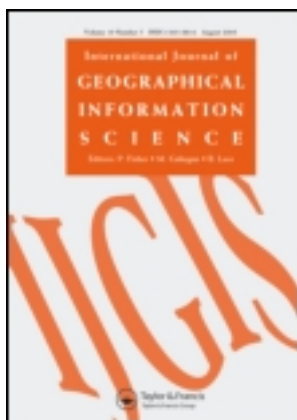


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Spatial structure analysis of a reptile community with airborne LiDAR data

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The analysis of the spatial structure of animal communities requires spatial data to determine the distribution of individuals and their limiting factors. New technologies like very precise GPS as well as satellite imagery and aerial photographs of very high spatial resolution are now available. Data from airborne LiDAR (Light Detection and Ranging) sensors can provide digital models of ground and vegetation surfaces with pixel sizes of less than 1 m. We present the first study in terrestrial herpetology using LiDAR data. We aim to identify the spatial patterns of a community of four species of lizards (*Lacerta schreiberi*, *Timon lepidus*, *Podarcis bocagei*, and *P. hispanica*), and to determine how the habitat is influencing the distribution of the species spatially. The study area is located in Northern Portugal. The position of each lizard was recorded during 16 surveys of 1 h with a very precise GPS (error < 1 m). LiDAR data provided digital models of surface, terrain, and normalised height. From these data, we derived slope, ruggedness, orientation, and hill-shading variables. We applied spatial statistics to determine the spatial structure of the community. We computed Maxent ecological niche models to determine the importance of environmental variables. The community and its species presented a clustered distribution. We identified 14 clusters, composed of 1–3 species. Species records showed two distribution patterns, with clusters associated with steep and flat areas. Cluster outliers had the same patterns. Juveniles and subadults were associated with areas of low quality, while sexes used space in similar ways. Maxent models identified suitable habitats across the study area for two species and in the flat areas for the other two species. LiDAR allowed us to understand the local distributions of a lizard community. Remotely sensed data and LiDAR are giving new insights into the study of species ecology. Images of higher spatial resolutions are necessary to map important factors such as refuges.

Keywords: GIS; Iberia; spatial statistics; digital elevation or terrain models; remote sensing; landscape ecology

1. Introduction

Animals do not live in isolation. They live inside an environment composed of sources of energy (food and sunlight). In these places, they find shelter and rest, avoid predators, find mates, and have offspring. The complete set of components of the environment are located and distributed inside a particular space. For an individual, its home range is the spatial representation of the distribution of all the items needed for the survival of that individual (Burt 1943). If we consider a community, its spatial representation is the

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addition of the home ranges of all the individuals belonging to that community. The distribution of an environmental component may affect and influence the distribution of another component (e.g. the distribution of a predator depends on its prey). This is very important from a spatial point of view because ‘everything is related to everything else, but near things are more related than distant things’, as Tobler (1970) proposed in the First Law of Geography. This means that the network of influences among the components that form the home range of an individual or the space shared by all the members of a community is in fact a network determined by distances.

Animals’ home ranges have been widely studied, and the scientific literature is very abundant in this field of research (e.g. Selkirk and Bishop 2002, Laver and Kelly 2008). However, to our knowledge, the spatial structure analysis of animal communities by spatial statistics is less frequent (e.g. Azovsky *et al.* 2000, Frost and Bergmann 2012). On the other hand, tree communities have been analysed spatially for their economic value (e.g. He *et al.* 1997, Wells and Getis 1999; for a revision see Stoyan and Penttinen (2000)). For this purpose, it is necessary to have spatial data on individuals’ home ranges, or at least on their distributional ranges, as well as on the factors influencing these individuals, such as temperature, habitat, refuges, and prey. These types of data are not frequently used, even in home range studies (Anderson *et al.* 2005).

Reptiles are a good model to study the spatial structure of a community due to their strong dependence on weather conditions and low mobility (Sillero *et al.* 2009). Although it is very difficult to perform telemetry studies of small reptiles (Diaz *et al.* 2006), it is currently possible to obtain accurate distribution data with GPS devices. Very accurate hand-held GPS can provide an accuracy on horizontal coordinates lesser than 1 m, enough to record positions of many individuals in little time. Until now, home ranges of very small reptiles have been determined by measuring distances to each individual position manually from fixed marks in a plot (Diego-Rasilla and Pérez-Mellado 2003, Scoular *et al.* 2011). Other studies have used GPS devices, but with a high error in the spatial coordinates (e.g. 5 m in Frost and Bergmann 2012).

