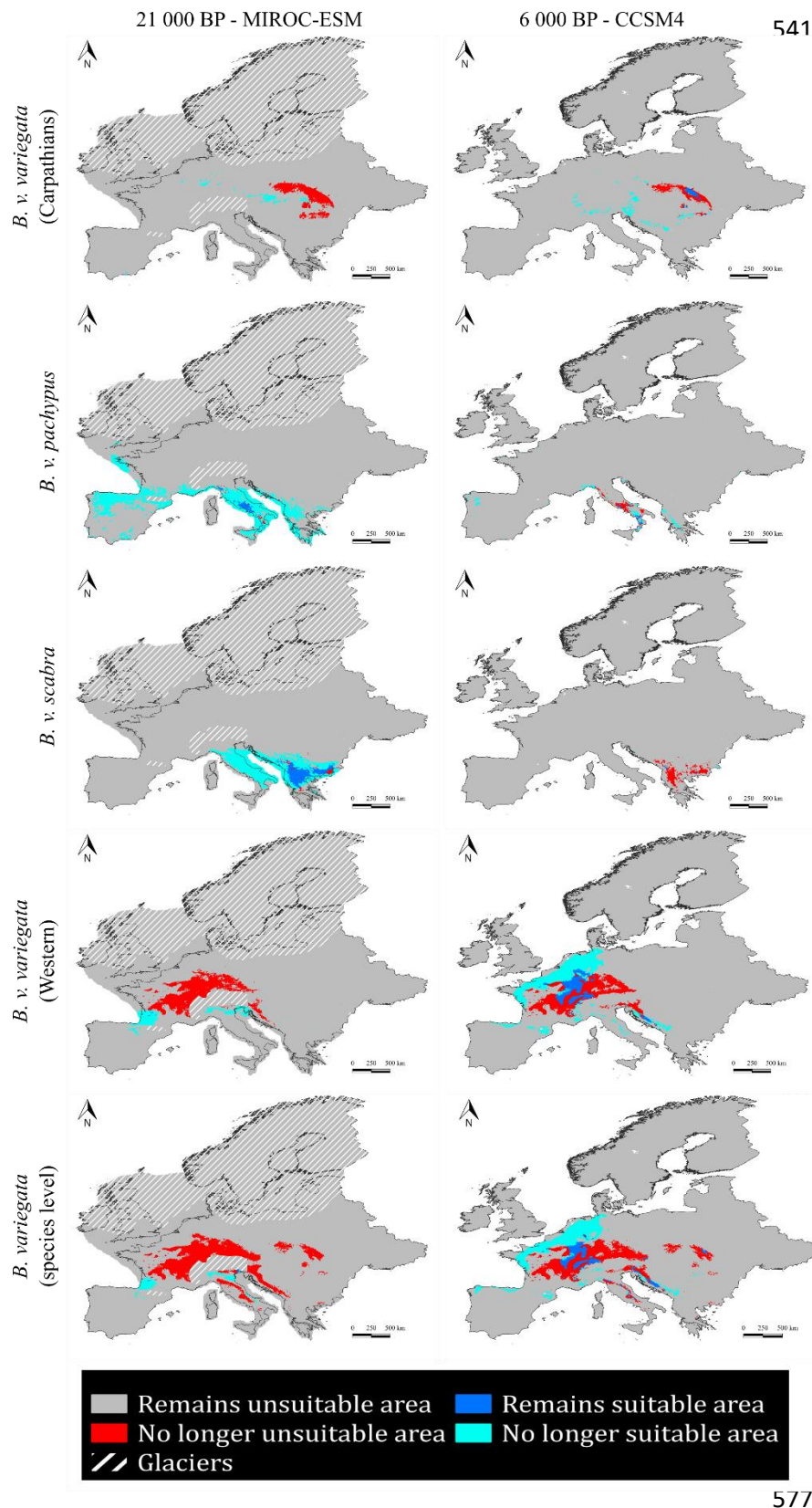


FIGURE 3 Predicted changes in habitat suitability for *Bombina variegata* lineages in Europe during 21,000 and 6,000 bp in comparison to the current period. Red indicates areas that were previously unsuitable but are currently suitable, dark blue indicates areas that have been suitable and are still 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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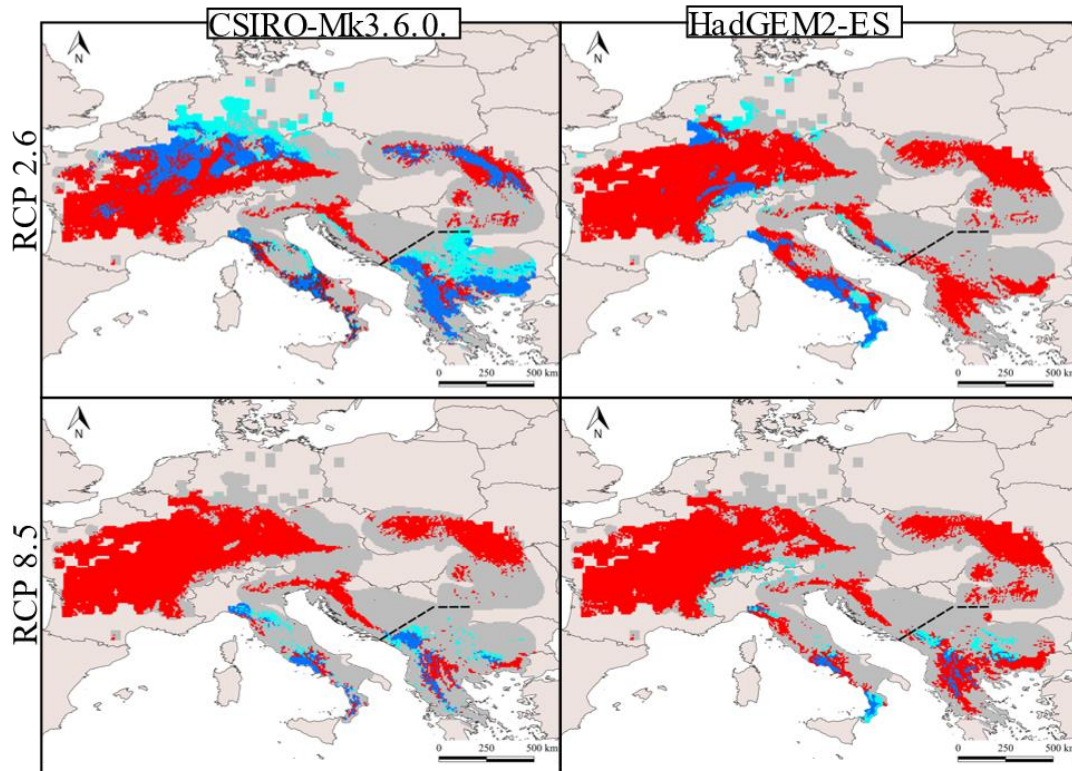


