RESEARCH ARTICLE

Patch analysis of atlas data reveals pattern and process of species replacement

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Abstract

The dynamics of species range borders may be difficult to study due to the local rarity of populations and individuals. This hindrance applies less when range borders are parapatric contact zones. Analysis of species in parapatry has the further advantages of no (inferred) absence data and that shortcomings in data gathering such as uneven sampling apply to the counterpart species about equally. The large-bodied newts *Triturus cristatus* and *T. marmaratus* are spatially segregated within a wide area of range overlap in the west of France. They locally show abutting or slightly overlapping distributions with many isolated occurrences (here called 'patches') of either species within the continuous range section of the other. Historical and genetic data suggest that *T. cristatus* has been superseding *T. marmoratus*. Species replacement should be also discernible from local species distributions, with more, larger and more distantly positioned patches in the receding than the advancing species. Atlas data for France and from the French region Pays de la Loire largely confirm these predictions. The data also indicate that *T. marmoratus* patches may be void of *T. cristatus*, suggesting that they are persisting strongholds, whereas the more admixed *T. cristatus* patches are in flux. The species' differential ecological signature is that of forested, hilly terrain for *T. marmoratus* and open, flat terrain for *T. cristatus*. Accordingly, the main dispersal route for *T. cristatus* towards the Atlantic coast has been through the valley of the Loire River, with a secondary, intraspecific contact zone at the Normandy coast. A literature survey revealed several other species pairs of European herpetofauna that may be amenable to patch analysis, as will be species pairs in other groups of organisms characterized by limited, habitat dependent dispersal. In such efforts the availability of species occurrence data from atlases and digital databases is an indispensable asset.

Highlights

- When related species engage in parapatry it is appropriate to forego species distribution modelling and instead focus on the ecography of the contact zone, such as in 'two-species distribution modelling' in which presence data for counterpart species are contrasted against the background of environmental data.

- In such systems, shifting range borders may be discernable from species occurrences (here called 'patches') that are disconnected from the continuous section of the species range, as interrupted by the counterpart species.

- Across the west of France, patches emerging from a two-species distribution model were found to be large, pure and isolated in the newt *Triturus marmoratus*, as opposed to small, admixed and closer to the continuous range section in the counterpart species *T. cristatus*, suggesting regressing and expanding ranges, respectively.

- Patches of *T. marmoratus* are relict strongholds positioned in hilly and forested terrain whereas *T. cristatus* patches are advanced positions in flat and open terrain, suggesting that species replacement perpetuated along the Loire River to eventually reach the French Atlantic coast.

- Patch analysis is a promising method applicable to all kinds of organisms with limited, habitat dependent dispersal, to which the availability of species occurrence data in atlases and digital databases is an indispensable asset.

Keywords: Clinal hybrid zones, enclaves, France, large-bodied newts, mosaic hybrid zones, parapatry, peripheral populations, *Triturus cristatus*, *Triturus marmoratus*, two-species distribution models

Introduction

Species range borders and their dynamics are important in the study of biodiversity. Although often depicted as simple outlines on a map, species range limits typically summarize a gradient of densities. One scheme suggested for understanding the structure of species borders (Gorodkov 1986, reproduced as Figure 2.1 in Gaston 2003) recognizes several density zones (from continuous, through 'disjunct', etc., to the absence of populations), with in the middle of the gradient the 'generalized limit of distribution' which is equivalent to the 'simple outline' mentioned above.

The gradual reduction in density of individuals and populations at the range periphery is crucial to, but also hinders research in pattern and process of change. However, the edge of one taxon's distribution often abuts that of another, closely related taxon (Darwin 1859, Rapoport 1982, Bull 1991, Case and Taper 2000). On this account, a scheme such as that of Gorodkov may advantageously be extended to accommodate – or mirror – *two* species, on the conditions that they negatively affect one another (with competitive exclusion as an ultimate outcome), and do not frequently hybridize (as not to form wide species intergradations). The generalized species border in Gorodkov's scheme is therewith to be seen as the parapatric species border. The advantages of studying two-species systems for range border dynamics are that: i) the species are not necessarily rare, ii) analyses can be performed without (inferred) absence data, and iii) shortcomings in data gathering such as uneven sampling plausibly apply to either species in equal terms (Arntzen 2023).

One avenue of research is 'two-species distribution modelling', as applied to the large-bodied newts *Triturus cristatus* (Laurenti 1768) and *T. marmoratus* (Latreille 1800) in France (Arntzen 2023). I here expand on this analysis by an ecogeographical analysis of these species' patched distributions, with the aim to gain insight into range border dynamics and the process of species replacement. The French *Triturus* species make an outstanding system for putting 'patch analysis' to the test, because historical and genetic data indicate that *T. cristatus* has been superseding *T. marmoratus* at the edge of its range (Arntzen and Wallis 1991). If species replacement has taken place, this should be discernible from local species distributions, with more, larger and more distantly positioned patches in the receding than the advancing species. Finally, a published literature survey on species pairs in European amphibians and reptiles was used to assess the wider scope for patch analysis to the study of dynamic species borders.

