

Niche conservatism determines the occurrence of allopatric populations of *Hyla meridionalis* in different biogeographical scenarios

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Abstract. Niche conservatism controls the distribution of many amphibians during both speciation and invasion processes. In a few species it is possible to investigate the ecological divergence between isolated populations. *Hyla meridionalis* is an anuran with a distribution pattern of one group of alien populations in southwestern Europe and two allopatric groups of populations in northern Africa that have been diverging for an estimated period of between 2 and 12 million years. In this study we tested the hypothesis that niche conservatism determines the occurrence of a species on two distinct niche scales and in separate geographical regions. Our results indicate that *H. meridionalis* in some places occupies aquatic habitats that are suboptimal for other anuran species. This fact may have favoured its persistence in this niche and establishment in regions where no equivalent species occur. The two lineages of *H. meridionalis* overlap extensively in the climate space, even though the western lineage has spread into more marginal niches. Overall, our results support the hypotheses that niche conservatism controls the dispersal and distribution of populations and that a species' niche can be stable on an evolutionary time scale.

Key words. Amphibia, Anura, Hylidae, alien species, larval habitat, Mediterranean tree frog, range limits.

Introduction

It has recently been observed that although some genera of vertebrates are highly diverse, this diversity is not reflected in their niche radiation and some related species share the same ecological space (WIENS 2004, HAWKINS et al. 2006, COOPER et al. 2011). The ranges of these conservative species are maintained by interspecific competition or environmental barriers including steep thermal or aridity gradients that species are unable to overcome, which promote further genetic isolation (KOZAK & WIENS 2006, AHMADZADEH et al. 2013). This niche conservatism also controls the invasive dispersal of several alien species (WIENS & GRAHAM 2005). Several aliens have spread into niches that are similar to those they occupy in their native ranges and offer conditions that are within their eco-physiological ranges of tolerance (RODDA et al. 2011). In the case of amphibians there is also evidence of phylogenetic patterns in the worldwide niche space (HOF et al. 2010), possibly determined by their poor capacity for dispersal and their relatively strict physiological requirements (WELSH & LIND 1996, ARAÚJO & PEARSON 2005). For these reasons many alien amphibians occupy niches that are similar or identical to those in their native range (GOVINDARAJULU et al. 2006, ESCORIZA et al. 2014).

In this study we investigated the niches of an anuran species, the Mediterranean tree frog *Hyla meridionalis* BOETTGER, 1874, with the aim of identifying whether niche conservatism is a trait shared by the allo-parapatric populations of this species. In North Africa *H. meridionalis* occurs from northern Tunisia to the Atlantic coast of Morocco (SALVADOR 1996, BEN HASSINE & NOUIRA 2012). It also occurs in Europe, where it occupies a discontinuous range: one group of populations inhabits southern France, northwestern Italy, and the northern Iberian Peninsula, and the other group occurs in the southwest of the Iberian Peninsula (GASC et al. 1997). These European populations may be the result of a relatively recent invasion from Morocco, probably associated with human activities (RECUERO et al. 2007). In Europe *H. meridionalis* maintains a nearly parapatric range with native hylids, except in the southwest of the Iberian Peninsula, where there is a large overlap between *H. meridionalis* and *H. molleri* (GASC et al. 1997, PLEGUEZUELOS et al. 2002, LOUREIRO et al. 2008). The African populations show a high degree of genetic divergence with the populations of Tunisia and northeastern Algeria having separated from the Moroccan populations 2–12 mya (RECUERO et al. 2007, STÖCK et al. 2008). In fact such high degree of divergence has implicitly been suggested to be indicative of specific separation, but the identity of

the lineage of the populations from western and central Algeria is as yet still unknown (STÖCK et al. 2012, GVOŽDÍK et al. 2015). In Morocco a genetic gradient extends from north to south and European populations belong to two distinct haplotypes, with one apparently having its origins in the southern High Atlas (populations in the southwest of the Iberian Peninsula) and the other in the Rif (populations in the north of the Iberian Peninsula, France, and on the Canary Islands; RECUERO et al. 2007). This biogeographical pattern allows for testing some hypotheses about whether niche conservatism has determined the present distribution of *H. meridionalis*. We expected that these populations occurred in relatively similar niches, because amphibian lineages show an important conservatism at several niche levels even on time scales of millions of years (KOZAK et al. 2005, KOZAK & WIENS 2010). However, the northernmost range limits of *H. meridionalis* cannot be predicted from ecological models based on the native range of the species (SILLERO 2010). Similarly, populations of *H. meridionalis* from Tunisia are mainly restricted to meso-thermal climates, while in Morocco they reach the marginal zones of the Saharan region (BONS & GENIEZ 1996, BEN HASSINE & NOUIRA 2012). These differences could indicate niche shifts or cryptic niche conservatism, whereby the native distribution does not include the entire fundamental niche of the species (SCHULTE et al. 2012).

We analysed the niche occupied by *H. meridionalis* at two spatial scales (local and regional), because the occupancy of niches at these scales is controlled by different factors (HUSTON 1999). At local level (spatial extent below 25 km²; COWLEY et al. 2001) we studied the selection of aquatic habitats, as they are key to explaining the local occurrence of an anuran species (PARRIS & MCCARTHY 1999). We also considered the type of terrestrial habitat surrounding these habitats, as this also determines the amphibian composition in the aquatic habitats (HOULAHAN & FINDLAY 2003). Furthermore, the investigation of habitat use has relevance not only to an understanding of the process of niche diversification. The existence of broad ranges in habitat selection or the occurrence in a suboptimal niche in native species may reveal some of the factors that could favour the successful establishment of an alien species (KIESECKER et al. 2001, KORSU et al. 2012). The regional niche was quantified on the basis of the species' presence at each locality and data extracted from environmental layers were used to characterize these localities. These layers describe some aspects of the climate space that are assumed to be ecologically relevant to the species (RÖDDER & LÖTTERS 2010); in amphibians these factors are related to the water-energy balance and temperature extremes (ESCORIZA & RUHÍ 2014). This quantification of the climate space occupied by species belonging to the same lineage can provide important insights into the environmental drivers that promote species diversification (RISSLER & APODACA 2007).

In summary, in this study we used *H. meridionalis* to investigate niche stability in different evolutionary and environmental scenarios. We first assessed the selected aquatic habitat on the basis of key characters of the water bodies

and the cover of adjacent terrestrial habitats, expecting to find similar preferences in the European (alien group) and the two main African lineages (hypothesis i). Additionally, we compared the habitat use of *H. meridionalis* to that of sympatric species. This study may provide some insights into the factors controlling the establishment of *H. meridionalis* in southwestern Europe. In this sense, and given the local absence of other hylid species, we expected *H. meridionalis* to occur in a vacant niche or a niche that is underused by other anuran species (hypothesis ii). Finally, we described the climate niches quantitatively and calculated whether there was niche divergence by comparing the population groups, predicting that niche conservatism determines this species' range (hypothesis iii).

