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Uncovering the rules of (reptile) species coexistence in transition zones between bioregions

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Abstract. Transition zones between bioregions can sustain the coexistence of species with different biogeographic affinities through ecological niche segregation at a finer scale. Reptiles can serve as a good model group to evaluate the mechanisms behind such coexistence patterns especially due to their thermal sensibility to microhabitat structure. We examined whether reptile species spatially segregate in their microhabitat use and whether this segregation reflects the biogeographic affinities of species. Reptiles were surveyed across a 1.5-km transect located in the Peneda-Gerês National Park. We used 478 GPS observations of nine sympatric non-Mediterranean and Mediterranean species collected during field surveys in 2012 and 2013. Each observation was assigned to a microhabitat-openness measurement. Differences in microhabitat selection between Mediterranean and non-Mediterranean species were studied with factorial ANOVA analyses. The similarity in microhabitat selection between pairs of species was compared with the similarity in their Iberian distributions by a Partial Mantel test checking for the genetic distances between species pairs in a phylogenetic framework. Comparing a random selection of points along transect, we found that non-Mediterranean species used more closed microhabitats than Mediterranean species. No differences in this pattern were found between snakes and lizards. The Mantel test showed that microhabitat selection was correlated with the Iberian geographic distributional patterns of species. The complex vegetation structure of this area is most likely responsible for the availability of different microhabitats, which promotes high reptile species richness and governs their sympatric coexistence at a finer scale.

Key words. Squamata, distribution pattern, biogeographic affinities, habitat selection, community ecology.

Introduction

Transition zones between bioregions are areas of exceptional species and habitat diversity across many taxonomic groups (Spector 2002). In this context, an intriguing question in community ecology is to understand the reasons behind this pattern of generally high species coexistence in such "bioregion crossroads". Often, the mechanism of release of potential interactions between community members is spatial segregation (e.g., Langklide & Shine 2004). On this spatial axis, species can avoid interactions by subtle differences in microhabitat use (Pianka 1973) that are in turn also connected with species' eco-physiological constrains (e.g., Žagar et al. 2015a) or with species-specific behavioural responses (e.g., differential chemical recognition of predators, van Damme & Quick 2001).

Reptiles can serve as a good model group to evaluate mechanisms that govern the rules of species coexistence taking into account the spatial axis (Pianka 1973, Carretero 2004). Spatial segregation is only rarely complete in reptile communities, thus, areas of distributional overlap of several reptile species are common in nature (e.g., Luiselli 2006, Žagar et al. 2013). In such areas of coexistence, species can either segregate by occupying ecological niches that are separated at a fine-scale (e.g., Pianka 1986) or display and increased level of interaction (e.g., Downes & Bauwens 2002). Interactions between sympatric species of lizards and snakes can be promoted either by interference competition (e.g., Downes & Bauwens 2002, Lailvaux et al. 2012, Žagar et al. 2015b) or indirectly by exploitative competition for limited resources such as food or refuges and basking sites (e.g., Luiselli 2006, Metzger et al. 2009). Alongside interactions, segregation patterns, as a consequence of avoidance of interaction, have already been observed between several reptile species pairs (e.g., Toft 1985, Luiselli 2006).

The Iberian Peninsula was identified as one of the world's biodiversity hotspots (Myers et al. 2000), hosting almost 50% of the European plant and terrestrial vertebrate species (Araújo et al. 2007). It has a high spatial heterogeneity (Pascual et al. 2011) and being the limit between two major bioregions, namely Mediterranean and Atlantic (EEA 2012), it features a notable environmental gradient. Environmental heterogeneity, a major determinant of diversity, has been indicated as highly important to species richness (Begon et al. 2006). Habitat heterogeneity, marked by different habitats from one spot to another, have also been linked to animal species diversity (see review in Tews et al. 2004) but not in the case of some of the Iberian faunae (Moreno-Rueda & Pizarro 2009). However, in a transition zone between the two major Iberian bioregions, Soares & Brito (2007) demonstrated that the distribution of amphibian and reptile species richness was correlated with a mixture of climatic, topographical, and habitat factors depending on the biogeographic traits of species.