Materials & Methods

Underlying the present paper is a two-species distribution model that describes the *Triturus cristatus* and *T. marmoratus* mutual range border as it reticulates through France, from the Atlantic coast at the Contentin peninsula, Normandy to roughly the Mediterranean coast near Marseille (Arntzen 2023). However, both species have also been observed in a wide area of overlap and hybridization away from that border (Figure 1). Distribution data here analyzed are from two atlases covering France including the 'Area of Range Overlap' (FARO) with *Triturus* records from 1275 localities (Lescure and De Massary 2012, see also Arntzen 2023) and the administrative region Pays de la Loire (PDLL) with 3724 localities (Evrard et al. 2022). Interspecific hybrids were taken to represent both species (see Arntzen et al. 2021). Locality coordinates were in, or transformed to, the WGS84 system, with a nominal precision of two (FARO) and four decimal places (PDLL). A data overview is in Table 1.

Blanket distribution maps composed of so-called Dirichlet cells (Burroughs et al. 2015) were obtained by spatial data interpolation with the 'NearestPoint' procedure in ILWIS 3.8.6 (ILWIS 2019). This splits the *Triturus* records in five groups that represent the continuous ranges for both species (areas A and B in the schematic Figure 2), areas where the contiguous range border widens to potentially accommodate mixed (syntopic) as well as pure (allotopic) localities for either species (border area C) and 'patches' (areas D and E). Patches are single or conglomerates of cells for which the Dirichlet tessellation suggests that they
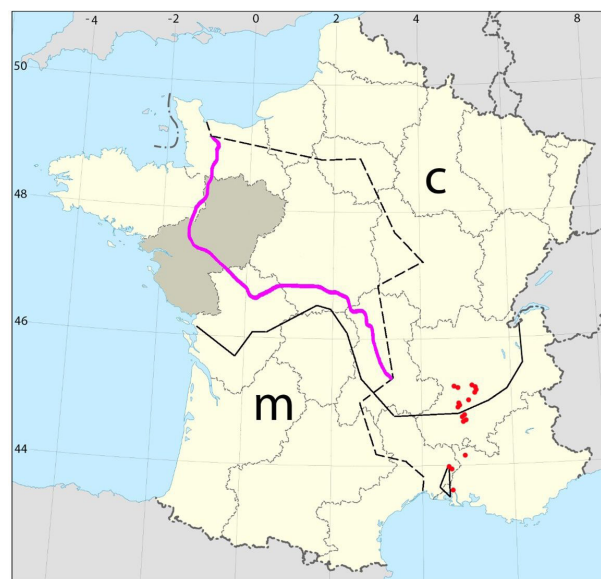

Figure 1. Range borders of the northern crested newt, *Triturus cristatus* (c, southern border shown by solid line) and the northern marbled newt, *T. marmoratus* (m, northern and eastern border shown by interrupted line) in continental France after Castanet and Guyetant (1989) and Lescure and De Massary (2012). The species' mutual range border as reconstructed with a two-species distribution model (Arntzen 2023) is shown by a purple curved line. New records for *T. cristatus* in the southern part of its range are shown by red dots (Priol et al. 2022). The region Pays de la Loire is marked by grey shading. The base map was downloaded from MapsLand at https://www.mapsland.com, under a Creative Commons Attribution-ShareAlike 3.0 Licence. Coordinates are in northern latitude and eastern longitude.

Table 1. Overview of atlas data available for the study of spatial organization in *Triturus cristatus* and *T. marmoratus* in France.

Administrative unit	France	Region within France
Study area	Area of range overlap	Pays de la Loire
Area acronym (N localities)	FARO (1275)	PDLL (3724)
Data source	Lescure and De Massary (2012)	Evrard et al. (2022)
Temporal window #	≤ 2010	2010-2020
Precision (decimal places in WSG-coordinates)	2	4
Number of localities with		
T. cristatus	728	2243
T. marmoratus	730	1758
Localities with both species and / or hybrids	7.4%	14.6%
Cell size		
Mean	119.20 km^2	8.61 km^2
Ratio (*T. cristatus / T. marmoratus*)	0.981	0.971
Number of patches (localities) of /at		
T. cristatus	30 (59)	30 (206)
T. marmoratus	21 (138)	51 (335)
Border areas	17 (188)	20 (285)

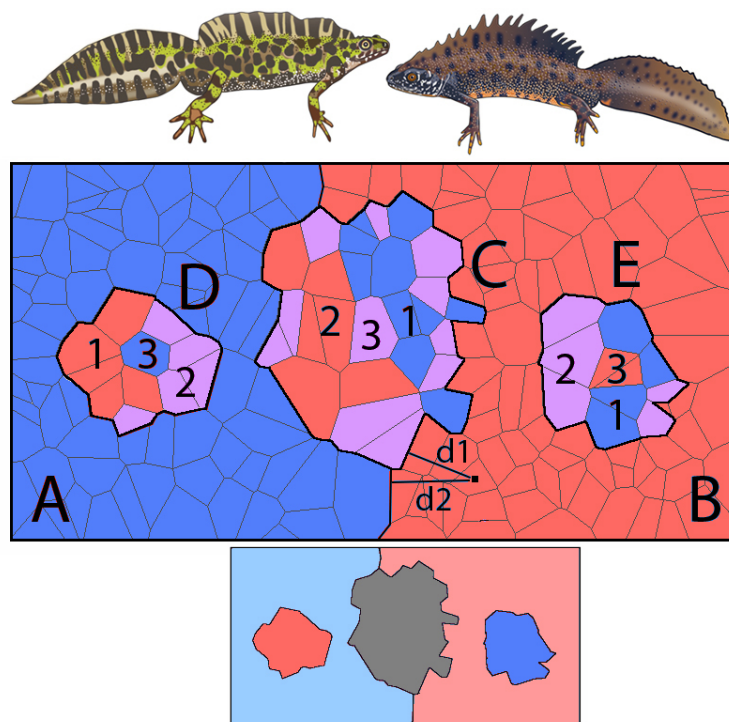\# For details see Supplementary Material Figure S2

