

# A two-species distribution model for parapatric newts, with inferences on their history of spatial replacement

Arntzen, J.W.

### Citation

Arntzen, J. W. (2022). A two-species distribution model for parapatric newts, with inferences on their history of spatial replacement. *Biological Journal Of The Linnean* Society, 138(1), 75-88. doi:10.1093/biolinnean/blac134

Version: Publisher's Version License: Creative Commons CC BY 4.0 license https://hdl.handle.net/1887/3674647 Downloaded from:

**Note:** To cite this publication please use the final published version (if applicable).

## A two-species distribution model for parapatric newts, with inferences on their history of spatial replacement

JAN W. ARNTZEN<sup>1,2,\*,0</sup>

<sup>1</sup>Institute of Biology, Leiden University, Sylvius Laboratory, Sylviusweg 72, 2333 BE Leiden, The Netherlands <sup>2</sup>Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands

Received 6 July 2022; revised 1 October 2022; accepted for publication 4 October 2022

Related species often engage in abutting or overlapping contact zones with various strengths of interspecific competition. Biotic interactions such as these preclude the registration of the full profile of environmental variables that would describe the otherwise larger species ranges. Here, I advocate to forego full range species distribution modelling and instead focus on the ecography of the contact zone, for example with 'two-species distribution models' (TSDMs), in which presence data are contrasted against the background of environmental data. The newts *Triturus cristatus* and *Triturus marmoratus* meet in the west of France. A countrywide TSDM suggests that the contact zone of the species is located at a climatic gradient, in line with their north-eastern vs. south-western ranges. The species are also ecologically segregated by elevation and forestation, which is in line with a documented movement of the contact zone caused by hedgerow removal in lowland areas. Hindcasts for the Holocene suggest that the species contact zone was positioned at either the same place as at present or more to the south, depending on the amount of forestation. A forecast under climate warming predicts a fast movement to the north, but this scenario is deemed unrealistic. One reason is that recent habitat loss compromises dispersal and range expansion. Other species pairs to which TSDMs have been applied are listed for comparison.

ADDITIONAL KEYWORDS: climate change – ecological segregation – forestation – France – genetic erosion – habitat deterioration – niche differentiation – *Triturus cristatus – Triturus marmoratus*.

#### INTRODUCTION

Species distribution modelling aims to identify the ecological factors that limit and define species distributions. The models can be used to evaluate the impact that environmental change might have on local and, eventually, species survival or to reconstruct past distributions (Franklin, 2010; Peterson et al., 2011; Guisan et al., 2017). As such, species distribution modelling has become a popular tool in fields as far apart as wildlife management and phylogeography. Many approaches have been proposed to construct species distribution models (SDMs), but the most prominent stumbling blocks remain spatial biases in the gathering of presence data and the inferred nature of 'absence data'. Moreover, SDMs are mostly constructed for individual 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 & Luoto, 2007; Meier *et al.*, 2010; Wisz *et al.*, 2013).

Biotic factors have been described as the set of interactions with other species that modify the ability of a species to maintain populations (Soberón & Peterson, 2005). Biotic interactions can either be exploitative or mutualistic with positive effect or they can be negative (e.g. through disease, predation and competition). By limiting or enhancing population processes, biotic interactions will affect species distributions. The main reasons for ignoring biotic factors in species distribution modelling are that they are difficult to parameterize and that blanket coverage is mostly unavailable. One notable exception is strong interspecific competition that dictates a mutual range border. Darwin (1859) observed that the location of a species border can be determined by the border of another species, in defiance of what would become known as the 'Eltonian noise hypothesis', which states that biotic interactions do not

<sup>\*</sup>E-mail: pim.arntzen@gmail.com

<sup>© 2022</sup> The Linnean Society of London.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

affect species distributions at large geographical scales. As we now know, parapatry is common, especially among related organisms with low dispersal capability (Key, 1981; Bull, 1991). Many of these situations will probably reflect competitive exclusion, although to demonstrate a case unequivocally, experimental field and laboratory studies would usually be required (Anderson *et al.*, 2002).

For species with truncated ranges, SDMs might be of limited value, in the same way that the edge of a continent is not helpful in understanding the ecological limitations of a species. In the case of parapatry, however, the drawback comes with a bonus, because species with abutting ranges offer the opportunity to contrast their ecological preferences. In, as here proposed, 'two-species distribution models' (TSDMs), presence data from each of the two species are compared against the background of environmental data to yield insights into species habitat differentiation. Twospecies distribution modelling thereby constitutes a shift from regular species distribution modelling and is not to be confused with wider approaches that incorporate multiple species co-occurrence data, as in 'multispecies interaction' (Kissling et al., 2012), 'joint species' (Pollock et al., 2014) and 'communitylevel' (Nieto-Lugilde et al., 2018) distribution models. By concentrating on the requirements of species (as opposed to their position and functioning in the ecosystem), TSDMs are not derived from 'Eltonian' niches, but from 'Grinellian' niches extended to include a single biotic variable, namely the presence of a closely related species.

An illustrative example of range restriction by competition is provided by some amphibian species in the Pannonian basin in central Europe, such as the fire-bellied toad (Bombina bombina) and the Danube crested newt (Triturus dobrogicus). For both of them, it could be argued that ranges would be wider (i.e. include localities at higher elevation) if it were not for the presence of one (Bombina) or several (Triturus) closely related species, with which they engage in long and narrow hybrid zones that envelop their lowland ranges (Arntzen, 1996; Arntzen et al., 2014; Vörös et al., 2016). With the advent of molecular genetic data in taxonomy, more mosaics of closely related species have been (Highton, 1998; Kaliontzopoulou et al., 2011; Pabijan et al., 2017; Dufresnes et al., 2018) and continue to be (Marzahn et al., 2016; Pyron et al., 2022; Yang *et al.*, 2022) resolved, underlining the ubiquity of parapatric contact zones and, therewith, the scope for TSDMs. Early examples of TSDMs are on toads and on vipers (Romero & Real, 1996; Brito & Crespo, 2002). For a list of taxon pairs subjected to species distribution modelling in European herpetology, see Table 1. Following Smith et al. (2019), this includes examples from beyond the species level.

Potentially most rewarding for TSDMs are closely related, negatively interacting yet possibly hybridizing species, with a wide but not unrestrained area of range overlap, such as found in the newts Lissotriton helveticus/Lissotriton vulgaris and Triturus cristatus/ Triturus marmoratus in France. In hybrid zone terminology, these are bimodal (or mosaic) and not unimodal (or clinal) species settings. In both systems, the counterparts show spatial isolation determined by a variety of ecological differences (Schoorl & Zuiderwijk, 1981; Arntzen, 2022). Historical data from the department Mayenne show that the T. cristatus-T. marmoratus contact zone has been moving southwards at a pace of ~1 km/year (Vallée, 1959; Arntzen & Wallis, 1991). The process has been associated with landscape reform over the post-World War II period, in particular hedgerow removal over the southern, flat part of Mayenne. This interpretation is in line with the ecological preferences for flat and open terrain for T. cristatus vs. hilly and forested terrain for T. marmoratus (Schoorl & Zuiderwijk, 1981). Yet, the system requires study over the wider area of range overlap.