Using climatic-factor preferences assigned to Iberian reptile species, Sillero et al. (2009) observed that Mediterranean and non-Mediterranean species segregate their habitats according to the degree of solar exposure or vegetation structure complexity. This environment-based mechanism of segregation implies that species would segregate at a large geographic scale by respecting the borders of bioregions (Sillero et al. 2009). However, the distribution ranges of species according to their biogeographic affinities are often not as precise as the borders of bioregions (Pleguezuelos et al. 2002, Loureiro et al. 2008), and several lizard and snake species distributions overlap and they coexist especially across the limits of bioregions (Sillero et al. 2009). In these transition zones, fieldwork-based studies can test the rules that govern species coexistence, hence predicting the likelihood of potential interactions (direct or indirect competition) using intra-guild species members.

Our study focused on the reptile assemblage located in the border zone of two bioregions (Mediterranean and Atlantic) in northern Portugal. The first aim was to identify whether species spatially segregate on a fine-scale habitat level by examining interspecific differences in microhabitat selection. The second aim was to test whether the spatial segregation between species was related to their distribution ranges across the Mediterranean and Atlantic bioregions in Iberia (i.e., biogeographic affinities). We predict that species with similar distribution patterns in Iberia will select similar microhabitats. Understanding the mechanisms behind high species' coexistence in the border area between bioregions can benefit the transfer of this knowledge as a conservation measure to areas with lower species richness.

Materials and methods

Study area

Our study was performed in the Homem River valley (41°48' N, 8°7' W; mean altitude 740 m above sea level), a fully protected area within the Peneda-Gerês National Park in northern Portugal (Fig. 1). The mean annual rainfall average is 3,200 mm with ranges from 55 mm in July to 457 mm in January on more than 130 rainy days per year, and mean air temperatures vary here between 7.9°C in January and 20.3°C in July (Godinho & Machado 1993, Vieira 1996). The park is located in a transition zone between the Atlantic and Mediterranean biogeographic regions (EEA 2012) and holds a microclimate mosaic that facilitates the existence of typical Mediterranean, Euro-Siberian, and Alpine species (ICN 1995, Araújo et al. 2006). The vegetation at the study site is composed of deciduous oak forests of *Quercus robur* and *Q. pyrenaica* (Honrado et al. 2001) interspersed with arbutus trees (*Arbutus unedo*) and scrubland of low shrubs of heath (*Erica* sp. and *Calluna vulgaris*), gorse (*Ulex* sp.), and tall scrubs of brooms (*Cytisus* sp. and *Genista* sp.) (Serra & Carvalho 1989). Among these vegetated areas are outcrops of large granite rock that are patchily distributed. This land-cover mosaic provides several microhabitats, which reptiles can freely select according to their ecological preferences or as a means of avoiding pressures such as competition.

The reptile community

The Peneda-Gerês National Park has a reptile community composed of 20 species (Soares et al. 2005, Soares & Brito 2007). Eleven of these species are present in the study area (Table 1), which reflects the high herpetological significance of this spot (Soares & Brito 2007) that is considered one of the most important sites in terms of reptile species richness in Portugal (Loureiro et al. 2008). The assemblage comprises a combination of Mediterranean and non-Mediterranean species, which reflects the transitional Mediterranean-Atlantic climatic character of the locality. The biogeographic affinity of each reptile species was designated following Sillero et al. (2009) in which "A species was considered as belonging to a particular biogeographical region when its presence in that region, expressed as percentage, exceeded its presence in the other region". Recent taxonomic advances recognized a number of species within the *Podarcis hispanica* complex (Geniez et al. 2014), clarifying that the populations of northern Portugal correspond to the species *P. guadarramae*. According to the distribution of this species in Iberia, we included it in the group of Mediterranean species.

Fieldwork procedures

We searched for reptiles along a 1.5 km linear transect along the bank of the Homem River. We conducted 40 replicate visits on this transect between spring and autumn of 2012 and 2013. We used time-constrained, area-constrained survey techniques (Heyer et al. 1994). Transects were walked by one observer between 09:00 and 13:00 GMT on days with favourable weather conditions (warm sunny days) to maximize reptile sightings. A consistent sampling effort was applied during every visit by experienced observers (DF or XS) during each survey to maintain consistent observer bias. Using visual encounter surveys, every reptile was identified (species, age, and sex if possible) and its position recorded with a GPS. We did not individually mark specimens, thus we did not discard that some could be re-observed during consecutive visits. To avoid pseudoreplication, we excluded records from visits on consecutive days and only considered those visits that were at least one week apart from each other, thus allowing reptiles to move and relocate freely in their preferred habitats. Although some reptile species found at the study site have small home ranges e.g., vipers and some lizard species, the heterogeneity of the microhabitat openness guarantees that two observations of the same individual during temporally spaced visits were independent.