Figure 2. Schematic representation on the distribution of two species, *in casu Triturus marmoratus* (drawing top left) and *T. cristatus* (top right), within a hypothetical area of range overlap. Dirichlet cells were drawn with PASSaGE 2 software (Rosenberg and Anderson 2011) for 200 random localities, with allotopic *T. marmoratus* in blue, allotopic *T. cristatus* in red, and both species (i.e., *T. marmoratus* and *T. cristatus* in syntopy and / or hybrids) in purple. Areas are composed of one or more cells and defined as follows: A – continuous allotopic *T. marmoratus*, B – continuous allotopic *T. cristatus*, C – border area (with 1 – only *T. marmoratus*, 2 – only *T. cristatus* and 3 – both species and/or hybrids), D and E – patches of *T. cristatus* and *T. marmoratus*, respectively (including allotopic (D1, E1) and syntopic localities (D2, E2)). Locality distance (d) is measured from the cell nadir up to the continuous part of the range as made up by pure and pure plus mixed localities (d=0.5*d1+0.5*d2). Distances from within border areas are given negative values. Admixture is the number of syntopic localities in the patch or border area divided by the total, to which counter patches (D3, E3) were included as syntopic. The inset illustrates how areas are summarized in Figure 3, along with the colour scheme applied. Animal drawings are by Bas Blankevoort, Naturalis Biodiversity Center.

are disconnected from the continuous section of the corresponding species range, as interrupted by the counterpart species. For convenience of writing, border areas may also be called border patches.

For all localities cell size was measured as a proxy to observed population density. Distance to the border (d) of the continuous stretches of species ranges (henceforth 'species border' or 'border') is the average of locality distances to the range edge (d=0.5*d1+0.5*d2, see Figure 2). Positive and negative values were given to data points outside and inside border areas, respectively. For patches, the corresponding measures were patch size and patch to border distance as measured from the nadir of the patch. For patches and border areas, species admixture was quantified as the number of syntopic localities divided by the total number (for details see Figure 2).

Following published work on *T. cristatus* and *T. marmoratus*, the environmental variables of interest are elevation, forest cover, hedgerow density and pond density (Schoorl and Zuiderwijk 1981, Visser et al. 2017, Arntzen 2023). Elevation data (in m a.s.l.) were extracted from the WorldClim global climate database v2, available at http://www.worldclim.org, with a spatial resolution of 30 arc seconds. 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, with a spatial resolution of 100 m. The parameter forestation (% cover) is composed of the Corine classes 22-25 and was measured over a 1 km^2 area surrounding the locality. Unfortunately, data for hedgerows and ponds were not available for the entire study areas. Data on percent forest cover and admixture proportion were arcsin transformed. The other data were log-transformed if this improved the normality of the distribution.

The PDLL and FARO data sets were both analyzed by Canonical Analysis of Principal coordinates (CAP) with Primer 7 and Permanova+ software, following the manuals (Anderson et al. 2008, Clarke and Gorley 2015). Aim of the analysis is to find axes through the multivariate cloud of points that are best at discriminating among the three spatially bounded groups of species occurrences (groups C, D and E in Figure 2). Univariate statistical analyses were carried out by analysis of variance (ANOVA) with Tukey's post-hoc test, or by the non-parametric Kruskal-Wallis procedure with the post-hoc pairwise testing procedure provided by SPSS 26 (IBM SPSS 2019). The association between the level of admixture and environmental and spatial data was investigated with the BEST-procedure in Primer 7 (Clarke and Gorley 2015), for patches of either species and border areas separately. Model choices were made based on significance levels obtained under 999 random permutations.

The unit of observation employed for statistical testing is either to be the locality or the patch (border areas included). Locality data will frequently be strongly autocorrelated so that their number exaggerates the number of independent observations. Conversely, patches are likely to deprecate that number on account of their frequently large size, number of localities involved and tangled shape. To settle this issue, statistical analyses involving patches were carried out with the patch as the unit of observation, weighted by the square root of the number of localities that they represent.

Results

The *Triturus cristatus – T. marmoratus* contact zone is characterized by abutting or somewhat overlapping continuous range sections, each describing about half of the length of the contact (Figure 1). Equally characteristic are numerous patches at either foreign side, altogether spanning a ca. 152,000 km^2 area positioned in between 45.5 – 49.5 degrees northern latitude. The five categories of species occupation anticipated in Figure 2 were all observed in both study areas. Cell sizes are not different between the species in either area (Table 1; FARO – t-test on log cell size, t=0.791, P>0.05; PDLL – Mann-Whitney U-test, standardized test-statistic 1.23, P>0.05). The distribution map for PDLL (Figure 3B) is roughly in line with that for the same area within FARO (Figure 3A), notwithstanding a nearly 14-fold increase in the density of records. The frequency of syntopic localities is 7.4% in FARO and 14.6% in PDLL.

Visual inspection of the results obtained with CAP resolves the three groups of interest (patched *T. cristatus* localities, localities in border areas and patched *T. marmoratus* localities) for both study areas in similar manner (Figure 4). Unsurprisingly, border localities associate negatively with distance to the range border, whereas *T. marmoratus* localities associate positively with distance to the range border, with *T. cristatus* in an intermediate position. *Triturus cristatus* and *T. marmoratus* localities are associated with low and high values for forestation and elevation, respectively. Finally, border areas associate with larger cell sizes, but the impact is small.