Materials and methods

Study area and species

The study area included the range of *H. meridionalis* in the western Mediterranean region, encompassing northwestern Africa and southwestern Europe between 28 and 46°N latitude (SCHLEICH et al. 1996, GASC et al. 1997). The region was limited by the temperate oceanic and subtropical desert climate belts, although it mainly has a Mediterranean-type climate (KOTTEK et al. 2006). In North Africa the populations of *H. meridionalis* occur from sea level to 2,650 m a.s.l. (BONS & GENIEZ 1996, BEN HASSINE & NOUIRA 2012), while in the Iberian Peninsula, northwestern Italy, and France they occur in lowlands, mainly below 700 m a.s.l. (TEJEDO & REQUES 2002, MALKMUS 2004, EMANUELI & SALVIDIO 2006, THIRION & GENIEZ 2013). The eastern and western lineages despite their high degree of genetic divergence are morphologically very similar in the two phases of their life cycles (Fig. 1), suggesting that they could be functionally conservative. *Hyla meridionalis* is a generalist that can breed in a wide range of water body types with reproduction occurring from winter to early spring in the south of its range and to late spring and midsummer in the north (PASTEUR & BONS 1959, DÍAZ-PANIAGUA 1990, REQUES & TEJEDO 1991, ETXEZARRETA & RUBIO 1998, JAKOB et al. 1998). It is abundant throughout most of its range, although some marginal populations are isolated and locally threatened (TEJEDO & REQUES 2002, ETXEZARRETA & RUBIO 2003, BEN HASSINE & NOUIRA 2012).

Aquatic and terrestrial habitat characterisation

The surveyed aquatic habitats included seasonal and permanent water bodies and stream pools. These habitats were sampled in February to April in Morocco and Tunisia and in April to July in Europe, based on previous surveys that had shown these months to cover most of the reproductive period of the species (BEN HASSINE & NOUIRA 2012, ESCORIZA & BOIX 2012, ESCORIZA & BEN HASSINE 2013). Details of the sampled water bodies are provided in Supplementary Table 1, and sampling localities are shown in Fig-

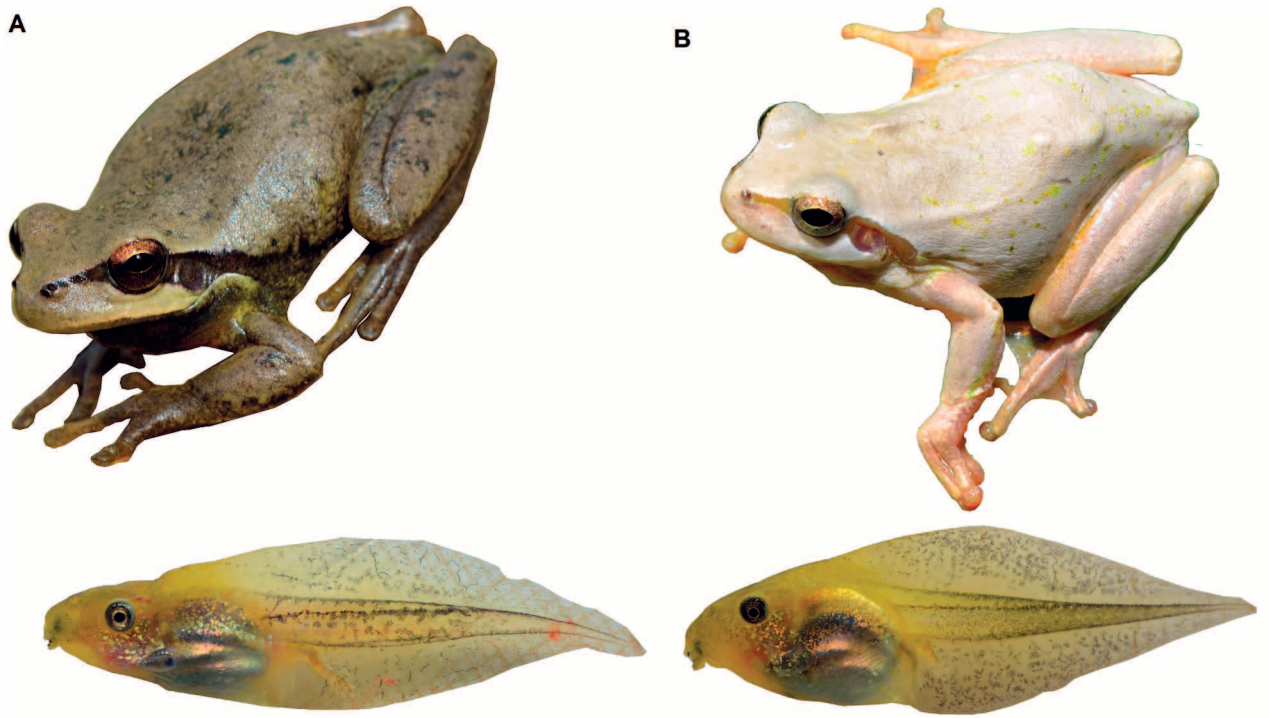


Figure 1. Adults and tadpoles of *H. meridionalis*. A) western lineage, Tangiers, northern Morocco (adult) and La Provence, France (tadpole); B) eastern lineage, Cap Bon, northeastern Tunisia (adult) and Annaba, northeastern Algeria (tadpole).

