Newts in time and space: the evolutionary history of Triturus newts at different temporal and spatial scales

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CHAPTER 8

ENVIRONMENTAL PARAMETERS THAT DETERMINE SPECIES GEOGRAPHICAL RANGE LIMITS AS A MATTER OF TIME AND SPACE

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Abstract

Aim To identify the ecological factors associated with the range borders of two amphibian species, to investigate geographical variation in environmental parameters that determine species range limits, and to develop a testable hypothesis on the species' biogeographical history.

Methods We documented the distribution of two species of marbled newts (*Triturus marmoratus* and *T. pygmaeus*) from atlas data, survey data and six latitudinal transects. Countrywide ecogeographical models were constructed from presence only data and a suite of 19 environmental parameters. Local ecogeographical models were constructed along the contact zone.

Results *Triturus marmoratus* and *T. pygmaeus* share a parapatric range border from coastal Portugal to central Spain. Ecogeographical models performed better in descriptive mode (i.e., for the country where it was developed) than in predictive mode (i.e., when extrapolated for the neighbouring country). This suggests the existence of spatial variation for parameters that determine the species range borders. Local models showed good performance in Spain and western Portugal. Parameters dominating the models were climatic (precipitation, temperature and solar radiation), geographical (altitude) and geophysical (soil permeability). Enclaves in the distribution of *T. marmoratus*/*T. pygmaeus* also corresponded with environmental parameters. Poor-fitting local models were found in central Portugal where the species' mutual range border coincides with the River Tejo.

Main conclusions The fit and predictive performance of the ecogeographical models suggest that equilibrium conditions have been reached over most of the contact zone. Parameter selection, field observations and natural history knowledge led us to identify, in terms of reproductive strategy, a stable species with regular, but low, annual recruitment (*T. marmoratus*) versus an opportunistic species with fluctuating 'all or nothing' annual recruitment (*T. pygmaeus*). Ecological parapatry derives from the use of permanent ponds for breeding in *T. marmoratus* versus ephemeral ponds used by *T. pygmaeus*. Enclaves in the distribution show that *T. pygmaeus* has been displacing *T. marmoratus* historically. In central Portugal, where model fit is poor, the advance of *T. pygmaeus* is currently impeded by the River Tejo. We predict that once this barrier has been crossed, the contact zone will move ca. 40 km to the north. Since *T. marmoratus* and *T. pygmaeus* are hybridizing species, we predict the occasional presence of *T. marmoratus* genes in areas that have changed occupancy.

Keywords: contact zone, ecological parapatry, enclave, geographical information system, Iberian Peninsula, newts, presence-only ecogeographical models, *Triturus*

Introduction

Species ranges are finite. They are delimited on all sides by a more or less sudden decrease in population density up to a point where no more individuals are present. One of the most important objectives in ecology is to understand why species exist in one place and not in another. Distributional models are based on (usually) limited records of presence and (presumed) absence, and they predict where species will occur given the correlation with one or a few ecological variables. However, the factors that determine these limits will not be the same over the entire edge of the distribution. A species may be bound by, for example, the lack of appropriate habitat in the north, a competing species in the east, an ocean in the south and a mountain range in the west. Such factors act on a local scale by influencing reproductive success, survivorship or the dispersal ability of individuals and populations. This is especially true when species ranges are large, when the habitat is heterogeneous or when the species have high genetic diversity. A corollary of these observations is that ecological models should not be extrapolated to other areas when significant ecological variability is present.

Many researchers have focused on the change in species distribution through time. This is notable in environmental research where the possible effects of man-made changes to the environment are assessed and predicted (TEIXEIRA and ARNTZEN, 2002; ARAUJO and RAHBEK, 2006; ACEVEDO and RESTREPO, 2008). However, few studies have focused on geographical variation in environmental correlates of species distributions. Those that have done this have reported that geographical variation is limited to, for example, differences between a small number of populations (AYRES and SCRIBER, 1994) or between the northern and southern edge of the range (GROSS and PRICE, 2000). In a study exploring data from a Portuguese atlas of amphibians and reptiles (GODINHO *et al.*, 1999), Arntzen (ARNTZEN) compared the precision of descriptive ecogeographical models for Portugal with the accuracy of the predictions in neighbouring Spain. Well-fitting descriptive models tended to predict distributions rather well. Hence, these models appear to convey biologically meaningful information that improve our understanding of species' ecological requirements and can be used in conservation management (ARNTZEN, 2006). An issue that has not yet been addressed is the presence of regional variation in environmental parameters that determine the geographical range limits of species. With geographical variation present, model fit in predictive mode would be relatively low, but that does not necessarily indicate poor modelling conditions.

The present paper deals with geographical variation in environmental parameters that determine species range limits. Firstly, we describe the distribution of two species of marbled newt (genus *Triturus*) in the Iberian Peninsula. The species' territories are parapatric (i.e., contiguous and only narrowly overlapping in relation to the vagility of the individuals). This makes it possible to contrast the presence of one species with that of the other without reference to absence data. Secondly, we document the existence of spatial variation in the environmental parameters determining a species' range. Thirdly, we present and discuss a hypothesis on the historical biogeography of Iberian *Triturus* species.