In addition to the ability to record a lizard’s spatial position, environmental information can be obtained from satellite imagery and aerial photographs of high spatial resolution. Another source of data is Airborne Laser Scanning (ALS) technology, also called light detection and ranging (LiDAR), used to obtain more accurate digital elevation and terrain models, with a larger spatial resolution. LiDAR is an active remote-sensing technique based on the measurements of range and precise orientation of laser reflection on ground surface from an aircraft (Baltsavias 1999; Wehr and Lohr 1999). The main result is a geo-referenced 3D point cloud. The principal advantage of LiDAR compared to photogrammetry and spectral images is that laser scanners are not dependent on the sun as a source of illumination (Baltsavias 1999). Consequently, the interpretation of the data is not hampered by shadows caused by clouds or neighbouring objects. Laser scanner pulses may travel unimpeded back and forth along the same path through small openings in a forest canopy, providing information about the forest ground. In contrast, optical images can only provide information about ground cover when it is visible through the forest canopy. Despite its numerous applications in different fields, LiDAR has been used in the area of animal ecology to generate variables of forest structure in order to model the distribution of birds (e.g. Bradbury *et al.* 2005, Graf *et al.* 2009, Tattoni *et al.* 2012). Yamamoto *et al.* (2012) generated topographical variables from LiDAR data to analyse the difference in the use of beaches by sea turtles.

In studies of small reptiles, the spatial resolution of data is important and LiDAR can be used to obtain more accurate digital terrain models (DTMs), to distinguish among

different vegetation layers, and to perform functional habitat and refuge maps, thereby addressing two key limiting factors in the analysis of the spatial structure of reptile communities. Accordingly, we present here the first study to our knowledge in terrestrial herpetology using LiDAR data. The study was performed on a lizard community composed of four species (*Lacerta schreiberi*, *Timon lepidus*, *Podarcis bocagei*, and *P. hispanica*) in Northern Portugal. Specifically, we aim

- (1) To identify the spatial patterns of a community of lizards, considering all species together and each species separately. We want to know if the species (together and separately) are distributed in clusters or not. We predict that the species are not distributed randomly across the study area, but in clusters, largely determined by the spatial structure of the area. We also aim to identify each cluster and its specific composition and how their distributions are correlated with the environment. We hypothesise that the individuals of each species are clustered in different ways due to age and not due to sex. Adults are able to obtain areas with better resources, whereas juveniles are relegated to the poorest parts of the community space (Frost and Bergmann 2012). On the other hand, both sexes should make a similar use of the space (Frost and Bergmann 2012).
- (2) To determine whether the habitat is influencing the distribution of the species. Here, we forecast that the four species have independent distributions due to different habitat requirements. In other words, each species will occupy different parts of the study area.
- (3) Finally, we aim to assess if LiDAR data is a reliable data source for spatial studies at the local scale.

2. Materials and methods

2.1. Study area

The study area was located in the valley of the River Camposinho, around the Monastery of Santa Maria de Pitões (Northern Portugal; Figure 1). The region belongs to the Atlantic biogeographical region (Sillero *et al.* 2009). The study area enclosed a sampling transect 250 m in length composed of two parts: a stony pathway and a flat area, with an approximate North–South orientation. The pathway began at the top of the valley and ended at the flat area, almost at the entrance of the Monastery. The pathway has an irregular stone wall (approximately 1 m high at its highest point) on the eastern side. The flat area encloses the Monastery and a grass area with some groups of stones, behind the buildings of the Monastery, and constitutes the right bank of the River Camposinho. The Monastery is partially in a ruinous state and is composed of a restored church and the remains of a cloister. The valley is composed of Mediterranean bushes (*Cytisus* sp.) on the western side and agricultural fields on eastern side. The pathway wall has some individuals of oaks, *Quercus pyrenaica*. The river has a very dense gallery forest. The top parts of the valley were burnt in 2007. The effects were still visible at the time of the survey.

2.2. Surveys

We performed 16 surveys of the study area for 3 days, at the end of May and the beginning of June 2012. Each survey took around 1 h. The survey started at one end of the study area (alternately the pathway at the top of the valley or the grass area behind the cloister remains) and finished at the other (the grass area behind the cloister remains or the pathway at the top of