Here, I present a case study with a TSDM on T. cristatus and T. marmoratus that stretches over France and includes a patchwork of allotopic and syntopic localities within the fairly wide area of range overlap. The aims of the case study are as follows: (1) to describe species ranges where they are in touch; (2) to gain insight into the ecological parameters that differentiate T. cristatus and T. marmoratus; and (3) to reconstruct and predict the spatiotemporal pattern of species replacement. The wider aim is to evaluate the advantages and disadvantages of the two-species distribution modelling approach.

#### MATERIAL AND METHODS

Data on the distribution of Triturus newts were taken from the most recent atlas of amphibians and reptiles in France (Lescure & De Massary, 2012). Records for introduced populations (one northern *T. marmoratus* locality and *T. carnifex* from near the Geneva basin) were discounted. Low-precision records that go back to the previous French atlas (Castanet & Guyetant, 1989) were ignored, except for the construction of the southern (*T. cristatus*) and northern (*T. marmoratus*) range borders of the species. Locality coordinates were in northern latitude and eastern longitude, with a precision of two decimal places. Duplicated records were removed. Triturus cristatus × T. marmoratus hybrids were taken to be the direct offspring of both species, because  $F_1$  individuals form the great majority of intermediate phenotypes (Arntzen et al., 2021). Records for hybrids were taken to represent both species.

Taxonomic level	Amphibian and reptile species or subspecies*	Research area	Method used in species distribution modelling†	Niche similarity	x	Source‡
				р	Ι	
Intraspecific						
	Chioglossa l. lusitanica/longipes	Iberian peninsula	LR			1
Introcentario	Discoglosses & galganoi/jeanneae	Iberian peninsula	LR			2
nu ageneric	Alvtes cistern asii / obstetrican s	Therian neninsula	GLM			c.
	Romhina hombina / wariesata	Central Furone	OA			4.5
		Pannonian basin	LR	0.804	0.972	6, ps
				(0.883)	(0.989)	•
	Bufo bufo/spinosus	North-western Europe	LR			7
		France and Italy	LR	0.488	0.794	8, 9, ps
				(0.836)	(0.974)	
		Europe	ME			10
	Hyla meridionalis/molleri	Iberian peninsula	GLM			11
	Lissotriton boscai/ helveticus	Western Europe	ME			12
	Lissotriton helveticus/vulgaris	Europe	ME			12
		Pas de Calais, France	OA			13
	Lissotriton italicus/vulgaris	Italy	BRT, ME			14
	Lissotriton montandoni/vulgaris	Carpathians	LR			15
	Psammodromus edwardsianus/hispanicus/	Spain	ENFA, MDE, ME			16
	occidentalis					
	Triturus cristatus / marmoratus	Mayenne, France	OA			5
		Europe	ME			12
		Mayenne, France	LR	0.451	0.716	17, ps
				(0.835)	(0.959)	
		Deux Sevres, France	ANN, CTA, FDA, GAM, GBM, GLM, MARS, RF			18
		France	LR	0.515	0.771	bs
			, ,	(0.912)	(766.0)	
	Triturus dobrogicus / (carnifex-cristatus- macedonicus-ivanbureschi)	Pannonian basin	LR	0.815 (0.904)	0.974 (0.988)	6, ps
	Triturus marmoratus   pygmaeus	Iberian peninsula	LR	0.583	0.829	19, 20, ps
				(0.688)	(0.907)	
		Western Europe	ME			12
	Vipera aspis/latastei/seoanei	Northern Spain	ME			21
		Iberian peninsula	LR			22
		Northern Spain	ANN			23
		North-western Iberian peninsula	LR			24

**Table 1.** Methods used in distribution modelling of species pairs of European amphibians and reptiles

Table 1. Cor	itinued					
Taxonomic level	Amphibian and reptile species or subspecies*	Research area	Method used in species distribution modelling†	Niche similarity		Source‡
				D	I	
Intergeneric	Bufo bufo / Epidalia calamita	Southern Spain	LR			25
Niche similari Niche similari	ty averaged over six parapatric species pairs ty averaged over 26 allopatric species pairs in	Mexico (butterflies, birds and mammal	s; climatic variables)	0.609 0.163	0.843 0.447	ps 26
For some taxa, <sup>1</sup> permutations w given at the bot	niche similarities over the studied part of the ran 7th ENMTOOLS (Warren <i>et al.</i> , 2010). Results in 5tom of the table for comparison.	ges could be quantified (with Schoener's $D$ dicate that the observed similarities are a	and Warren's $D$ . Values in parentheses deno all different from random expectations at $P$	ote the lowest score of < 0.01. Average value	otained under es from anoth	100 random er study are
*For species lis †Methods used lysis; GAM, gro multidimension	t with full names, see the Supporting Information are as follows: ANN, artificial neural networks; B uping generalized additive models; GBM, general al envelopes; ME, maximum entropy; OA, overlar follows: (1) Arntean & Alexandrino (2004); (2) Rec follows: (1) Arntean & Alexandrino (2004); (2) Rec	(Table S2). RT, boosted regression trees, CTA, classifc ized boosting models; GLM, general linear p analysis; RF, random forests.	cation tree analysis; ENFA, ecological niche r methods; LR, logistic regression; MARS, m rmtzen (1978); (5) Armtzen (1996); (6) Vörös et	factor analysis; FDA, ultivariate adaptative <i>al.</i> (2016); (7) Arntze	flexible discri regression sj n (2019); (8) A	minant ana- dines; MDE, rntzen <i>et al.</i>
(2020a), (J) ALAL	$1260 \ et \ at$ . (20200); (10) Duffesties et $at$ . (2020); (1)	T) Velho et $a_i$ . (2011): (12) Vielles et $a_i$ . (20)	J3); (13) ATHVZEII (2022); (14) IAIIIIEIIA 6( 01) (2	701/2 (01/2/107	dl. (2013), (11)	) I IUZE EL UL.

(2011); (17) Visser *et al.* (2017); (18) Preau *et al.* (2020); (19) Arntzen & Espregueira Themudo (2008); (20) Arntzen (2018); (21) Martinez-Freiria *et al.* (2008); (22) Chamorro *et al.* (2021); (23) Tarroso *et al.* (2014); (24) Brito & Crespo (2002); (25) Romero & Real (1996); (26) Warren *et al.* (2008); ps, present study.

