International Journal of
Geo-Information

Article

Local Segregation of Realised Niches in Lizards

**Neftalí Sillero [1,*], Elena Argaña [1], Cátia Matos [1], Marc Franch [1],
Antigoni Kaliontzopoulou [2] and Miguel A. Carretero [2,3]**

[1] CICGE, Centro de Investigação em Ciências Geo-Espaciais, Faculdade de Ciências da Universidade do Porto, Alameda do Monte da Virgem, 4430-146 Vila Nova de Gaia, Portugal; elenutis82@gmail.com (E.A.); c.matos@2013.hull.ac.uk (C.M.); marc.franch@udg.edu (M.F.)
[2] CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, Vila do Conde, 7 4485–661 Vairão, Portugal; antigoni@cibio.up.pt (A.K.); carretero@cibio.up.pt (M.A.C.)
[3] Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, Rua do Campo Alegre, 4169-007 Porto, Portugal
* Correspondence: neftali.sillero@gmail.com

Received: 28 October 2020; Accepted: 18 December 2020; Published: 21 December 2020

Abstract: Species can occupy different realised niches when sharing the space with other congeneric species or when living in allopatry. Ecological niche models are powerful tools to analyse species niches and their changes over time and space. Analysing how species' realised niches shift is paramount in ecology. Here, we examine the ecological realised niche of three species of wall lizards in six study areas: three areas where each species occurs alone; and three areas where they occur together in pairs. We compared the species' realised niches and how they vary depending on species' coexistence, by quantifying niche overlap between pairs of species or populations with the R package ecospat. For this, we considered three environmental variables (temperature, humidity, and wind speed) recorded at each lizard re-sighting location. Realised niches were very similar when comparing syntopic species occurring in the same study area. However, realised niches differed when comparing conspecific populations across areas. In each of the three areas of syntopy, the less abundant species shift its realised niche. Our study demonstrates that sympatry may shift species' realised niche.

Keywords: Iberian peninsula; niche conservatism; reptiles; R package ecospat; spatial segregation

---

1. Introduction

Species frequently live in communities composed of two or more congeneric species [1,2]. When a species is sharing resources with another species, it may be forced to shift its niche to minimise competition or stress and to maximise success in resource acquisition and/or mating [3]. This segregation may occur in time, space, or in any other dimension of the niche (e.g., food resources, biotic interactions) [4]. When the species segregate temporally, they avoid using the same resources at the same time [5]. When species segregate spatially, they may use resources from different locations [2], for instance by taking advantage of different microhabitats. The microhabitats may have different structural characteristics [6,7]: microclimate (e.g., temperature, humidity), food availability, predation pressure, parasite exposure, or abundance of refuges.

The set of microhabitats where the species occurs constitutes the species niche [8], i.e., the subset of the environment containing the (micro) habitat conditions that allow the individuals of the species to survive and reproduce [8]. Hutchinson [4] provided the first mathematical definition for species niche: the fundamental niche is the n-dimensional hypervolume on the abiotic environmental space where a species can maintain a viable population and persist over time without immigration. Each dimension is an environmental variable. Hutchinson [4] also defined the realised niche as the subset of the fundamental niche where the species is not excluded by competition. Pearson [9] included other biotic interactions (e.g., predation, parasitism, symbiosis), dispersal ability, as well as geographical and historical constraints. Therefore, a species can use a specific microhabitat if the environmental conditions fall within its realised niche, as any environmental condition outside it cannot be occupied [4,9]. Consequently, the degree of local segregation between two coexisting species can be approached by quantifying the differences between their realised niches [10].

Numerous studies have analysed how species segregate spatially when occurring with other species [11–15], but not from a species ecological niche perspective, i.e., without modelling the ecological niche. The reason for this lay in the difficulty to obtain fine-scale spatial data for micro-habitat occurrence and use [10,16]. Numerous studies have examined niche conservatism (i.e., the species' realised niche is maintained without changes over space and time) at the species distribution level [17–20] using ecological niche models (ENMs) [21,22]. ENMs are powerful statistical tools for analysing species niches and their changes over time and space [22]. However, very few studies have applied ENMs at very high spatial resolution [23–28] and even less have compared several species composing a community [10].

The microhabitats used by two species in syntopy may differ from those used by the same species when living alone. From a niche perspective, ecological character displacement [29] can be observed when the species' realised niche, sharing the space with a congeneric species, may be different from the species' realised niche when living alone. In both situations, the species uses its fundamental niche, but it is occupying parts of the realised niche with different intensity. The parts of the realised niche the species is occupying differently depend on the factors driving the realised niche [9]. This process is similar to niche shifts observed in invasive species: the species' realised niche in the native area can be different from the niche in the introduced area if released, for instance, from predation in the latter area [30,31]. Similarly, two congeneric species living in strict syntopy might tend to shift their realised niches [10]. In this case, the relative abundance of each congeneric species may influence the niche segregation: the less abundant species might be the one shifting its realised niche.

To our knowledge, no study has analysed the differences in microhabitat use between species in syntopy and allopatry situations from an ecological niche perspective. The main aim of this work is to examine whether species use the same microhabitat when in syntopy with other congeneric species compared with allopatric situations (areas with only one species). For this, we compared the microhabitat of three species of Iberian wall lizards in a matrix of syntopic/allopatric populations: the three species do not occur all together but can rather be found in combinations of two species when in sympatry. We considered six study areas: three areas have a single species each (allopatric areas); the other three areas have combinations of two species (sympatric areas). We predict that:

(1) Species occurring in syntopy might use microhabitats in the same way, as Iberian wall lizards are considered generalists [32].
(2) When comparing the microhabitat use in populations of the same species between a sympatric and an allopatric area, the species may use the same microhabitats as in the sympatric area when being the more abundant of the two species [33,34].
(3) When comparing the microhabitat use of a species between a sympatric and an allopatric area, the least abundant species within the community will shift its realised niche [33,34].

To verify these predictions, we compared the climatic characteristics (temperature, humidity, and wind speed) of the microhabitats across the study areas using the R software package ecospat methodology [35,36]. Ecospat quantifies the niche overlap between two entities, either species or populations. This approach allows us to assess the degree and direction of realised niche shift when different species pairs co-occur.

2. Materials and Methods

2.1. Study Species

We considered three endemic species of Iberian wall lizards: *Podarcis bocagei* (Seoane, 1885), a generalist species distributed in Atlantic habitats of the northwestern part of the Iberian Peninsula [37]; *P. carbonelli* Pérez-Mellado, 1981, a ground-dwelling species inhabiting Atlantic habitats with a fragmented distribution in western Iberia [37]; and *P. guadarramae* (Boscá, 1916), a saxicolous species of Atlantic and Mediterranean habitats of northwestern and north-central Iberia [38]. Each species can be found alone or coexisting with one of the other two species, but the three species never occur all together [39].