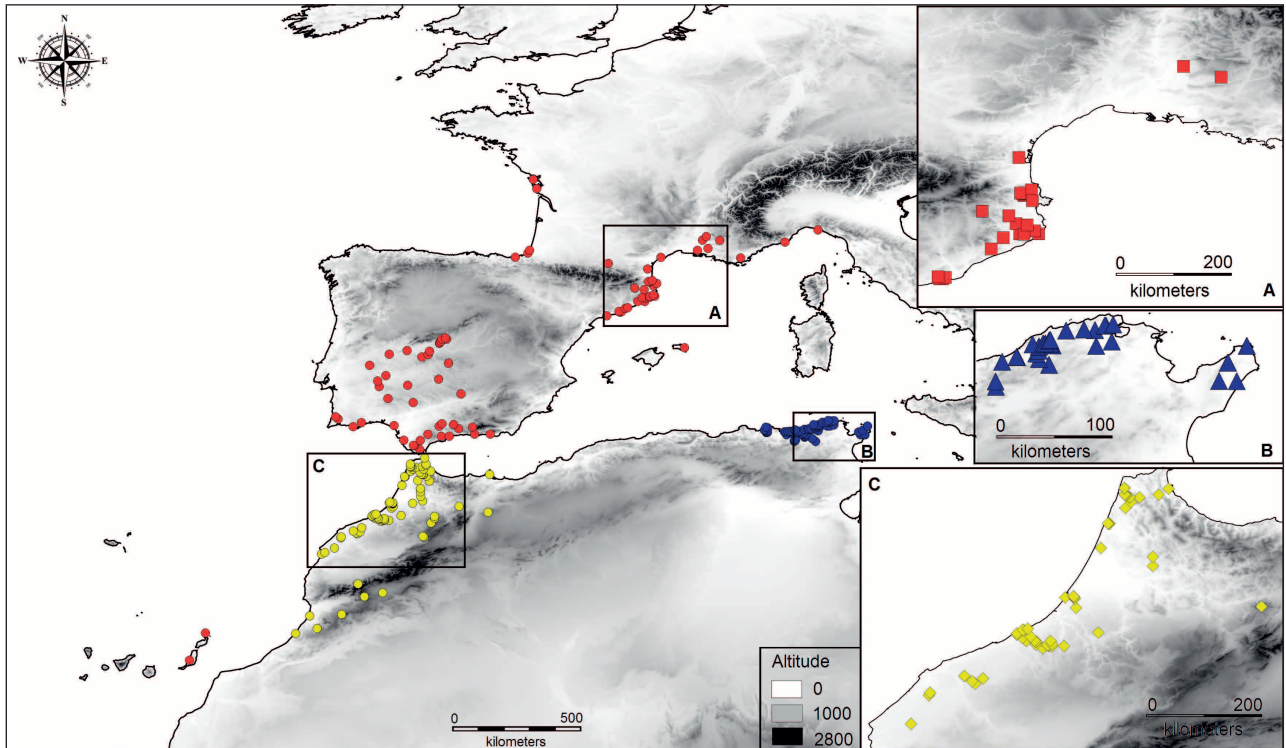


Figure 2. Study area. The coloured circles show the locations included in our climate models (yellow – western lineage native; red – western lineage alien; blue – eastern lineage). The thumbnails illustrate the locations where aquatic habitats were sampled. A) north-eastern Spain and southern France; B) northern Tunisia; C) Morocco.

ure 2. The presence of larvae was inferred from the yields of a minimum of 10 sweeps with dip nets in water bodies with a surface area less than 50 m² and up to 60 sweeps with dip nets in water bodies larger than 1,000 m², while we tried to cover all possible mesohabitats (from unvegetated to vegetated zones). The physical and chemical variables measured were the average water body surface area (m²), water column depth (cm), temperature (°C), dissolved oxygen (mg·l⁻¹), pH, and conductivity (µS·cm⁻¹). The average depth was taken as the mean value of five successive measurements from the shore to the centre. Surface area was calculated from the maximum length and width of the water body and assuming an elliptical shape. In water bodies larger than 100 m² the surface area was estimated using a Garmin Dakota 100. Chemical water parameters were measured in situ, using a Crison 524 conductivity meter (for conductivity), an EcoScan ph6 (for pH), and a Hach HQ10 Portable LDO meter (for the dissolved oxygen content). Aquatic habitats were sampled between 12 and 15 h (local time) in order to maintain maximum homogeneity in the measurements.

The land cover types surrounding each aquatic habitat were obtained from the GlobCover 2009 database (BONTEMPS et al. 2011). The categories were extracted from the coordinates of each aquatic habitat by using the Quantum-GIS 2.0 package (QGIS Development Core Team 2013) and describe the terrestrial habitat surrounding the aquatic habitats. This database classifies the land cover into 23 categories from forests to urban areas, and is based on satellite photographs having a spatial resolution of 300 m.

Climatic data

Climate data were obtained from 264 records, 83 from Western Europe and the Canary Islands, 94 from Morocco, and 87 from Tunisia and Algeria, covering most of the range of *H. meridionalis* (Fig. 2 and Supplementary Table 2). Of these records 226 were collected in situ by using a Garmin Dakota 100 navigator, while 38 records from Spain, France, and Algeria were obtained from previously published data (BARBADILLO & LAPEÑA 2003, IRAOLA et al. 2003, DUFRESNES et al. 2011, SAMRAOUI et al. 2012). We characterized the environmental water-energy balance by using an aridity index (AIT): mean annual precipitation/mean annual potential evapotranspiration (TRABUCCO & ZOMER 2009). Thermal ranges were assessed based on the mean temperature of the warmest quarter (MTWQ), i.e., a 3-month period, and the mean temperature of the coldest quarter (MTCQ). These climatic data were obtained from the WorldClim database (HIJMANS et al. 2011) and the Consortium for Spatial Information (TRABUCCO & ZOMER 2009). Using the Quantum-GIS 2.0 package (QGIS Development Core Team 2013), data from these variables was extracted for each locality with a spatial resolution of 30 arc-seconds.

Data analyses

Habitat selection: The degree of resemblance in the selection of aquatic habitats within groups and relative to other anuran species was assessed by performing an Outlying Mean Index (OMI) analysis. This method explores the tendency of a species to occupy a specific habitat, pinpointing the position of a species within the available niche space and its niche breadth (DOLÉDEC et al. 2000). The OMI measures the marginality of the niche (those species that show high values of OMI) and the tolerance of a species (high tolerance values indicate that a given species has a broad niche). These indices were computed for the three groups of populations and for an outgroup (absences), on the basis of the characteristics of aquatic habitats. Habitats with species absence were defined as those water bodies within the range of *H. meridionalis* where we could find no larvae of this species, but in which at least one other anuran species was observed. The statistical significance of the OMI indices was obtained after 999 Monte-Carlo randomisations.

The relative contribution of environmental factors (aquatic habitat descriptors and the type of land cover) to explaining the occurrence of *H. meridionalis* was established using binomial generalised linear models (GLM). The best explanatory models were selected based on Akaike's Information Criterion (AIC) (BURNHAM & ANDERSON 2002) by comparing all possible combinations of variables. The variables included land cover type, the first axis of the principal component analysis (PCA) obtained for the variables 'surface area' and 'average depth' (water body size), and the first axis obtained by PCA for the physical and chemical properties of the water (water parameters). The models were compared using AIC values and two associated measures: delta AIC (Δ_i) and Akaike weights (w_i). In general, a Δ_i value < 2 is strong evidence for the model, while the best model among the various candidates has the w_i value closest to 1. The relative contribution of each variable was estimated by the sum of w_i for those models in which this variable was included (BURNHAM & ANDERSON 2002). These statistics were calculated by using the package AICcmodavg (MAZEROLLE 2013) for the software R (R DEVELOPMENT CORE TEAM 2011).

Climate space: Climate space based on the three climatic variables was visualised by using a Principal Component Analysis ordination. To evaluate niche divergence we conducted niche equivalency and background similarity tests, comparing the actual ecological niche model (ENM) with random models generated from pseudoreplicate datasets (WARREN et al. 2008). The niche equivalency test (NET) assesses whether the ENMs drawn from allopatric populations of two species are more similar than expected for the null hypothesis that their ENMs are not equivalent. The background similarity test (BST) reveals whether ENMs based on the distribution of two geographically separated species resemble each other more than expected in relation to the local environmental background available to

each population (WARREN et al. 2010). These models were created by using the climatic variables AIT, MTWQ, and MTCQ. The statistical significance of the values for niche overlap (based on Schoener's D and modified Hellinger distances I) was assessed from 99 permutations (WARREN et al. 2008). The ENMs for the various population groups (native for the western lineage and native and alien for the western, eastern lineages, and two Moroccan haplotypes) were run with 75% of the locations allocated to training and with a regularisation value of 1, enabling linear, quadratic, and hinge features based on the number of presence records for the species (ANDERSON & GONZALEZ 2011). In the projection the 10th percentile of the predicted training values indicated species presence (PEARSON et al. 2007). The accuracy of the model was calculated based on the area under the ROC curve (AUC). These analyses were performed by using the package phycoclim (HEIBL & CALENGE 2013) for R (R Development Core Team 2011) and MaxEnt 3.3.3k (PHILLIPS et al. 2006).

