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Long Term Hybrid Zone Dynamics in Fire-Bellied Toads Estimated From Environmental Data at Allopatric and Parapatric Scales

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Keywords: *Bombina variegata* | enclave formation | genetic footprints | geographical clines | moving hybrid zone | pen-enclave | post-glacial recolonization | species replacement | two-species distribution modelling

ABSTRACT

Aim: Aims of the study are to identify environmental variables underlying the mutual distribution of a species pair engaged in a long and winding hybrid zone, to reconstruct pattern and process of species' range developments following the Last Glacial Maximum (LGM), and to open research lines for the study of hybrid zone dynamics in a model system.

Location: Central and Eastern Europe, Croatia.

Taxon: The red-bellied toad *Bombina bombina* and the yellow-bellied toad *Bombina variegata*.

Methods: The construction of two-species distribution models (TSDM) at allopatric and parapatric scales and the reconstruction of geographical clines across a low mountain range, in transects with and without extensive lowland forest.

Results: It is confirmed that *B. variegata* is a mountain species and *B. bombina* is a lowland dweller, with hybrid populations in between, but traditional distribution models are oversimplistic. Environmental parameters selected with TSDM at both allopatric and parapatric scales are elevation and forest cover. At transects with lowland forestation, hybrid zones are positioned further away from elevated areas than in the absence of lowland forest. *Bombina variegata* stronghold areas are characterised not just by elevation but also by forestation. Eighteen historical studies (< 2000) with quantitative data are evaluated for their promise in the further study of *Bombina* hybrid zone dynamics.

Conclusions: The overall species mosaic with isolated mountain strongholds (enclaves) suggests that *B. variegata* was displaced from the surrounding lowlands upon its counterparts' northward advance, following post-LGM climate amelioration. Initial hybrid zone formation would have been along the lower Danube river, distant from present-day positions. Because lowland forestation constitutes a buffering effect to species replacement, current hybrid zones may not have reached equilibrium conditions, depending on deforestation history and other characteristics of the landscape. Future genetic work on *B. variegata* enclaves may shed light on the pattern and process of hybrid zone movement and species replacement, though timing and the size and environmental signature of the enclaves will affect genetic introgression in ways that may be hard to disentangle.

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1 | Introduction

Species distribution modelling (SDM) aims to identify the ecological factors that limit and define species ranges and can be used across temporal windows to reconstruct past distributions and to evaluate the impact that environmental change might have on species extinction probabilities. Therewith, SDM has become a popular tool in fields as far apart as phylogeography and wildlife management (Franklin 2010; Peterson et al. 2011; Guisan et al. 2017). The most notable obstacles to meaningful SDM remain identification error, spatial biases in presence data, the inferred nature of absence data and the selection of explanatory variables (Lobo et al. 2010; Dormann et al. 2013; Soley-Guardia et al. 2024).

Species distribution models are frequently constructed for single species without reference to biotic interactions, although it has been noted that such disregard might give rise to misleading results (Davis et al. 1998; Leathwick 2002; Araújo and Luoto 2007; Meier et al. 2010; Wisz et al. 2013). Biotic interactions can be exploitative or mutualistic with positive effect or they can be negative through disease, predation and competition, thereby enhancing or limiting population processes and, ultimately, species distributions. The main reasons for ignoring biotic factors in species distribution modelling are that they may be difficult to parameterise and that blanket coverage is mostly unavailable, such as in, for example, the distribution of bromeliads for a bromeliad-breeding frog (Vasconcelos et al. 2017). For species that interact to the extent that their ranges are mutually exclusive, ordinary SDM may be of limited value, in the same way that the edge of a continent is not helpful in understanding the ecological limitations of a terrestrial species (e.g., Iannella et al. 2017; Dufresnes, Litvinchuk, et al. 2020; Dufresnes, Suchan, et al. 2020; Kalaentzis et al. 2023). It has, for example, been found that related salamander species can occur in a wider range of conditions than found at their parapatric contact (Werner et al. 2013). Similarly, for *B. variegata* it was observed that its ecological amplitude is wider in allopatry than in parapatry with *B. bombina* (von Méhély 1905; Mertens 1928), for the present day exemplified by remnant populations in the southwest of France (Berroneau et al. 2010) and in the Po Valley in Italy (Barbieri et al. 2004) and in *B. bombina*, a thriving population outside the native range is known for the northeast of France (Vacher et al. 2020; Cogălniceanu et al. 2024).

In cases of parapatry the drawback of incomplete environmental sampling may, however, be turned into an advantage, because species with abutting ranges offer the opportunity to *contrast* their ecological preferences such as in 'two-species distribution modelling' (TSDM), in which presence data from two species are compared against the background of environmental data, to yield insights into species habitat differentiation. Parapatry is common, especially among related organisms with low dispersal capability (Key 1981; Bull 1991; Weir and Price 2011). With the advent of molecular genetic data in systematics, mosaics of closely related species continue to be resolved (Marzahn et al. 2016; Pyron et al. 2022; Yang et al. 2022), underlining the ubiquity of parapatric contact zones and, therewith, the scope for TSDMs (for a review in European amphibians and reptiles see Arntzen 2023a).

Another dimension to parapatry is the occurrence of narrow hybrid zones at the species interface. Hybridization offers insight into speciation and the forces that maintain barriers to reproduction (Ravinet et al. 2017; Peñalba et al. 2024). Hybrid zones provide excellent opportunities to test how the environment shapes barriers to reproduction and hybrid fitness, and how differences in reproductive barriers between two species influence their relative success across habitats. I here apply TSDM and hybrid zone cline analyses to a species pair of fire-bellied toads (genus *Bombina*) that represents a model system in speciation research. Aims of the study are to identify environmental variables that determine the mutual distribution of *B. bombina* and *B. variegata* that engage in a long and winding hybrid zone across central Europe, and to reconstruct the pattern and process of species' range developments following the Last Glacial Maximum (LGM). It will be argued that, by ignoring important components of the species' environments, or relying on few variables, existing species distribution models (Arntzen 1978; Dufresnes, Suchan, et al. 2020) are oversimplistic and that a process of hybrid zone movement is ongoing, depending on characteristics of the landscape, therewith opening research lines for the study of hybrid zone dynamics in a model system.

2 | Materials and Methods

2.1 | Study Areas and Species Distribution Data

The research area conforms to the region of *Bombina* species range overlap in central and eastern Europe, bounded by the 14–28 eastern longitude and 43–51 northern latitude coordinates (Figure 1). This includes central Croatia with the sections Jastrebarsko and Peščenica at opposite flanks of the Vukomerić hills (Figure 2). It may be noted that the 'Jastrebarsko area' is also known as the 'Karlovac depression' (Magyar et al. 1999). All species distribution data, used to *construct* a two-species distribution model (see below) and independent data for *testing* model performance, are publicly available. The model for central Europe is based upon 171 nominally high precision records (with two or more decimal places, from Dufresnes, Suchan, et al. 2020; data available at https://doi.org/10.1111/jbi.14018 and Appendix S8). Model evaluation was done with the online databases of the Global Biodiversity Information Facility (available at https://www.gbif.org/species; data downloaded on 1 January 2025 under references https://doi.org/10.15468/dl.ux3zcu and https://doi.org/10.15468/dl.msznks) and the Societas Europaea Herpetologica (Sillero et al. 2014 and https://www.seh-herpetology.org/distribution-atlas). See Appendix S9. Also consulted were databases for Hungary and Croatia (Herpterkep 2025; available at http://herpterkep.mme.hu and https://biologer.hr/groups/16/species/126 and 127), two countries with otherwise low data coverage. Atlas grid cell data with both species were ignored in the analyses, as were records for Ukraine and Moldavia for which countries Corine land cover data are not available. Species distribution data for central Croatia are available online (Atkinson 2001, https://era.ed.ac.uk/handle/1842/13662 and Appendix S8) with species identifications based on a genetic hybrid index that runs from zero (pure *B. bombina*) to unity (pure *B. variegata*) with a 0.5 cut-off point (see also Nürnberger et al. 1995; MacCallum