The microhabitat openness was measured at 10 m intervals along our transect (N = 136 intervals). At each 10-m point, we used a measuring tape to take four measures of the canopy height at two and four metres distant from the midline of the transect to either side (left and right). We measured the height to the nearest 0.1 m from the ground to the first branch with leaves of trees at each point, or in the case of bushes or herbs the total height of the plant (a similar approach as in Carrascal et al. 1989). Afterwards, we averaged the four measurements of the canopy height to assign to each 10-m segment a corresponding quantitative measurement of microhabitat openness. We then associated GPS points of every reptile find with the microhabitat openness measurements by attributing it to one of the 10-m segments. The microhabitat selection of each reptile species was then characterized by a set of microhabitat-openness scores. Juveniles were excluded from the analysis due to their distinctive activity and thermal patterns, which can differ from adults (e.g., Castilla & Bauwens 1991, Carrascal et al. 1992, Díaz 1994). To characterize the available microhabitat openness in the study area, we used measurements from all 136 points distributed equally at 10 m segments along our transect.

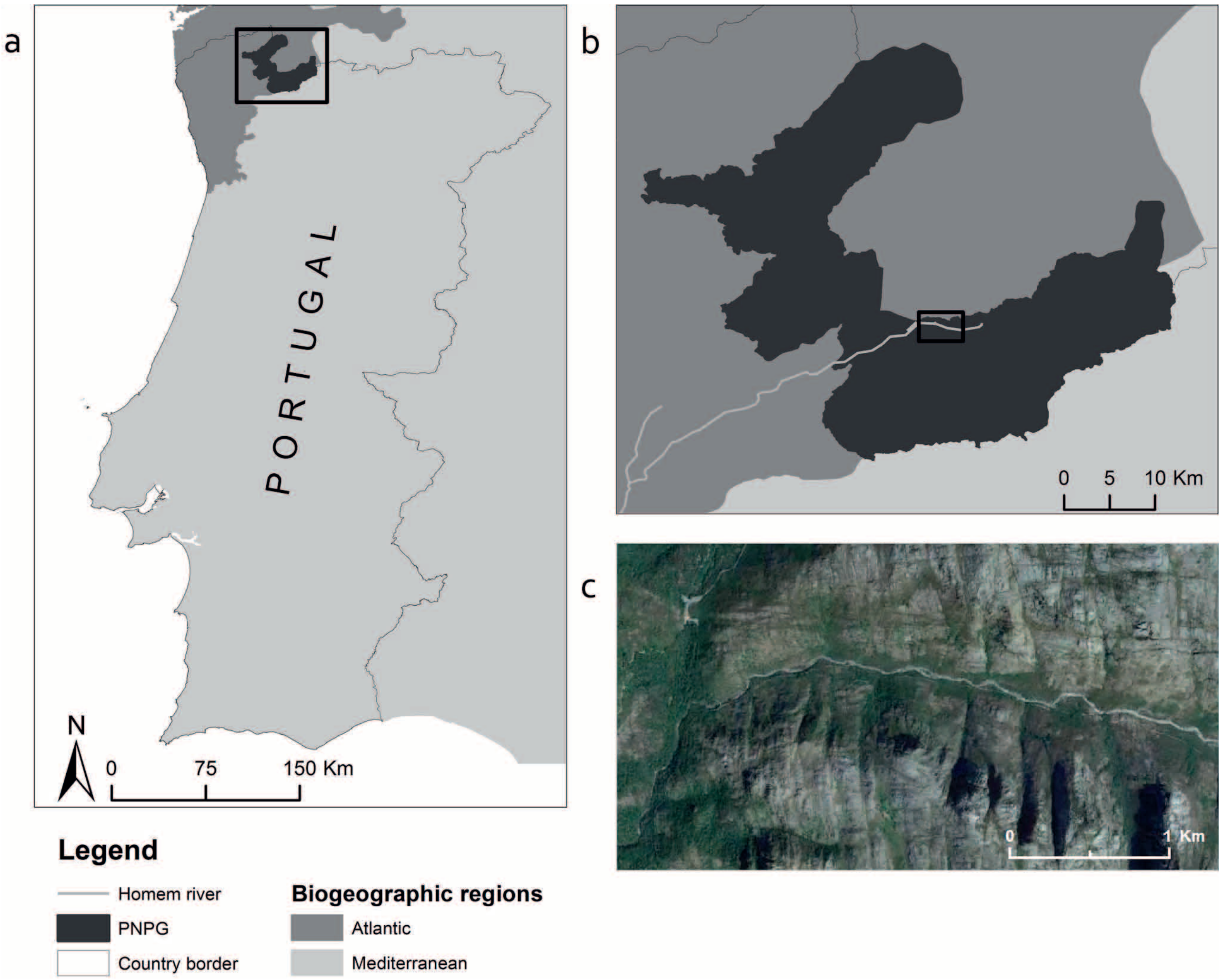

Figure 1. Location of study area. (A) The Peneda-Gerês National Park (PGNP) is located in extreme northern Portugal where two biogeographic regions meet, the Atlantic and the Mediterranean (EEA, 2012); (B) Within PGNP, the Homem River valley is a fully protected area; (C) Satellite image of the study area from 2013 (Google Earth).

Table 1. List of reptile species found during this field study in the Homem River valley in the Peneda-Gerês National Park, number of observations recorded (N_1), number of observations used for further analyses after excluding juveniles and records from consecutive days (N_2), average ± standard error of the habitat openness (HO), and biogeographic affinity according to percentage (%) of UTM 10 × 10 km squares located in