Materials and methods

Biological data

The current knowledge of the distribution of Iberian amphibians is organised in atlases for Spain (PLEGUEZUELOS *et al.*, 2004) and Portugal (LOUREIRO *et al.*, 2008). Both employ the Universal Transverse Mercator grid with a spatial resolution of 10 x 10 km (UTM10). Marbled newts (*T. marmoratus* and *T. pygmaeus*) are recorded in > 2000 grid cells. The Spanish data suggest that the distributions of *T. marmoratus* and *T. pygmaeus* are mutually exclusive and that their ranges are parapatric. For Portugal this is unclear because the data are pooled across species, due to the fact that *T. pygmaeus* was until recently considered a subspecies of *T. marmoratus*. In order to clarify the distributions of *T. marmoratus* and *T. pygmaeus*, we studied six approximately north to south orientated transects, and surveyed the areas around Aveiro and Caldas da Rainha (Fig. 1A). Species identification was based on adult morphology, and the molecular genetic analysis of embryo and larval tissue samples (CHAPTER 7).

Environmental data

The environmental variables considered for ecogeographical modelling are those provided by Teixeira & Arntzen (2002), Real *et al.* (2005) and the EROS program

(Earth Resources Observation and Science - Global Land Cover Characterization, Version 2.0. available at http://eros.usgs.gov/products/landcover.html). Variables that

