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

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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

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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. Two-species 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 ‘community-level’ (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 ‘Grinnellian’ 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 & Guyétant, 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 F₁ individuals form the great majority of intermediate phenotypes (Arntzen *et al.*, 2021). Records for hybrids were taken to represent both species.

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

Taxonomic level	Amphibian and reptile species or subspecies*	Research area	Method used in species distribution modelling†	Niche similarity	Source‡
<i>D</i> <i>I</i>					
Intraspecific	<i>Chioglossa l. lusitanica / longipes</i>	Iberian peninsula	LR		1
	<i>Discoglossus g. galganoi / jeanneae</i>	Iberian peninsula	LR		2
Intragenetic	<i>Alytes cisternasi / obstetricans</i>	Iberian peninsula	GLM		3
	<i>Bombina bombina / variegata</i>	Central Europe Pannonian basin	OA LR	0.804 (0.883)	4, 5 6, ps
	<i>Bufo bufo / spinosus</i>	North-western Europe France and Italy	LR LR		7
				0.794 (0.974)	8, 9, ps
		Europe	ME		10
	<i>Hyla meridionalis / malleri</i>	Iberian peninsula	GLM		11
	<i>Lissotriton boscai / helveticus</i>	Western Europe	ME		12
	<i>Lissotriton helveticus / vulgaris</i>	Europe	ME		12
		Pas de Calais, France	OA		13
	<i>Lissotriton italicus / vulgaris</i>	Italy	BRT, ME		14
	<i>Lissotriton montandoni / vulgaris</i>	Carpathians	LR		15
	<i>Psammotromus edwardsianus / hispanicus / occidentalis</i>	Spain	ENFA, MDE, ME		16
	<i>Triturus cristatus / marmoratus</i>	Mayenne, France	OA		5
		Europe	ME		12
		Mayenne, France	LR	0.451 (0.835)	17, ps
		Deux Sevres, France	ANN, CTA, FDA, GAM, GBM, GLM, MARS, RF		18
		France	LR	0.515 (0.919)	ps
	<i>Triturus dobrogicus / (carnifex-cristatus-macedonicus-ivanbureschi)</i>	Pannonian basin	LR	0.815 (0.904)	6, ps
	<i>Triturus marmoratus / pygmaeus</i>	Iberian peninsula	LR	0.583 (0.688)	19, 20, ps
	<i>Vipera aspis / latastei / seoanei</i>	Western Europe Northern Spain Iberian peninsula Northern Spain North-western Iberian peninsula	ME ME LR ANN LR		12 21 22 23 24

Table 1. Continued

Taxonomic level	Amphibian and reptile species or subspecies*	Research area	Method used in species distribution modelling†	Niche similarity	Source‡
Intergeneric	<i>Bufo bufo</i> / <i>Epidaleia calamita</i>	Southern Spain	LR	<i>D</i>	<i>I</i>
					25
	Niche similarity averaged over six parapatric species pairs			0.609	ps
	Niche similarity averaged over 26 allopatric species pairs in Mexico (butterflies, birds and mammals; climatic variables)			0.163	0.447
					26

For some taxa, niche similarities over the studied part of the ranges could be quantified (with Schoener's *D* and Warren's *D*). Values in parentheses denote the lowest score obtained under 100 random permutations with ENMTOOLS (Warren *et al.*, 2010). Results indicate that the observed similarities are all different from random expectations at $P < 0.01$. Average values from another study are given at the bottom of the table for comparison.

*For species list with full names, see the Supporting Information (Table S2).

†Methods used are as follows: ANN, artificial neural networks; BRT, boosted regression trees; CTA, classification tree analysis; ENFA, ecological niche factor analysis; FDA, flexible discriminant analysis; GAM, grouping generalized additive models; GBM, generalized boosting models; GLM, general linear models; LR, logistic regression; MARS, multivariate adaptive regression splines; MDE, multidimensional envelopes; ME, maximum entropy; OA, overlap analysis; RF, random forests.