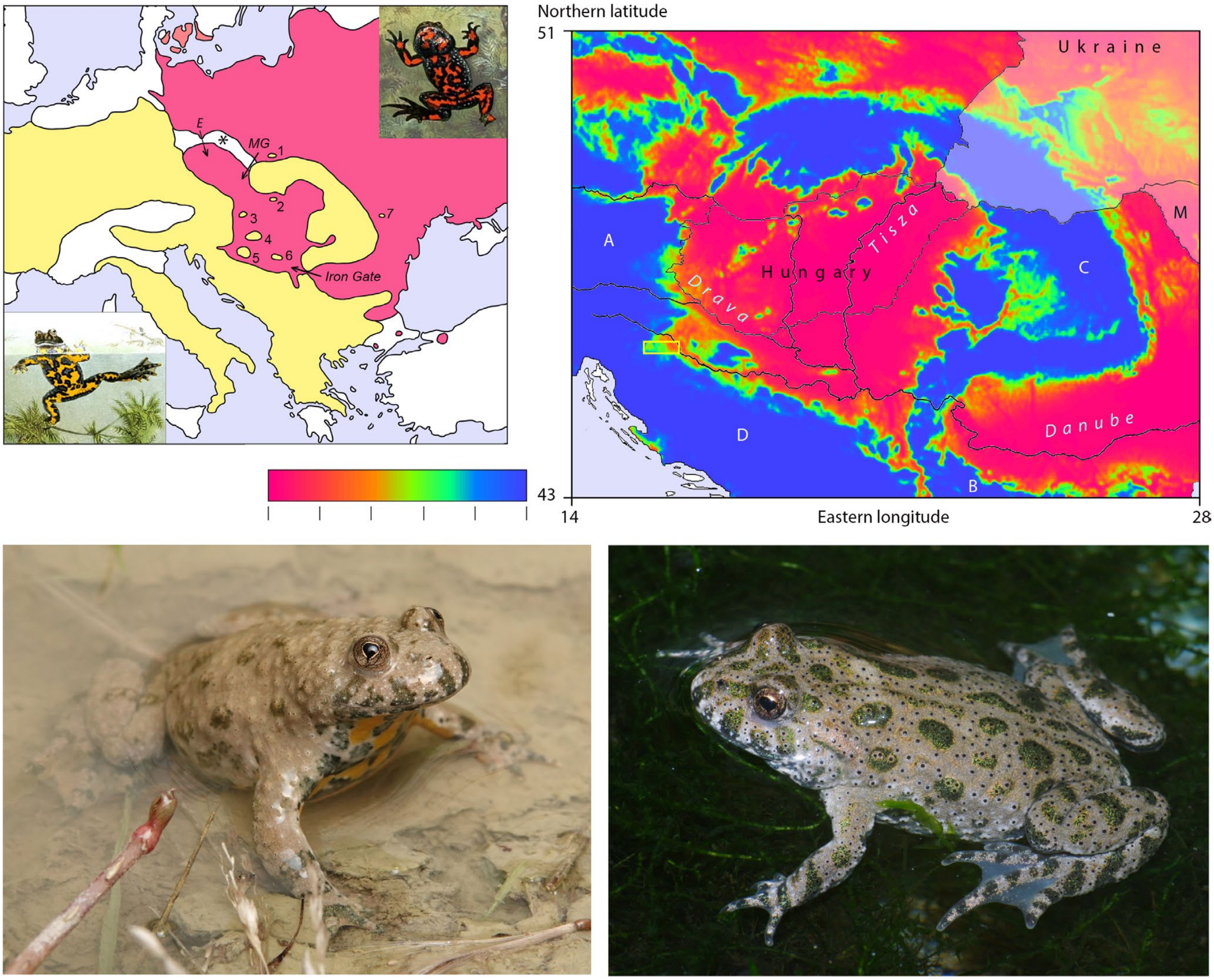

FIGURE 1 | Panel top left—Distribution map for the red-bellied toad *Bombina bombina* (in red) and the yellow-bellied toad *B. variegata* (in yellow). The animal pictures are from Boulenger (1897) with *B. bombina* top right and *B. variegata* bottom left and used to indicate the matching colours of species and their distributions. Note the absence of either species in the Ore mountains and the western Sudetes (asterisk) as supported by atlas data of the Czech Republic and Germany (https://portal23.nature.cz/nd, http://www.feldherpetologie.de/atlas/maps.php?art=Gelbbauchunke%20(Bombina%20variegata)&zeitschnitt=1900-2018&raster=mtbq and http://www.feldherpetologie.de/atlas/maps.php?art=Rotbauchunke%20(Bombina%20bombina)&zeitschnitt=1900-2018&raster=mtbq). Documented enclaves for *Bombina variegata* are at (1) the Kraków-Chrzanów ridge, (2) Mátra mountains, (3) Bákony forest, (4) Mecsek moutains, (5) Bilo Gora, (6) Fruška Gora and (7) Iaşi. Supporting data for and recognition of the enclaves is by von Méhély (1905), Fuhn (1960), Michałowski (1961), Arntzen (1978), Szymura (1993), Cogălniceanu et al. (2013) and Arntzen et al. (2025). Supporting data for the presence of *B. variegata* in northern Dobrogea, Romania (Mertens 1928; Arntzen 1978) have not since become available and this occurrence was suppressed. Note that more recent and detailed data on the distribution of European *Bombina* species are available (e.g., Appendix S2), but the production of an updated map is outside the scope of the paper. The southern arrow indicates the post-glacial dispersal route of *Bombina bombina* along the Danube and across the Iron Gate from Dobrogea and the lower Danubian plains into the Carpathian basin (Arntzen 1978; Vörös et al. 2006; Dufresnes, Suchan, et al. 2020). An alternative but unsupported dispersal route follows the Moravian Gate (MG) whereas the area around Prague may have been colonised from the north, following the Elbe (E) (Schreiber 1912; Madej 1964a; Arntzen 1978). Panel top right—two-species distribution model (TSDM) for *B. bombina* and *B. variegata* in central Europe. Areas shown in red represent *B. bombina*, areas in blue represent *B. variegata* and ecological transition areas are shown in orange and green ($0.2 < P < 0.8$, see colour legend bottom left with increments of 0.2). The model is smoothened for presentation purposes. The main mountain systems are the Alps (A), Balkans (B), Carpathians (C) and Dinarides (Dinaric Alps, D) and the main rivers are the Danube, the Tisza and the Drava. For the Sava and Kupa rivers see Figure 2. Country borders of Hungary, Moldavia (M) and Ukraine are shown for reference (for other countries see Appendix S2B). Moldavia and Ukraine are white shaded to indicate the absence of Corine land cover data. The small yellow box in central Croatia indicates the Jastrebarsko–Peščenica study area (as in Figure 2). Bottom row left—*B. variegata* from Marche-en-Famenne, Belgium; photographer and image copyright owner Frank Pasmans. Bottom row right—*B. bombina* from the northeast of France (population outside the native range, see Vacher et al. 2020); photographer and image copyright owner Sergé Bogaerts.

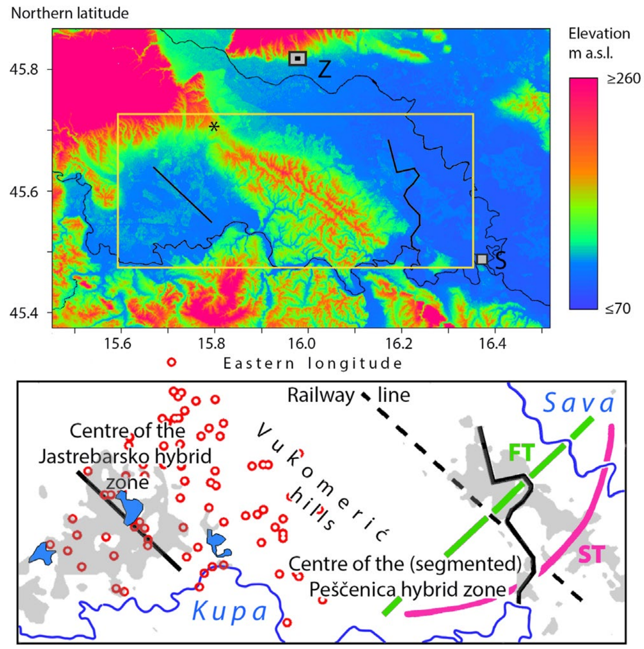

FIGURE 2 | Study area of *Bombina* toads in Croatia south of Zagreb (Z) and west of Sisak (S). The top panel shows elevation from lower (in blue) to higher elevations (in red) with the adjoining Jastrebarsko and Peščenica areas boxed. The thick black lines show the inferred centres of the *B. bombina*–*B. variegata* hybrid zones at either side of the Vukomerić hills and relative to the rivers Kupa and Sava and the Zagreb–Sisak railway line. The segmented hybrid zone at Peščenica is after Atkinson (2001). The open red symbols in the lower panel are investigated *Bombina* populations in the Jastrebarsko area and the thick lines summarise the forest transect (FT, in green) and the southern transect (ST, in purple) at Peščenica. Areas with lowland forest are shaded. Three fish lake complexes of which the central one is Crna Mlaka are shown by blue surfaces. Potential corridors that connect the pocket of *B. bombina* occurences at Jastrebarko with the main distribution in the Sava river lowland are over the saddle of the Vukomerić hills (asterisk) and the river Kupa. For the detailed distribution of *Bombina* species at Jastrebarsko see Appendix S3. For the species distribution following the geographical clines see Figure 4.

et al. 1998). For the Jastrebarsko area, species identification was based on 'spot scores' that describe the species' differentiated ventral colouration patterns. Spot scores are based on the extent of the coloured spots at the toads' ventral sides and on the degree to which these patches are interconnected (see Vörös et al. 2007 for a review). Spot scores are concordant with results from genetic markers (Nürnberger et al. 1995; MacCallum et al. 1998; Atkinson 2001). Finally, an 'enclave' is here defined as a distinct part of a species range that is enclosed by the range of a related, competing species.

2.2 | Environmental Data and Two-Species Distribution Modelling

Environmental data considered as candidate explanatory variables to the reciprocal distribution of *B. bombina* and *B. variegata* (and with that the position of the species' hybrid zone) included 19 climate variables (bio01–bio19) extracted from the WorldClim global climate database v.2 (available at https://www.worldclim.org/data/index.html) (bio01–19, Hijmans et al. 2005, see also Busby 1991 and Booth 2018). For elevation I used the Copernicus digital elevation model (European Space Agency 2024, available at https://doi.org/10.5069/G9028PQB). 'Hilliness' is the standard deviation of elevation derived with a 9*9-pixel wide filter, covering ca. 7.3 ha. Vegetation data were from the Corine land cover database of the European Environment Agency (available at https://land.copernicus.eu/pan-european/corine-land-cover, in particular https://doi.org/10.2909/71fc9d1b-479f-4da1-aa66-662a2fff2cf7) (Büttner et al. 2021). The nominal resolution of the data is 30 arc-seconds for climate, 30 m for elevation and 10 m for land cover. However, land cover data for Croatia were from 1998, corresponding to the period that the *Bombina* data were collected (available at https://doi.org/10.2909/c89324ef-7729-4477-9f1b-623f5f88eaa1). The distinction was made between variables that operate at coarse spatial scales (i.e., the climate variables) versus elevation, hilliness and land cover that take effect at more local scales, because it was shown that the latter variables have superior predictive power in central European *Bombina* (Arntzen et al. 2025).

To identify and subsequently reduce collinearity among the environmental variables, a half-matrix of the pairwise absolute Spearman correlation coefficients was subjected to clustering using the unweighted pair group method with arithmetic mean clustering method in Primer 7 (Clarke and Gorley 2015). Variables were retained using criteria of partial independence at $|r| < 0.75$ and selected in alphanumerical order (Appendix S1). Two-species distribution models (TSDM) in which the presence of one species is contrasted with the presence of the counterpart species were derived with stepwise logistic regression analysis in SPSS v. 30 (IBM Corp. 2024). Variable selection was in the forward stepwise mode under criteria of entry ($p_{\mathrm{in}} = 0.05$) and removal of terms ($p_{\mathrm{out}} = 0.10$) under the likelihood ratio criterion. When species sample sizes were uneven (as at Jastrebarsko) a weighing procedure was applied that sets the number of records for species at par. The fit of the model to the underlying data was assessed by the area under the curve (AUC) statistic. Spatial models were analysed and visualised with ILWIS v.3.8.6 (ILWIS 2019). The data to construct TSDMs and the SPSS command lines are shown in Appendix S8.

2.3 | Hybrid Zone Analysis

The *B. bombina*–*B. variegata* species profile is made up of four diagnostic allozyme genetic markers in a hybrid index that runs from 0 to 1, and from 'spot scores' for which population averages fall in the 0.075–0.875 range (Atkinson 2001). Parallel data on species identity determined with allozymes (MacCallum et al. 1998) suggest a spot score cut-off point at 0.45 (see Figure 3 and Appendix S7).

Classic equilibrium cline models, describing a sigmoid change in phenotypes or allele frequencies across hybrid zones (Szymura and Barton 1991), were fitted with the R package HZAR (Derryberry et al. 2014) with details as described earlier (e.g., Arntzen et al. 2016). At Peščenica, two transects were studied from the lowlands into the hills as guided by a segmented *Bombina* hybrid zone reconstruction (Figure 2).