Results

Aquatic and terrestrial habitat selection

The descriptive statistics obtained from the characterisation of larval habitats are shown in Supplementary Table 1. The three groups of populations exhibited a wide range in terms of the selection of water body morphology (i.e., surface area and depth) and water parameters. The results of the OMI analysis revealed that the first axis was related to the water body morphology, while the second axis was related to water parameters (Fig. 3). Depth was the most important factor explaining the occurrence of *H. meridionalis* when compared with absence groups. The position on the first factorial plane indicated that the European populations occupy a more marginal niche that will be differenti-

Table 1. Habitat selection of the studied groups of populations of *H. meridionalis*. The variability of species niche (Inertia), the group centroid (OMI, Outlying Mean Index), the group tolerance (Tol), the residual tolerance (Rtol), the percentages of variability (%), and their significances (p-values) are shown. Significant values marked in bold.

	Inertia		OMI	Tol	Rtol	p
Europe	5.17	index	0.43	0.81	3.92	0.023
		%	8.5	15.6	75.9	
Morocco	4.28	index	0.23	1.03	3.02	0.014
		%	5.3	24.1	70.50	
Tunisia	5.40	index	0.26	1.27	3.87	0.07
		%	4.8	23.5	71.7	
Absence	7.63	index	0.16	1.19	6.28	0.004
		%	2.1	15.6	82.2	

ated from native groups by the water body depth (Table 1 and Fig. 4). However, the three groups had an important overlap in niche space (Fig. 4).

With regard to land cover our data indicated that all three groups were associated with open terrestrial habitats: mosaic cropland (59% of total habitat area) and rain-fed cropland (32%) in Tunisia, mosaic cropland (38%), rain-fed cropland (23%), and mosaic vegetation (17%) in Morocco, and rain-fed cropland (21%), mosaic cropland (17%), mosaic vegetation (17%), and closed broad-leaved deciduous forest (10%) in Europe. In the three study regions, the variables 'water body size' and 'water parameters' made similar contributions to both PCAs (Supplementary Table 3). Only one model for Tunisia was supported (Table 2). The variable that most explained the occurrence of *H. meridionalis* was 'water body size' ($w_i = 0.96$), with the contributions of the variables 'land cover' ($w_i = 0.26$) and 'water parameters' ($w_i = 0.26$) being less important. Two models for Morocco

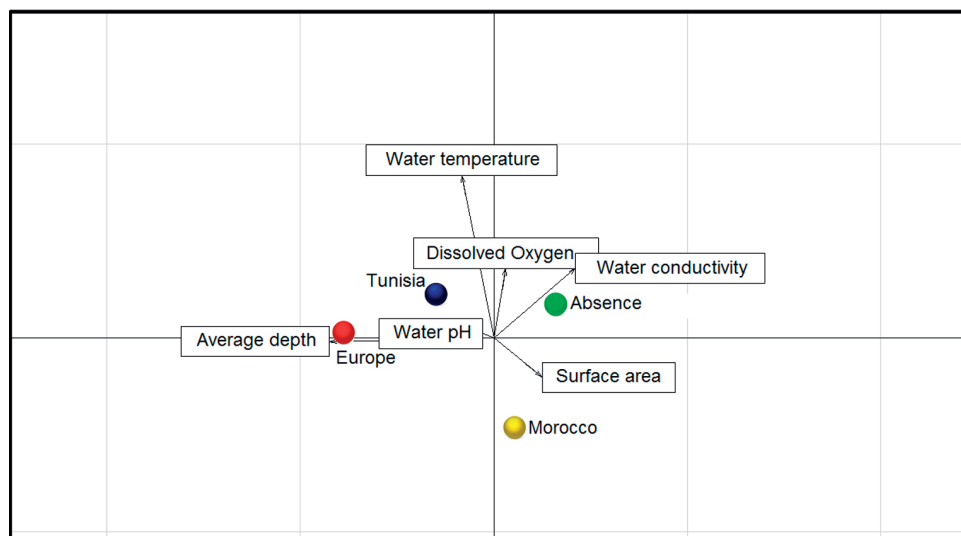


Figure 3. Aquatic habitat selection. Position of the *H. meridionalis* groups and environmental vectors on the first two axes of an Outlying Mean Index analysis. Percentages of explained variation Axis 1 = 64.2%, Axis 2 = 31.9%.

Table 2. Generalised linear model of *H. meridionalis* occurrence using the best subset of variables. Size – values of axis 1 of PCA based on water body size variables; water chemistry – values of axis 1 of PCA based on physical and chemical water parameters; land cover – vegetation categories. Δ_i – delta AIC; w_i – Akaike weights. Most supported models are those that showed $\Delta_i < 2$.

	Model	AIC	Δ_i	w_i
Tunisia	1 size	131.50	0.00	0.54
	2 size + water chem	133.60	2.10	0.19
Morocco	1 size	64.68	0.00	0.47
	2 size + land cover	66.53	1.86	0.19
	3 size + water chem	66.76	2.08	0.17
Europe	1 size	100.55	0.00	0.48
	2 size + water chem	101.88	1.33	0.25
	3 size + land cover	102.60	2.05	0.17

were supported, although the w_i values suggested that the first model was better (Table 2). The variable that most explained the occurrence of *H. meridionalis* was ‘water body size’ ($w_i = 0.79$), whereas the contributions by ‘land cover’ ($w_i = 0.28$) and ‘water parameters’ ($w_i = 0.26$) were less important. Two models for Europe were well supported, although the w_i values suggested that the first model was better (Table 2). The variable that most explained the occurrence of *H. meridionalis* was ‘water body size’ ($w_i = 0.99$), whereas the contributions by ‘land cover’ ($w_i = 0.27$) and ‘water parameters’ ($w_i = 0.34$) were less important.

Climate space

The PCA results showed an important overlap in the climate space among the three population groups. The eastern lineage was fully contained within the range of the

Table 3. Results of a background similarity test based on three climatic variables: mean temperature of the warmest quarter, mean temperature of the coldest quarter, and aridity index. 95% CI – confidence intervals obtained after 99 permutations; S/N haplotype – haplotypes from southern and northern Morocco, including the alien range; D – Schoener’s D; I – modified Hellinger distances; S haplotype – southern Morocco haplotype; N haplotype – northern Morocco haplotype.