Mediterranean climate areas following the procedure by Sillero et al. (2009). [a)] The percentage of squares of *Podarcis guadarramae* within Mediterranean-climate areas has not been calculated due to its recent taxonomic elevation to full species, but its biogeographic affinity was determined according to its previous taxonomic affinity (*P. hispanica*); [b)] Although 73.4% of the distribution range of *Natrix natrix* in Iberia lies within Mediterranean areas, its freshwater dependence and distribution outside Iberia justified considering it a non-Mediterranean species.

Species	N_1	N_2	HO	Biogeography (%)
Lizards				
Anguis fragilis	14	12	4.00±0.71	non-Med (0.8%)
Lacerta schreiberi	160	112	2.80±0.20	non-Med (1.7%)
Podarcis bocagei	447	270	2.53±0.13	non-Med (0%)
Podarcis guadarramae	53	21	2.19±0.51	Med (–)[a]
Psammodromus algirus	9	7	2.03±0.97	Med (95.3%)
Timon lepidus	28	6	2.89±0.54	Med (88.3%)
Snakes				
Coronella girondica	1	0	–	Med (83.5%)
Coronella austriaca	7	5	2.37±1.24	Non-Med (0%)
Natrix natrix	20	15	3.79±0.89	Non-Med (73.4%)[b]
Natrix maura	1	0	–	Med (67.1%)
Vipera latastei	45	30	1.59±0.26	Med (68.9%)

Statistical analyses

Interspecific differences in the microhabitat-openness selection were assessed by a Kruskall-Wallis test. This nonparametric test was applied since the homogeneity of variances is compromised by the unbalanced number of sightings recorded for each reptile species. When interspecific differences were significant, we examined them post-hoc with Mann-Whitney U tests between species pairs. A factorial ANOVA was performed to test for differences in microhabitat-openness selection between species according to Taxa (snakes and lizards) and Biogeographic Affinity (Mediterranean and Non-Mediterranean). The factor Taxa was included due to the different ecological requirements of both groups (i.e., snakes are mostly vertebrativores whereas lizards are largely insectivores). The factorial ANOVA also allows for examination of interactions between both factors. All the statistical analyses were performed with STATISTICA v.10.0 (Statsoft Inc. 2010).