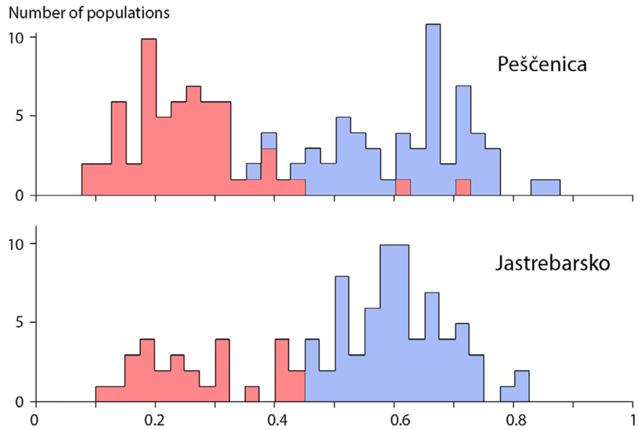

FIGURE 3 | Histograms of spot scores of *Bombina* toads for the Peščenica and Jastrebarsko areas in central Croatia. Data are taken from Atkinson (2001). The cut-off point is set at 0.45 based on genetic data from Peščenica (top panel) and then applied to Jastrebarsko, with *Bombina bombina* in red and *B. variegata* in blue (bottom panel) (details see text).

The transects were projected through a lowland forest (the 'forest transect' with 40 investigated populations) and no forest adjoining the hills (the 'southern transect' with 27 populations) and included eight end-of-transect populations figuring in both analyses.

At Jastrebarsko, a single, wide transect was studied with spot score data for 78 populations (leaving out 19 populations with southwestern and south-eastern positions that belong to an opposite stretch of the species contact zone). Spatial reference is to the long straight stretch of the Zagreb–Sisak railway line that runs in parallel to the Vukomerić hills.

3 | Results

The TSDM for *Bombina* toads across central Europe has ten environmental variables available for selection (uncorrelated to the level at $|r|=0.75$, Appendix S1). The obtained model is $P=(1/(1+\exp.(0.0129*\text{bio12}+0.0109*\text{elevation}-2.159*\text{forest\_cover}+0.0437*\text{hilliness}-12.494)))$ in which 'bio12' describes annual precipitation. Model fit is $\text{AUC}=0.941\pm0.020$. The position of the species contact zone corresponds to range borders reconstructed earlier, whereas the width of the ecological transition over $0.2<P<0.8$ varies widely (Figure 1) (P-values were chosen in parallel to customary cut-off values in the analysis of hybrid zone genetics, Endler 1977). The fit of reference data to the model is $\text{AUC}>0.95$ (for a detailed account see Appendix S2 panels C,D).

In central Croatia also ten environmental variables are available for selection. The TSDM at Peščenica is $P=(1/(1+\exp.(-44.587*\text{bio01}+0.239*\text{bio12}-0.185*\text{elevation}+0.0297*\text{forest\_cover}-0.529*\text{hilliness}+287.662)))$ in which 'bio01' describes annual mean temperature. The model fit is $\text{AUC}=0.955\pm0.017$. Testing the model with reference data was not possible for the lack of records for central Croatia (cf. Appendix S2 panel E). Application of the 'global model' to the Peščenica data yields a significantly reduced fit (AUC <0.5; DeLong test, $z=14.1$, $p<0.001$). Implementation of the spot score criterion to *Bombina* species in the Jastrebarsko area (where genetic data are unavailable) suggests that ca. a third of populations is at the *B. bombina* side of the species bimodality (Figure 3 and Appendix S3). In this area just bio01 and bio12 make it into the model as $P=(1/(1+\exp.(-15.251*\text{bio01}-0.0861*\text{bio12}+249.436)))$, with $\text{AUC}=0.942\pm0.029$.

At Peščenica the cline centres for the two transects are set apart over 5.4 km on either side of the railway line and positioned at elevations of ca. 111 m for the forest transect and ca. 105 m at the southern transect. At Jastrebarso the centre of the cline is positioned at a parallel distance of −24.3 km from the railway line at an elevation of ca. 125 m (Figure 4). A two-dimensional plot of spot scores at Jastrebarsko is near-equivalent to the linear hybrid zone representation (Appendices S3 and S4). Estimated hybrid zone widths range from 1.26 to 3.32 km (for details see Appendix S4).

4 | Discussion

Single-species distribution modelling is a popular research tool, also frequently applied to species for which the full ecological amplitude cannot be determined such as when the species range is bounded by that of a closely related species. This then is unfortunate because, if species are affected to the extent that their ranges are interdependent, such a biotic interaction is better not ignored. Two-species distribution modelling, in contrast, highlights the ecological differences that come into play among competing taxa and neatly aligns with hybrid zone and species delimitation research. Yet, modelling results away from the contact zone are possibly compromised and, at the extreme, a TSDM will project species where there are none such as for *Bombina* toads in the Ore mountains and the western Sudetes (Figure 1).

4.1 | Species Ecological Differentiation

Bombina bombina and *B. variegata* are closely related species that are spatially separated yet engage in extensive hybridisation. The species are also deeply differentiated across a wide variety of life history traits (see Szymura 1993: table 1). A fundamental difference between them is the aquatic versus more terrestrial lifestyle that is reflected in typical breeding habitats found at opposite ends of the large and permanent (for *B. bombina*) to small-and-ephemeral continuum (for *B. variegata*). Common habitat types for *B. bombina* are flooded areas in river valleys, swamps and boggy wetlands and medium- to large-sized ponds (Gollmann et al. 2012 and references therein). Habitat types used by *B. variegata* are drinking troughs in farmland and quarry puddles as well as naturally formed rocky pools on riverbanks and pools at landslides (Cayuela et al. 2011; Cayuela et al. 2020; Cayuela et al. 2022) and tip-up pools formed when large trees fall over. Typical breeding habitats of ponds and ruts are shown in Appendix S6. These different aquatic habitats place opposing demands on the tadpoles (Werner and Anholt 1993), namely rapid growth and development in ephemeral and early-stage aquatic habitats where desiccation looms versus cryptic behaviour in larger ponds and flooded areas at later successional stages where to avoid invertebrate predators, with accompanying

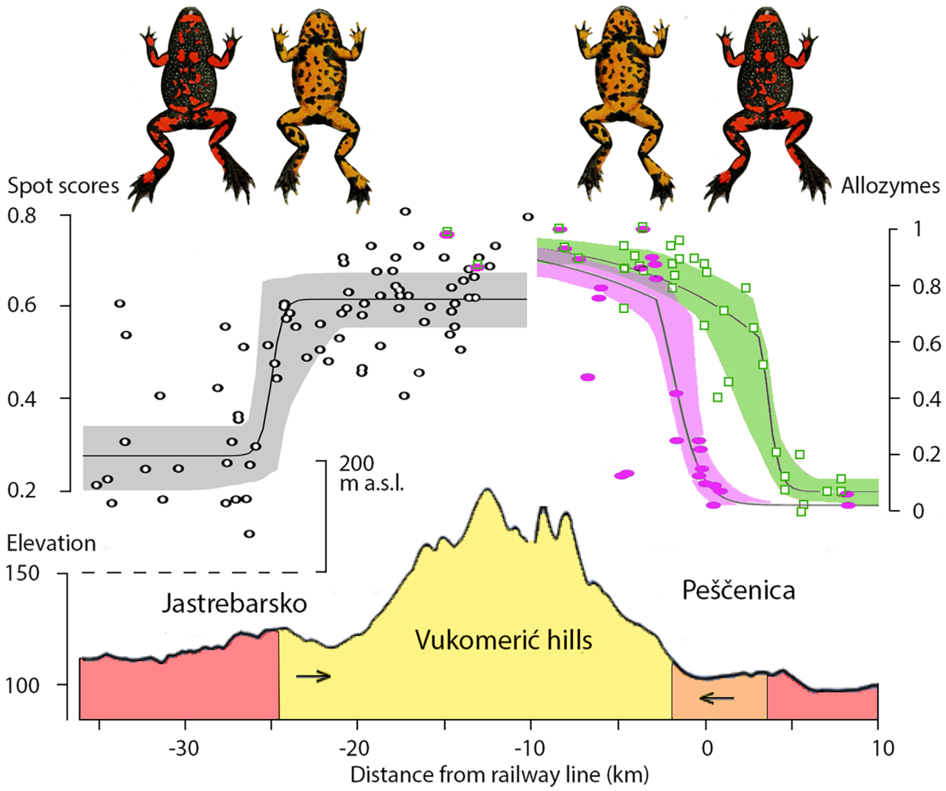

FIGURE 4 | Distribution of *Bombina bombina* and *B. variegata* across the Vukomerić hills, combined for the Jastrobarsko and Peščenica areas in central Croatia. Top panel—geographical clines as reconstructed with HZAR software based on a spot score hybrid index at Jastrebarsko and an allozyme hybrid index at Peščenica (for details see Appendix S4). Results for the forest transect (FT, in green) and southern transect populations (ST, in purple; colours as in Figure 2) are shown by open square and solid ellipsoid symbols, respectively. The shaded area represents the 95% credibility interval of the estimate. Bottom panel—elevation profile. Areas are coloured yellow or red according to the majority presence of one species or the other (*Bombina bombina* in red and *B. variegata* in yellow). The orange part of the elevation profile at Peščenica is occupied by *B. variegata* across the forest transect and by *B. bombina* across the southern transect. The hypothesis eventually to be tested is that the hybrid zones would find a new position at the foothills if the local lowland forests were to become disconnected from the *B. variegata* range or would disappear altogether (see arrows). Animal figures at the very top are from Boulenger (1886) and used to indicate the matching colours of species and their distributions.

developmental, morphological and behavioural differences between the tadpoles (Rafińska 1991; Vorndran et al. 2002; Nürnberger et al. 2016; Smolinský et al. 2020). The emphasis on the breeding habitat as a local factor that affects the species' interaction and local distribution (MacCallum et al. 1998; Vines et al. 2003; Yanchukov et al. 2006) is informative but may be temporally biased because most puddles are car-tracks and ruts from forest management and large, stable ponds are frequently purposefully made (Hartel et al. 2025). Such anthropogenic influences may have assisted the persistence of *B. variegata* in forests and of *B. bombina* in lowlands, therewith strengthening the species' ecological segregation.

4.2 | Modelling Results

The 'global' TSDM for European *Bombina* includes the parameters elevation, hilliness, forest cover and annual precipitation and is strongly supported by reference distribution data (Appendix S2). The three locally operating parameters elevation, hilliness and forest cover provide the model with substantial projected detail. The model is nevertheless frequently inaccurate, such as, for example, at the Mecsek Mountains in southern Hungary, where the realised *B. variegata* enclave is larger than projected (see Appendix S2 panels A,E). This is probably because the *Bombina* hybrid zone is not positioned at one particular elevation contour. While the model sets the elevation separating the species at around 300 m, in the field it varies from ca. 115 m in central Croatia (present study) to ca. 330 m in western Ukraine (Yanchukov et al. 2006) and to ca. 450 m at the Slovak–Hungarian border (Gollmann et al. 1988). In mosaic hybrid zone sections, an elevation threshold is more difficult to determine, but, for example, at Apahida, Romania, a hybrid belt is found at ca. 450 m (Vines et al. 2003). Another example of elevation operating at different thresholds is shown in the *Bufo bufo*–*B. spinosus* hybrid zone that is positioned at ca. 200 m in the west of France, at ca. 500 m at the Plateau Central, and at ca. 1200 m in the Ligurian Alps (Arntzen et al. 2020). In these systems, the mutual species borders seem better described by the transition from flat to hilly than by elevation per se, and global models are limited in the fit they can achieve. This is also shown at Peščenica, where the 'global model' yields a poor fit despite a strong overlap in variable selection. The TSDM for Jastrebarsko does not include elevation and forest cover, which makes sense because the hybrid zone cuts straight through the lowland forest (Figure 2) and is not set at an incline (Figure 4). Instead, the model relies on the variables annual mean temperature and annual precipitation that, however, do a poor job in predictive TSDM (Arntzen 2025) and such gradual thresholds are unlikely to stop the hybrid zone from moving.