Observed range	Background range	Similarity statistics	Observed value	95% CI
Tunisia	Morocco	D	0.23	0.12–0.13
		I	0.48	0.34–0.35
Morocco	Tunisia	D	0.23	0.45–0.47
		I	0.48	0.70–0.72
Europe	Morocco	D	0.49	0.35–0.36
		I	0.80	0.60–0.62
Morocco	Europe	D	0.49	0.47–0.48
		I	0.80	0.71–0.72
S haplotype	N haplotype	D	0.44	0.43–0.45
		I	0.77	0.72–0.74
N haplotype	S haplotype	D	0.44	0.26–0.27
		I	0.77	0.52–0.54

western lineage (Fig. 5). The results of NET indicated that the ENMs for the Tunisian and Moroccan lineages were not ecologically equivalent for the two similarity metrics (similarity p values = 1). The BST revealed that the ENMs for the Tunisian group were more similar than expected, given the available climate space for the Moroccan populations, but the Moroccan ENMs were less similar than expected, given the available background of the Tunisian populations (Table 3). NET comparison of the alien and native populations within the western lineage also revealed that both

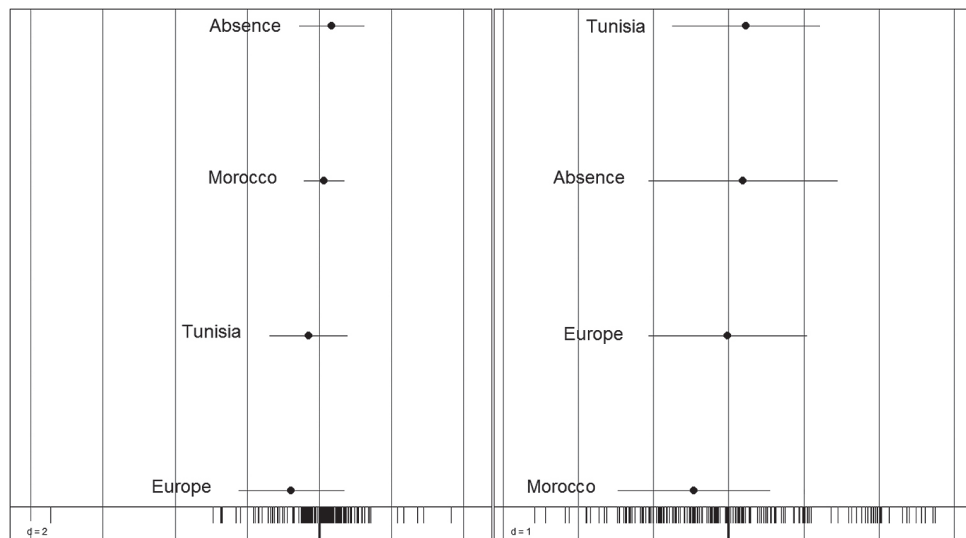


Figure 4. Niche position and niche breadth on the first two axes of an Outlying Mean Index analysis.

ENMs were not ecologically equivalent (similarity p value = 1). The BST indicated that the ENMs for the alien populations were more similar to the Moroccan ENMs than expected by chance, and reciprocally, the ENMs for the Moroccan group were more similar to the alien ENMs than expected by chance (Table 3). The results of NET indicated that the ENMs for both Moroccan haplotypes were not equivalent for the two similarity metrics (similarity p value = 1). The BST indicated that the ENMs for both Moroccan haplotypes were more similar than expected by chance (Table 3). The ENMs produced an AUC of 0.93 for the native group in the western lineage (Fig. 6A), 0.92 for the western lineage (alien and native localities, Fig. 6B), 0.96 for the eastern lineage (Fig. 6C), 0.88 for the southern Morocco haplotype (Fig. 6D), and 0.95 for the northern Morocco haplotype (Fig. 6E), indicating a high predictive value for these models. These results also indicated that aridity contributed similarly in the full-scale western (Fig. 6B) and eastern (Fig. 6C) lineage models, whereas the contribution of temperature was more variable (Table 4). The model only involving the native populations of the western group failed to predict part of the invasive range, while the

model involving both native and alien populations overestimated the range of the species, specifically in the west and southeast of the Iberian Peninsula (Figs. 6A and 6B). The projections for both main lineages in North Africa were similar, but the suitable conditions for the western lineage extended farther south in Morocco to near the margins of the Sahara (Figs 6B+C). There were also differences in the projections obtained for both Moroccan haplotypes and the model generated for the southern haplotype predicted a larger suitable area in Morocco (Figs 6D+E).

Discussion

Habitat selection and species invasiveness

Our results demonstrate that the three groups of populations of *H. meridionalis* occupy similar aquatic habitats and that their local presence is determined mainly by water body size (or the hydroperiod, as both variables are related; BROOKS & HAYASHI 2002). This is probably related to this species requiring a minimum aquatic period of 2–4 months to facilitate complete larval development (DÍAZ-