Environmental data considered as candidate explanatory variables to the reciprocal distribution of T. cristatus and T. marmoratus were the same as in a parallel paper on the distribution of another pair of hybridizing amphibians with a roughly similar area of species interaction, namely the common toad and the spined toad (Bufo bufo and Bufo spinosus) (Arntzen et al., 2020a). In brief, elevation and 19 climate variables (bio01-bio19) were extracted from the WorldClim global climate database v.2, obtained from the paper by Hijmans et al. (2005) (see also Fick & Hijmans, 2017). The parameter 'slope' was derived from elevation with the 'DFDX' and 'DFDY' filters in ILWIS v.3.8.6 (ILWIS, 2019). Data on a variety of soil properties were considered as far as parameter values could be ordered (i.e. strictly categorical data were excluded) from the ESDAC European soil Database v.2.0 (available at: https://esdac.jrc.ec.europa.eu; see also Panagos et al., 2012). Vegetation data were from the CORINE land cover database version CLC 2012 of the European Environment Agency (available at: https://land. copernicus.eu/pan-european/corine-land-cover) and grouped in the classes 'crop growing', 'forestation' and 'pasture'. The spatial resolution of the environmental data is reported as 30 arc-seconds for WorldClim, 1 km for ESDAC and 100 m for CORINE. To identify and, subsequently, reduce collinearity among the environmental variables, a half-matrix of the pairwise Pearson correlation coefficients was subjected to clustering using the unweighted pair group method with arithmetic mean clustering method in Primer 7 (Clarke & Gorley, 2015). Variables were retained using criteria of partial independence at r < 0.7 and selected in alphanumerical order. The selected variables were the same as in the paper on Bufo mentioned above, with the addition of the variables 'clay', 'silt' and 'coarse fragments' (Supporting Information, Table S1). Furthermore, the distinction is made between variables that operate at large spatial scales (the climate variables) and the others (such as elevation, land use and geomorphological characteristics), which operate at more local scales.

Two-species distribution models, in which the presence of one species was contrasted with the presence of the other species, were derived with stepwise logistic regression analysis in SPSS v.26 (IBM SPSS, 2019). Localities with both species were ignored. Parameter selection was in the forward stepwise mode under criteria of entry ( $P_{in} = 0.05$ ) and removal of terms ( $P_{out} = 0.10$ ) with the likelihood ratio method. Spatial models were analysed and visualized with ILWIS v.3.8.6 (ILWIS, 2019). The discriminatory ability of the model was assessed by the area under the curve (AUC) statistic. The AUC values were assessed for statistical significance by comparison with a null model derived under 100

random permutations (Raes & Ter Steege, 2007). Niche similarity for the species was quantified by the measures D and I (also known as Schoener's D and Warren's I) and assessed for statistical significance with ENMTOOLS (Warren *et al.*, 2010), again using a null model derived under 100 permutations. For the purpose of comparison, niche similarities were also calculated for other species pairs in European herpetology, to the extent that the constituting data could be retrieved. To gain an impression of the power of the model to predict the differential species distribution accurately, 70% of the data were used to build a model, the performance of which was tested with the remaining 30% of the data.

The countrywide TSDM obtained for the present day (based on all data) was used for 'hindcasting', with climatic conditions as reconstructed for the mid-Holocene at ~6000 years before present, and for forecasting, in climatic conditions as predicted for 50 years from now, under the assumption that 'elevation' did not and will not change much over this temporal window. The TSDMs were re-estimated under the assumption that western Europe would be entirely forested ('full forest') or entirely deforested ('zero forest'), because blanket data on forestation are available only for the present day. In the absence of firm guidance on which Holocene climate reconstruction would be most appropriate to apply (Guevara et al., 2019), model projections were obtained for all nine of them and eventually considered in combination. Likewise, no explicit guidance is available on what future climate scenario(s) would be best to choose (Beaumont et al., 2008). Out of the 25 currently available, one scenario was selected arbitrarily for each of four 'shared socio-economic pathways' (SSPs), namely CMCC-ESM2 under SSP 126, BCC-CSM2-MR under SSP 246, UKESM1-0-LL under SSP 370 and MIROC-ES2L under SSP 585. However, the data for BCC-CSM2RR deviated erratically from the others, and this scenario was replaced by EC-EARTH3-VEG. Species distribution models for the Last Glacial Maximum are already in place (Wielstra et al., 2013). Vernacular names and authorities for species names are given the Supporting Information (Table S2).

#### RESULTS

The distribution data indicate the existence of a ~250-km-wide and 600-km-long area of range overlap in the west of France, with areas of allopatry to the north with *T. cristatus* and to the south with *T. marmoratus* (Fig. 1; the atlas data are available for inspection at: https://atlas.lashf.org/espece/139 and https://atlas.lashf.org/espece/163). The area of range overlap has records for 545 allotopic *T. cristatus* localities (42%), 547 allotopic *T. marmoratus* localities (43%) and 192 localities with both species and/or hybrids (15%). The northern and southern areas of allopatry have 754 and 578 records for *T. cristatus* and *T. marmoratus*, respectively. The environmental variables significantly associated with the differential distributions of *T. cristatus* and *T. marmoratus* across France describe temperature (bio01, bio03 and bio06), precipitation (bio12, bio14 and bio15), elevation and forestation, whereas none of the geomorphological parameters enters the model. The TSDM equation is:

$$P_{
m c} = \left\{ 1 / \left[ 1 + \exp \left( egin{array}{c} 0.369 imes {
m bio06} + 0.0324 imes \ {
m elevation} + 0.0308 imes {
m forest} + \ 0.553 imes {
m bio03} - 0.476 imes {
m bio15} + \ 0.0222 imes {
m bio12} + 0.113 imes {
m bio1} - \ 0.298 imes {
m bio14} - 36.192 } 
ight) 
ight] 
ight\}$$

in which  $P_{i}$  is the probability for any eligible locality to be occupied by T. cristatus (Fig. 2A). The eight selected variables are ordered according to the impact they have on the model. The discriminatory ability of the model is AUC = 0.880; this value is outside the range obtained from 100 random permutations and is therefore statistically significant (P < 0.01). Visual inspection of the associated environmental profiles reveals a south-west to north-east gradient in temperature, with generally higher and less fluctuating values for T. marmoratus than for T. cristatus, whereas forestation increases over the perpendicular, north-west to southeast axis. The three selected precipitation variables show more fine-scale local gradients, frequently with high values for coastal and mountainous areas. The model obtained from the training data and applied to the test data yielded AUC values that overlapped in their 95% confidence intervals, suggesting that model overfitting is not a major issue.