At Peščenica the elevation contour is followed, except where extensive lowland forestation is connected to the main *B. variegata* range (Bugter et al. 1997; MacCallum et al. 1998; Atkinson 2001). A wider *B. variegata* range than predicted from the lowland to mountain transition is also found at the densely forested Jastrebarsko area (Figures 2 and 4). The notion that forestation extends the position of the species hybrid zone into the lowland such as at Peščenica—thus in favour of *B. variegata*—is here supported by analyses at coarse (central Europe) and fine spatial scale (Jastrebarsko). The importance of forestation to the presence of *B. variegata* is further supported by a TSDM for *Bombina* species from the Hungarian atlas data (Arntzen et al. 2025). Forestation was also mentioned as an explanatory variable at the opposite side of the parapatric species interaction at Stryi in western Ukraine (Yanchukov et al. 2006) along with elevation, but because the variables are locally strongly correlated, effects could not be disentangled. The transects in central Croatia yield hybrid zones that at 1.3–3.3 km are narrower than elsewhere (average width 6.7 km, range 2.1–11.4, data compiled by Dufresnes, Suchan, et al. 2020) and it is probably not coincidental that the other most-narrow hybrid zone at Stryi (width of 2.1 km) also yields a convoluted and sharp parapatric species contour set by forestation and elevation (Yanchukov et al. 2006). Other locally operating variables such as soil (e.g., accommodated in the 'Hupka' line that describes hybrid zone position west of Kraków, see Michałowski 1958; Appendix S5) are problematic to employ for blanket mapping (Arntzen et al. 2025).

The hybrid zone at Jastrebarsko runs through the centre of the lowland forest at ca. 5 km from the lowland–mountain transition, so that (forested) areas close to the Kupa river have *B. bombina* and areas adjacent to the Vukomerić hills have *B. variegata* (Figure 4). The pocket of *B. bombina* at Jastrebarsko is thinly connected to the species' main range by the Kupa river corridor and for such a situation I propose the term 'peninsular enclave' or 'pen-enclave'. This Jastrebarsko pen-enclave forms a miniature representation of *Bombina* across central Europe, with a potential corridor in the north (the saddle at the Vukomerić hills versus the Moravian Gate that interconnects Poland and the Czech Republic) and a river that forms the actual corridor (Kupa river valley versus the Danube at the Iron Gate) (Figures 1 and 2). However, at Jastrebarsko the presence of *B. bombina* is limited to the Kupa river region whereas the Carpathian basin is almost entirely taken.

Clinal hybrid zones, to which *B. bombina* and *B. variegata* contribute prime examples (Szymura and Barton 1986, 1991), are characterised by an equilibrium between dispersal into the zone and selection against hybrids (Bazykin 1969; Endler 1977; Barton and Hewitt 1985). For the Jastrebarsko zone to move towards the Vukomerić hills requires that *B. bombina* colonises more of the forested lowland (the left arrow in Figure 4) to which, however, the species pool is in short supply. While the Carpathian basin can also be seen as a pen-enclave (*B. bombina* surrounded by *B. variegata* except for a riverine corridor), *B. bombina* populations are widespread so that at the opposite site of the Vukomerić hills (the other arrow in Figure 4) dispersal into the hybrid zone and colonisation of forested lowlands is not compromised by small population sizes (other than through recent population decline from habitat degradation). A complicating factor at Jastrebarsko is the presence of three fish pond complexes positioned at various distances from the centre of the hybrid zone (Figure 2). Fish ponds generally constitute *B. bombina* habitat and are avoided by *B. variegata* (von Méhély 1905; Dolgener et al. 2012). While an introduced origin of *B. bombina* associated with pisciculture cannot be excluded, the natural explanation is that these lakes were colonised from along the Kupa river.

4.3 | From Holocene to the Present

Consensus exists that during the most recent Pleistocene glaciation at 20 Kyr BP refugia were in Dobrogea and at the Black Sea coast for *B. bombina* and in the southern Carpathians and the Balkan and Apennine Peninsulas for *B. variegata* (Arntzen 1978; Fijarczyk et al. 2011; Dufresnes, Suchan, et al. 2020). A Pannonian refugium for *B. bombina* is contradicted by the occurrence of enclaves of *B. variegata* in this area, suggesting that the latter species was there first (Vörös et al. 2016). The Holocene colonisation of the Carpathian basin by *B. bombina* is thought to have taken place from the southeast, following the Lower Danube Corridor through the Iron Gate (Arntzen 1978; Magyari et al. 2010). While Dufresnes, Suchan, et al. (2020) support this scenario, they assume that studied sections of the *B. bombina*–*B. variegata* hybrid zone formed at their current position 'post LGM', following climate amelioration with a timing governed by the distance to the *B. bombina* LGM refugium. Distances range from 500 to 1000 km for eastern European localities and from 1100 to 1400 km for central European (Pannonian) localities. I take issue with this scheme because it ignores the buffering effect of forestation on the *B. bombina* range expansion.

The research question here addressed resembles the debate on the biogeographic origin of the species-rich steppe grasslands in central Europe, to which the alternative hypotheses are long-term species persistence in situ versus immigration from the southeast, either shortly after the last glacial maximum or along with the Neolithic landscape deforestation (Divíšek et al. 2022). At 6 Kyr BP, most of the Pannonian and Danube plains were forested (Bohn et al. 2003; Molnár et al. 2018; Feurdean et al. 2021). The prime *B. bombina* habitats of open wetlands were located mostly adjacent to the Danube and Tisza rivers (Figure 5). Given the relatively strong position of *B. variegata* in lowland forests uncovered in the present study, these forests may have been strongholds that remained occupied by *B. variegata* for longer than the surrounding deforested areas. For example, Cayuela et al. (2015) observed that *B. variegata* is negatively affected by loss of forest cover to agricultural land, even in the absence of the congener. Hence, an extensive patchwork of *B. variegata* occurrences may have existed over the Pannonian and Danubian plains, of which forested patches of occurrence eventually dissolved and elevation enclaves persisted. However, ambiguity exists on the tempo and mode of the deforestation process. First settlers at the Carpathian basin are reported at 8 Kyr BP (Anders and Siklósi 2012). More widespread anthropogenic influences developed from 3.1 Kyr BP (Magyari et al. 2010), with cultural inequalities (Bogaard et al. 2019; Duffy et al. 2025) further contributing to habitat complexity and a patchy environment. In spite of the advance of farming, woodland cover was high

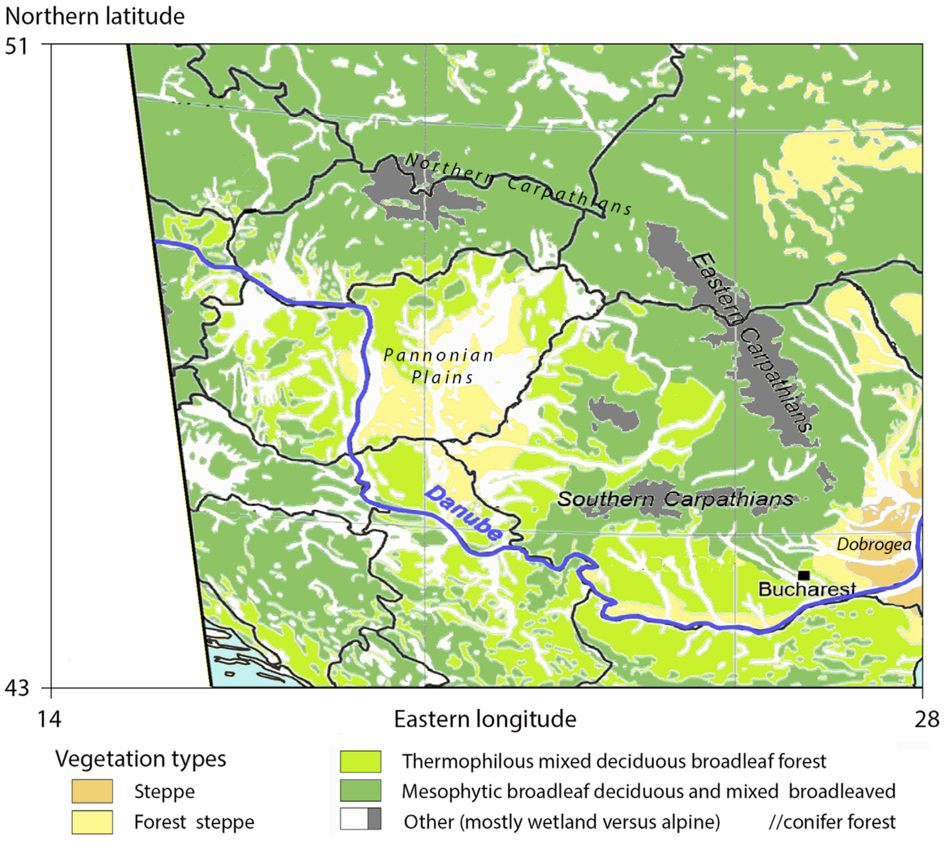

FIGURE 5 | Potential natural vegetation cover showing the extent of wetlands, forestation and steppes in central Europe at 6000 year BP (after Bohn et al. 2003; Feurdean et al. 2021). *Bombina bombina* prime habitats are lowland wetlands, shown in white. Forested areas shown in yellow and green, at the time widespread over the Pannonian plains including the current range of *B. bombina* (cf. Figure 1) were, possibly until recently, inhabited by *B. variegata*.

until the Middle Ages (Sundseth 2009) and the absence of *B. variegata* in the Pannonia lowland may have been relatively recent. By the late 18th century, forest cover in the Pannonian lowland was down to ca. 10% cover, further down to ca. 3% in 1942, with a recent upsurge of secondary forest at the expense of semi-natural forest (Biró et al. 2022). The relative recency of the deforestation process and the subsequent latter-day advance of *B. bombina* over *B. variegata* offers opportunities for molecular genetic research (see below).