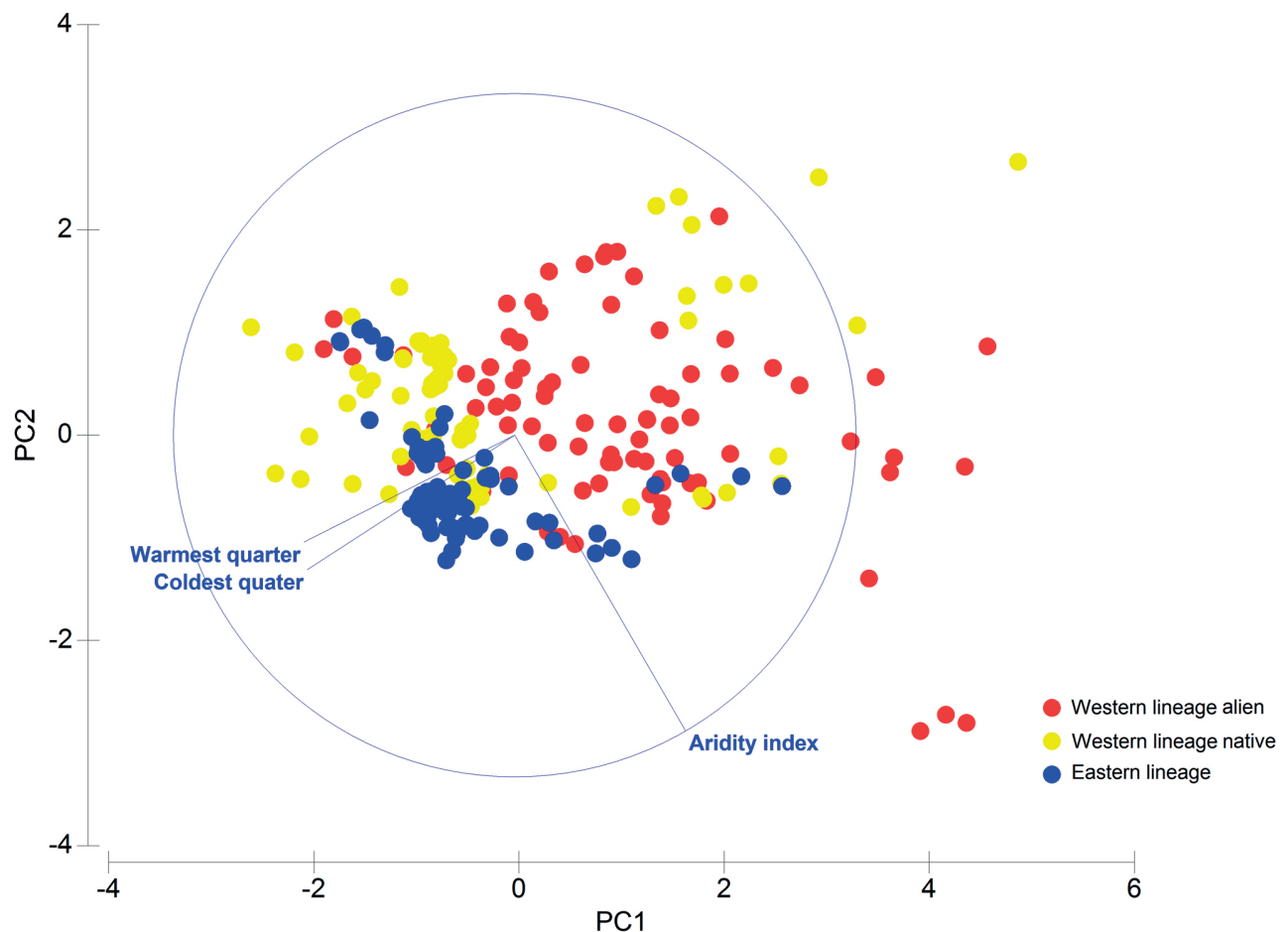


Figure 5. Climate space obtained from three bioclimatic layers (aridity index, mean temperature of the warmest quarter, and mean temperature of the coldest quarter). PCA ordination including populations and environmental variables (arrows). Percentages of explained variation PC1 = 63%, PC2 = 24%.

Table 4. Relative contributions of climate variables to the ENMs shown in Figure 6.

	Variables	Percent contribution	Permutation importance
Model A (Native western lineage)	Aridity index	43.3	40.0
	Temp. warmest quarter	15.5	13.7
	Temp. coldest quarter	41.2	46.3
Model B (Western lineage native + alien)	Aridity index	38.2	50.2
	Temp. warmest quarter	34.4	22.7
	Temp. coldest quarter	27.4	27.1
Model C (Eastern lineage)	Aridity index	36.6	44.8
	Temp. warmest quarter	56.0	48.6
	Temp. coldest quarter	7.4	6.5
Model D (Southern Morocco haplotype native + alien)	Aridity index	33.7	73.0
	Temp. warmest quarter	62.5	14.9
	Temp. coldest quarter	3.8	12.2
Model E (Northern Morocco haplotype native + alien)	Aridity index	58.7	79.7
	Temp. warmest quarter	24.7	18.8
	Temp. coldest quarter	16.7	1.8

PANIAGUA 1986). Although this species is able to reproduce in a wide range of water bodies (DÍAZ-PANIAGUA et al. 2005), our results indicate that it tends to occupy deeper water bodies than other anuran species. This suggests that *H. meridionalis* exploits a suboptimally occupied niche, corresponding to medium-sized nektonic larvae (DÍAZ-PANIAGUA 1985). Several factors could control this segregation, including the greater diversity of predators in this type of water body, which greatly reduces the presence of other amphibian species (BABBITT et al. 2003). In this sense species of the genus *Hyla* display some strategies to reduce predation (e.g., active swimming behaviour; CHOVANEC 1992). Moreover, the analysis of land cover data appeared to indicated that the terrestrial habitat did not con-

tribute to the occurrence of the species, which contrasts with observations for other anuran species that are sensitive to changes in the vegetation structure through anthropogenic disturbance (GUERRY & HUNTER 2002, POREJ et al. 2004). This may also have favoured the invasive potential of *H. meridionalis*, which has managed to successfully colonize agricultural and urban landscapes in southwestern Europe (BEJA & ALCAZAR 2003, THIRION & GENIEZ 2013).

Divergence in the realised niches

The result of our analysis of climate data indicate that the allo-parapatric groups of populations occupy different re-

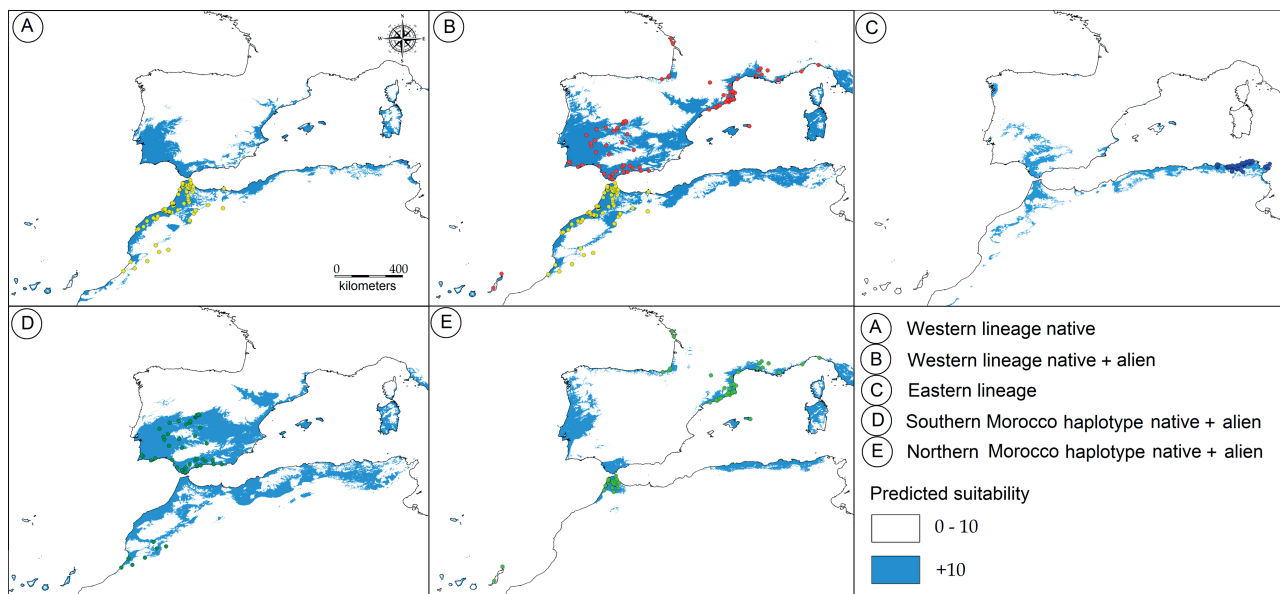


Figure 6. Ecological niche models for lineages in *H. meridionalis*, using three bioclimatic layers (aridity index, mean temperature of the warmest quarter, and mean temperature of the coldest quarter). The blue layer marks the 10th percentile of the predicted training values.