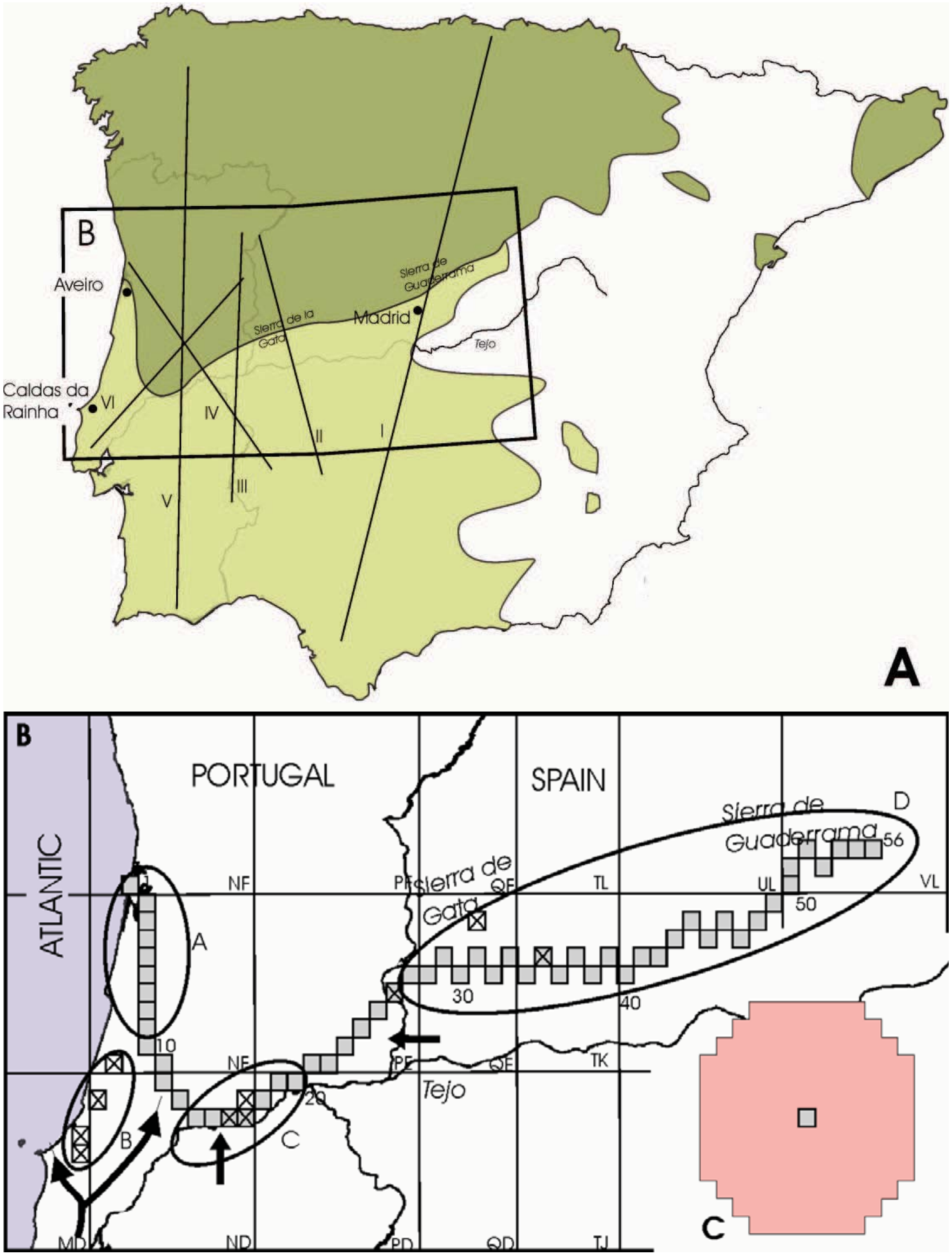

Figure 1 (a) Geographical distribution of the marbled newts Triturus marmoratus (dark shading) and Triturus pygmaeus (light shading) in the Iberian Peninsula. Six latitudinal transects perpendicular to the mutual species boundary (I–VI, continuous lines) showed sharp morphological and genetic transitions. (b) The inferred parapatric range border is shown by shaded UTM10 grid cells. Cells for which both species were actually observed are marked by a cross, including five such cells outside the continuous contact zone. Ellipses A–D refer to areas discussed in the text. (c) Shape and size of a window, the central point of which is moved over the string of shaded grid cells, in 56 steps. The 145 grid cells enclosed in each of the 56 steps were used to build a series of distribution models (see text for details).

were deemed biologically uninformative (e.g., distance to urban centres and highways) or not available for both countries were deleted. A further selection was made with UPGMA cluster analysis, using the criterion of parameter redundancy at the level of Spearman's rank correlation coefficient, $r_s > 0.8$, as follows : the 'mean annual number of frost days' (minimum temperature ≤ 0.5 ºC; code DFRO) was chosen over 'mean temperature in January'; the 'mean relative air humidity in July at 07h00' (HJUL, in %) was chosen over the 'annual relative air humidity range'; the 'mean annual precipitation' (PREC, in mm) was chosen over 'mean annual actual evapotranspiration'; the 'mean annual temperature' (TEMP, in ºC) was chosen over 'mean annual potential evapotranspiration'; and the 'mean temperature in July' (TJUL, in ºC) was chosen over 'mean annual insolation'. Other selected variables were 'altitude' (ALTI, in m a.s.l.); 'mean annual number of days with precipitation ≥ 0.1 mm' (DPRE); 'mean relative air humidity in January at 07h00' (HJAN, in %); 'permeability of the soil' in three categories of increasing permeability (PERM); 'relative maximum precipitation' (RMP, equalling MP24/PREC); 'maximum precipitation in 24 h' (MP24, in mm); 'slope' in degrees, calculated from ALTI (SLOP); 'mean annual solar radiation' (SRAD, in $\mathrm{kWh.m^{-2}.day^{-1}}$); and 'annual temperature range' (TRAN, in ºC, equalling 'mean temperature in July' minus its equivalent for January). From EROS we chose the 'Running Vegetation Lifeforms Classification' (RUNNING *et al.*, 1994 7 and 8 pooled) and 12 monthly vegetation index composites from April 1992 to March 1993. With UPGMA, the 12 NDVIs clustered in three seasonal groups from which we chose the April (NDVI04), August (NDVI08) and December (NDVI12) images. The two most dissimilar images were used to calculate an annual NDVI range, as dNDVI = NDVI03 - NDVI12. The 19 variables listed in Table 1 were introduced into the GIS software ILWIS 3.0 (ITC, 2001) as raster layers with 1 km spatial resolution. Mean values for UTM10 grid cells were obtained by averaging the data (modal values were used for the categorical variable RVLC).

Modelling and analysis

Logistic regression was performed with SPSS 14 (SPSS, 2005) with a forward stepwise addition of explanatory variables and with Bonferroni correction to the initial α=0.05 (HOLM, 1979). The latter, guarded against overfitting the models. For specific models, sets of variables were entered simultaneously. The presence of *T. marmoratus* versus that of *T. pygmaeus* was the (binary) response variable. The numerical impact of the recorded presence of one species versus the other was equilibrated through a weighting variable, using the 'weight cases' option in SPSS, resulting in a balanced dataset with a fifty/fifty representation. Ten cells with both species recorded (<1% of the data) were deleted from the analysis. The continuous and ordered variables were standardized to an average of zero and standard deviation of unity, to increase the comparability of their effects. To test their spatial predictive performance, models were constructed from data in one country and applied to the neighbouring country (from Portugal to Spain and *vice versa*). A significant change in model performance from descriptive to predictive mode would indicate spatial variation in the ecological determinants of the contact zone position. To investigate this phenomenon in detail, a circular window with a surface of 145 grid cells was

Table 1 Environmental parameters used to model the distribution of Marbled newts on the Iberian Peninsula.