Triturus cristatus and T. marmoratus localities that, according to the countrywide model, have environmental conditions rather typical for the counterpart species are shown in Figure 1B (40 T. cristatus localities with  $P_{c} \leq 0.2$  and 34 T. marmoratus localities with  $P_c \ge 0.8$ ). Alternative projections suggest that T. marmoratus would have a wider range to the north if western Europe were to be entirely forested (Fig. 2B), whereas differences in comparison to the base model are minor if forestation were to be entirely absent (Fig. 2C). Triturus cristatus and T. marmoratus differ significantly in their habitat associations (observed *D* = 0.515, null model *D* > 0.919, *P* < 0.01; observed *I* = 0.771, null model *I* > 0.992, *P* < 0.01). Analysed for areas separately, these niche similarity metrics are equally high for the area of range overlap (observed D = 0.503, null model D > 0.926, P < 0.01; observed *I* = 0.766, null model *I* > 0.994, *P* < 0.01) and much lower in allopatry (observed D = 0.195, null



**Figure 1.** A, the outer range borders of the crested newt, *Triturus cristatus* (c; southern border shown by continuous line) and the marbled newt, *Triturus marmoratus* (m; northern and eastern border shown by dashed line) in continental France, after Castanet & Guyetant (1989) and Lescure & De Massary (2012). Departments mentioned in the text are as follows: DS, Deux-Sevres; M, Mayenne; V, Vienne. The Lower Rhône *T. cristatus* population is indicated by LR. The base map was downloaded from MapsLand (https://www.mapsland.com), under a Creative Commons Attribution-ShareAlike 3.0 Licence. B, the area of *T. cristatus*-*T. marmoratus* range overlap in Mercator projection, with the generalized species border as inferred from a two-species distribution model (see Fig. 2). The open circles represent documented species occurrences that strongly contradict the model, for *T. cristatus* (probability of occurrence,  $P_c \leq 0.2$ , in red) and *T. marmoratus* ( $P_c \geq 0.8$ , in blue). Large symbols represent multiple observations at close range. The drawings of animals, with *T. cristatus* at the top and *T. marmoratus* at the bottom, are by Bas Blankevoort, Naturalis Biodiversity Center.

model D > 0.892, P < 0.01; observed I = 0.427, null model I > 0.984, P < 0.01). The difference appears to be instigated by the climate variables and not by elevation and forestation (Table 2).

Hindcasting results for the nine climate reconstructions available for the mid-Holocene are summarized in Figure 3, which shows that the variation among the nine projections is limited (see also Supporting Information, Fig. S1). The suite of full-forest scenarios suggests a reciprocal species distribution similar to that observed at present, whereas the zeroforest scenarios suggest that T. cristatus had a wider range to the south. The presence of *T. cristatus* in the lower Rhône valley (see the triangle marked LR in Fig. 1) is marginally supported under the full-forestation scenario and well supported under the zero-forestation scenario. Among the four TSDMs under future climate change, the CMCC-ESM2 scenario yields the most conservative result, but still suggests a range expansion of T. marmoratus into Germany and the Netherlands, at the expense of *T. cristatus* (Fig. 4). For the other three, more drastic scenarios, see the Supporting Information (Fig. S2).

#### DISCUSSION

Distribution modelling is frequently performed on species for which the full ecological amplitude cannot be determined, for example when the range is truncated, as in island endemics, or is bounded by that of a closely related species. In the latter case, twospecies distribution modelling might be considered. In a loose sense, 'two-species distribution modelling' applies to all instances where closely related, nonallopatric species are compared in spatial models (for examples from European herpetology, see Table 1). However, if species are affected to the extent that their ranges are interdependent, this interaction is better not ignored. Accordingly, here I advocate



Figure 2. Two-species distribution model derived from Triturus cristatus and Triturus marmoratus records over France along with a suite of environmental variable (for details, see main text), extrapolated over neighbouring areas. The colours show the probability for any eligible locality to be occupied by T. cristatus (P.), from deep red for T. cristatus to deep blue for T. marmoratus. Intermediate colours, such as orange and green, represent intermediate probabilities (see the colour scale, which ranges from  $P_{e}$  at zero to  $P_{e}$  at unity). Areas in black have an elevation of > 1500 m a.s.l. A, model with forestation as documented. B, C, the mutual species distribution under the assumption that western Europe would be completely forested (full forest; B) and devoid of forestation (zero forest; C). The white line approximates the mutual species border as modelled in A. Note that large areas in the south-east of France are devoid of Triturus newts (cf. Fig. 1) and that Italy has another crested newt species (Triturus carnifex), but that a parapatric contact zone is being modelled nevertheless.

the use of TSDMs to highlight ecological differences among species that come about in parapatry, while realizing that this attention diverts from the quest to uncover the fundamental niches of species and, more pragmatically, that this focus is at the expense of modelling results away from the contact zone. At the extreme, TDSMs will describe a species contact zone

even in areas where neither species is present (e.g. Figs 1, 2). Another inherent drawback of two-species distribution modelling is that parameters for which the counterpart species are undifferentiated, possibly including many biotic ones, will remain unnoticed, although they might be crucial for population and species survival.

#### 82 J. W. ARNTZEN

**Table 2.** Niche similarities estimated with Schoener's *D* and Warren's *I* for the newts *Triturus cristatus* and *Triturus marmoratus* in France, cross-tabulated for areas and environmental variables

Area(s) within France	Range overlap		Allopatry	
Niche similarity metric	D	Ι	D	Ι
Environmental variables considered				
Climatic (bio01, bio03, bio06, bio12, bio14 and bio15)	0.738	0.940	0.220	0.450
	(0.894)	(0.983)	(0.904)	(0.989)
Elevation and forestation	0.854	0.981	0.772	0.955
	(0.940)	(0.995)	(0.925)	(0.993)

Values in parentheses denote the lowest score obtained under 100 random permutations with ENMTOOLS (Warren *et al.*, 2010). The results indicate that the observed similarities are all different from random expectations at P < 0.01.



**Figure 3.** Models of the two-species distribution of *Triturus cristatus* and *Triturus marmoratus* for climatic conditions as reconstructed for the Holocene, under the assumption that western Europe would be entirely forested (left panel) or entirely deforested (right panel). Colour key as in Figure 2. Results for nine different scenarios (for details, see main text) were averaged; for scenarios shown individually, see the Supporting Information (Fig. S1). The white line approximates the mutual species border as modelled for the present day in Figure 2.

The focal species engage in a long and wide contact, but do they restrict one another spatially such that TSDM is duly applied? The answer is positive because, firstly, syntopic localities for *T. cristatus* and *T. marmoratus* are uncommon (~15% of the total; note that the measure is dependent on sample size). Secondly, a recent range expansion of *T. cristatus* involved the concomitant range reduction of *T. marmoratus*, suggesting that the species range borders are not independent (Arntzen & Wallis, 1991). Thirdly, the presence of *T. cristatus* in the lower Rhône valley demonstrates that the species can occur at more southerly latitudes if *T. marmoratus* is absent (Fig. 1A).