We selected wall lizards as model organisms because (1) they occur in communities with high density of individuals over relatively small areas, (2) their communities are usually composed of a low number of species, sometimes belonging to the same genus, and (3) they are easy to capture and handle [40]. Further, wall lizards are ectothermic organisms and have strong dependence on environmental conditions [41], which facilitates studies of habitat and niche flexibility.

2.2. Study Areas

We performed the systematic sampling in six different locations (Table 1 and Figure 1), three with only one species (hereafter allopatric study areas), and three with two species (hereafter syntopic study areas). The allopatric study areas were:

1. **Coronado**: an agricultural area of irrigated crops separated by high stone walls (>150 cm) inside a lax urban matrix. Only *P. bocagei* is present. Lizards were captured on 9 and 10 June 2013, and resighted between 12 and 17 June 2013.
2. **Padrão**: area composed by restored ruined walls (always lower than 50 cm) of a prehistorical village and surrounded by a forest of oaks and cork trees. Only *P. guadarramae* is present. Lizards are more frequent on the walls. Lizards were captured on 26 May 2013 and resighted between 28 May and 4 June 2013.
3. **Torreira**: area of coastal dunes with wooden boardwalks. Only *P. carbonelli* is present. Lizards can be found everywhere, but more frequently on the woody passages. Lizards were captured on 11 and 12 May 2013 and resighted between 14 and 23 May 2013.

The sympatric areas are:

4. **Moledo**: agricultural area of irrigated crops with stone walls (~150 cm) separating the crops. *Podarcis bocagei* and *P. guadarramae* occur sympatrically, although the latter in lesser numbers. Lizards occur in the walls. Lizards were captured on 10 June 2014 and resighted between 12 and 20 June 2014.
5. **Espinho**: area of coastal dunes with wooden boardwalks. *P. carbonelli* and *P. bocagei* are present, although the latter in lesser numbers. This is the only known point of syntopy for both species [42,43]. Lizards were captured on 23 April 2013 and resighted between 25 of April and 24 May 2013.
6. **Estrela**: area composed by rock boulders on the shore of a reservoir. *P. guadarramae* and *P. carbonelli* are present in this area, although the latter in less number. Lizards were captured on 16 and 17 May 2012, and resighted between 19 and 24 May 2012.

Table 1. Matrix of species combinations by study area. In each study area occur either one (across the diagonal, shaded in grey) or two of the three species analysed. The study areas of Espinho, Estrela, and Moledo host two species. The study areas of Coronado, Padrão, and Torreira (background in grey) host a single species.

Species	***Podarcis bocagei***	***Podarcis carbonelli***	***Podarcis guadarramae***
Podarcis bocagei	Coronado		
Podarcis carbonelli	Espinho	Torreira	
Podarcis guadarramae	Moledo	Estrela	Padrão

2.3. Fieldwork

Sampling was performed during the reproductive period (spring) of wall lizards [39,44–46]. We captured the wall lizards by noose [47], and marked each individual temporally on the belly with a number using a non-toxic permanent marker. We identified the capture site for each wall lizard with the number of the lizard in a plastic tape. For visual identification of wall lizards during re-sighting sampling, we marked each individual with non-toxic coloured inks using a unique code made of three coloured dots on their back [48–50]. All preliminary field procedures took one day, except in Torreira and Estrela where two days were necessary to capture enough individuals (i.e., at least 30 individuals). We concentrated sampling effort in a short time period to minimise dispersal events of captured individuals [51]. After all procedures were completed, we released the wall lizards in the exact site of capture. We left lizards undisturbed for one or more days (depending on weather conditions) to ensure that they had returned to their normal activities after being captured. After that, animals were resighted over several days until coloured inks disappeared.

We recorded the position of each wall lizard (capture and resighting locations) for 60 s with a Trimble GeoExplorer GT GPS receiver with a horizontal error around 10 cm after postprocessing. We corrected all GPS positions by a differential procedure using Trimble GPS Pathfinder office software 5.0. In each lizard position, we recorded local weather measurements with a portable meteorological station SkyMate SM-18 at substrate level for temperature (measured always at in the shade), humidity, and wind speed. We selected these variables as they are main drivers of lizards' biogeography and activity patterns [16,38].

In each study area, we searched for marked wall lizards in favourable climatic conditions (warm, no rain and strong winds) from the beginning until the end of their daily activity. We performed multiple haphazard routes (see Figure 1 for an example in each study area), as routes could not be completely random in the wooden boardwalks and walls. We started and finished each route in a different place of the study area. In each route, we sampled the study area only once per survey to avoid pseudoreplication [52], allowing wall lizards to recover their normal activity after disturbance by the observer and to prevent resightings being too close in time to keep independence. Searching for marked wall lizards always involved two people: one person actively searched for lizards and recorded the local weather data; the second person recorded the wall lizard location, waiting always some meters behind to avoid disturbance until the moment of using the GPS receptor. Minimum time between two consecutive sightings of the same wall lizard was one hour. Based on our own experience, we consider this interval long enough for a lizard to displace between two consecutive positions. Consequently, a position could not be predicted from the previous one, independently of whether the wall lizard effectively moved or not. We checked the independence of the locations using the Moran's I test in spdep R package [53] for each of the three local weather measures (humidity, temperature, and wind).

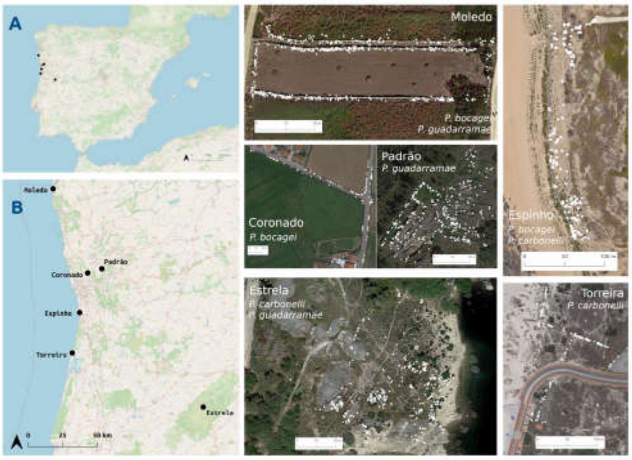

Figure 1. Location of the six study areas in the Iberian peninsula (**A**) and in Portugal (**B**). Backgrounds from OpenStreetMaps. Distribution of individual records (white dots) in each of the six study areas: Moledo, Padrão, Coronado, Espinho, Torreira, and Estrela (from north to south). Backgrounds from Google Maps.

2.4. Niche Segregation between Species

Estimations of species' realised niche were compared using the procedures implemented in the ecospat R package version 3.1 [35,36]. We performed two sets of pairwise analyses with ecospat (Table 1): (1) comparisons between pairs of species in the syntopic study areas (*P. bocagei*–*P. carbonelli* in Espinho; *P. carbonelli*–*P. guadarramae* in Estrela; and *P. bocagei*–*P. guadarramae* in Moledo); and (2) comparisons between populations of the same species between study areas (e.g., for *P. bocagei*: Coronado–Moledo; Espinho–Moledo; Coronado–Espinho).