Code	Variable description	Source
ALTI	altitude, in m a.s.l.	1
DFRO	mean annual number of frost days, minimum temperature ≤ 0.5 ºC	1
dNDVI	annual NDVI range, NDVI March 1993 minus NDVI December 1992	2
DPRE	mean annual number of days with precipitation ≥ 0.1 mm	1
HJAN	mean relative air humidity in January at 07h00, in %	1
HJUL	mean relative air humidity in July at 07h00, in %	1
MP24	maximum precipitation in 24 h, in mm	1
NDVI04	monthly vegetation index composite April 1992	2
NDVI08	monthly vegetation index composite August 1992	1
NDVI12	monthly vegetation index composite December 1992	1
PERM	permeability of the soil in three categories of increasing permeability	1
PREC	mean annual precipitation, in mm	1
RMP	relative maximum precipitation, equalling $MP24*PREC^{-1}$	1
RVLC	Running Vegetation Lifeforms Classification	2
SLOP	slope in degrees, calculated from ALTI	1
SRAD	mean annual solar radiation, in $kWh*m^{-2}*day^{-1}$	1
TEMP	mean annual temperature, in ºC	1
TJUL	mean temperature in July, in ºC	1
TRAN	annual temperature range, in ºC, equalling mean temperature in July minus its equivalent for January	1

References : (1) Real *et al*. (REAL *et al.*), (2) Earth Resources Observation and Science Program into Global Land Cover Characterization, Version 2.0. The rare classes 6, 7 and 8 were pooled with class 3 (RUNNING *et al.*, 1994).

moved with the nadir point from cell 1 to cell 56 along the reconstructed contact zone of the species (Fig. 1). Inside the window, marbled newts were presumed present (including 'pseudo-presences') in all cells north (*T. marmoratus*) and south (*T. pygmaeus*) of the contact zone. The strength of agreement among distribution models and distribution data was summarized with 'Area Under the Curve' statistics (PEARCE and FERRIER, 2000; FIELDING and BELL, 2002) and their asymptotic standard errors (SE).

Results

Distribution of *Triturus marmoratus* and *T. pygmaeus* in the Iberian Peninsula and characterization of the contact zone from field observations

We observed a steep transition from *T. marmoratus* in the north to *T. pygmaeus* in the south in each of six transects (Fig. 1A). The abruptness of the transition suggested the absence of wide areas of intergradation and confirmed the essentially parapatric species distribution suggested by the Spanish atlas data. Both species together were observed in five grid cells of the contact zone and in five grid cells outside the contact zone (Fig. 1B: MD95, MD96, ND08, ND87, ND97, ND98, NE10, PE84, QE38 and TK16). Spatial interpolation of the contact zone was straightforward in Portugal. It was somewhat equivocal in data deficient areas of Spain, which is reflected in a sub-optimally resolved ‘zig-zag’ pattern. The overall result allows an analysis in which the presence of one species is contrasted with that of another, without reference to so-called ‘soft’, potentially problematic absence data.

Around Aveiro, *T. pygmaeus* occurs inside and *T. marmoratus* outside the coastal dunes (Fig. 1B, area A). In western Portugal, an exception to strict parapatry was observed north of Caldas da Rainha in area B, where one or more pockets of *T. marmoratus* were found surrounded by *T. pygmaeus*, although this was not resolved at the UTM10 grid scale (The fine scale distribution and environmental analysis is dealt with in CHAPTER 9). In central Portugal, the position of the contact zone appears to be associated with the River Tejo (area C). The local distribution is, however, asymmetric, with *T. pygmaeus* occurring over the river northwards and *T. marmoratus* not crossing it southwards. In Spain, the contact zone runs along the southern edge of the Central System, from the Sierra de Gata (and adjacent Serra da Gata in Portugal) in the west to the Sierra de Guadarrama in central Spain (area D).

The species transition is situated at ca. 1000 m a.s.l. in transect I and at ca. 500 m a.s.l. in transect II.

Table 2 Distribution models for the parapatric range border of Marbled newts (*Triturus marmoratus* and *T. pygmaeus*) by logistic regression of presence-only data.

	Model *						
	1	2	3	4	5	6	7
Distribution data from	Iberia	Portugal	Spain	window			
				1-4	5-13	23-27	28-56
Parameter code							
Constant	9,504	-16,649	33,695	-14,160	-20,287	-1,319	1,831
ALTI				-13,498			0,201
DFRO	2,824	6,729	17,172		-16,468		-4,906
dNDVI	2,309	4,081	3,427				
DPRE	4,106		12,765				
HJAN			-2,679				
HJUL			7,565				
MP24	-5,297		-10,396				-0,124
NDVI04	1,441						
NDVI08							
NDVI12							
PERM	-1,731	-2,969			1,797		1,669
PREC	9,011	7,381	19,495				
RMP	5,301	3,806	11,746	8,837			-1,662
RVLC1	1,578	29,697					
RVLC2	-0,884	30,123					
RVLC4	0,200	31,425					
RVLC5	2,063	30,978					
RVLC3678	0,000	0,000					
SLOP							
SRAD	-12,114	-7,937	-39,183			20,207	
TEMP	2,508		9,913				
TJUL							
TRAN							
Model fit							
Descriptive mode				window			
	Iberia	Portugal	Spain	1-4	5-13	23-27	28-56
AUC	0,996	0,996	1,000	0,995	0,936	0,986	0,970
SE	0,001	0,002	0,000	0,004	0,017	0,006	0,007
Predictive mode	Iberia	Spain	Portugal	all 56 windows			
AUC	not	0,932	0,898	0,822	0,824	0,969	0,825
SE	applicable	0,007	0,016	0,015	0,015	0,006	0,016

Environmental data are standardized, except for the categorical variable RVLC that is represented by four binary variables. The fit of the models to the distribution data is expressed by the 'Area Under the Curve in Receiver Operating Characteristic' plots (AUC) and asymptotic standard error (SE).