The number of patches resolved is 51 for FARO and 81 for PDLL (Table 1). Numbers do not significantly differ from neutral expectations in FARO (30 *T. cristatus* versus 21 *T. marmoratus*, Chi^2-test for equal proportions, Chi^2=2.59, P>0.05) and are higher for *T. marmoratus* (N=51) than *T. cristatus* (N=30) in PDLL (Chi^2=5.44, P<0.05). *Triturus marmoratus* patches are on average significantly higher in elevation, denser in forestation and more distant to the species border than *T. cristatus* patches, in both areas (Table 2). In FARO, *T. marmoratus* patches are larger whereas admixture is higher in *T. cristatus* patches than in *T. marmoratus* patches. Border areas keep intermediate positions in elevation and forestation in one or the other area. Finally, cell sizes are consistently larger (and thus observed population densities lower) in border areas than for patches of either species.

Within patches and border areas a suite of statistically significant correlations was obtained for admixture with environmental and spatial variables (Table 3). More admixture was found in habitats *atypical* for the species (e.g., *T. cristatus* patches at higher elevations in PDLL) whereas less admixture was found in habitats *typical* for the species (i.e.,
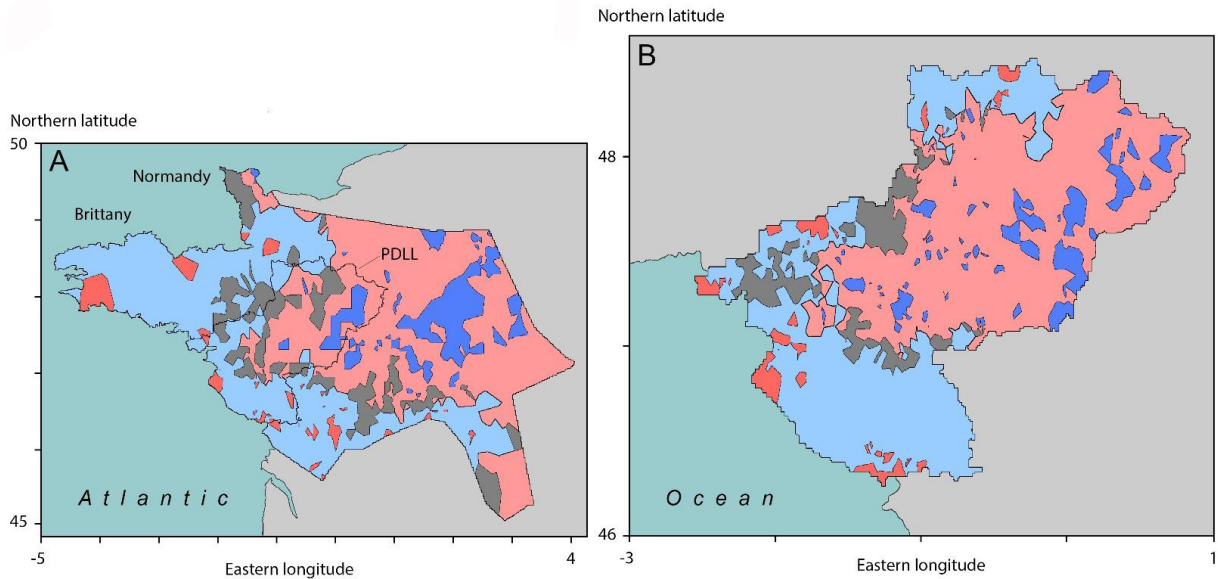
Figure 3. Distribution of *Triturus cristatus* and *T. marmoratus* obtained by interpolation of published distribution data over A – the area of range overlap in the west of France (FARO) and B – Pays de la Loire (PDLL). Colors are as in Figure 2 (inset), with the Atlantic Ocean in petrol blue and areas outside FARO and PDLL in light grey. Note that patches of small size do not always show up. Western and northern *T. marmoratus* areas positioned at the regional border were interpreted as representing the continuous part of the range in Brittany and Normandy. Some *T. cristatus* patches that were only resolved as a by-product of the reticulated coastline were suppressed. For the southernmost set of *T. cristatus* (semi) patches at coordinates around 1.2 W, 46.3 N, it may be wondered if they link up with *T. cristatus* in PDLL or rather to a more eastern stretch of the *T. cristatus* range.
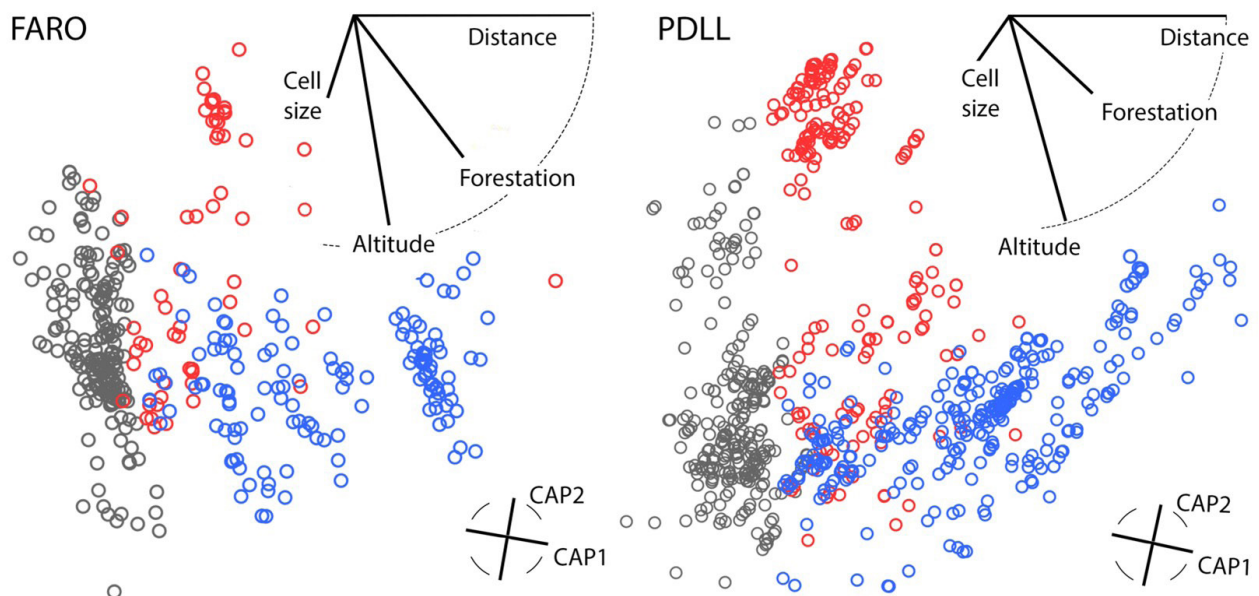