‡Sources are as follows: (1) Arntzen & Alexandrino (2004); (2) Real *et al.* (2005); (3) Reino *et al.* (2017); (4) Arntzen (1978); (5) Arntzen (1996); (6) Vörös *et al.* (2016); (7) Arntzen (2019); (8) Arntzen *et al.* (2020a); (9) Arntzen *et al.* (2020b); (10) Dufresnes *et al.* (2020); (11) Reino *et al.* (2017); (12) Vietes *et al.* (2009); (13) Arntzen (2022); (14) Iannella *et al.* (2017); (15) Zielinski *et al.* (2019); (16) Fitze *et al.* (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) Iarrosa *et al.* (2014); (24) Brito & Crespo (2002); (25) Romero *et al.* (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:

$$P_c = \left\{ 1 / \left[1 + \exp \left(\begin{array}{l} 0.369 \times \text{bio06} + 0.0324 \times \\ \text{elevation} + 0.0308 \times \text{forest} + \\ 0.553 \times \text{bio03} - 0.476 \times \text{bio15} + \\ 0.0222 \times \text{bio12} + 0.113 \times \text{bio01} - \\ 0.298 \times \text{bio14} - 36.192 \end{array} \right) \right] \right\},$$

in which P_c 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 south-east 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 $P_c \geq 0.8$). 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

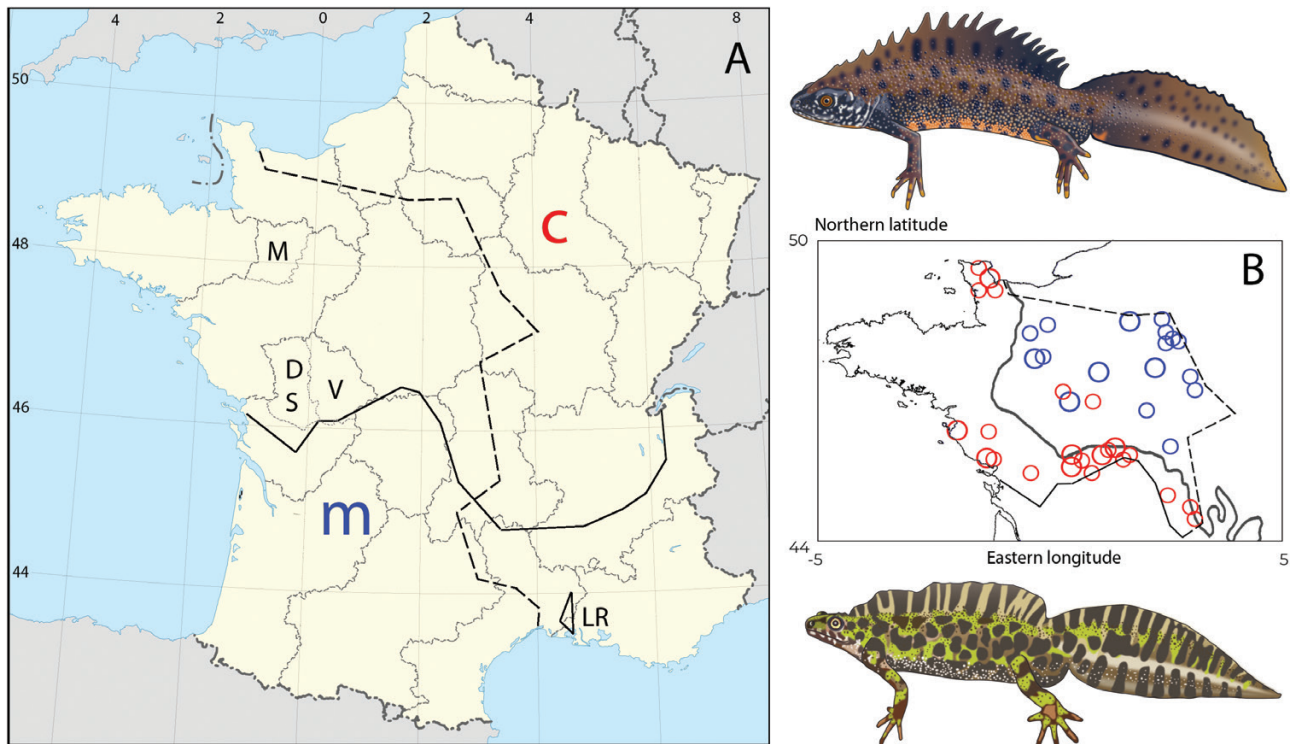


Figure 1. A, the outer range borders of the crested newt, *Triturus cristatus* (c; southern border shown by continuous line) and the marbled newt, *Triturus marmoratus* (m; northern and eastern border shown by dashed line) in continental France, after Castanet & Guyétant (1989) and Lescure & De Massary (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 zero-forest 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, two-species distribution modelling might be considered. In a loose sense, ‘two-species distribution modelling’ applies to all instances where closely related, non-allopatric 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