Ecospat includes tools to support spatial analyses and modelling of species' realised niches. It quantifies the niche overlap between two entities, either species or populations (e.g., between sympatry and allopatry, or between species sharing a location). The package works in three steps [36]: (1) it extracts environmental values corresponding to the observation records of the species pair, calculates a PCA, and transforms the first two components of the PCA into densities by kernel smoothers; (2) it measures the niche overlap along the gradients of the PCA; and (3) it applies the statistical tests of niche equivalency and similarity [35,54]. The background data for each pairwise comparison is the set of all study areas. Niche overlap is calculated using the Schoener's D metric [55], which varies from 0 (no overlap) to 1 (complete overlap). Ecospat also measures the distance between the centroids of each species' realised niche, represented by the kernel densities. The larger this distance, the smaller the overlap between the species' realised niches.

The niche equivalency test determines whether two species' realised niches are less equivalent than random by permuting randomly 100 times the occurrences between entities. The niche similarity test examines whether two species' realised niches are less similar than expected by chance by shifting randomly 100 times the niches within the available conditions in the study area [35,54,55]. For both tests, when the observed overlap is lower than 95% of the simulated values, both entities occupy environments more dissimilar than expected by chance.

Finally, ecospat quantifies in three components how the niches overlap in the environment space [18]: Stability (S), the proportion of the niche that is shared by both species; unfilling (U), the proportion of the niche of the first species that is not occupied by the second one; and expansion (E), the proportion of the niche of the second species that is not occupied by the first one.

We analysed the differences of humidity, temperature, and wind measures between species and localities with Kruskal–Wallis test. When significant, we applied the Dunn post-hoc test to search for significant pairwise comparisons. All analyses were performed with R version 4.0.3 [56].

3. Results

We captured a total of 219 individuals, with 1785 resightings (Table 2): 68 individuals and 625 resightings for *P. bocagei*; 61 individuals and 331 resightings for *P. carbonelli*; and 90 individuals and 829 resightings for *P. guadarramae*. We collected more records from all allopatric populations; all syntopic communities presented one species population with a large number of records and the other one with a low number of records (Table 2). All locations were spatially independent as all Moran's I estimates were close to 0 (Table S1).

When comparing syntopic species occurring in the same study area (Espinho, Estrela, Moledo), the equivalency tests indicated a high degree of niche similarity: all Schoener's D indices were higher than 0.6 (Table 3). Humidity, temperature, and wind were not different in these areas during the study period (Tables S2 and S3, Figure S1). When comparing a species between different study areas, the equivalency tests for all pairwise comparisons were dissimilar: all Schoener's D indices were lower than 0.4 (Table 3). However, the similarity tests showed that the species' realised niches were not more dissimilar than expected by chance (Table 3). All tests were nonsignificant, except for the Estrela area comparison. Humidity, temperature, and wind were significantly different for most of the combinations between species from different areas (Tables S2 and S3, Figure S1).

Three main patterns can be observed in ecospat results:

(1) When comparing species between syntopic areas (Espinho, Estrela, Moledo), all species pairs occupied very similar niches (Table 3): Schoener's D indices were high, stability values were close or equal to 1, and the unfilling and expansion indices were very low (<0.1). The overlaps between niches were almost complete, while the distances between centroids were very small (Figure 2).

(2) When comparing populations of the same species between a syntopic (Espinho, Estrela, Moledo) and an allopatric area (Coronado, Padrão, Torreira), similarities were intermediate (Table 3): Schoener's D indices were close to 0.3 and stability indices were very high (around 0.8–0.9). Here, the exception is the comparison between Torreira and Espinho populations of *P. carbonelli*, which presented always lower values (below 0.2). Niche overlaps across areas were high, but not total, while the distances between centroids were large (Figures 3–5).

(3) When comparing populations of the same species between syntopic study areas (Espinho, Estrela, Moledo), similarities values were very low (Table 3): Schoener's D indices were lower than 0.15 and stability indices were lower than 0.8–0.9 (except the comparison between Espinho and Moledo for *P. bocagei*). The expansion and unfilling indices presented the maximum values considering all comparisons. Niche overlaps were moderate while the distances between centroids were very large (see the red arrows in Figures 3–5).

Table 2. Number of individuals and sightings per species and study area. The study areas of Espinho, Estrela, and Moledo host two species. The study areas of Coronado, Padrão, and Torreira host a single species.

	P. bocagei		***P. carbonelli***		***P. guadarramae***			
Locality	**Individuals**	**Sightings**	**Individuals**	**Sightings**	**Individuals**	**Sightings**	**All individuals**	**All sightings**
Moledo	37	419			6	70	43	489
Padrão					38	391	38	391
Coronado	25	174					25	174
Espinho	6	32	32	118			38	150
Torreira			20	184			20	184
Estrela			9	29	46	368	55	397
Total	68	625	61	331	90	829	219	1785

Table 3. Summary of ecospat results: Schoener's D index, p values for the equivalency and similarity tests, and values of the observed overlaps between realised niches (expansion, stability, and unfilling). The study areas of Espinho, Estrela, and Moledo host two species. The study areas of Coronado, Padrão, and Torreira host a single species. The first three lines correspond to the comparisons of the realised niches between pairs of species in sympatry. The next nine lines correspond to the comparisons of the realised niches of a single species between the pairs of study areas. PB: *Podarcis bocagei*; PC: *Podarcis carbonelli*; PG: *Podarcis guadarramae*. ET: equivalency test; ST: similarity test. *p*: *p* values. Note that the similarity test is not symmetrical, and therefore it is performed from species 1 to 2 and from species 2 to 1. * significant *p* value (<0.05).