Figure 4. Results of analyses with Canonical Analysis of Principal coordinates (CAP) for atlas data on *Triturus cristatus* and *T. marmoratus* from France, for the area of range overlap (FARO, 385 localities) and the Pays de la Loire (PDLL, 826 localities). Localities from *T. cristatus* patches (red open symbols), *T. marmoratus* patches (blue open symbols) and from border areas (grey open symbols) are shown as positioned along the first (CAP1) and the second (CAP2) axis. Images are rotated clockwise by 10 degrees (FARO) and 14 degrees (PDLL) for presentation purposes. Lines within the quarter circles indicate the impact (by length relative to the maximum) and the strength of association (by orientation) of the parameters listed.

Table 2. Summary of univariate statistical analyses for differences among spatial groups of *Triturus cristatus* and *T. marmoratus* in the area of range overlap (FARO, top panel) and Pays de la Loire (PDLL, bottom panel). The spatial group listed in post-hoc comparisons (*T. cristatus* patches, border areas and *T. marmoratus* patches) is the one with the higher average value, for statistically significant pairwise comparisons only.

Environmental, spatial and demographic variables	Data transformation	Test applied -overall significance $	Post-hoc comparisons for spatial groups			Summary #
			T. cristatus patches - *T. marmoratus* patches	Border areas - *T. cristatus* patches	Border areas - *T. marmoratus* patches	
FARO						
Cell size	Log	ANOVA - ***	*T. marmoratus* ***	Border ***	Border **	b > m > c
Patch size	Log	Student t-test - *	NA	NA	NA	m > c
Distance to border	None	MWU - ***	NA	NA	NA	m > c
Elevation	Log	KW - *	*T. marmoratus* *	NS	NS	m > c
Forestation	Arcsin	KW - ***	*T. marmoratus* ***	Border *	*T. marmoratus* ***	m > b > c
Admixture	Arcsin	KW - *	*T. cristatus* *	NS	Border *	m > b = c
PDLL						
Cell size	Log	KW - ***	NS	Border ***	Border ***	b > c = m
Patch size	Log	MWU - NS	NA	NA	NA	c = m
Distance to border	None	MWU - ***	NA	NA	NA	m > c
Elevation	Log	KW -***	*T. marmoratus* ***	Border *	*T. marmoratus* *	m > b > c
Forestation	Arcsin	KW - ***	*T. marmoratus* ***	Border **	NS	b = m > c
Admixture	Arcsin	KW - NS	NS	NS	NS	c = b = m

$ ANOVA - Analysis of variance, KW - Kruskal-Wallis test and MWU - Mann-Whitney *U*-test. Post-hoc tests are Tukey's HSD in ANOVA and 'pairwise comparisons' in KW, as provided by SPSS 26. Significance levels are * - $P < 0.05$, ** - $P < 0.01$, ***- $P < 0.001$ and NS - $P > 0.05$; NA - not applicable. # Abbreviations are c - *T. cristatu*s, b - both species and m - *T. marmoratu*s. The equal sign is to be read as 'not significantly different from'

Table 3. Associations between the level of *Triturus cristatus* and *T. marmoratus* species admixture and environmental and spatial characteristics for within species patches and border areas in the area of range overlap (FARO) and the region Pays de la Loire (PDLL). Values shown are Spearman's correlation coefficients for the model selected with the BEST procedure in Primer 7 software, and for the admixture x environmental variables individually, as far as selected in the model.

	T. cristatus patches		*T. marmoratus* patches		Border areas	
	FARO	**PDLL**	**FARO**	**PDLL**	**FARO**	**PDLL**
Model characteristics						
Spearman's correlation coefficient	0.139	0.354	0.316	0.234	0.302	0.527
Parameters in the model	2	3	2	2	2	2
Statistical significance	NS	***	***	***	***	***
Environmental variables						
Elevation		0.467				
Forestation	0.258		- 0.337	- 0.327	- 0.582	0.146
Spatial variables						
Cell size		- 0.446			0.365	- 0.524
Distance to border					NA	NA
Patch size	0.283	- 0.513	- 0.430	- 0.288	NA	NA

Significance levels are: *** - $P < 0.001$ and NS - not significant; NA - not studied

T. marmoratus patches at denser forestation in FARO and PDLL) (Table 3). A tendency was observed for less admixture when patches were larger, regardless of patch type and study area.