* Example - considering data over window 23-27, the probability of occurrence of *T. marmoratus* is estimated as (1/(1+exp(20.207*SRAD-1.319))).

Ecogeographical models

The minimal adequate model (sensu CRAWLEY, 2002) for the Iberia-wide differential *T. marmoratus–T. pygmaeus* distribution is described as model 1 in Table 2. For countries separately, the models were slightly better fitting for Spain (model 3) than for Portugal (model 2). Extrapolating the models to the neighbouring country showed that model fit is poorer in predictive mode than in descriptive mode in both directions – Spain to Portugal and Portugal to Spain. This suggests spatial variation in the variables that determine the species' geographical range limit. We therefore proceeded with 56 models that were constructed by moving a circular window over the contact zone, with the focal point stepping from position 1 to 56 (Fig. 1B and 1C). In those models, the variables ALTI and RMP dominated in the coastal zone of Aveiro. Variables frequently selected were DFRO (29 times) and SRAD (22 times). DFRO was often accompanied by MP24 (10 times) or PERM (11 times). Explanatory variables other than these six entered the models occasionally and were spatially incoherent. We therefore restricted the variable evaluation to the following sets: ALTI+RMP, DFRO, DFRO+MP24, DFRO+PERM and SRAD (Fig. 2). Four models were calculated over areas where variable sets performed best and had high values of fit: ALTI+RMP over windows 1-4 (model 4); DFRO+PERM over windows 5-13 (model 5); SRAD over windows 23-27 (model 6); and ALTI, DFRO, MP24, PERM and RMP over windows 28-56 (model 7; Table 2). No model was formalized for area C, where model fit was low. Models 4-7 performed better in local mode than in spatial extrapolation (Table 2). The *T. marmoratus–T. pygmaeus* interspecific range limit described by the models is shown in Fig. 3.

Discussion

We document the distribution of *T. marmoratus* and *T. pygmaeus* from field surveys and atlas data and from the study of six latitudinal transects. *Triturus marmoratus* and *T. pygmaeus* are shown to have parapatric ranges. No further analysis is required to conclude that the single factor affecting the mutual geographical range limit in central Iberia is the presence of the sister species. This raises the question of what keeps the species separate. Key (1981) distinguished 'hybridization parapatry' and 'ecological parapatry'. In hybridization parapatry, the lack of admixture results primarily from the populations [species] mating more or less freely with each other, but either