Species	Locality 1	Locality 2	D	ET p	ST 1 → 2p	ST 2 → 1p	Expansion	Stability	Unfilling
PB-PC	Espinho	Espinho	0.745	0.446	0.941	0.951	0.003	0.997	0.077
PC-PG	Estrela	Estrela	0.619	0.673	0.960	0.960	0.000	1.000	0.063
PB-PG	Moledo	Moledo	0.693	0.446	0.901	0.911	0.011	0.989	0.021
PB	Coronado	Moledo	0.320	0.009 *	0.653	0.653	0.126	0.874	0.093
PB	Espinho	Moledo	0.114	0.009 *	0.317	0.416	0.108	0.892	0.461
PB	Coronado	Espinho	0.232	0.009 *	0.574	0.535	0.336	0.664	0.048
PC	Torreira	Espinho	0.032	0.009 *	0.188	0.238	0.024	0.976	0.790
PC	Estrela	Espinho	0.004	0.009 *	0.067	0.089	0.395	0.605	0.919
PC	Torreira	Estrela	0.170	0.009 *	0.614	0.713	0.368	0.632	0.419
PG	Padrão	Estrela	0.366	0.009 *	0.822	0.792	0.042	0.958	0.077
PG	Moledo	Estrela	0.133	0.009 *	0.465	0.564	0.476	0.524	0.286
PG	Padrão	Moledo	0.304	0.009 *	0.743	0.634	0.062	0.938	0.243

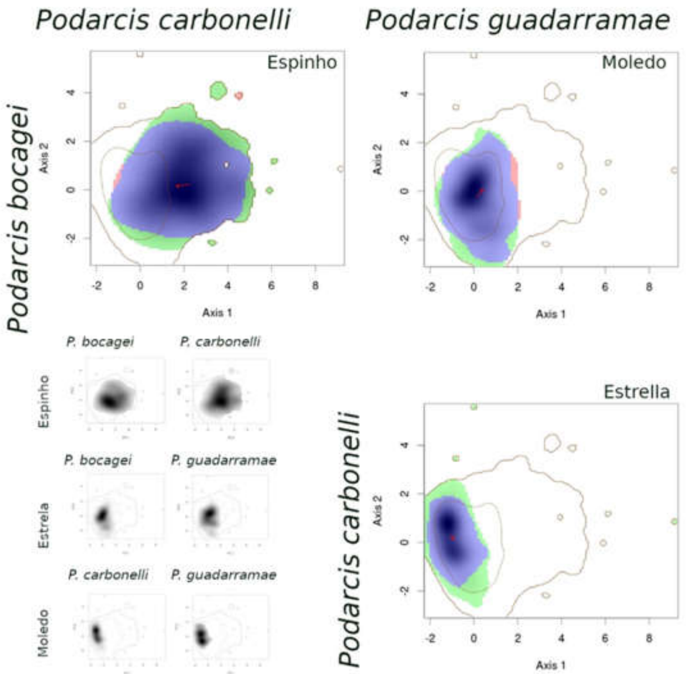

Figure 2. Matrix of ecospat overlap plots of the realised niches of *P. bocagei*, *P. carbonelli*, and *P. guadarramae* in the sympatric study areas where two of them occur together: Moledo, Espinho, and Estrela. The small plots correspond to the individual species' realised niche in each study area. Stability is represented in blue, unfilling in green, and expansion in red. The red arrow is the distance between centroids.

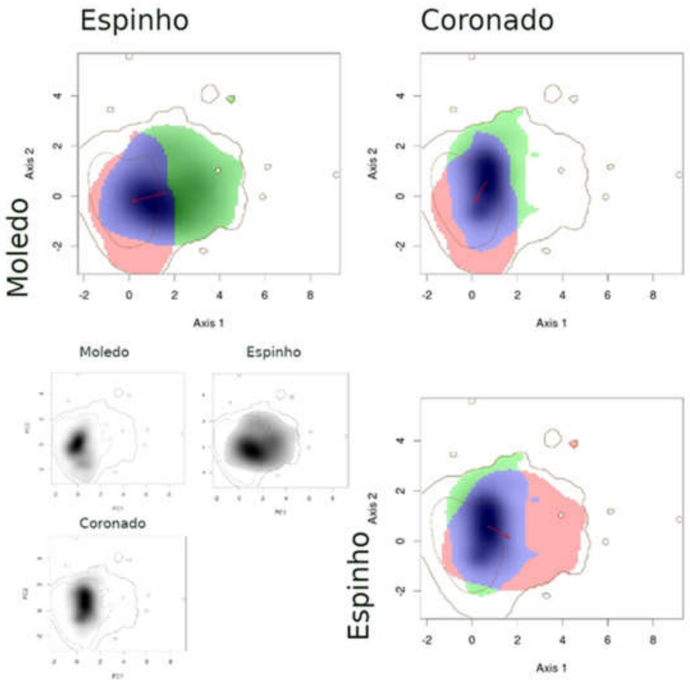

Figure 3. Matrix of ecospat overlap plots of the realised niches of *P. bocagei* between the study areas where it occurs: Coronado (allopatric area), Moledo, and Espinho (both sympatric areas). The small plots correspond to the species' realised niche in each study area. Stability is represented in blue, unfilling in green, and expansion in red. The red arrow is the distance between centroids.

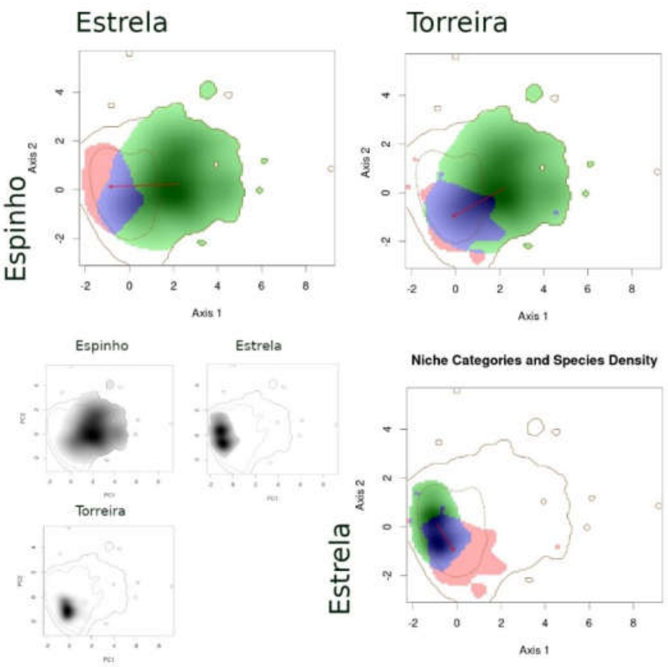

Figure 4. Matrix of ecospat overlap plots of the realised niches of *P. carbonelli* between the study areas where it occurs: Torreira (allopatric area), Espinho, and Estrela (both sympatric areas). The small plots correspond to the species' realised niche in each study area. Stability is represented in blue, unfilling in green, and expansion in red. The red arrow is the distance between centroids.