Habitat and distribution similarity matrices

According to the frequency of observations at each 10-m segment, microhabitat-openness similarities between species were calculated using the Bray-Curtis index, and a Habitat Similarity Matrix (HABIT) was built with all pairwise comparisons. Distribution patterns of species in Iberia were established from the Asociación Herpetologica Española data set with presence/absence of each species in 10 × 10 km UTM squares (Pleguezuelos et al. 2002). Distribution similarities between species were calculated using the Jaccard index, which takes into account presences and absences in each UTM square (see Sillero et al. 2009). A Distribution Similarity Matrix (DIST) was constructed with all pairwise comparisons.

Correlations of HABIT versus DIST similarity matrices were examined with a Partial Mantel test (Manly 1997) using the genetic distance matrix (GENET) between species pairs as a covariate. The genetic distances between the species found at the study site were calculated as the evolutionary divergence based on Pyron et al. (2013) using the pairwise p-distance (the proportion of sites that are different) incorporated in MEGA v.6 (Tamura et al. 2013). The Partial Mantel test correlation of HABIT, DIST, and GENET was performed with Passage v.2 (Rosenberg & Anderson 2011). The Mantel test was performed for the whole reptile community as well as for lacertid lizards separately.

Results

In total, we observed 785 individuals (all ages) representing 11 species: six lizard and five snake (Table 1, N_1). After excluding species with very low frequency of occurrence (*Coronella girondica* and *Natrix maura*), juveniles, and individuals recorded during consecutive visits, we used a data set of 478 records of nine species (six lizards and three snakes) for further analyses (Table 1, N_2).

We detected interspecific differences in the selection of microhabitat according to the openness measurement (Kruskal-Wallis test, $H_{8,478} = 17.26$, $P = 0.03$). Post-hoc Mann-Whitney U tests detected differences between some Mediterranean–non-Mediterranean pairs ($P < 0.05$). The only significant difference between two Mediterranean species was the *V. latastei*–*T. lepidus* pair ($P = 0.04$). The microhabitat openness of the studied transect (Random class in Fig. 2) varied from forested (i.e., microhabitat-openness score up to 13 m) to open points (i.e., microhabitat-openness score less than 1 m). Apparently, only two species, *Podarcis bocagei* and *Natrix natrix* "used" the complete range of available microhabitats with regard to their openness (Fig. 2). All non-Mediterranean reptiles showed a higher upper range limit of habitat openness (Fig. 2), suggesting that they were more frequently observed in forested areas of the transect than Mediterranean reptiles.

The factorial ANOVA demonstrated that Mediterranean and non-Mediterranean species showed differences in the selection of points according to the microhabitat openness ($F_{1,474} = 8.94$, $P = 0.003$). We did not find differences in this pattern between lizards and snakes ($F_{1,474} = 0.02$, $P = 0.9$), although the interaction between both factors was marginally significant ($F_{1,474} = 3.93$, $P = 0.05$) with Mediterranean and Non-Mediterranean snakes demonstrating a clearer segregation pattern than lizards (Fig. 3).

Partial Mantel tests showed that HABIT (Habitat Similarity Matrix) was correlated to DIST (Distribution Similarity Matrix) with GENET (Genetic distance matrix) being constant (r = 0.38, P = 0.01, 999 permutations). These results marginally persisted when lizards were examined separately (HABIT vs. DIST: r = 0.65, P = 0.06, 999 permutations).

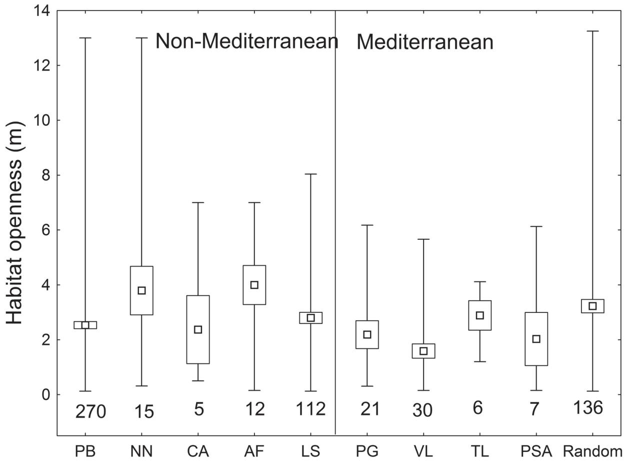

Figure 2. Mean, standard error (box), and minimum-maximum (whisker) values of the use of microhabitats by Mediterranean and non-Mediterranean reptiles according to openness measurements made on a 1.5-km transect along the Homem River (Peneda-Gerês National Park, Northen Portugal). The rightmost column indicates values obtained from 136 equally distributed points along the transect; they represent the available microhabitat according to the openness measurements. Numbers below whiskers reflect sample sizes.