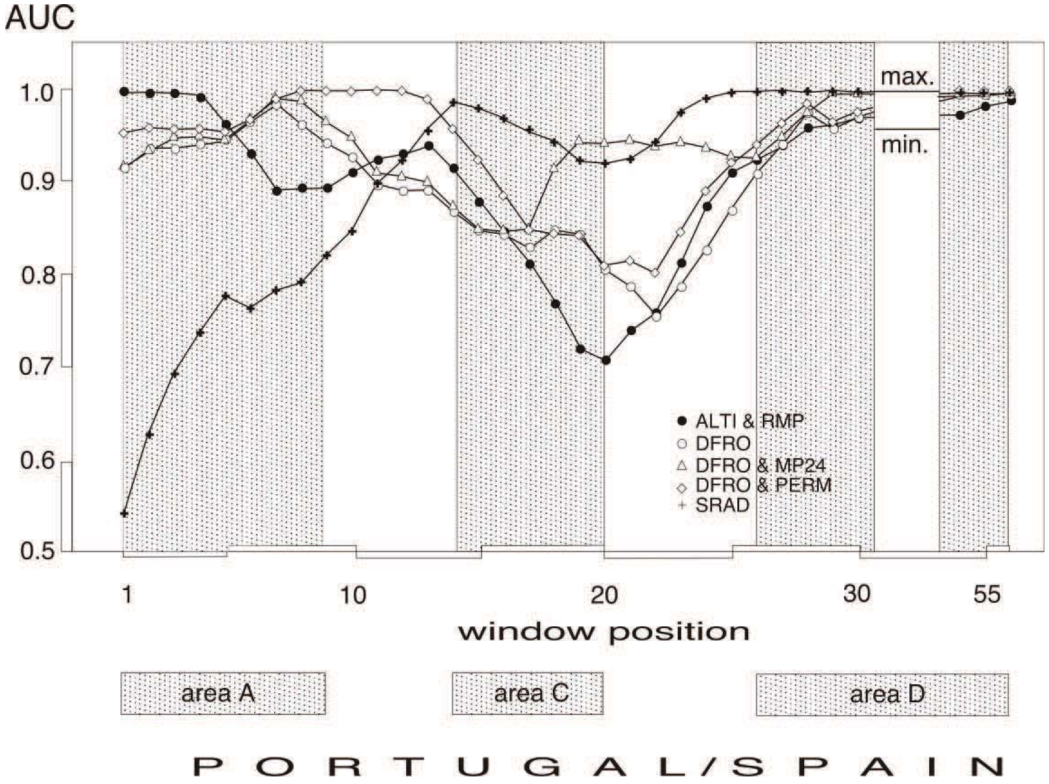

Figure 2. Area under the curve values describing the fit of 56 models constructed with a window (Fig. 1c) moving over the contact zone of Triturus marmoratus and Triturus pygmaeus, from position 1 near Aveiro to position 56 north of Madrid (Fig. 1b). Ecogeographical models were generated with logistic regression for the independent variable Triturus with character states marmoratus range vs. pygmaeus range and selected environmental variables in five sets (see text for details).

leaving no fertile progeny or leaving progeny of reduced fertility. In ecological parapatry, the lack of admixture results primarily from a sharp ecological interface between the habitats of the two populations [species], perhaps reinforced by competition between them. Hybridization between *T. marmoratus* and *T. pygmaeus* has so far been documented in central Portugal (J. W. Arntzen & G. Espregueira Themudo, unpublished data) and perhaps in eastern Portugal also (MALKMUS and LOUREIRO, 2007). One marbled newt of mixed *T. marmoratus–T. pygmaeus* ancestry was found in a survey around Caldas da Rainha in western Portugal (area B in Figure 1; CHAPTER 9). Considering the coverage of the studies, we conclude that hybridization between *T. marmoratus* and *T. pygmaeus* is rare and that the observed distribution pattern does not qualify as hybridization parapatry.

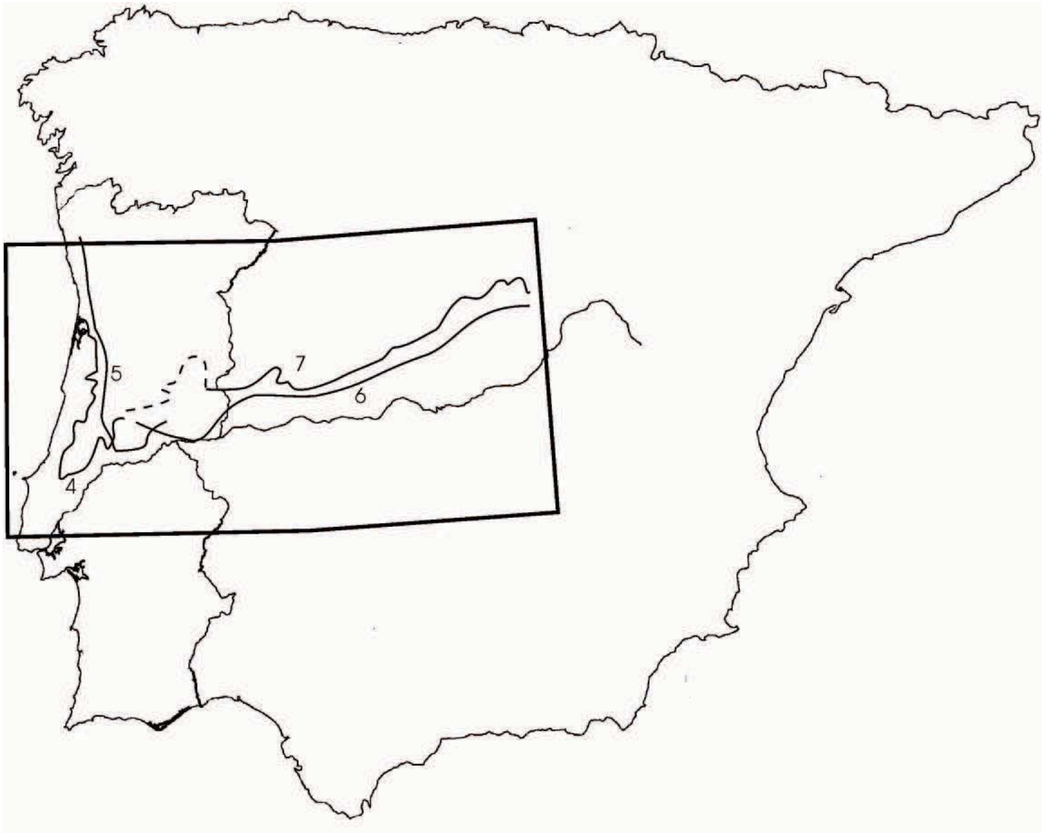

Figure 3. Local limit of the Triturus marmoratus–Triturus pygmaeus differential distribution as modelled from variable sets ALTI + RMP (model 4) and DFRO + PERM (model 5) in western Portugal, SRAD (model 6) in eastern Portugal and adjacent Spain, and ALTI, DFRO, MP24, PERM and RMP in Spain (model 7). The variables are described in Table 1 and the models in Table 2. The dashed line shows the predicted mutual range limits of the species assuming no impeding effect of the River Tejo on the northward range extension of T. pygmaeus. This links model 4 and model 7 and is based on the Iberia-wide model 1.