The model for the reciprocal distribution of *T. cristatus* and *T. marmoratus* across France shows

a good correspondence to the data, suggesting that the selected variables might genuinely underlie the presence of one species vs. the other (Fig. 2). Unsurprisingly, with T. marmoratus distributed in the south-west and *T. cristatus* in the north-east of France, the TSDM follows a temperature gradient that is captured by bio01 (mean annual temperature), bio03 (isothermality) and bio06 (minimum temperature of coldest month), with some fine-tuning by the precipitation variables bio12 (annual precipitation), bio14 (precipitation of driest month) and bio15 (precipitation seasonality), along with elevation and forestation yielding an essentially bimodal representation (Fig. 2A). The TSDM, however, fails to accommodate a fair number of documented localities that show the environmental characteristics typical

#### Northern latitude



**Figure 4.** Model of the two-species distribution of *Triturus* cristatus and *Triturus marmoratus* for climatic conditions as foreseen for 50 years from now under the CMCC-ESM2\_SSP126 scenario. Results were simplified to a binary representation, with red for *T. cristatus* (probability of occurrence,  $P_c > 0.5$ ) and blue for *T. marmoratus* ( $P_c < 0.5$ ). Grey areas predict the presence of one species or the other, depending on zero or full forestation (for details, see main text). The white line approximates the mutual species border as modelled for the present day (Fig. 2A). Note that the contact zone would have to move at a pace of > 10 km/ year to keep up with the projected change. Three other scenarios yielded even larger contact zone displacements (Supporting Information, Fig. S2).

for the counterpart species (Fig. 2B). The discrepancy is probably best explained by parameters that operate locally, such as forestation and, to a lesser degree, elevation, which might override the influence of the more large-scale climatic parameters. Accordingly, a better-fitting model would possibly have been achieved by the inclusion of additional, locally relevant variables, such as landscape elements. In particular, small water bodies and hedgerows have been shown to affect the local distribution of *Triturus* newts (Schoorl & Zuiderwijk, 1981; Arntzen, 1996; Visser *et al.*, 2017; Préau *et al.*, 2020; Gauffre *et al.*, 2022) and other salamander species (Arntzen & Van Belkom, 2020; Arntzen 2022). The detailed data are, however, not currently available for the whole country.

Using both the D and I metrics, the hypothesis of niche equivalence for T. cristatus and T. marmoratus was rejected (Table 1), in line with the results from ecological studies mentioned above. These and other niche similarity values obtained for parapatrically distributed European amphibians are, on average, significantly higher than was observed for a suite of animal species pairs in Mexico (butterflies, birds and mammals, table 1, column Bioclim in the paper by Warren *et al.*, 2008; Student's *t*-test, *D*, d.f. = 5.86, P < 0.001; *I*, d.f. = 30, P < 0.0001; Table 1). The difference might be attributable to the deliberate choice of species with allopatric ranges that, in pairwise fashion, encounter different climatic regimes at either side of the Isthmus of Tehuantepec (Warren *et al.*, 2008; Butler *et al.*, 2022). Likewise, climatic niches in the allopatric sections of the French *Triturus* distribution are (much) less similar than within the area of range overlap (Table 2). That no such difference was observed for elevation and forestation squares with the notion that these variables operate at smaller, and possibly more meaningful, spatial scales.

Two-species distribution models under zero forestation are near-equivalent to those that account for the real data (Fig. 2A, C). Conversely, the fullforestation projection supports a wider distribution of T. marmoratus to the north (Fig. 2A, B), from which it might be argued that deforestation is (and has been) in favour of *T. cristatus*. Although the surface of forested terrain across France has recently increased, from  $\sim 13\%$  in the 18<sup>th</sup> century to 31% in the present day (Cinotti, 1996; Vallauri et al., 2012; IGN, 2020), the bigger impact on the species distributions will probably have been the large-scale change from dense forestation in the Holocene to the scarce and patchy forestation found at 200+ years ago (Badré, 1983; Marchant et al., 2009). Refugia during the Last Glacial Maximum were in the Balkan peninsula for T. cristatus and in the Iberian peninsula for T. marmoratus (Wielstra et al., 2013), meaning that the species were widely allopatric at that time. The application of a TSDM in the mid-Holocene is subject to the (reasonable) assumption that the ranges of T. cristatus and T. marmoratus were already in contact, following range expansion after the Last Glacial Maximum. The results are, however, somewhat ambiguous, owing to the uncertainty in the climate reconstructions, as brought about by the availability of nine different Holocene scenarios (Supporting Information, Fig. S1). Depending on the climate scenario and on the amount of forestation, the mutual species border is reconstructed at its current position or more to the south, with a prong towards the Pyrenees, or anywhere in between (Fig. 4). Although it is disputed among palaeobotanists whether forest cover in the Holocene was continuous or half-open (Bradshaw & Mitchell, 1999; Vera, 2000), this is of little concern here, because half-open forestation would also favour T. marmoratus over T. cristatus. All reconstructed contact zone positions are in central or southern France, which argues against dispersal of T. marmoratus over the Doggerland into the UK, as was proposed from genetic data for the spined toad, Bufo spinosus, which, along with the common toad,

*Bufo bufo*, has a similar overall distribution (Arntzen, 2019; Arntzen *et al.*, 2020a). Finally, a long-term persistence of *T. cristatus* in the lower Rhône valley is more strongly supported by the zero-forest than by the full-forest scenario, suggesting that deforestation helped *T. cristatus* to establish this southernmost area.

In a study on *T. marmoratus* populations of the French department Deux-Sevres, populations in the flat and increasingly deforested southern section were found to be genetically impoverished (Gauffre et al., 2022). The loss of genetic diversity was attributed to agricultural intensification. A shortcoming of this explanation is, however, the limited time, nominally ~60 years since World War II, available for the change to take place. Considering a generation time for T. marmoratus of 6.3 years (cf. Francillon-Viellot et al., 1990) fewer than ten generations would be involved. A massive loss of alleles over a shallow genealogy is possible, but strong genetic drift is typical for small and very small populations (Wright, **1931**). The 'agricultural intensification' hypothesis is therefore not entirely compatible with the currently wide distribution of T. marmoratus in Deux-Sevres and the sample sizes obtained in the study. According to the Faune-France database (faune-france.org) T. marmoratus is present across the department (1470 records), whereas T. cristatus (468 records) and hybrids (46 records) are most numerous in the south, with, unfortunately, no standardized information on species co-occurrences. An alternative explanation for the inferred genetic erosion in T. marmoratus in the south of Deux-Sevres could be range and population size fluctuations resulting from competition with T. cristatus, for which process the available temporal window is several orders of magnitude larger. A negative effect on the genetic diversity of T. marmoratus, not inflicted by modern agriculture, but by an also endangered and legally protected counterpart species, would change the perspective on nature conservation. The first steps to select among the alternative explanations could be to model the population genetic data and to review the analytical approaches that document genetic erosion (Epps & Keyghobadi, 2015; Jensen & Leigh, 2022).