FIGURE 4 Predicted changes in habitat suitability in Europe for *Bombina variegata* lineages by 2050 (period 2041–2060) under dispersal limitation. Because predictions for each lineage were made in different areas, they were pooled in the same map. The colours show the differences from the current distributions: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

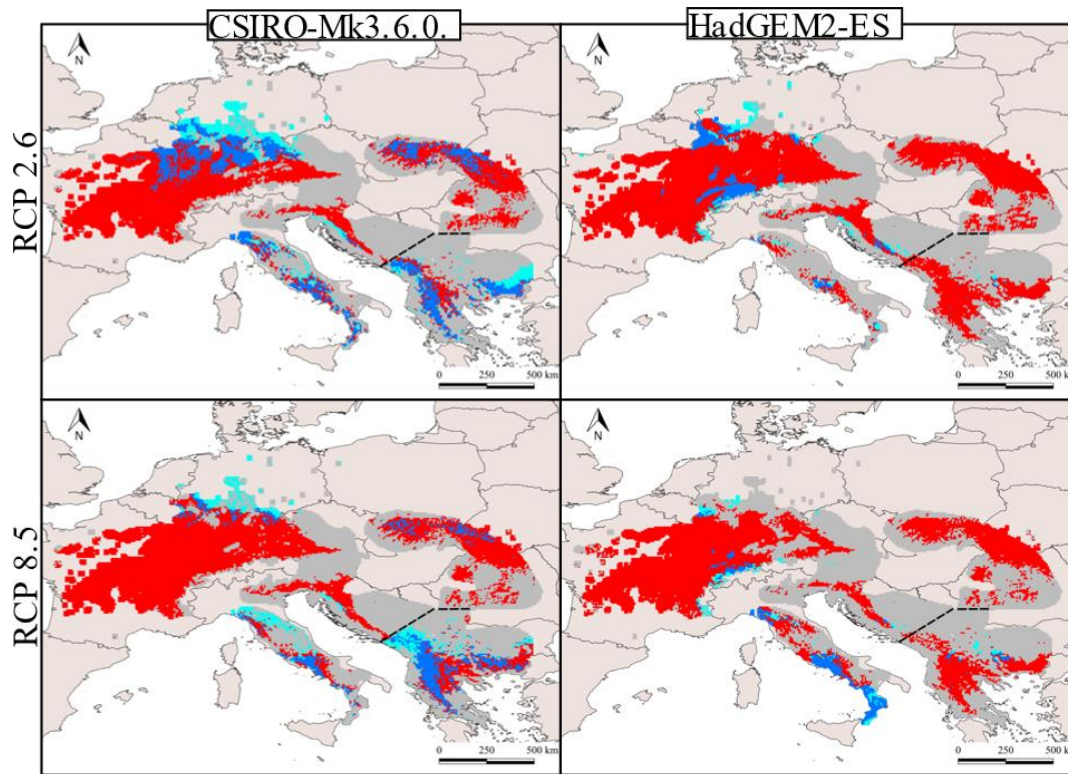


FIGURE 5 Predicted distribution change in Europe by 2070 (period 2061–2080) for *Bombina variegata* lineages under dispersal limitation (see details in Figure 4).

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