If ecological parapatry is the case, have we been able to identify a more or less sharp ecological interface (ecotone) associated with the mutual species border?

The field observations and ecogeographical analyses provide us with a clear positive answer, but, interestingly, the variables associated with the position of the mutual species border vary from one region to the other. The primary factors suggested by field observation are soil composition (coastal dunes versus other soil types inland) in area A, the River Tejo in area C, and the southern slopes of the Central Iberian Mountain System over area D. In area B the primary ecological correlate of *T. marmoratus* presence is the agricultural practice of fruit growing (CHAPTER 9). No obvious correlates of the differential *T. marmoratus –T. pygmaeus* distribution were apparent for the regions flanking area C.

From the statistical perspective, the dominating explanatory parameters are ALTI + RMP (model 4) and DFRO + PERM (model 5) in area A. Model 4 has stronger appeal than model 5 because: 1) its local descriptive performance is better (Table 2); 2) it makes significantly better predictions at the Iberian-wide scale (Table 2); 3) it does not describe the presence of *T. pygmaeus* along the Atlantic coast north of Aveiro as does model 5 (Fig. 3); and 4) it is the only model that predicts the presence of *T. marmoratus* over area B (Fig. 3; remember that records for the grid cells MD95, MD96, ND08 and NE10 were excluded from the analysis on the basis of species syntopy at the UTM10 scale). As yet no UTM10 grid cells are known south of the River Tejo with *T. marmoratus* present and *T. pygmaeus* absent. No explanatory parameters are strongly associated with the position of the contact zone in area C (Fig. 2). Model 6 with SRAD is the only model that performs well over windows 23-27 (for which it was designed), but otherwise has little appeal because in western Portugal it performs no better than random data (Fig. 2). The differential *T. marmoratus*–*T. pygmaeus* distribution along the Central Iberian Mountain System is captured by SRAD in model 6 and by five variables in model 7. These variables are locally strongly correlated and will be difficult to disentangle.

Can the results from the more or less intuitive field observations and the formal ecogeographical analysis be reconciled?

In area A the species breeding localities are drastically different. The dune ponds with *T. pygmaeus* are usually wide, shallow and ephemeral whereas *T. marmoratus* breeding sites outside the dunes are mostly smaller, deeper and more permanent. The dunes represent an unstable system for amphibian breeding. In wet years reproductive success could be great, because of low predation pressure by fish and aquatic insects, but in dry years many ponds desiccate before the larvae reach metamorphosis or do not form at all. We predict that the breeding success of *T. pygmaeus* inside the dunes is subject to large fluctuations and that the annual reproductive output of *T. marmoratus* is comparatively steady. This hypothesis can be tested through a demographic study, for example using the skeletochronological approach for determining individual age (FRANCILLON-VIEILLOT *et al.*, ; CAETANO and CASTANET, 1993; JAKOB *et al.*, 2003). Soil type also differentiates the terrestrial shelter it provides to the (postmetamorphic) juveniles and adults. Shelter may be readily available through active burrowing in sand, but not through the availability of cracks and fissures in hilly and mountainous terrain. The alternative model 4 is composed of

ALTI and RMP. We interpret low altitude as a proxy to the coastal zone and, hence, ALTI as an indirect descriptor of soil structure that locally differentiates between the dune and inland areas. The alternative model 5, composed of DFRO and PERM, also distinguishes the conditions inside the dunes (with a higher than average temperature and permeable soil) and outside the dunes. The steady moisture conditions described by high RMP values are in line with the field based interpretation that point to more constant (reproductive and foraging) conditions for *T. marmoratus* than for *T. pygmaeus*. This variable was particularly successful in predicting the presence of *T. marmoratus* in area B. Area C is characterized by the absence of a strong ecogeographical signal associated with the differential species distribution. The River Tejo (not an explanatory variable in the GIS analysis) locally separates the species, which suggests that the river acts as a barrier to dispersal. In area D, the distribution of *T. pygmaeus* extends northwards into the foothills of the Central Iberian mountain system where *T. marmoratus* occupies the higher slopes. The altitude at which the species transition takes place varies and we observed more permeable soils in the south than in the north. Since we are dealing with a latitudinal divide running along a mountain range, it is no surprise that the species transition is also described by climatic conditions of rainfall (MP24 and RMP), temperature (DFRO) and solar radiation (SRAD). The observed species differential ecology is similar to that in area A, with relatively small and permanent ponds in the mountains, and large, often temporary ponds in the plains accompanied by a soil structure and opportunities for hiding that are also similar to those in area A. The essential difference between the species appears to be an opportunistic life history (r-strategy) of *T. pygmaeus* and a more stable life history of *T. marmoratus* (K-strategy), consistent with their occurrence in habitats providing more fluctuating ‘all-or-nothing’ and more predictable opportunities for reproduction, respectively. The difference in life histories does not seem to be important in central Portugal where the mutual species border is bounded by the River Tejo. We suggest that reciprocal transplant experiments and laboratory experiments would be required to test our interpretations. The agreement between the field-raised biological interpretation in areas A and D would further suggest that the selected ecogeographical parameters only indirectly relate to the differential *T. marmoratus–T. pygmaeus* geographical range limit. It follows that the intuitive field approach and the formal ecogeographical approach have complementary strengths, with respect to a straightforward interpretation vs. a formal statistical evaluation and spatial extrapolation, respectively. The joint results indicate that in some areas the environment determines the outcome of interspecific competition whereas elsewhere it is a physical barrier (a river) that explains the current distributions. Other studies have dealt with variation in environmental parameters that govern the geographical range limit of species. However, these only compare the northern vs. southern edge of the range (GROSS and PRICE, 2000), coastal vs. oceanic, or presence vs. absence of a parapatric competitor (BULLOCK *et al.*, 2000). Competition is the most likely cause for reciprocal range boundaries in parapatric species, but here we see that local ecological conditions are determining which species has the competitive advantage.