The TSDM forecast under a climate change scenario (Fig. 4) is almost certainly unrealistic. Firstly, the forecast is built on the (as yet unsubstantiated) assumption that climate parameters are not only correlated with, but also drive the process of species replacement, although it must be noted that this objection also applies to the other models and projections. Secondly, a *T. cristatus-T. marmoratus* range border this far to the north-east would require contact zone movement at a pace of > 10 km/year, which is an order of magnitude faster (and in the opposite direction) to that documented so far (Arntzen

& Wallis, 1991). Another well-documented example based on historical data is the avian hybrid zone of the red- and yellow-shafted flicker, which moved over the plains of North America with an estimated speed of slightly > 1 km/year (Aguillon & Rohwer, 2022). However, even with no competition, 10 km/year is beyond the dispersal capability of most amphibians (Smith & Green, 2005), hence a formal analysis, with dispersal integrated in species distribution modelling (Engler et al., 2012), seems unwarranted. Thirdly, niche modelling in the department Vienne suggests that under climate change large areas will become unfavourable for either species, in particular through a reduced connectivity of local populations, which would preclude dispersal, range expansion and species replacement (Collingham & Huntley, 2000; Préau et al., 2020). Fourthly, the envisaged deterioration in habitat suitability owing to climate change is already largely overwritten by recent anthropogenic habitat loss. Over the last few decades, the decline in amphibian populations has been severe, in particular through the disappearance of small water bodies in which the species reproduce, to the extent that, in Mayenne, the T. cristatus-T. marmoratus hybrid zone has largely disintegrated (Visser et al., 2017). Rampant habitat degradation has also been noted for the adjacent region of Normandie (Astruc et al., 2021). In summary, as far as can be reconstructed currently, shifts in the contact zone of T. cristatus and T. marmoratus have not extended over a wide area, but might, nevertheless, have been explicit. The latter notion is exemplified by the speedy shift and subsequent stasis in the mutual species distribution in Mayenne observed since World War II although, at ~70 years, this concerns less than a centile of the period of post-glacial species contact.

#### CLOSING CONSIDERATION

Two fundamental problems of regular species distribution modelling are the inferred nature of absence data and geographically structured detection probabilities (i.e. uneven sampling). Auspiciously, absence data play no role in TSDMs, whereas uneven sampling will, very possibly, apply in an unbiased manner to both taxa, meaning that, in the long-held tradition of the comparative method (Mayr, 1982), shortcomings in the presence/presence dataset might be evened out.

#### ACKNOWLEDGEMENTS

I thank J. C. de Massary and J. Lescure for making distribution data available in digital format, N. Sillero for expert advice and three anonymous reviewers for constructive comments on an earlier version of the manuscript. I have no conflict of interest to declare.

#### DATA AVAILABILITY

Core to this paper are the newt distribution data for France, as compiled by J. Lescure and J. C. de Massary (both at the 'Muséum National d'Histoire Naturelle', Paris, France). The database is currently curated by and accessible through the Société Herpétologique de France (https://atlas.lashf.org). Web resources for environmental data are cited in the Material and Methods.

#### REFERENCES

- Aguillon SM, Rohwer VG. 2022. Revisiting a classic hybrid zone: movement of the northern flicker hybrid zone in contemporary times. *Evolution* **76**: 1082–1090.
- Anderson RP, Peterson AT, Gómez-Laverde M. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* **98**: 3–16.
- Araújo MB, Luoto M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16: 743–753.
- Arntzen JW. 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.
- Arntzen JW. 1996. Parameters of ecology and scale integrate the gradient and mosaic models of hybrid zone structure in *Bombina* toads and *Triturus* newts. *Israel Journal of Zoology* 42: 111–119.
- **Arntzen JW. 2018**. Morphological and molecular characters to describe a marbled newt hybrid zone in the Iberian peninsula. *Contributions to Zoology* **87**: 167–185.
- Arntzen JW. 2019. An amphibian species pushed out of Britain by a moving hybrid zone. *Molecular Ecology* 28: 5145–5154.
- Arntzen JW. 2022. Coexistence of two newt species in a transition zone of range overlap. *Contributions to Zoology* 91: 133–151.
- Arntzen JW, Alexandrino J. 2004. Ecological modelling of genetically differentiated forms of the Iberian endemic golden-striped salamander, *Chioglossa lusitanica*. *Herpetological Journal* 14: 137-142.
- Arntzen JW, Canestrelli D, Martínez-Solano I. 2020a. Environmental correlates of the European common toad hybrid zone. *Contributions to Zoology* **89**: 270–281.
- **Arntzen JW**, **Espregueira Themudo G. 2008**. Environmental parameters that determine species geographical range limits as a matter of time and space. *Journal of Biogeography* **35**: 1177–1186.
- Arntzen JW, Jehle R, Wielstra B. 2021. Genetic and morphological data demonstrate hybridization and backcrossing in a pair of salamanders at the far end of

the speciation continuum. *Evolutionary Applications* 14: 2784–2793.

- Arntzen JW, Van Belkom J. 2020. 'Mainland-island' population structure of a terrestrial salamander in a forestbocage landscape with little evidence for *in situ* ecological speciation. *Scientific Reports* 10: 1700.
- Arntzen JW, Vries WD, Canestrelli D, Martínez-Solano I. 2020b. Genetic and morphological differentiation of common toads in the Alps and the Apennines. In: Pontarotti P, ed. *Evolutionary biology – a transdisciplinary approach*. Cham: Springer.
- Arntzen JW, Wallis GP. 1991. Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in western France. *Evolution* 45: 805–826.
- Arntzen JW, Wielstra B, Wallis GP. 2014. The modality of nine *Triturus* newt hybrid zones assessed with nuclear, mitochondrial and morphological data. *Biological Journal of the Linnean Society* 113: 604–622.
- Astruc G, Miaud C, Besnard A, Barrioz M. 2021. Le déclin alarmant des amphibiens de France: l'exemple étayé e la Normandie. *Bulletin de la Société Herpétologique de France* 178: 57–74.
- **Badré L. 1983**. *Histoire de la Forêt Française*. Paris: Éditions Arthaud.
- Beaumont LJ, Hughes L, Pitman AJ. 2008. Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters* **11**: 1135–1146.
- **Bradshaw R**, **Mitchell FJ. 1999**. The palaeoecological approach to reconstructing former grazing-vegetation interactions. *Forest Ecology and Management* **120**: 3–12.
- **Brito JC**, **Crespo EG. 2002**. Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the northwestern Mediterranean basin. In: Schuett GW, Hoggren M, Douglas ME, Greene HW, eds. *Biology of the vipers*. Eagle Mountain: Eagle Mountain.
- Bull CM. 1991. Ecology of parapatric distributions. Annual Review of Ecology and Systematics 22: 19–36.
- Butler BO, Smith LL, Flores-Villela O. 2022. Phylogeography and taxonomy of *Coleonyx elegans* Gray 1845 (Squamata: Eublepharidae) in Mesoamerica: the Isthmus of Tehuantepec as an environmental barrier. *Molecular Phylogenetics and Evolution* 178: 107632.
- Castanet J, Guyetant R, eds. 1989. Atlas de repartition des amphibiens et reptiles de France. Paris: Société Herpetologique de France and Université de Paris VII, Laboratoire d'Anatomie comparée.
- Chamorro D, Martínez-Freiría F, Real R, Muñoz AR. 2021. Understanding parapatry: how do environment and competitive interactions shape Iberian vipers' distributions? *Journal of Biogeography* 48: 1322–1335.
- **Cinotti B. 1996**. Evolution des surfaces boisées en France: proposition de reconstitution depuis le début du XIXe siècle. *Revue Forestière Française* **48**: 547–562.
- Clarke KR, Gorley RN. 2015. PRIMER v7: user manual/ tutorial. Plymouth: PRIMER-E.
- **Collingham YC**, **Huntley B. 2000**. Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications* **10**: 131–144.