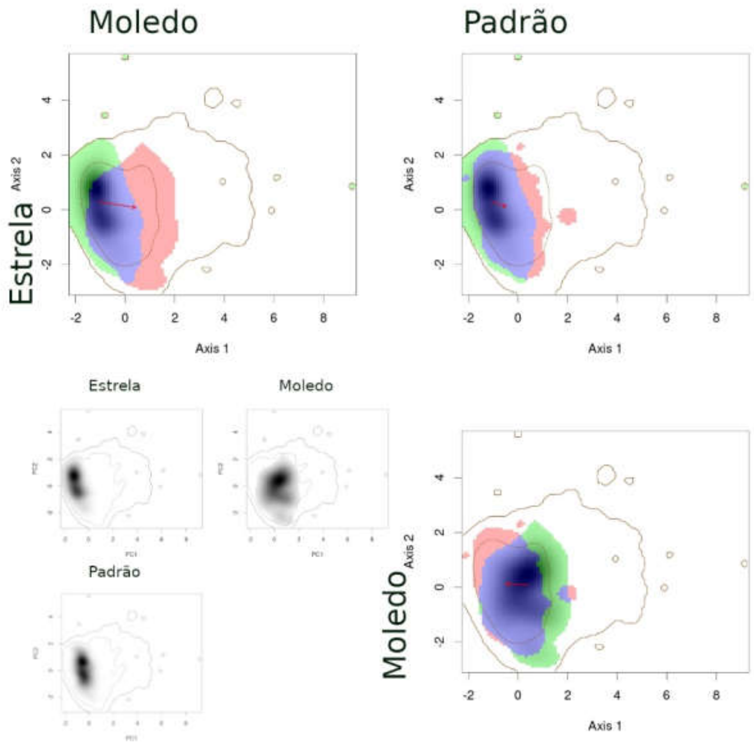

Figure 5. Matrix of ecospat overlap plots of the realised niches of *P. guadarramae* between the study areas where it occurs: Padrão (allopatric area), Moledo, and Estrela (both sympatric areas). The small plots correspond to the individual species' realised niche in each study area. Stability is represented in blue, unfilling in green, and expansion in red. The red arrow is the distance between centroids.

4. Discussion

Our initial hypotheses were confirmed: niches were very similar when comparing syntopic species in the same study area (Espinho, Estrela, Moledo), but the same species shifted their realised niches across different study areas. In this last case, the niches could be considered dissimilar when involving less abundant populations. In other words, allopatric populations and abundant populations in sympatry from the same species have similar niches. Therefore, different ecological responses may depend on the syntopic species presence and on their relative abundance. We can draw two main conclusions:

(1) Considering the environmental micro-niche variables analysed here, all *Podarcis* species tend to use similar microhabitats, as indicated by ecospat results between syntopic populations.
(2) When in syntopy with another congeneric species, a species tends to occupy different microhabitats if it is relatively less abundant.

The overlap between species in the same study area (Espinho, Estrela, Moledo) were the highest in all comparisons. The overlap between populations of the same species were high but not total as when comparing populations of different species. Therefore, proportions of niche shared (i.e., stability) by populations from the same species were high when comparing allopatric with syntopic populations: Coronado against the syntopic populations of Espinho and Moledo for *P. bocagei*; Torreira against the syntopic populations of Estrela and Espinho for *P. carbonelli*; and Padrão against the syntopic populations of Moledo and Estrela for *P. guadarramae*. The comparisons between syntopic populations of the same species had the lowest proportion of niche shared (i.e., stability) in all comparisons: the less abundant population of Espinho against the abundant population of Moledo for *P. bocagei* (Figure 3); the less abundant population of Estrela against the abundant population of Espinho for *P. carbonelli* (Figure 4); and the less abundant population of Moledo against the abundant population of Estrela for *P. guadarramae* (Figure 5). Comparisons including the population of *P. carbonelli* from Espinho were always more dissimilar than the rest, probably due to the higher climatic variability characterizing the records of this sampling, which lasted for four weeks.

We used only three environmental microniche variables (humidity, temperature, and wind) as these variables are main drivers of the lizards' biogeography and activity patterns [16,38]. Other variables can be selected, more related to vegetation cover and microtopography features [10]. Future research may clarify whether other variables might lead to niche segregation in *Podarcis* species. Despite some variation across species, *Podarcis* species are generalists compared to other southern European lizards [32]: they tend to use similar microhabitats. For example, *P. guadarramae* is a saxicolous lizard, but *P. bocagei* and *P. carbonelli*, both ground-dwelling lizards, will use also walls if available [39,46,57]. Moledo is a coastal agricultural area where *P. bocagei* and *P. guadarramae* occur in walls separating fields. There, *P. bocagei* is more abundant than *P. guadarramae* despite the latter being a rock specialist [48,57–59]. Indeed, the allopatric study area of *P. bocagei* (Coronado) is composed as well by walls separating agricultural fields. Thus, the habitat structure of the study areas alone does not fully explain the ecospat results. Although the study areas are clearly different, they did not differ so much in terms of habitat potentially or effectively used by wall lizards. We can divide the study areas in two groups: (1) Coronado (allopatric area) is a rural area with high walls separating agricultural fields, Padrão (allopatric area) is an archaeological site with small walls, Moledo (sympatric area) is a coastal agricultural area with medium-sized walls, Estrela (sympatric area) is an area of rock boulders, thus, all rocky; and (2) Torreira (allopatric area) and Espinho (sympatric area) are coastal dune systems, thus, habitats of sparse vegetation. Consequently, we found species highly overlapping (i.e., stability) their realised niches between study areas which are structurally different: Coronado and Espinho for *P. bocagei*, and Torreira and Estrela for *P. carbonelli*. Even the comparison between Estrela and Espinho for *P. carbonelli*, provided medium stability values despite Estrela being a continental rocky area and Espinho a coastal dune system. *P. carbonelli* is distributed in oak forests through the Iberian Central System mountain range and in Atlantic coastal dune systems [37]. Although both habitats are clearly different, the microhabitats are very similar: both are very humid at the time the species is active [60,61].

The discrepancy between the equivalency and similarity tests were expectable: similarity results indicated that the equivalency tests identified the species niche as different because the analyses focused on comparing different study areas, not because the niches are in fact significantly different. In other words, comparing different study areas forced the equivalency test to identify the niches as different [54,55].

Previous studies found similar results. Sillero and Gonçalves-Seco [10] modelled the local distribution of four species of wall lizards in northern Portugal, including *P. bocagei* and *P. guadarramae*. Despite not being identical, the distribution models for both species widely overlap: the former was widespread and the latter showed a clear preference for walls. However, when considering study areas with diversified habitats, species of the same genus (e.g., *Podarcis guadarramae and P. carbonelli*) segregate almost totally, inhabiting different habitats, while species of different genera (e.g., *Lacerta* and *Timon*) presented partial segregation, sharing some habitats [2]. Therefore, it is not surprising that we did not find niche segregation when comparing different species in the syntopic areas (Espinho, Estrela, Moledo). In these three areas, the two *Podarcis* species occurring there are using the same microhabitats as recovered for the environmental variables analysed.