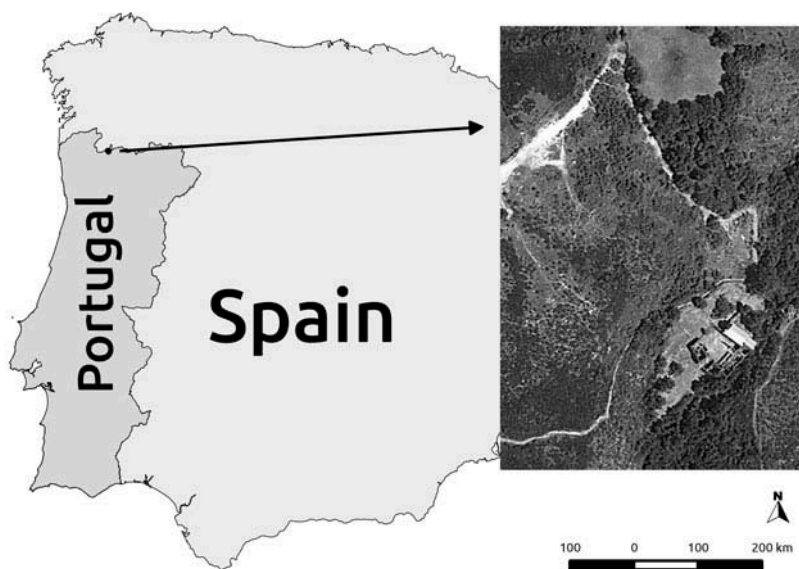


Figure 1. Location of the Monastery of Santa Maria de Pitões (Northern Portugal).

the valley). We then waited 15 min before beginning another survey from the final point to the initial one. This waiting time allowed the lizards to recover their normal position in the event that they were disturbed by our presence. We recorded the position of each lizard with a GPS unit (Trimble GeoExplorer 2008 HX) with an accuracy around 10 cm after post-processing.

2.3. Species community composition

The lizard community was composed of two medium-size species (*L. schreiberi* and *T. lepidus*), and two small species (*P. bocagei* and *P. hispanica*) of the Lacertid family. *L. schreiberi* is associated with very wet habitats, like river banks (Pérez-Mellado 1998c). *T. lepidus* (the biggest Lacertid species of the Iberian Peninsula) is typically a Mediterranean species; when in Atlantic regions, it is associated with open and sunny areas (Pérez-Mellado 1998a). *P. hispanica* prefers rocky habitats and is very frequently found in human buildings (Pérez-Mellado 1998b). *P. bocagei* is a ground-dwelling lizard of Atlantic habitats; it can use also rocky habitats (Pérez-Mellado 1998d).

2.4. LiDAR data

We obtained LiDAR data from the PNOA (Plan Nacional de Ortofotografía Area) project (<ftp://ftp.pnoa.ign.es/>). LiDAR data (Ministerio de Fomento 2010) were acquired in September 2009 using an IGI LM 5600 sensor, operated at a laser wavelength of 1064 nm from a flight altitude of 1000–1800 m (above sea level). The beam divergence was 0.5 mrad, the pulsing frequency 70 kHz, the scan frequency 50 Hz, and the scan angle $\pm 10^\circ$. The first and last return pulses were registered. The entire study area was flown in 18 strips and each strip was flown three times, which gave an average measuring density of about 0.5 pulses/m².

We interpolated a digital surface model (DSM) from the first LiDAR return. Then, we applied the adaptive morphological filter (AMF) proposed by Gonçalves-Seco *et al.* (2011) to classify the LiDAR data point cloud into terrain points and non-terrain points

(Sithole and Vosselman 2004). After applying the AMF, the final DTM was interpolated from the points classified as terrain. We obtained a digital height model (DHM) by subtracting the original DSM from the morphologically filtered DTM (see Supplementary material Figure S1). All data were interpolated in Golden Surfer[®] software (version 8) using the kriging method.

We derived slope, ruggedness, and orientation (in radians) variables from the LiDAR DTM (see Supplementary material Figure S1). We calculated for each DSM and DTM a hill-shading model per day and for the each sun position every 15 min, from sunrise to sunset. After that, all hill-shading models of each day were summed to obtain a surrogate of the accumulated number of hours of sun (see Supplementary material video S1). All procedures were performed in Quantum GIS 1.8.0.

2.5. Distribution spatial pattern analysis

In order to know how the species were spatially distributed, we applied several tests of spatial statistics. First, we analysed the distance threshold of clustering for all the species together and for each species individually. For this, we used the G distance function (Rogerson 2001, Bivand *et al.* 2008), which measures the distribution of the distances from an arbitrary event to its nearest event. The results of the G-function depend on the shape of the study area considered. For this, we calculated a buffer of 20 m around the species points (corresponding to the visual field of surveying). In addition, a complete spatial randomness (CSR) point process with the same estimated intensity in the study area was repeatedly simulated (with 999 iterations) to check whether the empirical function is contained inside. The G-function was calculated using the envelope function within the R software (R Development Core Team 2012).