- **Darwin C. 1859**. On the origin of species by means of natural selection, 6th edn, 1869. London: Murray.
- Davis AJ, Lawton JH, Shorrocks B, Jenkinson LS. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* 67:600-612.
- Dufresnes C, Litvinchuk SN, Rozenblut-Kościsty B, Rodrigues N, Perrin N, Crochet PA, Jeffries DL. 2020. Hybridization and introgression between toads with different sex chromosome systems. *Evolution Letters* 4: 444–456.
- Dufresnes C, Mazepa G, Rodrigues N, Brelsford A, Litvinchuk SN, Sermier R, Lavanchy G, Betto-Colliard C, Blaser O, Borzée A, Cavoto E. 2018. Genomic evidence for cryptic speciation in tree frogs from the Apennine Peninsula, with description of *Hyla perrini* sp. nov. *Frontiers in Ecology and Evolution* 6: 144.
- Engler R, Hordijk W, Guisan A. 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. *Ecography* 35: 872–878.
- **Epps CW**, **Keyghobadi N. 2015**. Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. *Molecular Ecology* **24**: 6021–6040.
- Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302–4315.
- Fitze PS, Gonzalez-Jimena V, San-Jose LM, San Mauro D, Aragón P, Suarez T, Zardoya R. 2011. Integrative analyses of speciation and divergence in *Psammodromus hispanicus* (Squamata: Lacertidae). *BMC Evolutionary Biology* 11: 347.
- **Francillon-Viellot H**, **Arntzen JW**, **Geraudie J. 1990**. Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): a skeletochronological comparison. *Journal of Herpetology* **24**: 3–22.
- Franklin J. 2010. *Mapping species distributions*. Cambridge: Cambridge University Press.
- Gauffre B, Boissinot A, Quiquempois V, Leblois R, Grillet P, Morin S, Picard D, Ribout C, Lourdais O. 2022. Agricultural intensification alters marbled newt genetic diversity and gene flow through density and dispersal reduction. *Molecular Ecology* 31: 119–133.
- **Guevara L, Morrone JJ, León-Paniagua L. 2019.** Spatial variability in species' potential distributions during the Last Glacial Maximum under different Global Circulation Models: relevance in evolutionary biology. *Journal of Zoological Systematics and Evolutionary Research* **57**: 113–126.
- Guisan A, Thuiller W, Zimmermann NE. 2017. Habitat suitability and distribution models: with applications in R. Cambridge: Cambridge University Press.
- Highton R. 1998. Is *Ensatina escholtzii* a ring species? *Herpetologica* 54: 254–278.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

- Iannella M, Cerasoli F, Biondi M. 2017. Unraveling climate influences on the distribution of the parapatric newts *Lissotriton vulgaris meridionalis* and *L. italicus. Frontiers in Zoology* 14: 55.
- **IBM SPSS. 2019**. *IBM SPSS statistics for Windows*. Armonk: IBM Corporation.
- IGN. 2020. Forest inventory. Paris: Institut National de l'Information Géographique et Forestière. Available at: https://inventaire-forestier.ign.fr/spip.php?rubrique216
- **ILWIS. 2019**. Integrated land and watershed management information system. Enschede: International Institute for Aerospace Survey and Earth Sciences.
- Jensen EL, Leigh DM. 2022. Using temporal genomics to understand contemporary climate change responses in wildlife. *Ecology and Evolution* **12**: e9340.
- Kaliontzopoulou A, Pinho C, Harris DJ, Carretero MA. 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African Podarcis wall lizards. Biological Journal of the Linnean Society 103: 779–800.
- Key KHL. 1981. Species, parapatry, and the morabine grasshoppers. *Systematic Biology* **30**: 425–458.
- Kissling WD, Dormann CF, Groeneveld J, Hickler T, Kühn I, McInerny GJ, Montoya JM, Römermann C, Schiffers K, Schurr FM, Singer A, Svenning J-C, Zimmermann NE, O'Hara RB. 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography 39: 2163–2178.
- Leathwick JR. 2002. Intra-generic competition among Nothofagus in New Zealand's primary indigenous forests. Biodiversity and Conservation 11: 2117–2187.
- Lescure J, De Massary JC, eds. 2012. Atlas des amphibiens et reptiles de France. Mèze: Biotope.
- Marchant R, Brewer S, Webb T, Turvey ST. 2009. Holocene deforestation: a history of human-environmental interactions, climate change, and extinction. In: Turvey S, ed. *Holocene extinctions*. Oxford: Oxford University Press.
- Martínez-Freiría F, Sillero N, Lizana M, Brito JC. 2008. GIS-based niche models identify environmental correlates sustaining a contact zone between three species of European vipers: environmental correlates in contact zones. *Diversity* and Distributions 14: 452–461.
- Marzahn E, Mayer W, Joger U, Ilgaz C, Jablonski D, Kindler C, Kumlutaş Y, Nistri A, Schneeweiss N, Vamberger M, Žagar A, Fritz U. 2016. Phylogeographyofthe Lacerta viridis complex: mitochondrial and nuclear markers provide taxonomic insights. Journal of Zoological Systematics and Evolutionary Research 54: 85-105.
- **Mayr E. 1982**. The growth of biological thought: diversity, evolution, and inheritance. Cambridge: Harvard University Press.
- Meier ES, Kienast F, Pearman PB, Svenning JC, Thuiller W, Araújo MB, Guisan A, Zimmermann NE. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33: 1038–1048.