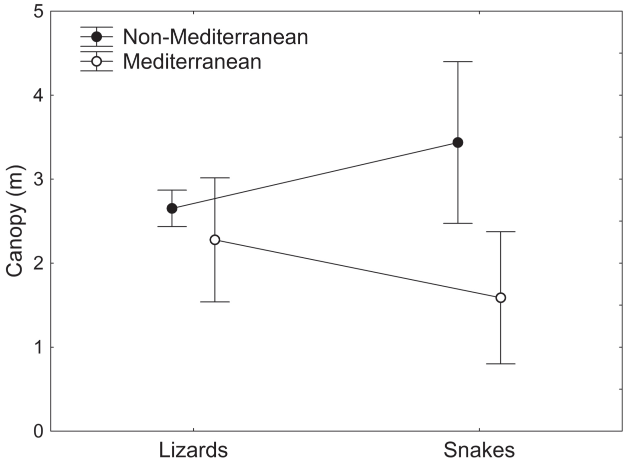

Figure 3. Mean and standard error values of the microhabitat openness measurement with pooled records of lizards and snakes according to their biogeographic affinities, namely Mediterranean and non-Mediterranean.

Discussion

Sympatric Mediterranean and non-Mediterranean species of the reptile assemblage at the Homem River valley differed in their microhabitat selection according to their biogeographic affinities, which likely promotes their coexistence in the area of spatial overlap in the transition zone between these bioregions. Our results strongly support the rule that fine-scale habitat selection (i.e., microhabitat) is governed by broader geographic species distributional patterns. Transition zones between bioregions, as in the case of our study, demonstrated that they sustain a mixed reptile community where species with different biogeographic affinities coexist. As expected, differences in the openness of used microhabitats found between species suggest that coexistence is promoted by spatial segregation between potentially interacting species to avoid competition.

Microhabitat segregation between reptile species in a transition zone between two bioregions follows the result of a previous study by Sillero et al. (2009) who showed that in the Iberian Peninsula, the Mediterranean species occupy climatically drier and hotter regions than the non-Mediterranean species. This correspondence of spatial segregation among coexisting reptiles with different geographic affinities relates two scales of spatial ecology and helps us to understand why and how species communities are richer in bioregional transition zones. The species with the strongest predilection for open habitats were the Mediterranean species: *Psammodromus algirus*, *Podarcis guadarramae*, and *Vipera latastei*. These results are largely congruent with previous ecological findings on these species. Carrascal & Díaz (1988) reported that *P. algirus* selected microhabitats with a plant cover of at maximum 10 cm above the ground. This Mediterranean lizard has a wide distribution range throughout Iberia and northern Morocco, with our study area being situated at the northernmost limit of its distribution (Sillero et al. 2014). This fact suggests marginal habitat suitability for *P. algirus* in the Homem River valley that probably promotes a strong predilection for the most open and hotter microhabitats available. The presence of *P. algirus* in the Homem River valley could also have been promoted by a wildfire in 2009 (ICNF; http://www.icnf.pt/portal/florestas/dfci/inc/info-geo) that denuded the habitat from south to north (authors, unpublished data) and in its wake allowed this Mediterranean species to colonize previously unsuitable habitats. The absence of this species in previous surveys along the same transect conducted in the period before the fire (1999–2001) supports our statement (authors, unpublished data). *Podarcis guadarramae* was reported to select microhabitats with rocks or rock walls, with a preference for open surroundings (Martín & Lopez 2002). This pattern of microhabitat preference of *P. guadarramae* seems to be consistent throughout the Peneda-Gerês National Park since this species has been shown to be able to cope with habitat simplification due to wildfires (authors' personal observations). The Iberian viper *V. latastei* is usually found in rocky areas within a wide range of habitats from open to forested spots (Brito & Crespo 2002). Brito (2003) also reported that male *V. latastei* in northern Portugal used different habitats from forested areas to open forest with bushes. Non-Mediterranean species opted for more closed microhabitats than Mediterranean ones. This result also agrees with previous studies that examined environmental preferences of these species (Brito et al. 1999, Sá-Sousa 2001, Santos et al. 2009, Sillero et al. 2009). *Natrix natrix* was found to select a wide range of microhabitats, suggesting a considerable generality in its habitat use as has been observed in northernmost localities of its distribution (e.g., Madsen 1984, Reading & Jofré 2009). Its predilection for more covered habitats might also be related to the presence of its most commonly taken prey species, toads of the genus *Bufo* (Filippi et al. 1996) in these habitats (authors' personal observations in the study area). *Anguis fragilis* has a preference for areas with high vegetation cover (Loureiro et al. 2008). It is an active forager that searches for food under objects and inside vegetation (Arnold & Ovenden 2002); these ecological preferences are in agreement with the microhabitat where it was found along the studied transect. The lacertid lizards *P. bocagei* and *L. schreiberi* are both endemic to northwestern Iberia and likely found in rocky microhabitats covered with vegetation (Loureiro et al. 2008). This combination can be found across the whole studied transect and for this reason these species, and *P. bocagei* in particular, were found in the widest range of available microhabitats.