2.6. Spatial clustering analysis

We used a topological clustering method to spatially identify the clusters of species locations. The definition of what constitutes a cluster inside a cloud of points depends exclusively on a threshold distance, i.e. the distances among the points inside the cluster are shorter than the distances to any other point outside the cluster. Many solutions are possible, depending mainly on how many points are included in the cluster and in the size of the study area. Therefore, this threshold distance should be determined statistically, for example using distance functions like the G-function (Rogerson 2001, Bivand *et al.* 2008). We used the nearest neighbour index (NNI) (Clark and Evans 1954) to determine the threshold distance because of its easier interpretation. The NNI considers that a cloud of points are clustered when the mean nearest neighbour distance among points is lower than the expected one. We computed the length of the lines of a Delaunay triangulation among all points, selecting those Delaunay lines shorter than the expected nearest neighbour distance (Clark and Evans 1954). The points intersecting the selected Delaunay lines were considered as clustered.

2.7. Spatial autocorrelation analysis

Spatial autocorrelation means that 'the values of a given variable are a function of the spatial distances between them or their locations in space' (Fortin and Dale 2005; for a review see Getis 2008). Thus, we measured the spatial autocorrelation among the species location points and the environment using a global method (Moran's I) and a local method

(Local Indicators of Spatial Association (LISA); Anselin 1995). LISA identifies the outliers of the clusters. We represented the environment by using the first component of a spatial principal component analysis (SPCA; Sillero *et al.* 2009) of all the topographical variables (DTM, DSM, DHM, slope, orientation, ruggedness, and both hill-shading models from DTM and DSM). We applied these analyses to identify how the environment influences the distribution of clusters by species and age class. In order to verify if there were differences in the spatial structure among sexes, we applied an LISA analysis per species, considering sex as environmental variable. Males were classified as 0 and females as 1. All spatial statistics were calculated with GeoDa software (Anselin *et al.* 2006).

2.8. Habitat analysis

We analysed how the habitats influence the spatial structure of the community by modelling the realised niche of each species (*sensu* Sillero 2011) with maximum entropy (Maxent 3.3.2 software), a general-purpose machine learning method that uses presence-only occurrence data (Phillips *et al.* 2006, Phillips and Dudík 2008). Maxent looks for the statistical model with the most uniform distribution but still infers as accurately as possible the observed data, selecting at random uniformly distributed data from the background pixels. Here, background sample does not mean species absence at the selected sites, but rather provides a spectrum of the available conditions (Phillips *et al.* 2009). As Maxent results depend on random background selection, the final model of each species was the average of 10 slightly different models (for a review on consensus models see Marmion *et al.* 2009). We chose 10 models as a compromise among statistical analysis power, computation time, and physical storage. We ran Maxent with autofeatures selecting at random 70% of the presence records as training data and 30% as test data. We tested model results with the area under the curve (AUC) of the receiver operating characteristics (ROC) plots (Liu *et al.* 2005), as AUC is independent of prevalence (the proportion of presence in relation with the total data set size) as assessed by its mathematical definition (Bradley 1997). However, AUC values are sensitive to the proportion between the size of the species distribution and the size of the study area: the larger this proportion, the larger the value of AUC (Lobo *et al.* 2008). Due to this reason, comparing ROC results among species of different study areas is not appropriate (VanDerWal *et al.* 2009). Maxent determined the importance of each environmental variable on models by jackknife resampling of the training and test gain and of AUC values. For this purpose, Maxent excluded each variable in turn and created a model with the remaining variables; then Maxent created another model using each individual variable. Finally, Maxent obtained an average percentage contribution of each environmental factor to the models.

3. Results

3.1. Distribution spatial pattern analysis

We collected a total of 173 records, divided as follows (see Supplementary material Table S1): 97 *P. bocagei*, 42 *T. lepidus*, 19 *P. hispanica* type 1A, and 15 *L. schreiberi*. From these 173 records, 164 were adults, eight subadults, and only one juvenile. *P. bocagei* and *L. schreiberi* occurred throughout the study area (Figure 2), while *T. lepidus* and *P. hispanica* were restricted to the flat area, including the remains of the Monastery (Figure 2).