Discussion

Within the wide area of range overlap in western France, 'patches' of *Triturus cristatus* and *T. marmoratus* are differentially found in flat and open versus hilly and forested terrain. The local mosaic can be seen as superimposed on the species' broad distribution with *T. cristatus* in the northeast and *T. marmoratus* in the southwest of France, as described by a two-species distribution model that is determined by a set of climatic gradients, along with elevation and forestation (Arntzen 2023). The present-day *T. cristatus* – *T. marmoratus* species contact originated in the postglacial era, when western Europe became populated from refugia in the northern Balkan peninsula and the Iberian Peninsula, respectively

(Wielstra et al. 2013). Position and period of the initial contact are unknown, but species distribution modelling suggests that western France may have been occupied by both species since the mid-Holocene, with no evidence for large scale species replacements (Arntzen 2023). The question at stake is whether inferences on the local history of species occupation can be drawn from the contemporary *T. cristatus* − *T. marmoratus* distribution pattern.

Seen over both data sets, *T. marmoratus* patches are significantly larger, more isolated and purer than the smaller, less isolated and more frequently admixed *T. cristatus* patches. These spatial and demographic characteristics suggest that *T. marmoratus* patches are stable and persisting strongholds whereas *T. cristatus* patches are in flux and undependable. *Triturus marmoratus* patches will be difficult for *T. cristatus* to take over on account of their ecological characteristics. In actual terms, *T. marmoratus* patches frequently coincide with forested and hilly areas, including the 'Forêt d'Orleans' (coordinates ca. 2.0 E, 48.0 N) and the 'Parc naturel regional Loire – Anjou – Tourraine' (coordinates ca. 0.0 E, 47.5 N; Figure 5). It is worth noting that the single, large *T. marmoratus* patch in the latter region is resolved as a dozen of patches, presumably on account of the denser and more recent sampling for PDLL than for FARO (Figure 3, Supporting Material Figures 1 and 2). Conversely, *T. cristatus* patches have possibly formed recently by invaders

from the mostly nearby main stock, by dispersal into mostly flat and unforested terrain.

The inference on *T. cristatus* superseding *T. marmoratus* is supported by two independent observations. Firstly, species replacement has been demonstrated for the post-World War II era in the department Mayenne. Historical data show that *T. marmoratus* had the widest distribution, whereas nowadays *T. cristatus* is predominating (Vallée 1959, Visser et al. 2017). The takeover has been attributed to agricultural reform, in particular hedgerow removal in the southern, flat part of the department, where changes in species occupation were most pronounced (Schoorl and Zuiderwijk 1981, Arntzen and Wallis 1991). Secondly, an advance of *T. cristatus* is supported by the observation that the species' continuous range stretches to the Atlantic coast (Figure 3B), or almost so (Figure 3A), to the effect that the *T. marmoratus*-occupied region in Brittany and Normandy might be interpreted as a 'mega-patch', rather than forming part of the main *T. marmoratus* range. *Triturus cristatus* has also been observed in two patches (or semi-patches, because positioned at the coast) in Brittany, but this entire region is poorly investigated, so that it is difficult to judge how disconnected these patches really are (Figure 3A and Supporting Material Figure 1). The southernmost set of *T. cristatus* patches in PDLL appears isolated (coordinates ca. 1.2 W, 46.3 N; Figure 3A), but may actually form part of a *T. cristatus* southern coastal prong (Figure 3B).
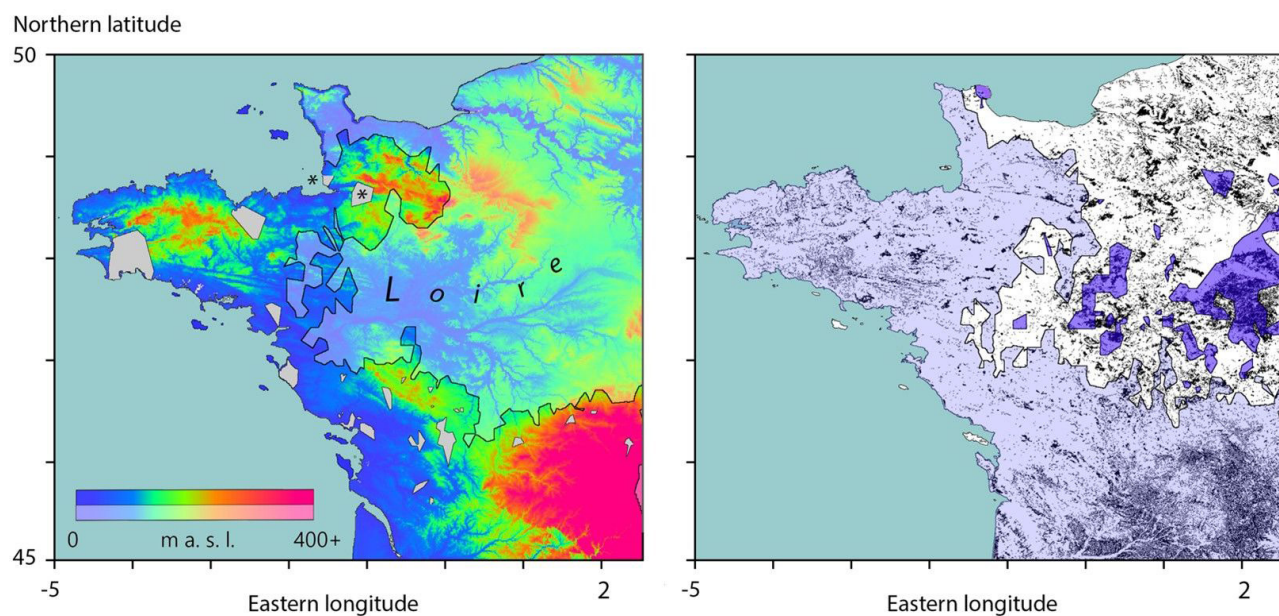