alised niches. The differences in climate space were mainly caused by the occurrence of the populations in separate geographic areas. This interpretation is supported by the results of the BST, which revealed a greater similarity between population groups than was expected by chance. The exception was the lineages in North Africa, where the native group of the western lineage occupied a wider niche than the eastern group. The two lineages present in North Africa occur in humid, sub-humid, and semiarid regions (BONS & GENIEZ 1996, BEN HASSINE & NOUIRA 2012). However, *H. meridionalis* extended its niche to arid regions in southern Morocco, but not in Tunisia, although regions with similar climatic conditions are present in Tunisia. This difference can be explained by a greater tolerance to aridity of the western native populations, suggesting a niche shift between these lineages. Alternatively, penetration into the arid regions of southwestern Morocco may be favoured by the local orography. *Hyla meridionalis* occurs up to the alpine areas in the Atlas Mountains (BONS & GENIEZ 1996), which extend in a northeastern to southwestern direction. The relatively humid conditions in these mountains have favoured the southern dispersal of several mesic species (COURTNEY & CHEW 1987, ALAOUI HARONI et al. 2009) that have followed river systems originating in the Atlas and Anti-Atlas mountains (oued Masa, oued Souss, and oued Draâ), where most of the records of *H. meridionalis* in the arid region of Morocco are concentrated. This explanation is supported by our ENM results, which indicate that aridity contributed similarly to the eastern/native-western models and were the variable with the greater explanatory capacity in the models generated for both Moroccan haplotypes.

The European populations occur mainly in Mediterranean-type climates and are favoured by conditions similar to those in the native range of the species. The boundaries of this invasion are probably determined by two factors: competition, mediated by the occurrence of other hylid species (GASC et al. 1997), and climatic ecotones. Interspecific competition is a mechanism that defines evolutionarily stable ranges between species that are not segregated by habitat use (CASE et al. 2005). *Hyla meridionalis* maintains a nearly parapatric distribution with other hylid species (*H. molleri*, *H. arborea*, and *H. intermedia*) throughout most of its European range, although some overlap occurs locally in southwestern Portugal, western and central Spain, and southwestern France (PATÓN 1989, MALKMUS 2004, LESCURE & DE MASSARY 2013). In Europe *H. meridionalis* is more tolerant of Mediterranean conditions than are native hylids, which as a consequence are absent under these climatic conditions (MALKMUS 2004, MORAND 2013). Our ENMs indicate that the suitable niche in the west of the Iberian Peninsula is larger than the actual range of the species. This can be explained by the presence of *H. molleri* in this region, which may prevent colonisation by *H. meridionalis*, and is supported by the fact that these species are ecologically equivalent, occupying similar larval and adult habitats (GARCÍA-PARÍS 1985, MALKMUS 2004). This convergent use of habitats produces occasional hybridisation

between *H. molleri* and *H. meridionalis* (OLIVEIRA et al. 1991). Our ENMs also indicate that suitable conditions for *H. meridionalis* exist in the east of the Iberian Peninsula, where only small isolated populations are present (EGEA-SERRANO et al. 2005). In this region, there are no native hylid species and it is possible that the prevalence of semi-arid climatic conditions together with the scarcity of suitable aquatic habitats (TORRALVA et al. 2005) have hindered the penetration by this species.

Our ENMs indicate that much of the invasive range of *H. meridionalis* cannot be predicted solely from the native locations of the species, as has been suggested by SILVERO (2010). This is a common finding in the analysis of the niches of alien species (MACK 1996, URBAN et al. 2007), as their native ranges do not always describe their fundamental niches (cryptic niche conservatism hypothesis; SCHULTE et al. 2012). The underlying reason for this being so is that the range limits of native populations can also be determined by interactions with other species or the presence of biogeographical barriers (SEXTON et al. 2009). At its northern range limits progressively decreasing temperatures have restricted the expansion of *H. meridionalis* to regions with a maritime influence (THIRION & GENIEZ 2013). Its expansion through the Atlantic plains is possibly related to the thermal buffering effect of the ocean, which attenuates extreme climatic phases (e.g., very cold winters) that are driving forces for rapid population turnover and the extinction of marginal populations (MEHLMAN 1997). These factors may have gradually shrunk the niche of *H. meridionalis*, limiting the size and connectivity of its populations and making them more sensitive to local extinction processes (including perturbation of aquatic habitats) and ultimately preventing the species' further expansion in Europe.

Conclusions

The analysis presented herein indicates the presence of evolutionary stability in the two niche dimensions of *H. meridionalis* examined. This stability could be related to the existence of a homogeneous niche in the region that has not promoted ecological divergence between the two lineages. Our study indicates that the European populations of *H. meridionalis* are restricted mainly to sub-Mediterranean and Mediterranean climates, and that their replacing native hylid species is unlikely. Indeed, this species has so far failed to invade regions outside the Mediterranean region (e.g., in Germany, where it was introduced in 1950; NOBANIS 2014). However, the capability exhibited by this species to colonise disturbed habitats in conjunction with the global rise in temperature could favour the expansion of *H. meridionalis* into the range of native hylids, promoting negative interactions (i.e., hybridisation and competition) between these species. It is for this reason that we consider it important to monitor the contact zones between *H. meridionalis* and other hylids, with particular emphasis on aquatic habitats, in order to assess whether there appears to be a decrease in the reproductive success of native hylid species.

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Supplementary material

Additional information is available in the online version of this article at <http://www.salamandra-journal.com>

Supplementary table 1. Descriptive statistics of water.

Supplementary table 2. List of localities included in the study.

Supplementary table 3. First component of the variables.

Supplementary table 1. Descriptive statistics of water body size and physical and chemical water parameters obtained from the characterisation of aquatic habitats. Aquatic habitats where we detected the presence of *H. meridionalis* were included in “presence”, while aquatic habitats where we did not detect the presence of *H. meridionalis* were included in “absence”. n – number of water bodies; area – pond surface area (m²); depth – average pond depth (cm); T – water temperature (°C); O₂ – dissolved oxygen in water (mg·l⁻¹); pH – water pH; Cond – water conductivity (μS·cm⁻¹).

	Area	Depth	T	O ₂	pH	Cond
Tunisia						
presence	797	39	19.0	7.7	7.9	789
(n = 41)	(19–9842)	(10–121)	(13.0–26.2)	(1.8–17.1)	(6.2–9.6)	(44–4650)
absence	963	20	18.9	8.3	7.9	1514
(n = 60)	(1–18656)	(3–126)	(10.0–27.8)	(1.6–20.0)	(6.6–9.4)	(86–11140)
Morocco						
presence	21422	29	16.9	6.9	7.9	676
(n = 53)	(13–515599)	(12–74)	(9.8–23.0)	(1.9–13.7)	(6.7–9.6)	(53–4930)
absence	1222	23	15.7	8.1	8.2	653
(n = 13)	(2–7125)	(9–43)	(10.9–24.0)	(3.2–14.1)	(6.3–10.2)	(26–3500)
Europe						
presence	1526	41	18.9	7.4	8.1	294
(n = 31)	(3–8715)	(9–95)	(12.0–27.7)	(0.3–18.5)	(5.8–10.3)	(60–1040)
absence	372	33	18.7	6.2	8.0	343
(n = 40)	(2–4032)	(5–225)	(12.8–29.9)	(0.4–18.2)	(6.6–9.8)	(30–1532)

Supplementary table 2. List of localities included in the study. References: * IRAOLA et al. (2003); + DUFRESNES et al. (2011); ++ BARBADILLO & LAPENA (2003); ** SAMRAOUI et al. (2012).