The combined effect of elevation and forest cover on the long-term dynamics of hybridising species as here shown for *B. bombina*–*B. variegata* is known from other systems. European amphibian species pairs in which a lowland species supersedes a closely related species from the hills, mountains and forests include *Triturus cristatus* and *T. pygmaeus* sandwiching *T. marmoratus* at opposite sides of its range (Arntzen and Wallis 1991; Espregueiro Themudo and Arntzen 2007; Arntzen and Espregueira Themudo 2008; Arntzen 2023a, 2023b) and *Bufo bufo* displacing *B. spinosus* (Arntzen 2019; Arntzen et al. 2020). Another candidate pair for the study of species replacement by a hybrid zone moving up an elevation-forestation gradient in a Carpathian setting is *Lissotriton vulgaris*–*L. montandoni* (Zieliński et al. 2019; Antunes, Dudek, et al. 2023; Antunes, Figueiredo-Vázquez, et al. 2023). This raises the question of whether the reverse situation of a mountain/terrestrial species taking over from a lowland/aquatic species is more difficult to document, that these cases are rare, or that we deal with a chance effect.

4.4 | Prospects for Research

If the current position of the *Bombina* hybrid zone would solely be determined by an elevation gradient, then the observed distributions possibly formed shortly after post-glacial climate warming (Arntzen 1978; Dufresnes, Suchan, et al. 2020). If, however, as suggested in the present paper, forestation and narrow river valleys tempered the *B. bombina* advance, the process may be recent (a couple of centuries, a time frame that was alluded to for the Apahida hybrid zone; Vines et al. 2003; Nürnberger et al. 2016) and ongoing. Hybrid zones not at equilibrium but in flux, moving or oscillating, would open new research possibilities. Three lines of argument have successfully been employed in the study of species replacement by moving hybrid zones, namely (i) historical data, (ii) spatial patterns of relict populations and (iii) introgression of genetic markers into the advancing taxon (Arntzen and Wallis 1991; Buggs 2007; Wielstra 2019). For the *Bombina* research program, this turns out as follows.

4.4.1 | Historical Data

The resurveying of an early documented *Bombina* distribution was carried out in south-eastern Poland and adjacent Ukraine (Horbulewicz 1933; Szymura and Barton 1986) whereas a survey a little more to the east (Yanchukov et al. 2006) is adjoining the very first *Bombina* hybrid zone inventory (Horbulewicz 1927; see

TABLE 1 | Overview of historical studies on *Bombina bombina* and *B. variegata* hybrid zones, considered for resurveying and additional research.

Number	Research area	Study	Spatial setting	Characters studied	Note/reworked by
1	Western Ukraine	Horbulewicz (1927)	Hybrid zone	Morphology	Isolines only/Yanchukov et al. (2006) (adjacent area)
2	Eastern Poland - western Ukraine	Horbulewicz (1933)	Hybrid zone	Morphology	Isolines, to some degree quantified/ Szymura and Barton (1991) (16)
3	Wider Krakow region, Poland	Michałowski (1958)	Hybrid zone	Spot scores	Large area covered, toad skins prepared
4	Slovakia	Lác (1961)	Hybrid zone	Spot scores and morphometry	Large area covered/Gollmann (1986) for two small areas (12)
5a	Carpathians south of Kraków transect, Poland	Michałowski (1961)	Hybrid zone	Spot scores	Toad skins prepared
5b	Kraków-Chrzanów ridge, Poland	Michałowski (1961)	Enclave	Spot scores	Toad skins prepared
6	Sądecki Beskid Mountains, Poland	Madej (1964a)	Hybrid zone edge	Spot scores	Sampling biased towards *B. variegata*
7	Upper Silesia and Moravian Gate, Poland	Madej (1964b)	Hybrid zone	Spot scores	Large area covered
8	Southwestern Slovakia	Lác and Lechovič (1965)	Hybrid zone	Spot scores and morphometry	Large area covered
9	Low Beskid Mountains, Poland	Madej (1966)	Hybrid zone	Spot scores	Toad skins prepared
10	Northeastern Austria	Gollmann (1984, 1996)	Hybrid zone	Spot scores, morphometry and allozymes	Sparse sampling in spite of an intensive search
11	Kraków transect, Poland	Szymura and Barton (1986)	Hybrid zone	Allozymes	Degraded, disappeared (J. Szymura, pers. comm.)
12	Laborec valley	Gollmann (1986)	Hybrid zone	Allozymes and spot scores	Possibly a local increase of *B. variegata*
13	Mátra Mountains, Hungary	Gollmann (1987)	Enclave	Allozymes, spot scores and morphometry	Sparse sampling
14	Slovak–Hungarian border	Gollmann (1986) and Gollmann et al. (1988)	Hybrid zone	Allozymes and spot scores	Detailed sampling with possibly a local increase of *B. variegata*
15	Kostajnica transect, Croatia	Szymura (1988, 1993)	Hybrid zone	Allozymes	Sparse sampling
16	Przemyśl area, south-eastern Poland	Szymura and Barton (1991)	Hybrid zone	Allozymes	Appears stable since 1933

(Continues)

TABLE 1 | (Continued)

Number	Research area	Study	Spatial setting	Characters studied	Note/reworked by
17	Peščenica, Croatia	Szymura (1988), Nürnberger et al. (1995), Bugter et al. (1997) and MacCallum et al. (1998)	Hybrid zone	Allozymes	With lowland forest in one section
18	Jastrebarsko, Croatia	Atkinson (2001)	Hybrid zone	Spot scores	With lowland forest

Note: The listed studies are based upon quantitative data, with fieldwork carried out prior to the year 2000.

Table 1). This yielded neutral results of no change, presumably because hybrid zones have locally stabilised against a sharp elevation profile. The large range covered by Lác (1961) was successfully resampled in two areas showing a possible local advance of *B. variegata* over *B. bombina* (Gollmann 1986). Among another six studies with spot score data (nos 3, 5–9 in Table 1, 1958–1966) the Polish ones stand out for a wide coverage. An especially promising setting for resurveying is the *B. variegata* enclave at the Kraków-Chrzanów ridge (no. 5b, Michałowski 1961; see also Figure 1 and Appendix S5), the more so if the toad skins that Dr. Michałowski prepared would be preserved, to a posteriori obtain genomic data and to corroborate his spot score classification. Among studies from the allozyme era (1984–1998, nos. 10–16) the one at the Slovak–Hungarian border stands out for sampling detail (Gollmann et al. 1988). Other promising venues are lowland forests close to or connected with the continuous *B. variegata* range such as at Peščenica and Jastrebarsko. In the latter area the hybrid zone appears unsettled, although it remains to be seen if the time span of 2–3 decades is not too short for movement of the hybrid zone to be detectable. Elsewhere, either sampling was sparse or transect habitats have become derelict (Table 1). Mosaic hybrid zones such as at Apahida, Romania (Vines et al. 2003) also yield promise because of more diverse, possibly fluctuating environmental conditions, but require detailed sampling to cope with the two dimensions. For *B. bombina*, Apahida is remote from its presumed source area Pannonia but has, as happens to be the case, been reachable by dispersal along the river Someş (see Appendix S2 panel F). Alternatively, the Apahida hybrid belt is an offshoot of the large *B. bombina* pen-enclave in central Romania that is connected to Pannonia by the river Mureş. This inference highlights that mere geographical distance to the LGM refugium is a poor indicator for the onset of hybrid zone formation.

4.4.2 | Spatial Patterns

Both *Bombina* species have ranges with isolated populations at the fringes of their ranges, such as for *B. variegata* across France (Lescure et al. 2011; Vacher et al. 2020) and for *B. bombina* in European and Asiatic Turkey (Figure 1) suggesting range regressions. Other isolated *B. variegata* occurrences are enclaves where the species is surrounded and thus isolated by *B. bombina*. These are an indication of the species' wider past distribution and the advance of its counterpart *B. bombina* (Arntzen 1978). The most promising areas for discovering enclaves are elevated, forested and data-deficient areas in north-eastern Romania, western Ukraine and Moldavia. So far, an association with *B. variegata* was found in the floodplain beech forests near the Dniester river in Ukraine (possibly as far east as the Medobory hills) and the Buciumeni forest in Romania (Appendix S2 panel E) but more data are needed to resolve more *B. variegata* enclaves, if they exist (Appendix S2 panel F). New surveys could be especially rewarding if they focus on the distinction between contact zones that are in flux and those that have stabilised, possibly guided by insights from this paper. Further information on habitat variables that play a role in the mutual species distribution can possibly be obtained in areas of the Czech Republic that currently stand out as sympatric, in particular the Moravian Gate area and the White Carpathians in the east of the country (Figure 1 and Appendix S2G). The modelling suggests that the Bohemian pen-enclave may be isolated from the Pannonian one, providing support for an independent colonisation even from the north by the river Elbe (Schreiber 1912). Resolving the *Bombina* species distributions in the Czech Republic may be straightforward from records with more precise locality information than shown in the gridded atlas (https://portal.nature.cz/).

4.4.3 | Genetic Footprints

Species replacement may also transpire from 'genetic footprints' (or perhaps 'genomic footprints', sensu Zacho et al. 2025) left behind by the regressing counterpart species (Scribner and Avise 1994; Currat et al. 2008). Dufresnes, Suchan, et al. (2020) point to 'genetic leakage' in the *Bombina* system but reported no asymmetries that would be indicative of spatio-temporal directionality, whereas no current introgression was observed in the Kraków transect (Nürnberger et al. 2016). A candidate area for research is the North Hungarian Mountain Range that is seemingly suitable for *B. variegata*, but where the species is present in some (Bakony, Mátra) and appears absent in other components (Bükk and Börszöny) (Arntzen et al. 2025; Herpterkep 2025). These areas may represent different stages in the process of species replacement and it is just a matter of perspective if the situation at Mátra (with possibly no pure *B. variegata*; Gollmann 1987) is best described as a deep genetic footprint or an eroded enclave. Other candidate research areas are persisting semi-natural lowland forests and areas where these disappeared recently, as can be traced in detail starting with the First Military Survey, that took place from 1782 to 1785 (Hungarian Military History Museum, Budapest, in Biró et al. 2018, 2022). Under the prevalent long-term scenario of an advancing *B. bombina* and a regressing *B. variegata* it is advisable that future molecular studies should include populations from the *B. bombina* LGM refugium areas at the western and northern Black Sea coast, to confirm that perceived *B. variegata* genetic traces are not actually *B. bombina* ancient polymorphisms persisting through incomplete lineage sorting. Future genetic work on *B. variegata* enclaves may shed some light on the pattern and process of species replacement though the timing and the size and environmental features of the enclave will both affect genetic introgression in ways that may be hard to disentangle. It may further be noted that 'pondscapes' are in serious decline from agrarian reform which compromises research opportunities, although this may be stronger so in western (e.g., Arntzen 2025) than in eastern Europe (Babai et al. 2015).

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Conflicts of Interest

The author declares no conflicts of interest.