The G-function for all the species showed that the species locations had a clustered distribution: from the beginning of the graph, the curve was always outside the CSR limits of the envelope analysis (Figure 3). The graph reached the asymptote close to the value of

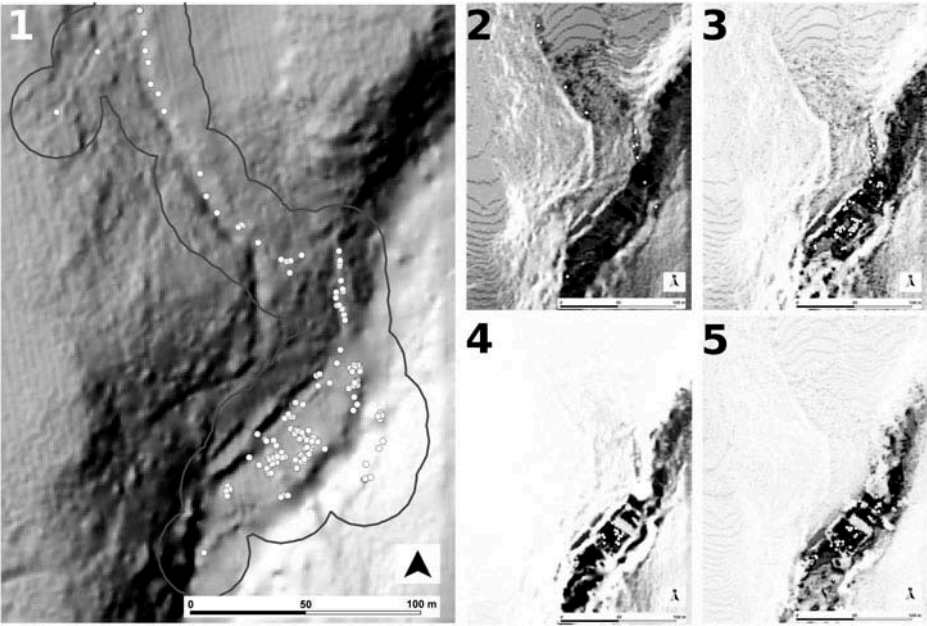


Figure 2. Map with the distribution of all records (1), and each species separately: *Lacerta schreiberi* (2); *Podarcis bocagei* (3); *P. hispanica* (4); *Timon lepidus* (5). The background of map 1 is a hill-shading model of the study area. Map 1 includes the study area used in G-function calculations (see methods for more details and Figure 3). The backgrounds of maps 2–5 correspond to the average Maxent models of each species. Dark shades represent more suitable habitats. Light shades represent more unsuitable habitats.

5 m of nearest neighbour distance. This clustered pattern was visible also when considering each species separately (Figure 3), although it was not so clear in the case of *P. hispanica* and *L. schreiberi*. The asymptote was reached at 3–6 m of nearest neighbour distance for all species except *L. schreiberi*, which was 25 m (Figure 3).

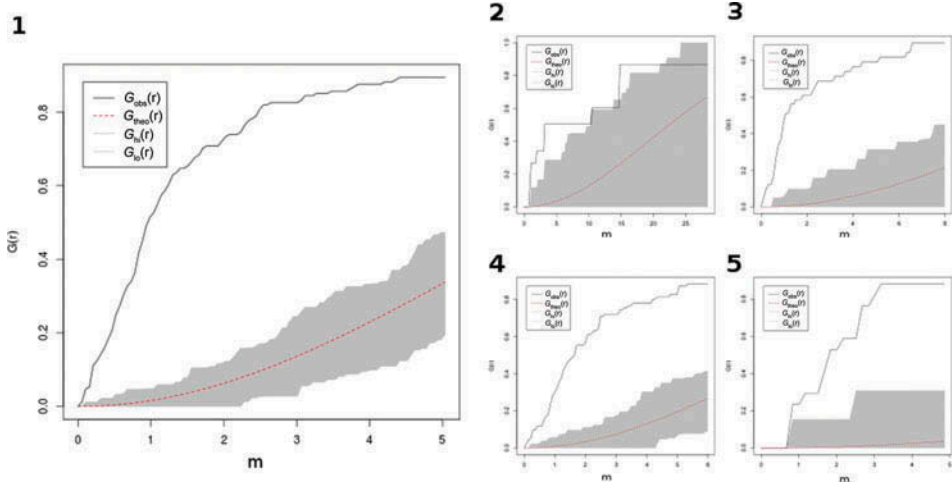


Figure 3. G-function graphs for all records (1), and each species separately: *Lacerta schreiberi* (2); *Podarcis bocagei* (3); *P. hispanica* (4); *Timon lepidus* (5).