- Nieto-Lugilde D, Maguire KC, Blois JL, Williams JW, Fitzpatrick MC. 2018. Multiresponse algorithms for community-level modelling: review of theory, applications, and comparison to species distribution models. *Methods in Ecology and Evolution* 9: 834–848.
- Pabijan M, Zieliński P, Dudek K, Stuglik M, Babik W. 2017. Isolation and gene flow in a speciation continuum in newts. *Molecular Phylogenetics and Evolution* 116: 1–12.
- Panagos P, Van Liedekerke M, Jones A, Montanarella L. 2012. European Soil Data Centre: response to European policy support and public data requirements. *Land Use Policy* 29: 329–338.
- Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB.
  2011. Ecological niches and geographical distributions. Monographs in population biology 49. Princeton: Princeton University Press.
- Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM, Vesk PA, McCarthy MA. 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* 5: 397–406.
- Préau C, Grandjean F, Sellier Y, Gailledrat M, Bertrand R, Isselin-Nondedeu F. 2020. Habitat patches for newts in the face of climate change: local scale assessment combining niche modelling and graph theory. *Scientific Reports* 10: 3570.
- Pyron RA, O'Connell KA, Lemmon EM, Lemmon AR, Beamer DA. 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.
- Raes N, ter Steege H. 2007. A null-model for significance testing of presence-only species distribution models. *Ecography* 30: 727-736.
- Real R, Barbosa AM, Martínez-Solano I, García-París M. 2005. Distinguishing the distributions of two cryptic frogs (Anura: Discoglossidae) using molecular data and environmental modeling. *Canadian Journal of Zoology* 83: 536–545.
- Reino L, Ferreira M, Martínez-Solano I, Segurado P, Xu C, Barbosa AM. 2017. Favourable areas for co-occurrence of parapatric species: niche conservatism and niche divergence in Iberian tree frogs and midwife toads. *Journal* of Biogeography 44: 88–98.
- **Romero J, Real R. 1996**. Macroenvironmental factors as ultimate determinants of distribution of common toad and natterjack toad in the south of Spain. *Ecography* **19**: 305–312.
- Schoorl J, Zuiderwijk A. 1981. Ecological isolation in Triturus cristatus and Triturus marmoratus (Amphibia: Salamandridae). Amphibia-Reptilia 1: 235–252.
- Smith AB, Godsoe W, Rodríguez-Sánchez F, Wang HH, Warren D. 2019. Niche estimation above and below the species level. *Trends in Ecology and Evolution* 34: 260–273.
- Smith AM, Green DM. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all

amphibian populations metapopulations? *Ecography* 28: 110–128.

- Soberón J, Peterson AT. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2: 1-10. https://doi. org/10.17161/bi.v2i0.4
- Tarroso P, Pereira RJ, Martínez-Freiría F, Godinho R, Brito JC. 2014. Hybridization at an ecotone: ecological and genetic barriers between three Iberian vipers. *Molecular Ecology* 23: 1108–1123.
- Vallauri D, Grel A, Granier E, Dupouey JL. 2012. Les forêts de Cassini. Analyse quantitative et comparaison avec les forêts actuelles. Rapport Technique. Marseille: World Wildlife Fund.
- Vallée L. 1959. Recherches sur Triturus blasii de l'Isle: hybride naturel de Triturus cristatus Laur. × Triturus marmoratus Latr. Mémoires Société Zoologique France 31: 1–95.
- **Vera FWM. 2000**. *Grazing ecology and forest history*. Wallingford: Cabi.
- Vieites DR, Nieto-Román S, Wake DB. 2009. Reconstruction of the climate envelopes of salamanders and their evolution through time. Proceedings of the National Academy of Sciences of the United States of America 106: 19715–19722.
- Visser M, de Leeuw M, Zuiderwijk A, Arntzen JW. 2017. Stabilization of a salamander moving hybrid zone. *Ecology and Evolution* 7: 689–696.
- Vörös J, Mikulíček P, Major A, Recuero E, Arntzen JW. 2016. Phylogeographic analysis reveals northerly refugia for the riverine amphibian *Triturus dobrogicus* (Caudata: Salamandridae). *Biological Journal of the Linnean Society* 119: 974–991.
- Warren DL, Glor RE, Turelli M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**: 2868–2883.
- Warren DL, Glor RE, Turelli M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33: 607–611.
- Wielstra B, Crnobrnja-Isailović J, Litvinchuk SN, Reijnen BT, Skidmore AK, Sotiropoulos K, Toxopeus AG, Tzankov N, Vukóv T, Arntzen JW. 2013. Tracing glacial refugia of *Triturus* newts based on mitochondrial DNA phylogeography and species distribution modeling. *Frontiers in Zoology* 10: 131–114.
- Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes J-A, Guisan A, Heikkinen RK, Høye TT, Kühn I, Luot M, Maiorano L, Nilsson M-C, Normand S, Ockinger E, Schmidt NM, Termanse M, Timmermann A, Wardl DA, Aastrup P, Svenning J-C. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15–30.
- Wright S. 1931. Evolution in Mendelian populations. *Genetics* 16: 97–159.
- Yang W, Feiner N, Salvi D, Laakkonen H, Jablonski D, Pinho C, Carretero MA, Sacchi R, Zuffi MAL, Scali S, Plavos K, Pafilis P, Poulakakis N, Lymberakis P,

Jandzik D, Schulte U, Aubret F, Badiane A, Perez i de Lanuza G, Abalos J, While GM, Uller T. 2022. Population genomics of wall lizards reflects the dynamic history of the Mediterranean Basin. *Molecular Biology and Evolution* **39**: msab311. Zieliński P, Dudek K, Arntzen JW, Palomar G, Niedzicka M, Fijarczyk A, Liana M, Cogalniceanu D, Babik W. 2019. Differential introgression across newt hybrid zones: evidence from replicated transects. *Molecular Ecology* 28: 4811–4824.

#### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Models on the two-species distribution of *Triturus cristatus* and *Triturus marmoratus* for climatic conditions as they are reconstructed for the Holocene, with the probability for any eligible locality to be occupied by *T. cristatus* ( $P_c$ ) in binary mode ( $P_c > 0.5$  in deep red and  $P_c < 0.5$  in deep blue). The nine different models were formulated under the assumption that western Europe would be entirely forested or entirely deforested, with areas of differential species occupation shown in grey. Under the full-forest setting, *T. marmoratus* consistently has a wider and northern-more hindcasted range than under the zero-forest setting. The model codes are BC, CC, CN, HE, HG, IP, ME, MG and MR. The scenarios are ordered relative to the generalized mutual species distribution (white line, as presented in Fig. 2) with, from top left to bottom right, a decreasing range of *T. cristatus* relative to that of *T. marmoratus*. Geographical coordinates are as in Figure 2.

**Figure S2.** Models of the two-species distribution of *Triturus cristatus* and *Triturus marmoratus* for climatic conditions as foreseen for 50 years from now under, from left to right, the scenarios EC-EARTH3-VEG/SSP246, MIROC-ESL2/SSP 585 and UKESM1-0-LL/SSP 370. Geographical coordinates are as in Figure 2, and the colour coding is as in Figure 4 and the Supporting Information (Fig. S1). The white line approximates the mutual species border, as modelled for the present day (Fig. 2A).

**Table S1.** Environmental variables considered for the construction of two-species distribution models for the northern crested newt, *Triturus cristatus*, and the northern marbled newt, *Triturus marmoratus*, across France. **Table S2.** European amphibian and reptile species referred to in the main text or in Table 1, by Latin name, taxonomic authority and vernacular name.