Many studies have identified shifts in the realised niches of invasive and introduced species when compared with their native ranges [30,31,62,63]. Although all these studies analysed whether there is niche conservatism, none showed shifts in the fundamental niche [4]. All niche shifts detected correspond to changes in the species' realised niche [17–20]. Here, we provided evidence that lizards shifted their realised niches when in syntopy, depending on the conspecific with which they coexisted. Based on previous knowledge of the examined species, phylogenetic relationships [64], morphology [65,66] and structural microhabitat use [57], and supported by character displacement theory [29], we might have expected *Podarcis bocagei* and *P. guadarramae* to exhibit the less intense niche shifts across areas, as they are sister species [64]. However, these species have quite different structural habitat preferences [57,59], which is hypothesized to have driven their morphological divergence. As such, they might have segregated their niches adaptively across their entire (and extensively overlapping) distribution areas [64], but not entering in direct competition when they meet in sympatry. By contrast, *P. bocagei* and *P. carbonelli* are much more similar in both morphology and structural habitat use [59,67], a fact that could be expected to trigger more intense niche shifts across this species pair. However, these predictions are not verified in our system. Instead, the most feasible explanation in our study case regards relative local abundance (see above) [34], where asymmetric competition may explain the pattern of ecological character displacement observed [33].

In this study, we only considered climatic dimensions of the species' realised niches. Other dimensions were not considered because of the difficulty of recording them spatially [16]. Habitat segregation may also occur in other niche dimensions such as diet, predation risk, refuge availability, or parasite exposure [66,68]. However, as stated before, *Podarcis* species tend to use the environment in a similar way [32], thus habitat segregation during the study period may be the same even if considering other niche dimensions. Moreover, our study is also limited by its own structure: there is not a place where our three *Podarcis* species occur together [41,69]. The current impossibility of ecospat performing comparisons between three or more entities constitutes a limitation [35,36]. Indeed, our results would gain in understandability if all study areas can be compared together. An alternative to ecospat is the hypervolume R package, which is able to compare several species at the same time [70]. However, tests for measuring niche overlap are not implemented in hypervolume. Furthermore, ecospat takes less statistical assumptions [35,36]. Nevertheless, ecological niche models are reliable and powerful statistical tools for analysing changes in species niches over time and space [22]. As our study demonstrates, biotic interactions among species may shift spatially the species' realised niches.

Supplementary Materials: The following are available online at www.mdpi.com/2220-9964/9/12/764/s1, Figure S1: Boxplots of humidity, temperature and wind for each location and species, Table S1: Table S1: Moran's I test results for each study area and local weather measures (humidity, temperature, wind), Table S2: Summary statistics for the local weather measurements collected in each lizard location, Table S3: Dunn test results (Z statistic and *p* value) for local weather measurements by species and study area.

Author Contributions: Conceptualization, Neftalí Sillero; methodology, Neftalí Sillero, Antigoni Kaliontzopoulou, Miguel A. Carretero; fieldwork, Neftalí Sillero, Elena Argaña, Cátia Matos, Marc Franch, Antigoni Kaliontzopoulou, Miguel A. Carretero; writing—original draft preparation, Neftalí Sillero; writing—review and editing, Neftalí Sillero, Elena Argaña, Cátia Matos, Marc Franch, Antigoni Kaliontzopoulou, Miguel A. Carretero; funding acquisition, Neftalí Sillero All authors have read and agreed to the published version of the manuscript.

Funding: This work was funded by Fundação para a Ciência e a Tecnologia (FCT, Portugal) through project HOUSE (PTDC/BIA-BEC/102280/2008). Collecting permits (180/2012/CAPT, 222/2013/CAPT, 564/2014/CAPT) were issued by Portuguese Conservation Authority (ICNF). NS is supported by a CEEC2017 contract (CEECIND/02213/2017) from FCT.

Acknowledgments: We thank all people that help us in the fieldwork and compiling the data: Verónica Gomes, Francisco Alves, Tjitske Gratama, Natascha Vreeken, Olatz San Sebastián, Nelson Pires, Miguel Salgado, João Campos.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Sillero, N.; Argaña, E.; Freitas, S.; García-Muñoz, E.; Arakelyan, M.; Corti, C.; Carretero, M.A. Short term spatial structure of a lizard (*Darevskia* sp.) community in Armenia. *Acta Herpetol.* **2018**, *13*, 155–163, doi:10.13128/Acta_Herpetol-22830.
2. Sillero, N.; Gomes, V. Living in clusters: The local spatial segregation of a lizard. *Basic Appl. Herpetol.* **2016**, *30*, 61–75.
3. Prinzing, A.; Durka, W.; Klotz, S.; Brandl, R. Geographic variability of ecological niches of plant species: Are competition and stress relevant? *Ecography* **2002**, *6*, 721–729.
4. Hutchinson, G.E. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* **1957**, *22*, 415–427.
5. Diaz-Paniagua, C. Temporal segregation in larval amphibian communities in temporary ponds at a locality in SW Spain. *Amphib. Reptil.* **1988**, *9*, 15–26.
6. Ficetola, G.F.; Pennati, R.; Manenti, R. Spatial segregation among age classes in cave salamanders: Habitat selection or social interactions? *Popul. Ecol.* **2013**, *55*, 217–226, doi:10.1007/s10144-012-0350-5.
7. Schenk, H.J.; Holzapfel, C.; Hamilton, J.G.; Mahall, B.E. Spatial ecology of a small desert shrub on adjacent geological substrates. *J. Ecol.* **2003**, *91*, 383–395.
8. Grinnell, J. The niche-relationships of the California Thrasher. *Auk* **1917**, *34*, 427–433.
9. Pearson, R.G. *Species' Distribution Modeling for Conservation Educators and Practitioners*; American Museum of Natural History: New York, NY, USA, 2007.
10. Sillero, N.; Gonçalves-Seco, L. Spatial structure analysis of a reptile community with airborne LiDAR data. *Int. J. Geogr. Inf. Sci.* **2014**, *28*, 1709–1722, doi:10.1080/13658816.2014.902062.
11. Frost, C.L.; Bergmann, P.J. Spatial Distribution and Habitat Utilization of the Zebra-tailed Lizard (*Callisaurus draconoides*). *J. Herpetol.* **2012**, *46*, 203–208, doi:10.1670/10-267.
12. Gray, L.; He, F. Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. *For. Ecol. Manag.* **2009**, *259*, 98–106, doi:10.1016/j.foreco.2009.09.048.
13. Getzin, S.; Dean, C.; He, F.; Trofymow, J.A.; Wiegand, K.; Wiegand, T. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* **2006**, *29*, 671–682.
14. Condit, R.; Ashton, P.S.; Baker, P.; Bunyavejchewin, S.; Gunatilleke, S.; Gunatilleke, N.; Hubbell, S.P.; Foster, R.B.; Itoh, A.; Lafrankie, J.V.; et al. Spatial Patterns in the Distribution of Tropical Tree Species. *Science* **2000**, *288*, 1414–1418.
15. Moody, A.L.; Thompson, W.A.; De Bruijin, B.; Houston, A.I.; Goss-Custard, J.D. The Analysis of the Spacing of Animals, with an Example Based on Oystercatchers during the Tidal Cycle. *J. Anim. Ecol.* **1997**, *66*, 615–628.
16. Sillero, N.; Dos Santos, R.; Teodoro, A.C.; Carretero, M. Ecological niche models improve home ranges estimations. *J. Zool.* **2020**, doi:10.1111/jzo.12844.
17. Pearman, P.B.; Guisan, A.; Broennimann, O.; Randin, C.F. Niche dynamics in space and time. *Trends Ecol. Evol.* **2008**, *23*, 149–158.
18. Guisan, A.; Petitpierre, B.; Broennimann, O.; Daehler, C.; Kueffer, C. Unifying niche shift studies: Insights from biological invasions. *Trends Ecol. Evol.* **2014**, *29*, 260–269, doi:10.1016/j.tree.2014.02.009.