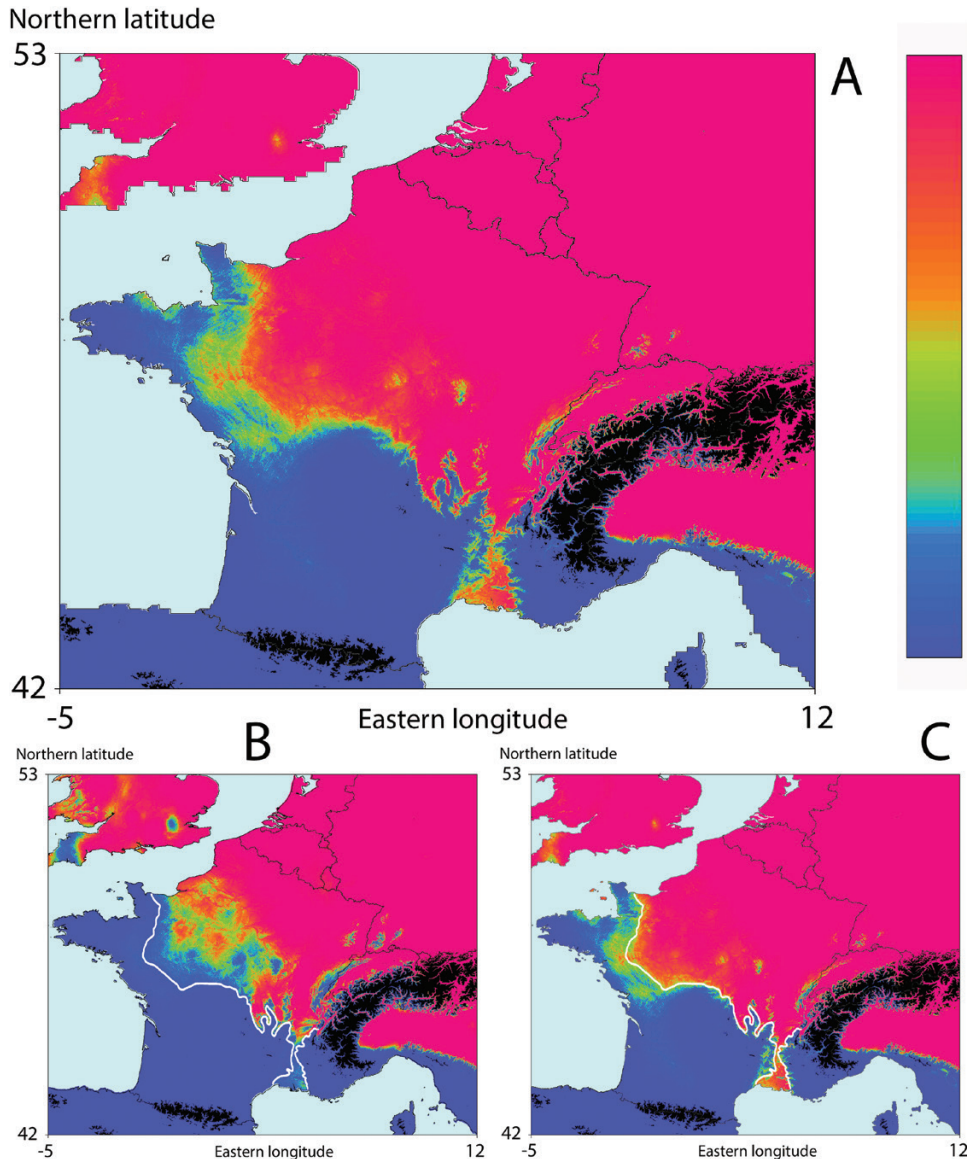


Figure 2. Two-species distribution model derived from *Triturus cristatus* and *Triturus marmoratus* records over France along with a suite of environmental variable (for details, see main text), extrapolated over neighbouring areas. The colours show the probability for any eligible locality to be occupied by *T. cristatus* (P_c), 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_c at zero to P_c 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, TSDMs 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.