Data Availability Statement

This article contains no new data. All data were taken from internet sources and those used to construct and test distribution models and geographical clines are reproduced in the Supporting Information.

References

Anders, A., and Z. Siklósi, eds. 2012. *The Körös Culture in Eastern Hungary, the First Neolithic Sites in Central/South-East European Transect. Volume III. The Körös Culture in Eastern Hungary*. Archaeopress. https://doi.org/10.30861/9781407309170.

Antunes, B., K. Dudek, M. Pabijan, P. Zieliński, and W. Babik. 2023. "Past Forest Cover Explains Current Genetic Differentiation in the Carpathian Newt (*Lissotriton montandoni*), but Not in the Smooth Newt (*L. vulgaris*)." *Diversity and Distributions* 29: 1129–1140. https://doi.org/10.30861/978140730917010.30861/9781407309170.

Antunes, B., C. Figueiredo-Vázquez, K. Dudek, et al. 2023. "Landscape Genetics Reveals Contrasting Patterns of Connectivity in Two Newt Species (*Lissotriton montandoni* and *L. vulgaris*)." *Molecular Ecology* 32: 4515–4530. https://doi.org/10.30861/9781407309170.

Araújo, M. B., and M. Luoto. 2007. "The Importance of Biotic Interactions for Modelling Species Distributions Under Climate Change." *Global Ecology and Biogeography* 16: 743–753. https://doi.org/10.1111/j.1466-8238.2007.00359.x.

Arntzen, J. W. 1978. "Some Hypotheses on Postglacial Migrations of the Fire-Bellied Toad, *Bombina bombina* (Linnaeus) and the Yellow-Bellied Toad, *Bombina variegata* (Linnaeus)." *Journal of Biogeography* 5: 339–345. https://doi.org/10.2307/3038027.

Arntzen, J. W. 2019. "An Amphibian Species Pushed out of Britain by a Moving Hybrid Zone." *Molecular Ecology* 28: 5145–5154. https://doi.org/10.1111/mec.15285.

Arntzen, J. W. 2023a. "A Two-Species Distribution Model for Parapatric Newts, With Inferences on Their History of Spatial Replacement." *Biological Journal of the Linnean Society* 138: 75–88. https://doi.org/10.1093/biolinnean/blac134.

Arntzen, J. W. 2023b. "Patch Analysis of Atlas Data Reveals Pattern and Process of Species Replacement." *Frontiers of Biogeography* 15: 3. https://doi.org/10.21425/F5FBG59627.

Arntzen, J. W. 2025. "Decadal Data Reveal Declines, Not Species Replacement, of Salamanders Under Agrarian Reform." *Global Ecology and Conservation* 59: e03567. https://doi.org/10.1016/j.gecco.2025.e03567.

Arntzen, J. W., D. Canestrelli, and I. Martínez-Solano. 2020. "Environmental Correlates of the European Common Toad Hybrid Zone." *Contributions to Zoology* 89: 270–281. https://doi.org/10.1163/18759866-bja10001.

Arntzen, J. W., and G. Espregueira Themudo. 2008. "Environmental Parameters That Determine Species Geographical Range Limits as a Matter of Time and Space." *Journal of Biogeography* 35: 1177–1186. https://doi.org/10.1111/j.1365-2699.2007.01875.x.

Arntzen, J. W., T. Trujillo, R. Butôt, et al. 2016. "Concordant Morphological and Molecular Clines in a Contact Zone of the Common and Spined Toad (*Bufo bufo* and *B. spinosus*) in the Northwest of France." *Frontiers in Zoology* 13: 1–12. https://doi.org/10.1186/s12983-016-0184-7.

Arntzen, J. W., J. Vörös, and K. Harmos. 2025. "Assessment of Environmental Variables for Species Distribution Modelling: Insight From a Mosaic Distribution in Central Europe (Red- and Yellow-Bellied Toads, Genus *Bombina*)." *Basic and Applied Ecology* 87: 120–127. https://doi.org/10.1016/j.baae.2025.06.005.

Arntzen, J. W., and G. P. Wallis. 1991. "Restricted Gene Flow in a Moving Hybrid Zone of the Newts *Triturus cristatus* and *T. marmoratus* in Western France." *Evolution* 45: 805–826. https://doi.org/10.2307/2409691.

Atkinson, N. W. 2001. "Ecological Parameters in a *Bombina* Hybrid Zone." PhD Thesis, University of Edinburgh, UK. http://hdl.handle.net/1842/13662.

Babai, D., A. Tóth, I. Szentirmai, et al. 2015. "Do Conservation and Agri-Environmental Regulations Effectively Support Traditional Small-Scale Farming in East-Central European Cultural Landscapes?" *Biodiversity and Conservation* 24: 3305–3327. https://doi.org/10.1007/s10531-015-0971-z.

Barbieri, F., F. Bernini, F. M. Guarino, and A. Venchi. 2004. "Distribution and Conservation Status of *Bombina variegata* in Italy (Amphibia, Bombinatoridae)." *Italian Journal of Zoology* 71, no. Suppl. 1: 83–90. https://doi.org/10.1080/11250003.2004.9525565.

Barton, N. H., and G. M. Hewitt. 1985. "Analysis of Hybrid Zones." *Annual Review of Ecology and Systematics* 16: 113–148. https://doi.org/10.1146/annurev.es.16.110185.000553.

Bazykin, A. D. 1969. "Hypothetical Mechanism of Speciation." *Evolution* 23: 685–687. https://doi.org/10.1111/j.1558-5646.1969.tb03550.x.

Berroneau, M., T. Armand, S. Bonifait, and M. Menay. 2010. "Redécouverte du Sonneur à Ventre Jaune (*Bombina variegata* Linné, 1758) dans le Département de la Gironde." *Bulletin de la Société Herpétologique de France* 133: 27–34.

Biró, M., J. Bölöni, and Z. Molnár. 2018. "Use of Long-Term Data to Evaluate Loss and Endangerment Status of Natura 2000 Habitats and Effects of Protected Areas." *Conservation Biology* 32: 660–671. https://doi.org/10.1111/cobi.13038.

Biró, M., Z. Molnár, K. Öllerer, L. Demeter, and J. Bölöni. 2022. "Behind the General Pattern of Forest Loss and Gain: A Long-Term Assessment of Semi-Natural and Secondary Forest Cover Change at Country Level." *Landscape and Urban Planning* 220: 104334. https://doi.org/10.1016/j.landurbplan.2021.104334.

Bogaard, A., M. Fochesato, and S. Bowles. 2019. "The Farming-Inequality Nexus: New Insights From Ancient Western Eurasia." *Antiquity* 93: 1129–1143. https://doi.org/10.15184/aqy.2019.105.

Bohn, U., G. Gollub, C. Hettwer, et al. 2003. *Map of the Natural Vegetation of Europe, Scale 1:2.500.000*. Landwirtschaftsverlag.

Booth, T. H. 2018. "Why Understanding the Pioneering and Continuing Contributions of BIOCLIM to Species Distribution Modelling Is Important." *Austral Ecology* 43: 852–860. https://doi.org/10.1111/aec.12628.

Boulenger, G. A. 1886. "On Two European Species of *Bombinator*." *Proceedings of the Scientific Meetings of the Zoological Society of London* 1886: 499–501.

Boulenger, G. A. 1897. *The Tailless Batrachians of Europe*. Ray Society. https://doi.org/10.5962/bhl.title.5774410.5962/bhl.title.57744.

Buggs, R. 2007. "Empirical Study of Hybrid Zone Movement." *Heredity* 99: 301–312. https://doi.org/10.1038/sj.hdy.6800997.

Bugter, R., C. J. MacCallum, J. W. Arntzen, and N. H. Barton. 1997. "An Analysis of Habitat Components in a *Bombina* Hybrids Zone Using Remote Sensing." In *Herpetologia Bonnensis*, edited by W. Böhme, W. Bischoff, and T. Ziegler, 35–42. Societas Europaea Herpetologica.

Bull, C. M. 1991. "Ecology of Parapatric Distributions." *Annual Review of Ecology and Systematics* 22: 19–36. https://doi.org/10.1146/annurev.es.22.110191.000315.

Busby, J. R. 1991. "BIOCLIM—A Bioclimatic Analysis and Prediction Tool." *Plant Protection Quarterly* 6: 8–9.

Büttner, G., B. Kosztra, G. Maucha, et al. 2021. *Copernicus Land Monitoring Service—CORINE Land Cover. User Manual*. Copernicus Publications.

Cayuela, H., A. Besnard, J. Cote, et al. 2020. "Anthropogenic Disturbance Drives Dispersal Syndromes, Demography, and Gene Flow in Amphibian Populations." *Ecological Monographs* 90: e01406. https://doi.org/10.1002/ecm.1406.

Cayuela, H., M. Cheylan, and P. Joly. 2011. "The Best of a Harsh Lot in a Specialized Species: Breeding Habitat Use by the Yellow-Bellied Toad (*Bombina variegata*) on Rocky Riverbanks." *Amphibia-Reptilia* 32: 533–539. https://doi.org/10.1163/156853811X614461.

Cayuela, H., J. Lambrey, J. P. Vacher, and C. Miaud. 2015. "Highlighting the Effects of Land-Use Change on a Threatened Amphibian in a Human-Dominated Landscape." *Population Ecology* 57: 433–443. https://doi.org/10.1007/s10144-015-0483-4.

Cayuela, H., B. Monod-Broca, J.-F. Lemaître, et al. 2022. "Compensatory Recruitment Allows Amphibian Population Persistence in Anthropogenic Habitats." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2206805119. https://doi.org/10.1073/pnas.2206805119.

Clarke, K. R., and R. N. Gorley. 2015. *PRIMER v7: User Manual/Tutorial*. PRIMER-E.

Cogălniceanu, D., F. Stănescu, and C. Eggert. 2024. "Aging and Growth Outside the Comfort Zone: The Case of Alien Fire-Bellied Toads in France." *European Zoological Journal* 91: 142–150. https://doi.org/10.1080/24750263.2024.2304269.

Cogălniceanu, D., P. Székely, C. Samoilă, et al. 2013. "Diversity and Distribution of Amphibians in Romania." *ZooKeys* 296: 35–58. https://doi.org/10.3897/zookeys.296.4872.

Currat, M., M. Ruedi, R. J. Petit, and L. Excoffier. 2008. "The Hidden Side of Invasions: Massive Introgression by Local Genes." *Evolution* 62: 1908–1920. https://doi.org/10.1111/j.1558-5646.2008.00413.x.

Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998. "Individualistic Species Responses Invalidate Simple Physiological Models of Community Dynamics Under Global Environmental Change." *Journal of Animal Ecology* 67: 600–612. https://doi.org/10.1046/j.1365-2656.1998.00223.x.

Derryberry, E. P., G. E. Derryberry, J. M. Maley, and R. T. Brumfield. 2014. "HZAR: Hybrid Zone Analysis Using an R Software Package." *Molecular Ecology Resources* 14: 652–663. https://doi.org/10.1111/1755-0998.12209.