Figure 5. Western France with the outermost ranges of *Triturus cristatus* plotted over an elevation map (A) and *T. marmoratus* plotted over a forestation map (B). In A, elevation is from sea level in deep blue to 400+ m a.s.l. in deep red, as shown in the color legend. The shaded area represents the continuous range of *T. cristatus* with non-translucent grey for *T. cristatus* patches. Hypothesized colonization routes are along the Loire River and along the Normandy coast. *Triturus cristatus* populations in starred patches are predicted to represent different invasion routes, in counterclockwise (Normandy coast) and clockwise (Loire River) directions. In B, forestation is shown in black. The shaded blue area represents the continuous range of *T. marmoratus* and the darker blue areas are *T. marmoratus* patches. Large *T. marmoratus* patches are associated with forestation and more likely to be remnants of a wider past distribution than that they would be newly colonized.

The parameters governing the most likely colonization routes of *T. cristatus* are scale dependent. Forests may be difficult to conquer, but scattered forestation will not have hindered the wider *T. cristatus* advance, so that the colonization route for *T. cristatus* will effectively have been determined by low elevation. This points to the Loire valley as the main corridor to the Atlantic coast, with another, less extensive advance along the Normandy coasts (Figure 5). This scenario predicts an area of secondary *T. cristatus-T. cristatus* contact situated in between the Atlantic coast and the 'Collines de Normandie' low mountain range (coordinates ca. 0.5 E, 48.7 N; Figure 5). The current distribution data also suggest that *T. marmoratus* strongholds in forested areas at higher elevations may eventually be taken over, such as seems to have been the case for the 'Collines du Perche' (coordinates ca. 0.5 E, 48.5 N). Long-distance dispersal of either *T. cristatus* or *T. marmoratus* to explain the patches (cf. Ibrahim et al. 1996) can be ruled out on the basis the limited dispersal capability of these small, ground-dwelling organisms (Smith and Green 2005, Trochet et al. 2014). Introductions may occasionally have taken place, but cannot account for the overall pattern. Patches may also be formed by (sub)species that differ in propensity and magnitude of dispersal (Rapoport 1982). For French *Triturus* species, however, differences in dispersal capability are not documented whereas differences in ecological preferences have repeatedly been demonstrated (Vallée 1959, Schoorl and Zuiderwijk, 1981).

Another scenario is that species occupancy has been oscillating over the area of range overlap following changes in the environment, with patches at either side constituting remnants of wider but largely ephemeral species distributions. However, environmental data provide little support for fluctuations. Temperatures have been gradually decreasing since the mid-Holocene (Kaufman et al. 2020), along with anthropogenic deforestation that started in the Holocene and led to the scarce and patchy forestation as it was in place until ca. 200 years ago (Badré 1983, Marchant et al. 2009). Both processes will have favored *T. cristatus* over *T. marmoratus*, whereas only recent reversals, such as reforestation (Cinotti 1996, Vallauri et al. 2012, IGN 2020) and climate warming (Kaufman et al. 2020) may be favoring *T. marmoratus*, even if just in a relative sense (Préau et al. 2022).

Parallel with hybrid zones

The *T. cristatus* – *T. marmoratus* contact zone has so far been described in biogeographical terms, but could equally well be interpreted as a (moving) hybrid zone, at least for the section for which historical and genetic data are available (Arntzen and Wallis 1991). Hybrid zones may be 'clinal', with unimodal character state frequency distributions, or be 'mosaic' with a bimodal profile (Harrison and Bogdanowicz 1997, Jiggins and Mallet 2000). In a clinal hybrid zone the narrow transition area will generally preclude gene exchange between the parental species ever since it was formed, other than through a string of hybrid populations. Conversely, in mosaic hybrid zones gene exchange is plausible in spatial terms, because populations of different species are frequently within one another's dispersal range. However, interspecific gene flow will often be precluded by assortative mating, or be hampered by genetic incompatibilities (Jiggins and Mallet 2000, Muraro et al. 2022).

When a hybrid zone is moving, it may leave behind 'relict pockets' attributable to the superseded species. In clinal hybrid zones, available terms for cases as this are 'internal parapatry' (Key 1981) and 'enclaves' (or 'exclaves', depending on the perspective), by virtue of the spatial separation imposed by the cline. However, in mosaic hybrid zones their spatial separation is questionable so that the term 'patches' seems appropriate, with which the earlier usage of 'enclaves' for the *T. cristatus* – *T. marmoratus* system (Arntzen and Wallis 1991) is amended. Signals for species replacement might also be obtained from genetic footprints (Scribner and Avise 1993), but gene flow between *T. cristatus* and *T. marmoratus* is limited (Arntzen et al. 2021) so that, to obtain an adequate signal, large samples are required (Arntzen and Wallis 1991, Arntzen et al. 2009).