The correlation between similarities in the microhabitat selection of reptiles in the Homem River valley and their Iberian distribution followed our predictions, also when the phylogenetic framework was accounted for in our analysis. Our results support the suggestion by Sillero et al. (2009) that reptiles are distributed according to the degree of solar exposure and vegetation structure complexity, here confirmed to also be the rule on a finer spatial scale.

The observed interspecific segregation pattern in microhabitat use can also be influenced by species-specific physiological constraints such as their thermal biology (Huey 1974). Several studies have already found that there is a strong connection between the thermal properties of habitats and habitat selection of different reptile species (i.e., Martín & Salvador 1995, Meik et al. 2002, Harvey & Weatherhead 2010, Monasterio et al. 2010, Gifford et al. 2012, but see Díaz et al. 2005). Furthermore, recent studies have reported that heterogeneity and spatial structure of a thermal landscape (available habitat) plays an important role in defining the quality of a habitat with regard to the thermoregulation of lizards (Sears & Angilletta 2015). More heterogeneous and structured habitats provide higher thermal quality, which reflect in higher lizard performance (Sears & Angilletta 2015). At community level, our study suggests that there is a link between microhabitat selection by reptiles and thermal properties of microhabitats. More open microhabitats are more sun-exposed and offer patches with a higher availability of solar energy, vs. less open habitats that are more shaded. In our case, the Mediterranean species were found in more open microhabitats than the non-Mediterranean species. In this respect, our results demonstrate at least for the studied transect that transition zones between bioregions are areas that provide high spatial structure and heterogeneity of microhabitats and so promote the coexistence of species with different climatic affinities.

In summary, it is known that an increased availability of resources generally promotes species coexistence and greater species richness (Pianka 1986, Vitt & Carvalho 1995). A complex vegetation structure is responsible for a high availability of different microhabitats in Homem River valley, which promotes a high diversity of reptiles. With this locality being a transition zone between two biogeographic regions and a hotspot for reptiles (Loureiro et al. 2008), our results indicate that coexistence of species at a microhabitat scale is governed by spatial segregation in microhabitat use and parallels their biogeographic affinities (Sillero et al. 2009).

Our study has practical applications for designing conservation plans for areas that feature naturally diverse communities or for describing the ecological requirements of endangered species (e.g., Martín & Salvador 1995). We have demonstrated that the coexistence of several reptile species is influenced by the availability of different habitats, in which each species can choose its preferred microhabitat according to its optimal conditions, but this also follows their broader-scale ecological preferences. Therefore, a correct management focused on preserving heterogeneity and structural complexity of existing microhabitats is necessary to maintain their capability of supporting natural communities and promoting the coexistence of species with different requirements. For example, any land alterations should be balanced; preventing increases in vegetation density as well as the clearing of vegetation.

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