Divíšek, J., M. Večeřa, E. Welk, et al. 2022. "Origin of the Central European Steppe Flora: Insights From Palaeodistribution Modelling and Migration Simulations." *Ecography* 2022: e06293. https://doi.org/10.1111/ecog.06293.

Dolgener, N., C. Schröder, N. Schneeweiss, and R. Tiedemann. 2012. "Genetic Population Structure of the Fire-Bellied Toad *Bombina bombina* in an Area of High Population Density: Implications for Conservation." *Hydrobiologia* 689: 111–120. https://doi.org/10.1007/s10750-012-1016-1.

Dormann, C. F., J. Elith, S. Bacher, et al. 2013. "Collinearity: A Review of Methods to Deal With It and a Simulation Study Evaluating Their Performance." *Ecography* 36: 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Duffy, P. R., F. Wilkes, H. Skorna, et al. 2025. "Five Thousand Years of Inequality in the Carpathian Basin." *Science Advances* 11: eadu0323. https://doi.org/10.1126/sciadv.adu0323.

Dufresnes, C., S. N. Litvinchuk, B. Rozenblut-Kościsty, et al. 2020. "Hybridization and Introgression Between Toads With Different Sex Chromosome Systems." *Evolution Letters* 4: 444–456. https://doi.org/10.1002/evl3.191.

Dufresnes, C., T. Suchan, N. A. Smirnov, M. Denoël, J. M. Rosanov, and S. N. Litvinchuk. 2020. "Revisiting a Speciation Classic: Comparative Analyses Support Sharp but Leaky Transitions Between *Bombina* Toads." *Journal of Biogeography* 48: 548–560. https://doi.org/10.1111/jbi.14018.

Endler, J. A. 1977. *Geographic Variation, Speciation, and Clines*. Princeton University Press.

Espregueiro Themudo, G., and J. W. Arntzen. 2007. "Newts Under Siege: Range Expansion of *Triturus pygmaeus* Isolates Populations of Its Sister Species." *Diversity and Distributions* 13: 580–586. https://doi.org/10.1111/j.1472-4642.2007.00373.x.

European Space Agency. 2024. “Copernicus Global Digital Elevation Model.” Distributed by OpenTopography. https://doi.org/10.5069/G9028PQB.

Feurdean, A., R. Grindean, G. Florescu, et al. 2021. “The Transformation of the Forest Steppe in the Lower Danube Plain of Southeastern Europe: 6000 Years of Vegetation and Land Use Dynamics.” *Biogeosciences* 18: 1081–1103. https://doi.org/10.5194/bg-18-1081-2021.

Fijarczyk, A., K. Nadachowska, S. Hofman, et al. 2011. “Nuclear and Mitochondrial Phylogeography of the European Fire-Bellied Toads *Bombina bombina* and *Bombina variegata* Supports Their Independent Histories.” *Molecular Ecology* 20: 3381–3398. https://doi.org/10.1111/j.1365-294X.2011.05175.x.

Franklin, J. 2010. *Mapping Species Distributions*. Cambridge University Press. https://doi.org/10.1017/CBO9780511810602.

Fuhn, I. 1960. *The Fauna of the People's Republic of Romania Amphibia, Volume XIV, Part 1, Amphibia*. Editura Academiei Republicii Populare Romine (in Romanian).

Gollmann, G. 1984. “Allozymic and Morphological Variation in the Hybrid Zone Between *Bombina bombina* and *Bombina variegata* (Anura, Discoglossidae) in Northeastern Austria.” *Journal of Zoological Systematics and Evolutionary Research* 22: 51–64. https://doi.org/10.1111/j.1439-0469.1984.tb00562.x.

Gollmann, G. 1986. “Genetic Analysis of *Bombina* Hybrids From Eastern Slovakia.” In *Studies in Herpetology*, edited by Z. Roček, 121–126. Charles University.

Gollmann, G. 1987. “*Bombina bombina* and *Bombina variegata* in the Matra Mountains (Hungary): New Data on Distribution and Hybridization (Amphibia, Anura, Discoglossidae).” *Amphibia-Reptilia* 8: 213–224. https://doi.org/10.1163/156853887X00252.

Gollmann, G. 1996. “Structure and Dynamics of a Hybrid Zone in *Bombina* (Amphibia: Anura: Discoglossidae).” *Israel Journal of Ecology & Evolution* 42: 121–133.

Gollmann, G., B. Gollmann, and K. Grossenbacher. 2012. “*Bombina bombina* (Linnaeus. 1761)—Rotbauchunke.” In *Handbuch der Reptilien und Amphibien Europas. Froschlurche I*, edited by K. Grossenbacher, 269–294. Aula-Verlag.

Gollmann, G., P. Roth, and W. Hödl. 1988. “Hybridization Between the Fire-Bellied Toads *Bombina bombina* and *Bombina variegata* in the Karst Regions of Slovakia and Hungary: Morphological and Allozyme Evidence.” *Journal of Evolutionary Biology* 1: 3–14. https://doi.org/10.1046/j.1420-9101.1988.1010003.x.

Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. *Habitat Suitability and Distribution Models: With Applications in R*. Cambridge University Press. https://doi.org/10.1017/9781139028271.

Hartel, T., C. V. Maloșn, E. Sevianu, and I. Pascu. 2025. “Persistence of an Endangered Amphibian in a Fully Anthropogenic Forested Pondscape.” *Ecology and Evolution* 15: e71608. https://doi.org/10.1002/ece3.71608.

Herpterkep. 2025. “Amphibian and Reptile Mapping of the Amphibian and Reptile Conservation Group, MME Birdlife Hungary.” http://herpterkep.mme.hu.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. “Very High Resolution Interpolated Climate Surfaces for Global Land Areas.” *International Journal of Climatology* 25: 1965–1978. https://doi.org/10.1002/joc.1276.

Horbulewicz, L. 1927. “Die Verbreitung der *Bombinator*-und *Triton*-Arten im Bereiche der Bezirke Sambor, Drohobycz, Stryj (Kleinpolen).” *Bulletin International de l'Académie Polonaise des Sciences et des Lettres, Classe des Sciences Mathématiques et Naturelles: Sciences Naturelles. Série B* 8: 87–112.

Horbulewicz, L. 1933. “Die Geographische Verbreitung der *Bombinator*-Arten im Bereiche der Bezirke Dobromil-Przemyśl-Jarosław.” *Kosmos, Lwów A* 58: 209–223.

Iannella, M., F. Cerasoli, and M. Biondi. 2017. “Unraveling Climate Influences on the Distribution of the Parapatric Newts *Lissotriton vulgaris meridionalis* and *L. italicus*.” *Frontiers in Zoology* 14: 55. https://doi.org/10.1186/s12983-017-0239-4.

IBM Corp. 2024. *IBM SPSS Statistics for Windows, Version 30.0*. IBM Corp.

ILWIS. 2019. *Integrated Land and Watershed Management Information System*. International Institute for Aerospace Survey and Earth Sciences.

Kalaentzis, K., J. W. Arntzen, A. Avcı, et al. 2023. “Hybrid Zone Analysis Confirms Cryptic Species of Banded Newt and Does Not Support Competitive Displacement Since Secondary Contact.” *Ecology and Evolution* 13: e10442.

Key, K. H. L. 1981. “Species, Parapatry, and the Morabine Grasshoppers.” *Systematic Biology* 30: 425–458.

Lác, J. 1961. “Verbreitung der Unken (Tiefland-Unke *Bombina bombina* L. und Berg-Unke *B. variegata* L.) in der Slowakei und Problematik Deren Gegenseitigen Kreuzung.” *Biologické Práce, Slovenskej Akademie Vied, Bratislava* 7: 5–32 (in Slovak).

Lác, J., and A. Lechovič. 1965. “Die Variabilität der Systematischen Merkmale bei den Unken-Populationen (*Bombina bombina* L. and *Bombina variegata* L.) in Berürhungszonen Des Flußgebietes Hron und Nitra.” *Zborník Slovenského Národného Múzea, Prírodné Vedy* 11: 107–122 (in Slovak).

Leathwick, J. R. 2002. “Intra-Generic Competition Among *Nothofagus* in New Zealand's Primary Indigenous Forests.” *Biodiversity and Conservation* 11: 2117–2187. https://doi.org/10.1023/A:1021394628607.

Lescure, J., J. Pichenot, and P.-O. Cochard. 2011. “Régression de *Bombina variegata* (Linné, 1758) en France par l'Analyse de Sa Répartition Passée et Présente.” *Bulletin de la Société Herpétologique de France* 137: 5–41.

Lobo, J. M., A. Jiménez-Valverde, and J. Hortal. 2010. “The Uncertain Nature of Absences and Their Importance in Species Distribution Modelling.” *Ecography* 33: 103–114. https://doi.org/10.1111/j.1600-0587.2009.06039.x.

MacCallum, C. J., B. Nürnberger, N. H. Barton, and J. M. Szymura. 1998. “Habitat Preference in the *Bombina* Hybrid Zone in Croatia.” *Evolution* 52: 227–239. https://doi.org/10.2307/2410938.

Madej, Z. 1964a. “Studies on the Fire–Bellied Toad (*Bombina bombina*) and Yellow–Bellied Toad (*Bombina variegata*) of Upper Silesia and Moravian Gate.” *Acta Zoologica Cracoviensia* 9: 291–334.

Madej, Z. 1964b. “Bellied Toads (*Bombina* Oken, 1816) of the Sądecki Beskid Mts.” *Acta Zoologica Cracoviensia* 9: 761–774 (in Polish).

Madej, Z. 1966. “Bellied Toads (*Bombina* Oken, 1816) of the Low Beskid Mts. and the Adjoining Regions.” *Acta Zoologica Cracoviensia* 11: 335–350.

Magyar, I., D. H. Geary, and P. Müller. 1999. “Paleogeographic Evolution of the Late Miocene Lake Pannon in Central Europe.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 147: 151–167. https://doi.org/10.1016/S0031-0182(98)00155-2.

Magyari, E. K., J. C. Chapman, D. G. Passmore, J. R. Allen, J. P. Huntley, and B. Huntley. 2010. “Holocene Persistence of Wooded Steppe in the Great Hungarian Plain.” *Journal of Biogeography* 37: 915–935. https://doi.org/10.1111/j.1365-2699.2009.02261.x.

Marzahn, E., W. Mayer, U. Joger, et al. 2016. “Phylogeography of the *Lacerta viridis* Complex: Mitochondrial and Nuclear Markers Provide Taxonomic Insights.” *Journal of Zoological Systematics and Evolutionary Research* 54: 85–105. https://doi.org/10.1111/jzs.12115.

Meier, E. S., F. Kienast, P. B. Pearman, et al. 2010. “Biotic and Abiotic Variables Show Little Redundancy in Explaining Tree Species Distributions.” *Ecography* 33: 1038–1048. https://doi.org/10.1111/j.1600-0587.2010.06229.x.