Is the species contact zone fixed or moving?

Species distributions change over time and a contemporary distribution map represents no more, so to speak, than one frame in a film covering the lifetime of a species. Thus, it is difficult to predict the direction and rate of change through time. Nevertheless, the isolated pockets in the easternmost part of the *T. marmoratus* and *T. pygmaeus* ranges have been interpreted as the signal of a receding range (GARCÍA-PARÍS *et al.*). This interpretation is reasonable, because drought conditions in these areas have been increasing (ESTRELA *et al.*, 1996) and newts have limited dispersal abilities that do not allow them to cross large areas of unsuitable habitat. An effective dispersal rate of one $km.y^{-1}$ is a fair estimate for *Triturus* newts (ARNTZEN and WALLIS, 1991; JEHLE and SINSCH, 2007). We used this line of reasoning to explain the isolated occurrence of *T. marmoratus* in western Portugal (area B in Fig. 1B), but the argument is stronger here because the surroundings are occupied by the sister species *T. pygmaeus* (ESPREGUEIRA THEMUDO and ARNTZEN, 2007). The isolated occurrence is effectively an enclave to *T. pygmaeus* (and an exclave to *T. marmoratus*). In species with low dispersal rates such as amphibians, enclaves are a signal of significant changes in the parapatric range border. The existence of this particular enclave is best explained by *T. pygmaeus* displacing *T. marmoratus*. The enclave is a remnant and appears to be associated with more favourable habitat for one species (*T. marmoratus*) and less favourable habitat for the other (*T. pygmaeus*). The most important environmental factor in the enclave is the extent to which the land is used for orchards. The growing of fruit trees in turn is selected for by higher moisture than in the surrounding areas (A. da Costa Pais, Caldas da Rainha, personal communication). Other examples of enclaves/exclaves for closely related, parapatric species are in *Bombina* toads in central Europe, and *Triturus* newts in western France and the northern Balkans. Ecological correlates of the distribution pattern are altitude and slope in *Bombina variegata* that is surrounded by *B. bombina* (ARNTZEN, 1978;1996), forestation and slope in *T. marmoratus* that is surrounded by *T. cristatus* (ARNTZEN and WALLIS, 1991), and as yet undetermined for a *T. karelinii* enclave that is sandwiched by *T. cristatus* and *T. carnifex* (ARNTZEN and WALLIS, 1999; ARNTZEN, 2003). The best explanation in each of these cases is the movement of the contact zone or hybrid zone in which the surrounded and isolated species is receding.

The distribution pattern of marbled newts on the Iberian Peninsula suggests that *T. pygmaeus* has been advancing at the expense of *T. marmoratus*. Given the change in range border, it further suggests that in central Portugal the advance of *T. pygmaeus* is stopped or impeded by the River Tejo. An essential difference between a river and other landscape elements that could act as barriers to dispersal is the linear aspect of the former. It is reasonable to assume that the strength of the barrier is related to the width of the river and that rivers are semi-permeable barriers. The actual strength of the barrier will be difficult to determine because it is possible that *T. marmoratus* in area C is not displaced from movements of *T. pygmaeus* across the River Tejo, but from the west and from the east (see arrows in Fig. 2B). Yet another possibility is that the newts do not cross the river, but that 'the river crosses the newts' through the redirection of its course or oxbow formation. Once the river has been passed and populations are settled, there is no impediment to further range expansion until the next barrier is encountered. Following this scenario of a northward advance of *T. pygmaeus* we can estimate from the models the position at which its advance will be stopped (Fig. 3, dashed line). If it was not for the barrier effect of the River Tejo, the position of the contact zone would be located ca. 40 km to the north. A corollary of this interpretation is that the *de novo* observation of geographical variation in the ecological parameters determining the range limit of species might reflect the non-equilibrium condition of the species and their environments.

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