19. Wiens, J.J.; Ackerly, D.D.; Allen, A.P.; Anacker, B.L.; Buckley, L.B.; Cornell, H.V.; Damschen, E.I.; Jonathan Davies, T.; Grytnes, J.-A.; Harrison, S.P.; et al. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **2010**, *10*, 1310–1324.
20. Peterson, A.T. Ecological niche conservatism: A time-structured review of evidence. *J. Biogeogr.* **2011**, *38*, 817–827, doi:10.1111/j.1365-2699.2010.02456.x.
21. Sillero, N. What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. *Ecol. Model.* **2011**, *222*, 1343–1346.
22. Barbosa, M.A.; Sillero, N.; Martínez-Freiría, F.; Real, R. Ecological niche models in Mediterranean herpetology: Past, present and future. In *Ecological Modelling*; Zhang, W., Ed.; Nova Publishers: Hauppauge, NY, USA, 2012; pp. 173–204.
23. Bogosian, V., III; Hellgren, E.C.; Sears, M.W.; Moody, R.W. High-resolution niche models via a correlative approach: Comparing and combining correlative and process-based information. *Ecol. Model.* **2012**, *237–238*, 63–73, doi:10.1016/j.ecolmodel.2012.04.017.
24. Descombes, P.; Petitpierre, B.; Morard, E.; Berthoud, M.; Guisan, A.; Vittoz, P. Monitoring and distribution modelling of invasive species along riverine habitats at very high resolution. *Biol. Invasions* **2016**, *18*, 3665–3679, doi:10.1007/s10530-016-1257-4.
25. Turner, J.A.; Babcock, R.C.; Kendrick, G.A.; Hovey, R.K. How does spatial resolution affect model performance? A case for ensemble approaches for marine benthic mesophotic communities. *J. Biogeogr.* **2019**, *46*, 1249–1259, doi:10.1111/jbi.13581.
26. Lassueur, T.; Joost, S.; Randin, C.F. Very high resolution digital elevation models: Do they improve models of plant species distribution? *Ecol. Model.* **2006**, *1–2*, 139–153.
27. Jiménez-Alfaro, B.; Draper, D.; Nogués-bravo, D. Modeling the potential area of occupancy at fine resolution may reduce uncertainty in species range estimates. *Divers. Distrib.* **2012**, *147*, 190–196, doi:10.1016/j.biocon.2011.12.030.
28. Svensson, J.R.; Jonsson, L.; Lindegarth, M. Excessive spatial resolution decreases performance of quantitative models, contrary to expectations from error analyses. *Mar. Ecol. Prog. Ser.* **2013**, *485*, 57–73, doi:10.3354/meps10307.
29. Brown, W.L.; Wilson, E.O. Character Displacement. *Syst. Zool.* **1956**, *5*, 49–64, doi:10.2307/2411924.
30. Beaumont, L.J.; Gallagher, R.V.; Thuiller, W.; Downey, P.O.; Leishman, M.R.; Hughes, L. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Divers. Distrib.* **2009**, *3*, 409–420.
31. Broennimann, O.; Treier, U.A.; Müller-Schärer, H.; Thuiller, W.; Peterson, A.T.; Guisan, A. Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* **2007**, *8*, 701–709.
32. Arnold, E.N. Resource partition among lacertid lizards in southern Europe. *J. Zool.* **1987**, *1*, 739–782, doi:10.1111/j.1096-3642.1987.tb00753.x.
33. Law, R.; Marrow, P.; Dieckmann, U. On evolution under asymmetric competition. *Evol. Ecol.* **1997**, *11*, 485–501, doi:10.1023/A:1018441108982.
34. Abrams, P.A. Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution* **1987**, *41*, 651–661, doi:10.1111/j.1558-5646.1987.tb05836.x.
35. Broennimann, O.; Fitzpatrick, M.C.; Pearman, P.B.; Petitpierre, B.; Pellissier, L.; Yoccoz, N.G.; Thuiller, W.; Fortin, M.-J.; Randin, C.; Zimmermann, N.E.; et al. Measuring ecological niche overlap from occurrence and spatial environmental data. *Glob. Ecol. Biogeogr.* **2012**, *21*, 481–497, doi:10.1111/j.1466-8238.2011.00698.x.
36. Di Cola, V.; Broennimann, O.; Petitpierre, B.; Breiner, F.T.; D'Amen, M.; Randin, C.; Engler, R.; Pottier, J.; Pio, D.; Dubuis, A.; et al. ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography* **2017**, *40*, 774–787, doi:10.1111/ecog.02671.
37. Pérez-Mellado, V. *Podarcis Bocagei (Seoane, 1884). Reptiles. Salvador, A. (Coordinador), 1998*; Fauna Ibérica, Ramos, M.A., Ed.; Museo Nacional Ciencias Naturales, CSIC: Madrid, Spain, 1998; Volume 10, pp. 243–257.
38. Geniez, P.; Sá-Sousa, P.; Guillaume, C.P.; Cluchier, A.; Crochet, P.A. Systematics of the *Podarcis hispanicus* complex (Sauria, Lacertidae) III: Valid nomina of the western and central Iberian forms. *Zootaxa* **2014**, *3794*, 1–51, doi:10.11646/zootaxa.3794.1.1.
39. Loureiro, A.; Ferrand, N.; Carretero, M.A.; Paulo, O. (Eds.) *Atlas dos Anfíbios e Répteis de Portugal*; Esfera do Caos: Lisboa, Portugal, 2010.