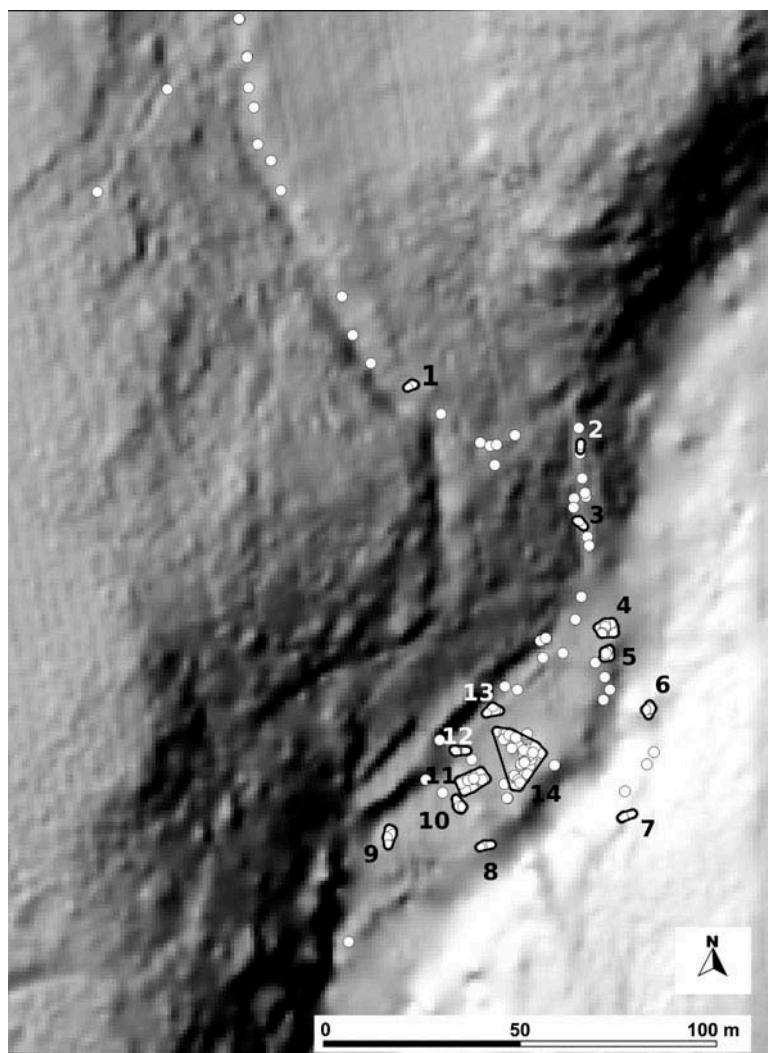


Figure 4. Distribution of clusters identified by the topological clustering method. Numbers refer to cluster numbers in Table S2.

3.2. Spatial clustering analysis

We identified 118 species points in 14 clusters (Figure 4). Three clusters were situated on the pathway, the rest on the flat area. The clusters were composed of one to three species, never of four species. The clusters with the most records were numbers 14 (44 records), 11 (15), and 4 (9) (see Supplementary material Table S2 and Figure 4).

3.3. Spatial autocorrelation analysis

The first component of the SPCA explained 78.49% of the variance. Both hill-shading variables had the highest eigenvalues, thus contributing most to the first component of the SPCA (see Supplementary material Table S3). Moran's I value indicated a low autocorrelation ($I = 0.0751$). The LISA analysis (Figure 5) identified outliers of low values (low

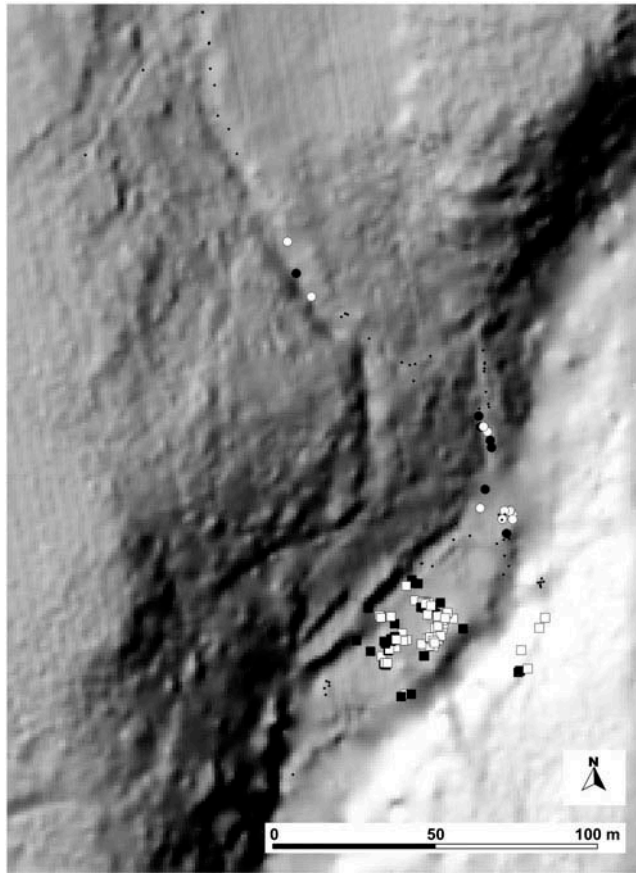


Figure 5. Map of the spatial autocorrelation between the first component of a principal component analysis (PCA) on environmental variables and the species records measured by LISA: small black points represent not clustered records; white circles are clustered records of high PCA values; white squares are clustered records of low PCA values; black circles are outliers of low PCA values (surrounded by high values); and black squares are outliers of high PCA values (surrounded by low values).