A remarkable result of the present study is the smaller number of observed localities in border areas, where levels of admixture are higher (Tables 2 and 3). An intriguing possibility is that a moving *T. cristatus* – *T. marmoratus* hybrid zone became trapped, stalled, or just slowed down in areas of lower population density, as is predicted by theory (Barton 1979, Goldberg and Lande 2007). This topic deserves further investigation, with quantitative data on admixture levels and with parameter intercorrelations considered.

Data considerations and the wider scope for patch analysis

Potential shortcomings in atlas data are identification error and localization inaccuracy, as well as limited and uneven sampling. The species under consideration have different morphological and coloration characteristics and will rarely be confused in their post-metamorphic phases (Figure 2). However, ca. 7% of the records is on pre-metamorphs. Species identification of eggs, embryos and larvae is possible, but requires expert knowledge that may, or may not have been available. Either way, it seems unwarranted to apply data filtering to high quality atlas data. Obviously, better sampling would yield more detailed maps. Larger samples would reveal more cases of syntopy, in particular when population species numbers are unbalanced, and would help to obtain more precise estimates on the level of species admixture. Syntopic localities make up ≤ 15% of the total, whereas inventories in Mayenne, with ca. threefold larger average sample sizes than in PDLL, observed 24-30% of the localities to be syntopic (Vallée 1959, Schoorl and Zuiderwijk 1981). It is, however, not evident how or why the above shortcomings in data gathering would affect *T. cristatus* and *T. marmoratus* differentially. A potential species bias is that forests ponds are more difficult to locate than field ponds, but locality densities are not

different for *T. cristatus* and *T. marmoratus* (see 'cell sizes' in Table 1). If spatial replacement and hybrid zone movement would take place within the period of data collecting the mosaic aspect may be exaggerated which presumably would inflate the number of *T. marmoratus* patches. This scenario is not supported by the data, because most *T. marmoratus* patches were found in PDLL for which the records are recent, and not in FARO where data collecting spanned an extended period (for the temporal profiles in data gathering see Supplementary Figure S2).

Finally, this study invites the question 'How common are systems available for patch analysis?'. The evaluation of a list of candidate taxon pairs in European amphibians and reptiles suggests that we are not spoiled for choice (Arntzen 2023: Table 1 and references therein). Species with widely overlapping distributions, possibly hybrid zones that 'collapsed into broad sympatry' (sensu Barton and Hewitt 1985), do not qualify. At the other side of the sympatry to parapatry spectrum are clinal hybrid zones, that also do not qualify. Enclave formation in these systems, as observed in fire-bellied toads (*Bombina*), common toads (*Bufo*) and several large-bodied newt species (*Triturus*), is an interesting phenomenon, but represent one-off situations that do not qualify for statistical analysis. Iberian midwife toads (*Alytes*) and tree frogs (*Hyla*) that have widely overlapping mosaic distributions, were studied for niche conservatism and niche divergence (Reino et al. 2017) but, with a 10 x 10 km grid as the unit of observation, local spatial-ecological segregations may have been obscured. Iberian vipers (*Vipera*) show long mosaic contact zones that though appear to be narrow (Chamorro et al. 2021) whereas Iberian sand racing lizards (*Psammodromus*) are subject to taxonomic uncertainty and present too many lacunes in their distributions for a meaningful analysis (Fitze et al. 2011, Doniol-Valcroze et al. 2023). French small bodied newts (*Lissotriton*) show a large area of range overlap, but the species mosaic is smooth which necessitates the quantitative analysis of species' relative frequencies (Arntzen 2022). One system that stands out for patch analysis is that of *Lissotriton vulgaris* (Linnaeus 1758) and *L. italicus* (Peracca 1898), that engage in a patchwork over a ca. 100 x 200 km area in central Italy (Iannella et al. 2017). Another promising system is that of *Lissotriton boscai* (Lataste 1879) – *L. helveticus* (Razoumowsky 1789) in the northwest of the Iberian Peninsula. These species' ranges overlap in a ca. 450 long and 150 km wide area, but precise locality data appear currently unavailable (Plegezuelos et al. 2002, Loureiro et al. 2008). Two-species distribution modelling and patch analysis are promising, yet underexplored approaches in the study of species' shifting range borders. Many species pairs in groups of crawling, walking, flying and swimming organisms characterized by limited, habitat dependent dispersal, along with the plant species, seeds and disease organisms they carry, are open for investigation, to which the wide availability of species occurrence data in atlases and digital databases is an indispensable asset.

Data Availability Statement

Core to this paper are distribution data for France and for the Pays de la Loire, as compiled by D. Angot, P. Evrard, J. Lescure, B. Marchadour, J. C. de Massary and M. Sineau. The databases are curated by and accessible through the 'Société Herpétologique de France' (https://atlas.lashf.org) and 'L'inventaire National du Patrimoine Naturel' (https://inpn.mnhn.fr/accueil/index), with data presented at the 10 x 10 km scale. Access to more detailed data may be obtained at the 'League pour la Protection des Oisseaux' (https://lpo.fr).

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Figure S1. Dirichlet cells established for localities in two areas in France for which atlas data on *Triturus* newts were analysed.
Figure S2. Increase in the number of *Triturus* records over time for two atlases on the herpetofauna of France.
Figure S3. Logos of the organizations that supported the atlas project for the Pays de la Loire.

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