40. Sillero, N.; Corti, C.; Carretero, M.A. Home ranges of parthenogenetic and bisexual species in a community of *Darevskia* lizards (Reptilia: Lacertidae). *Zool. Middle East* **2016**, *62*, 306–318, doi:10.1080/09397140.2016.1257403.
41. Sillero, N.; Skidmore, A.K.; Toxopeus, A.G.; Brito, J.C. Biogeographical patterns derived from remote sensing variables: The amphibians and reptiles of the Iberian Peninsula. *Amphib. Reptil.* **2009**, *30*, 185–206, doi:10.1163/156853809788201207.
42. Carretero, M.A.; Sá-Sousa, P.; Barbosa, D.; Harris, D.J.; Pinho, C. Sintopía estricta entre *P. bocagei* y *P. carbonelli*. *Boletín Asoc. Herpetol. Española* **2002**, *13*, 20–24.
43. Pinho, C.; Kaliontzopoulou, A.; Carretero, M.A.; Harris, D.J.; Ferrand, N. Genetic admixture between the Iberian endemic lizards *Podarcis bocagei* and *Podarcis carbonelli*: Evidence for limited natural hybridization and a bimodal hybrid zone. *J. Zool. Syst. Evol. Res.* **2009**, *47*, 368–377.
44. Galan, P. Reproductive ecology of the lacertid lizard *Podarcis bocagei*. *Ecography* **1997**, *20*, 197–209, doi:10.1111/j.1600-0587.1997.tb00362.x.
45. Carretero, M.; Ribeiro, R.; Barbosa, D.; Sá-Sousa, P.; Harris, D.J. Spermatogenesis in two Iberian *Podarcis* lizards: Relationships with male traits. *Anim. Biol.* **2006**, *56*, 1–12, doi:10.1163/157075606775904759.
46. Pérez-Mellado, V. *Podarcis Hispanica (Steindachner, 1870). Reptiles. Salvador, A. (Coordinador), 1998*; Fauna, Ibérica, Ramos, M.A., Ed.; Museo Nacinal Ciencias Naturales, CSIC: Madrid, Spain, 1998; Volume 10, pp. 258–272.
47. García-Muñoz, E.; Sillero, N. Two new types of noose for capturing herps. *Acta Herpetol.* **2010**, *5*, 259–263.
48. Stamps, J.A. Conspecifics as Cues to Territory Quality: A Preference of Juvenile Lizards (*Anolis aeneus*) for Previously Used Territories. *Am. Nat.* **1987**, *129*, 629–642.
49. Eifler, D.A.; Eifler, M.A. Foraging Behavior and Spacing Patterns of the Lizard *Cnemidophorus uniparens*. *J. Herpetol.* **1998**, *32*, 24–33.
50. Schoener, T.W.; Schoener, A. Intraspecific Variation in Home-Range Size in Some *Anolis* Lizards. *Ecology* **1982**, *63*, 809–823.
51. Boudjemadi, K.; Lecomte, J.; Clobert, J. Influence of connetivity on demography and dispersal in two contrasting habitats: An experimental approach. *J. Anim. Ecol.* **1999**, *68*, 1207–1224.
52. Hulbert, S. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **1984**, *54*, 187–211.
53. Bivand, R.S.; Pebesma, E.J.; Gómez-Rubio, V. *Applied Spatial Data Analysis with R*, 2nd ed.; Springer: New York, NY, USA, 2008. Available online: http://www.asdar-book.org/ (accessed on 21 December 2020).
54. Warren, D.L.; Glor, R.E.; Turelli, M. ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography* **2010**, *33*, 607–611, doi:10.1111/j.1600-0587.2009.06142.x.
55. Warren, D.L.; Glor, R.E.; Turelli, M. Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution* **2008**, *62*, 2868–2883, doi:10.1111/j.1558-5646.2008.00482.x.
56. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing; R Core Team: Vienna, Austria, 2020. Available online: https://www.R-project.org/ (accessed on 21/12/2020).
57. Gomes, V.; Carretero, M.A.; Kaliontzopoulou, A. The relevance of morphology for habitat use and locomotion in two species of wall lizards. *Acta Oecologica* **2016**, *70*, 87–95, doi:10.1016/j.actao.2015.12.005.
58. Kaliontzopoulou, A.; Carretero, M.A.; Llorente, G.A. Intraspecific ecomorphological variation: Linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. *J. Evol. Biol.* **2010**, *23*, 1234–1244, doi:10.1111/j.1420-9101.2010.01984.x.
59. Kaliontzopoulou, A.; Carretero, M.A.; Adams, D.C. Ecomorphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use. *J. Evol. Biol.* **2015**, *28*, 80–94, doi:10.1111/jeb.12540.
60. Román, R.; Ruiz, G.; Delibes, M.; Revilla, E. Factores ambientales condicionantes de la presencia de la lagartija de Carbonell *Podarcis carbonelli* (Pérez-Mellado, 1981) en la comarca de Doñana. *Anim. Biodivers. Conserv.* **2006**, *29*, 73–82.
61. Sillero, N.; Carretero, M.A. Modelling the past and future distribution of contracting species. The Iberian lizard *Podarcis carbonelli* (Squamata: Lacertidae) as a case study. *Zool. Anz.* **2013**, *252*, 289–298, doi:10.1016/j.jcz.2012.08.004.

62. Liu, X.; Petitpierre, B.; Broennimann, O.; Li, X.; Guisan, A.; Li, Y. Realized climatic niches are conserved along maximum temperatures among herpetofaunal invaders. *J. Biogeogr.* **2017**, *44*, 111–121, doi:10.1111/jbi.12808.
63. Petitpierre, B.; Kueffer, C.; Broennimann, O.; Randin, C.; Daehler, C.; Guisan, A. Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science* **2012**, *335*, 1344–1348, doi:10.1126/science.1215933.
64. Kaliontzopoulou, A.; Pinho, C.; Harris, D.J.; Carretero, M.A. When cryptic diversity blurs the picture: A cautionary tale from Iberian and North African *Podarcis* wall lizards. *Biol. J. Linn. Soc.* **2011**, *103*, 779–800.
65. Kaliontzopoulou, A.; Adams, D.C.; Meijden, A.; Perera, A.; Carretero, M.A. Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards. *Evol. Ecol.* **2012**, *26*, 825–845, doi:10.1007/s10682-011-9538-y.
66. Kaliontzopoulou, A.; Carretero, M.A.; Llorente, G.A. Morphology of the *Podarcis* wall lizards (Squamata: Lacertidae) from the Iberian Peninsula and North Africa: Patterns of variation in a putative cryptic species complex. *Zool. J. Linn. Soc.* **2012**, *164*, 173–193.
67. Kaliontzopoulou, A.; Carretero, M.A.; Llorente, G.A. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *J. Morphol.* **2007**, *268*, 152–165.
68. Carretero, M.A. An integrated assessment of the specific status in a group with complex systematics: The Iberomaghrebian lizards genus *Podarcis* (Squamata, Lacertidae). *Integr. Zool.* **2008**, *4*, 247–266.
69. Pleguezuelos, J.M.; Márquez, R.; Lizana, M. *Atlas de Distribución y Libro Rojo de los Anfibios y Reptiles de España*; Dirección de Conservación de la Naturaleza-Asociación Herpetológica Española: Madrid, Spain, 2002.
70. Blonder, B.; Lamanna, C.; Violle, C.; Enquist, B.J. The n-dimensional hypervolume. *Glob. Ecol. Biogeogr.* **2014**, *23*, 595–609, doi:10.1111/geb.12146.