values surrounded by high values) only in the pathway (composed of *P. bocagei*, *T. lepidus*, and *L. schreiberi*) and outliers of high values (high values surrounded by low values) only in the flat area (composed of *P. bocagei*, *P. hispanica*, and *T. lepidus*). LISA analysis associated the presence of juveniles and subadults to clusters of low values. LISA analysis per species and sex showed low autocorrelations for two species (*P. bocagei*: $I = -0.0889$; *T. lepidus* = 0.0015) and medium values for *P. hispanica* ($I = -0.3473$). In any case, LISA associated both males and females as outliers of low and high values.

3.4. Habitat analysis

Maxent models also identified two different patterns: suitable habitats for *P. bocagei* and *L. schreiberi* occurred throughout the study area, such as some slopes of the valley, but mainly in the flat area (Figure 2). However, *P. hispanica* and *T. lepidus* only had suitable habitats in the flat area (Figure 2). In any case, all models had training or testing AUC

Table 1. Main Maxent results for each lizard species.

Species	<i>L. schreiberi</i>	<i>P. bocagei</i>	<i>P. hispanica</i>	<i>T. lepidus</i>
Training samples	11	64	12	27
Training AUC	0.8379	0.9248	0.9701	0.9579
Test samples	4	27	5	11
Test AUC	0.7528	0.9112	0.9552	0.9168
AUC standard deviation	0.0875	0.0199	0.0126	0.0452
Hill-shading DSM sum	3.3035	9.2212	3.8787	4.7446
Hill-shading DTM sum	1.5476	1.5261	0.2389	3.133
DHM	35.2058	5.2806	3.7654	2.2441
DSM	33.8722	58.1503	68.7719	76.5038
Ruggedness	26.0709	25.8217	23.345	13.3745

Notes: The upper part of the table includes the number of records used to train and test the model as well as the value of the area under the curve (AUC) of the receiver operating characteristics (ROC) and its standard deviation for both training and test models. The bottom part of the table shows the contribution of each variable to the model. The two most important variables are indicated in bold.

values higher than 0.9, except in the case of *L. schreiberi* that had lower AUC values (Table 1). In fact, only this species presented DHM and DSM as the variable that contributed most to the models. For the rest of the species, DSM and ruggedness contributed most to the models (Table 1).

4. Discussion

Spatial statistics have been widely applied to forest communities (Stoyan and Penttinen 2000), applying as main statistical tools the Ripley's K-function (Wells and Getis 1999) and the NNI (He *et al.* 1997) to analyse the global spatial structure, or LISA to identify local patterns (Nelson and Boots 2008). In the case of reptiles, to our knowledge, the present work is the first to analyse the spatial community structure using spatial statistics. Frost and Bergmann (2012) used also the NNI, but exclusively to compare global distribution patterns (clustered, regular, or random) among sexes and ages of a lizard species. In the particular case of Iberian lizards, there are several works where community structure was analysed from an ecological point of view, but without a spatial component (Mellado *et al.* 1975, Mellado 1980).

In our study, the lizard community and their four species were not distributed randomly but in clusters, as indicated by the G-function. This result is expected because resources within home ranges are not distributed randomly (Mysterud *et al.* 1999, Kwiatkowski and Sullivan 2002). The species mainly presented two patterns of distribution: *P. bocagei* and *L. schreiberi* were widespread across the study area, while *P. hispanica* and *T. lepidus* were restricted to flat areas. There are a number of possible ecological explanations of these differences in the use of the space. *T. lepidus* occupies the highest trophic level inside the community, being present in open and flat areas (the top of the valley, the entrance to the Monastery, and the cloister; Pérez-Mellado 1998a). The Maxent model indicated effectively suitable habitats in open areas. *L. schreiberi* followed the path (where small lines of water are always flowing down) and the river in the bottom of the valley. In fact, this species is associated with water lines (Pérez-Mellado 1998c). *P. hispanica* is close to the northern limit of its distribution (Sá-Sousa and Pérez-Mellado 2002), being outcompeted by *P. bocagei*. Hence, *P. hispanica* exclusively occupied the most rocky area, i.e. the Monastery. Although it is always associated with rocky habitats,

P. hispanica can be found in less vertical rocks (Sá-Sousa and Pérez-Mellado 2002). The study area is included in the middle of the distribution of *P. bocagei*, and thus it is widespread, occupying all suitable areas, as proved by the Maxent model.