Latitude	Longitude	Latitude	Longitude	Latitude	Longitude	Latitude	Longitude
Canary Islands		33.80	-7.19	35.64	-5.33	41.27	1.84
28.39	-14.10*	33.86	-3.03	35.65	-5.91	41.27	1.88
29.40	-13.51 ⁺	34.02	-6.61	35.88	-5.38	41.29	1.91
Morocco		34.07	-6.55	Europe		41.30	1.82
29.38	-10.16	34.09	-4.11	36.19	-5.57	41.41	2.05
29.56	-9.37	34.18	-6.56	36.32	-5.77	41.44	2.14
30.03	-9.64	34.18	-6.57	36.34	-5.80	41.66	2.77
30.09	-8.46	34.18	-6.58	36.52	-5.55	41.67	2.52
30.74	-7.62	34.19	-6.57	36.53	-6.16	41.79	2.79
30.89	-6.94	34.19	-6.58	36.56	8.34	41.81	2.68
31.21	-7.85	34.20	-5.83	36.68	-4.47	41.81	2.95
32.32	-9.20	34.20	-6.57	36.68	-4.76	41.85	2.96
32.38	-9.08	34.20	-6.58	36.75	-5.26	41.86	3.14
32.54	-8.73	34.21	-6.57	36.76	-2.95	41.90	3.09
32.92	-8.49	34.21	-6.58	36.76	-3.53	42.10	2.75
32.95	-5.41	34.21	-6.70	36.96	-4.13	42.16	2.40
32.95	-8.48	34.22	-6.57	37.01	-3.61	42.24	3.10
32.97	-5.45	34.22	-6.58	37.03	-8.03	42.33	3.21
33.07	-7.88	34.24	-6.67	37.05	-4.85	42.38	2.96
33.10	-7.92	34.28	-5.46	37.07	-6.52	42.4	2.90
33.14	-7.78	34.45	-5.53	37.11	-4.31	42.4	2.97
33.17	-8.02	34.62	-5.54	37.14	-4.74	42.44	3.05
33.29	-7.72	34.74	-5.54	37.18	-7.73	42.87	2.88
33.47	-5.15	34.86	-6.23	37.32	-8.59	43.07	1.42
33.54	-6.99	35.02	-5.21	37.40	-8.69	43.28	6.32
33.57	-6.71	35.04	-5.64	37.92	-5.81	43.30	-2.03*
33.57	-6.87	35.18	-6.11	38.07	-6.74	43.30	3.37
33.57	-6.91	35.18	-6.12	38.24	-4.04	43.46	-1.56*
33.58	-6.91	35.18	-6.13	38.52	-7.07	43.56	-1.50*
33.58	-6.93	35.20	-5.31	38.56	-6.01	43.56	4.73
33.59	-6.87	35.26	-2.97	38.72	-7.12	43.63	5.11
33.59	-7.08	35.26	-5.42	38.79	-4.87	43.86	7.97
33.62	-7.06	35.27	-5.44	38.92	-6.82	43.93	4.91
33.62	-7.08	35.27	-5.49	39.30	-7.42	43.93	5.55
33.63	-6.89	35.28	-5.50	39.38	-4.50	44.07	5.05
33.63	-7.10	35.35	-5.55	39.33	-5.49 ⁺⁺	44.31	9.19
33.63	-7.21	35.39	-5.16	39.70	-5.25	45.84	-1.23
33.64	-7.10	35.39	-5.90	39.42	-6.70 ⁺⁺	46.18	-1.36
33.65	-5.02	35.46	-5.42	39.82	-5.20	Tunisia & Algeria	
33.68	-7.26	35.47	-5.83	39.85	-6.04	36.48	9.10
33.69	-7.15	35.52	-5.72	39.96	4.24	36.49	8.31
33.71	-5.02	35.53	-5.84	40.15	-5.24 ⁺⁺	36.50	8.31
33.72	-7.33	35.53	-5.85	40.28	-4.76 ⁺⁺	36.52	8.35
33.73	-7.33	35.55	-5.89	40.23	-4.62 ⁺⁺	36.59	8.98
33.74	-6.26	35.56	-5.46	40.27	-4.85 ⁺⁺	36.64	8.70
33.77	-7.25	35.56	-5.90	40.29	-4.83 ⁺⁺	36.67	8.70
33.78	-7.24	35.56	-5.91	40.23	-4.74 ⁺⁺	36.68	8.71
33.78	-7.25	35.60	-5.33	41.14	1.36	36.73	10.77

Latitude	Longitude	Latitude	Longitude
36.73	10.93	37.01	7.26**
36.73	8.03**	37.01	9.11
36.73	8.71	37.02	9.26
36.74	10.93	37.05	11.02
36.74	8.59	37.05	11.03
36.74	8.72	37.05	9.11
36.75	8.74	37.05	9.54
36.77	8.58	37.06	9.23
36.78	8.27**	37.06	9.63
36.79	8.23**	37.07	9.05
36.8	8.68	37.08	9.14
36.81	7.28**	37.08	9.16
36.81	8.44	37.08	9.21
36.82	7.32**	37.09	9.78
36.83	8.11**	37.1	9.2
36.84	10.69	37.11	9.03
36.84	7.28**	37.19	9.58
36.84	7.95**	37.20	9.36
36.84	7.98**	37.20	9.62
36.84	8.13**	37.21	9.52
36.84	8.15**	37.21	9.54
36.84	8.16**	37.24	9.71
36.84	8.42	37.24	9.72
36.84	8.44	37.25	9.79
36.85	8.07**	37.26	9.58
36.85	8.08**		
36.85	8.18**		
36.86	7.27**		
36.86	7.34**		
36.86	8.15**		
36.86	8.25**		
36.87	8.52		
36.88	7.30		
36.88	9.20		
36.89	7.32**		
36.9	10.85		
36.9	7.21**		
36.91	7.21**		
36.91	8.34		
36.91	8.77		
36.92	8.34		
36.92	8.94		
36.93	9.11		
36.94	8.69		
36.94	8.83		
36.95	8.85		
36.95	8.90		
36.95	8.92		
36.96	8.93		
36.98	9.08		
36.99	7.33**		

Supplementary table 3. First component of the variables included in the Generalised Linear Model. The table provides the explained variance (in %) and the factor loadings.

Dimension	First axis	Tunisia	Morocco
Water body size	Explained variance	50.4%	51.3%
	Surface area	0.71	0.72
	Average depth	-0.71	0.72
Water parameters	Explained variance	43.9%	45.3%
	Temperature	0.67	0.49
	O2	0.82	0.89
	pH	0.68	0.77
	Conductivity	0.42	0.41