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	
	<i>D</i>	<i>I</i>	<i>D</i>	<i>I</i>
Niche similarity metric				
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 $P < 0.01$.

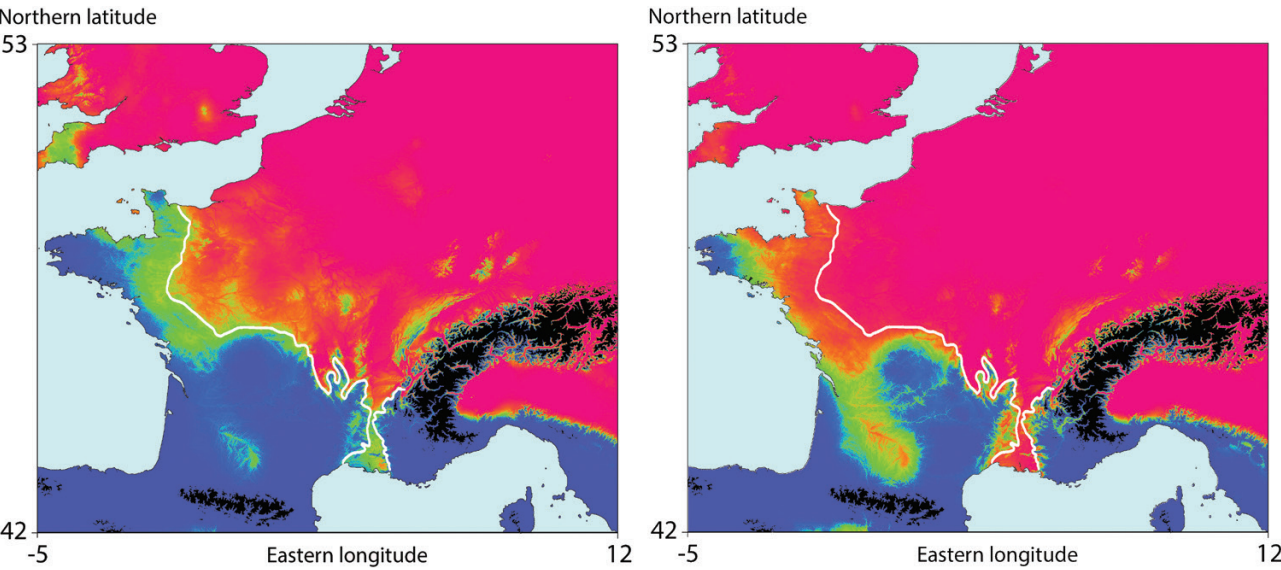


Figure 3. Models of the two-species distribution of *Triturus cristatus* and *Triturus marmoratus* for climatic conditions as reconstructed for the Holocene, under the assumption that western Europe would be entirely forested (left panel) or entirely deforested (right panel). Colour key as in Figure 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

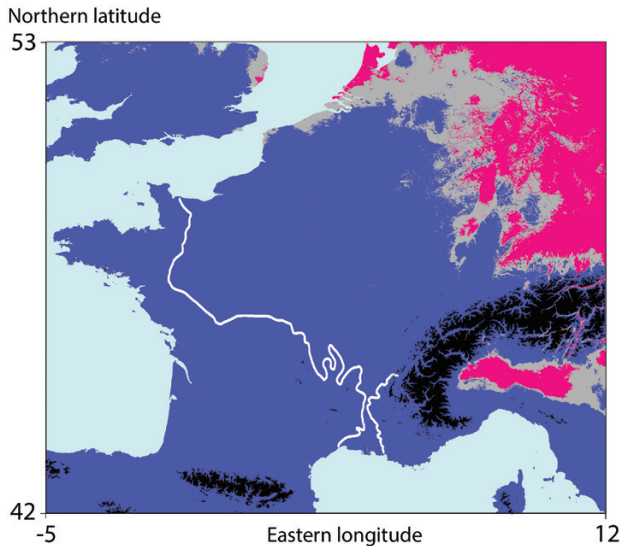


Figure 4. Model of the two-species distribution of *Triturus cristatus* and *Triturus marmoratus* for climatic conditions as foreseen for 50 years from now under the CMCC-ESM2_SSP126 scenario. Results were simplified to a binary representation, with red for *T. cristatus* (probability of occurrence, $P_c > 0.5$) 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 & Zuidervijk, 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 full-forestation 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 18th 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.

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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.

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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.