We identified 14 different clusters in the community, composed of three or fewer species, never four. Three were located on the path, but very close to the flat area of the valley. The remaining clusters were located in the flat area of the valley. *P. bocagei*, as a consequence of its widespread distribution within the study area, was found in almost all clusters, except one (cluster 5) composed exclusively of *T. lepidus*. Cluster 5 corresponded to one of the main thermoregulation places of two adults (male and female; Figure 4) near the entrance to the Monastery. Clusters 10–14 were situated in the cloister, and 2–6 in the last part of the pathway, where there is a stone wall. The remaining clusters are located in the flat area of the valley, always close to stone groups. Therefore, lizards followed the distribution of suitable areas. Effectively, Maxent models classified the main walls (e.g. the church and the cloister) as suitable habitats.

The global Moran's *I* among species detected a low spatial autocorrelation, a necessary condition to detect local clustering groups (Anselin 1995). The local autocorrelation analysis identified similar groups of clusters to the topological clustering method. LISA identified outliers of low values only on the path and of high values only in the flat area of the valley. The outliers of the path corresponded to shadowed places, while the outliers of the flat area corresponded to sunny places, mainly top of the walls, where individuals have better conditions for thermoregulation. All these places with better conditions were occupied by adults (Frost and Bergmann 2012). Subadults and juveniles were relegated to places with less solar radiation (Diego-Rasilla and Pérez-Mellado 2003, Frost and Bergmann 2012), but they did not form clusters. On the other hand, as previously hypothesised, males and females used the space in the same way (Frost and Bergmann 2012), as confirmed by LISA analysis. There are no studies on the home range of *P. bocagei*. Possible differences in the use of space between males and females of *L. schreiberi* remain unknown (Marco and Pérez-Mellado 1999). Díaz *et al.* (2006) studied habitat selection by *T. lepidus*, although they did not analyse differences between sexes. Both males and females of *P. hispanica* look for habitats of high quality (Gil *et al.* 1988), although females use different habitats depending on the season (Diego-Rasilla and Pérez-Mellado 2003).

The Maxent models showed that the environmental factors explaining the distributions of the species were different only for *L. schreiberi*. This species was limited by the variables DHM and DSM, while the others were limited by DSM and ruggedness. In fact, we were expecting that all the species should present different variable contributions. *P. bocagei* probably depends on the same environmental factors as *P. hispanica* and *T. lepidus*, due to its high prevalence in the flat area of the valley. The most important variables for the models were always related to altitude. Both DSM and ruggedness are related to the relative position of the objects on the surface of the study area. Consequently, *L. schreiberi* distribution was explained mostly by DHM, because most of the records were located on the wall of the path, thus at higher altitudes. The hill-shading DSM and DTM variables had low contributions to the species' distributions as they incorporated all shadow positions from sunrise to sunset. Partial models per hour or per transect might present these variables with higher contributions, as individuals look for sunny places during the day. Unfortunately, we do not have enough samples to split records. Nevertheless, the influence of sun as a source of heat is included in the digital elevation, surface, and height models. Our results showed that individuals look for suitable habitats, those with a large amount of energy from the sun.

LiDAR allowed the local analysis of the spatial distributions of the four species of lizards and their community. In fact, only with very high spatial resolution data (1 m or lower) is it possible to determine how home ranges are influenced by the spatial structure of microhabitats. In the case of lizards, LiDAR data can provide a good representation of terrain surface complexity, light/shadow places and movements, and possible refuges. These habitat characteristics are essential to understand which microhabitat features the lizards are actively selecting, and how this determines the spatial structure of the community. Our study helps to understand which microhabitat features explain the distribution of adults versus subadults and juveniles as well as of males and females. Although the raw LiDAR data used in this study were not prepared to be interpolated at a spatial resolution of 1 m², our results were reliable. Coarse spatial resolutions would not have allowed to identify, for instance, the importance of sunny places in the thermoregulation of individuals. Herpetologists have only an intuitive knowledge about microhabitat selection, but without spatial statistical support. In this sense, remotely sensed data and LiDAR in particular are opening new insights into the study of species ecology (Sillero *et al.* 2009, 2012). With this technology, we can analyse which are the spatial factors driving the distribution of individuals at the microhabitat level. Until now, such detailed analyses have not been performed. We hope, therefore, that space as an analytical component will be included more frequently in ecological studies.

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