Mertens, R. 1928. “Zur Naturgeschichte der Europäischen Unken (*Bombina*).” *Zeitschrift für Morphologie und Ökologie der Tiere* 11: 613–633. https://doi.org/10.1007/BF02424588.

Michałowski, J. 1958. “Geographische Verbreitung der Unken (*Bombina* Oken) Zwischen den Flüssen Weichsel, Skawa und Raba (Woiwodschaft Kraków).” *Acta Zoologica Cracoviensia* 3: 247–283 (in Polish).

Michałowski, J. 1961. “The Bombinators of the Kraków-Chrzanów Ridge and the Adjacent Part of the River Wisła Valley.” *Acta Zoologica Cracoviensia* 5: 699–714.

Molnár, Z., G. Király, R. Aszalós, et al. 2018. “Vegetation.” In *National Atlas of Hungary*, edited by K. Kocsis, 94–103. Hungarian Academy of Sciences.

Nürnberger, B., N. Barton, C. MacCallum, J. Gilchrist, and M. Appleby. 1995. “Natural Selection on Quantitative Traits in the *Bombina* Hybrid Zone.” *Evolution* 49: 1224–1238. https://doi.org/10.2307/2410447.

Nürnberger, B., K. Lohse, A. Fijarczyk, J. M. Szymura, and M. L. Blaxter. 2016. “Para-Allopatry in Hybridizing Fire-Bellied Toads (*Bombina bombina* and *B. variegata*): Inference From Transcriptome-Wide Coalescence Analyses.” *Evolution* 70: 1803–8018. https://doi.org/10.1111/evo.12978.

Peñalba, J. V., A. Runemark, J. I. Meier, et al. 2024. “The Role of Hybridization in Species Formation and Persistence.” *Cold Spring Harbor Perspectives in Biology* 16: a041445. https://doi.org/10.1101/cshperspect.a041445.

Peterson, A. T., J. Soberón, R. G. Pearson, et al. 2011. *Ecological Niches and Geographical Distributions*. Monographs in Population Biology 49. Princeton University Press. https://doi.org/10.23943/princeton/9780691136868.001.0001.

Pyron, R. A., K. A. O'Connell, E. M. Lemmon, A. R. Lemmon, and D. A. Beamer. 2022. “Candidate-Species Delimitation in *Desmognathus* Salamanders Reveals Gene Flow Across Lineage Boundaries, Confounding Phylogenetic Estimation and Clarifying Hybrid Zones.” *Ecology and Evolution* 12: e8574. https://doi.org/10.1002/ece3.8574.

Rafińska, A. 1991. “Reproductive Biology of the Fire-Bellied Toads, *Bombina bombina* and *B. variegata* (Anura: Discoglossidae): Egg Size, Clutch Size and Larval Period Length Differences.” *Biological Journal of the Linnean Society* 43: 197–210. https://doi.org/10.1111/j.1095-8312.1991.tb00593.x.

Ravinet, M., R. Faria, R. K. Butlin, et al. 2017. “Interpreting the Genomic Landscape of Speciation: A Road Map for Finding Barriers to Gene Flow.” *Journal of Evolutionary Biology* 30: 1450–1477. https://doi.org/10.1111/jeb.13047.

Schreiber, E. 1912. *Herpetologia Europaea*. Second ed. Gustav Fischer Verlag.

Scribner, K. T., and J. C. Avise. 1994. “Population Cage Experiments With a Vertebrate: The Temporal Demography and Cytonuclear Genetics of Hybridization in *Gambusia* Fishes.” *Evolution* 48: 155–171. https://doi.org/10.2307/2410011.

Sillero, N., J. Campos, A. Bonardi, et al. 2014. “Updated Distribution and Biogeography of Amphibians and Reptiles of Europe.” *Amphibia-Reptilia* 35: 1–31. https://doi.org/10.1163/15685381-00002935.

Smolinský, R., V. Baláž, and B. Nürnberger. 2020. “Tadpoles of Hybridising Fire-Bellied Toads (*B. bombina* and *B. variegata*) Differ in Their Susceptibility to Predation.” *PLoS One* 15: e0231804. https://doi.org/10.1371/journal.pone.0231804.

Soley-Guardia, M., D. F. Alvarado-Serrano, and R. P. Anderson. 2024. “Top Ten Hazards to Avoid When Modeling Species Distributions: A Didactic Guide of Assumptions, Problems, and Recommendations.” *Ecography* 2024: e06852. https://doi.org/10.1111/ecog.06852.

Sundseth, K. 2009. “Natura 2000 in the Pannonian Region.” Publications Office of the European Commission, Directorate-General for Environment, Brussels, Belgium.

Szymura, J. M. 1988. “Geographic Differentiation and Hybrid Zones Between the Fire-Bellied Toads *Bombina bombina* (L.) and *B. variegata* (L.) in Europe.” In *Rozprawy habilitacyjne*, vol. 147, 1–101. Uniwersytet Jagielloński (in Polish).

Szymura, J. M. 1993. “Analysis of Hybrid Zones With *Bombina*.” In *Hybrid Zones and the Evolutionary Process*, edited by R. G. Harrison, 261–289. Oxford University Press. https://doi.org/10.1093/oso/9780195069174.003.0010.

Szymura, J. M., and N. H. Barton. 1986. “Genetic Analysis of a Hybrid Zone Between the Fire-Bellied Toads, *Bombina bombina* and *B. variegata*, Near Cracow in Southern Poland.” *Evolution* 40: 1141–1159. https://doi.org/10.2307/2408943.

Szymura, J. M., and N. H. Barton. 1991. “The Genetic Structure of the Hybrid Zone Between the Fire-Bellied Toads *Bombina bombina* and *B. variegata*: Comparisons Between Transects and Between Loci.” *Evolution* 45: 237–261. https://doi.org/10.2307/2409660.

Vacher, J. P., D. Aumaître, and S. Ursenbacher. 2020. “Genetic Characteristics of an Introduced Population of *Bombina bombina* (Linnaeus, 1761) (Amphibia: Bombinatoridae) in Moselle, France.” *Acta Herpetologica* 15: 47–54.

Vasconcelos, T. S., C. P. Antonelli, and M. F. Napoli. 2017. “Mutualism Influences Species Distribution Predictions for a Bromeliad-Breeding Anuran Under Climate Change.” *Austral Ecology* 42: 869–877. https://doi.org/10.1111/aec.12509.

Vines, T. H., S. C. Kohler, M. Thiel, et al. 2003. “The Maintenance of Reproductive Isolation in a Mosaic Hybrid Zone Between the Fire-Bellied Toads *Bombina bombina* and *B. variegata*.” *Evolution* 57: 1876–1888. https://doi.org/10.1111/j.0014-3820.2003.tb00595.x.

von Méhély, L. 1905. “Die Herpetologischen Verhaltnisse des Mecsek-Gebirges und der Kapela.” *Annales Historico-Naturales Musei Nationalis Hungarici Budapest* 3: 256–316.

Vorndran, I. C., E. Reichwaldt, and B. Nürnberger. 2002. “Does Differential Susceptibility to Predation in Tadpoles Stabilize the *Bombina* Hybrid Zone ?” *Ecology* 83: 1648–1659. https://doi.org/10.1890/0012-9658(2002)083[1648:DDSTPI]2.0.CO;2.

Vörös, J., M. Alcobendas, I. Martínez-Solano, and M. García-París. 2006. “Evolution of *Bombina bombina* and *Bombina variegata* (Anura: Discoglossidae) in the Carpathian Basin: A History of Repeated Mt-DNA Introgression Across Species.” *Molecular Phylogenetics and Evolution* 38: 705–718. https://doi.org/10.1016/j.ympev.2005.08.010.

Vörös, J., P. Mikulíček, Á. Major, E. Recuero, and J. W. Arntzen. 2016. “Phylogeographic Analysis Reveals Northerly Refugia for the Riverine Amphibian *Triturus dobrogicus* (Caudata: Salamandridae).” *Biological Journal of the Linnean Society* 119: 974–991. https://doi.org/10.1111/bij.12866.

Vörös, J., F. Szalay, and L. Barabás. 2007. “A New Method for Quantitative Pattern Analysis Applied to Two European *Bombina* Species.” *Herpetological Journal* 17: 97–103.

Weir, J. T., and T. D. Price. 2011. “Limits to Speciation Inferred From Times to Secondary Sympatry and Ages of Hybridizing Species Along a Latitudinal Gradient.” *American Naturalist* 177: 462–469. https://doi.org/10.1086/658910.

Werner, E. E., and B. R. Anholt. 1993. “Ecological Consequences of the Trade-Off Between Growth and Mortality Rates Mediated by Foraging Activity.” *American Naturalist* 142: 242–272. https://doi.org/10.1086/285537.

Werner, P., S. Lötters, B. R. Schmidt, J. O. Engler, and D. Rödder. 2013. “The Role of Climate for the Range Limits of Parapatric European Land

Salamanders." *Ecography* 36: 1127–1137. https://doi.org/10.1111/j.1600-0587.2013.00242.x.

Wielstra, B. 2019. "Historical Hybrid Zone Movement: More Pervasive Than Appreciated." *Journal of Biogeography* 46: 1300–1305. https://doi.org/10.1111/jbi.13600.

Wisz, M. S., J. Pottier, W. D. Kissling, et al. 2013. "The Role of Biotic Interactions in Shaping Distributions and Realised Assemblages of Species: Implications for Species Distribution Modelling." *Biological Reviews* 88: 15–30. https://doi.org/10.1111/j.1469-185X.2012.00235.x.

Yanchukov, A., S. Hofman, J. M. Szymura, et al. 2006. "Hybridization of *Bombina bombina* and *B. variegata* (Anura, Discoglossidae) at a Sharp Ecotone in Western Ukraine: Comparisons Across Transects and Over Time." *Evolution* 60: 583–600. https://doi.org/10.1554/04-739.1.

Yang, W., N. Feiner, D. Salvi, et al. 2022. "Population Genomics of Wall Lizards Reflects the Dynamic History of the Mediterranean Basin." *Molecular Biology and Evolution* 39: msab311. https://doi.org/10.1093/molbev/msab311.

Zacho, C., I. van Riemsdijk, B. de Cahsan, J. Vörös, and M. E. Allentoft. 2025. "The *Bombina* Hybrid Zone: A Review of the Legacy and Future Research Directions." *Amphibia-Reptilia* 46: 141–167. https://doi.org/10.1163/15685381-bja10225.

Zieliński, P., K. Dudek, J. W. Arntzen, et al. 2019. "Differential Introgression Across Newt Hybrid Zones: Evidence From Replicated Transects." *Molecular Ecology* 28: 4811–4824. https://doi.org/10.1111/mec.15251.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendices S1–S9:** jbi70058-sup-0001-AppendicesS1-S9.zip.