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Habitat use patterns of three lacertid lizards in the Balearic Islands: insights from native and alien species

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Abstract. Three lacertid lizards inhabit Menorca and nearby islets: the endemic *Podarcis lilfordi*, restricted to small satellite islands, alongside the introduced *Podarcis siculus* and *Scelarcis perspicillata.* In this study, we investigated patterns of habitat use by these species within this insular system. Lizards were detected through visual surveys, and at each observation point, we measured meteorological, vegetation, and perch-use variables. We used the Outlying Mean Index to visualise multidimensional niche patterns and spatial probit regression to identify the environmental variables driving species separation. All three species were active under similar meteorological conditions and showed no segregation along topographic properties; however, their use of vegetation and perch types showed both shared and species-specific patterns. *Podarcis lilfordi* and *P. siculus* used similar perches but diverged in their responses to vegetation structure, with *P. siculus* more frequently recorded in more diverse, vegetated areas and *P. lilfordi* predominantly found in bush-dominated environments. *Scelarcis perspicillata* occupied sparsely vegetated rocky areas and vertical rocky perches. Broad distribution patterns indicate that *S. perspicillata* persists in patchy colonies, suggesting limited invasive potential, whereas *P. siculus* is highly adaptable and widespread. These findings suggest that the potential for *P. siculus* to compete with *P. lilfordi* over similar habitats exists if it reaches the islets, while such a scenario appears far less likely for *S. perspicillata*.

Keywords. Alien, competition, Menorca, *Podarcis lilfordi*, *Podarcis siculus*, *Scelarcis perspicillata*

INTRODUCTION

The Mediterranean islands possess a rich endemic fauna, but since the Late Pleistocene and into the Holocene, this richness has steadily diminished, mainly due to the disappearance of large vertebrates (Masini et al., 2008; Galetti et al., 2018). These extinctions have been driven primarily by human activity, including hunting, habitat destruction, and the introduction of non-native predators (Bover and Alcover, 2008; Spatz et al., 2017; Palombo et al., 2021).

Compared to mammals and birds, reptiles have been less severely affected by these extinction processes, with the possible exception of tortoises (Alcover, 2000; Valenti et al., 2022; Vlachos, 2022). Yet, in both historical and recent times, some endemic lizard species of the Mediterranean islands have experienced drastic population declines, and on certain islands or islets, they have disappeared altogether (Capula et al., 2002; Pérez-Cembranos et al., 2020). The introduction of predators has been a major cause of these extinctions, as some species lack effective escape or defence mechanisms (Mencía et al., 2017). More recent declines among lacertid populations are linked to the spread of generalist competitors, particularly *Podarcis siculus*. This species exhibits significant ecological overlap with native lacertids, potentially outcompeting them for resources. Furthermore, *P. siculus* demonstrates greater resilience in anthropogenically modified environments and higher tolerance to synanthropic predators (Gippoliti et al., 2017; Escoriza, 2021).

This study examined the habitat use patterns of three lacertid species (*Podarcis lilfordi*, *P. siculus*, and *Scelarcis perspicillata*) distributed in the Balearic archipelago (Mallorca and Menorca), with a particular focus on Menorca and its satellite islets. Among these, *P. lilfordi* is the only native species, endemic to the Balearic Islands, and part of a well-differentiated phylogenetic clade that includes other insular species from

the western Mediterranean (Yang et al., 2021). This lacertid was present on the main islands of the Gymnesic archipelago until the period of Roman colonisation (approximately 2.2 ka; Alcover et al., 1981), but currently, it only survives on 18 satellite islands and islets of Menorca and 26 satellite islands and islets of Mallorca (Salvador and Pleguezuelos, 2002; Escoriza, 2020).

The remaining two species are almost certainly introduced (Alcover and Mayol, 1982). First recorded on Menorca in 1928 (Mertens, 1929), *S. perspicillata* may have been introduced as early as the 18th century, with present-day populations likely originating from northwestern Algeria (Mateo et al., 2011). This species remains largely restricted to western Menorca, particularly around the port of Ciutadella and adjacent areas, with its occurrence elsewhere on the island considered doubtful (Perera, 2015). By contrast, *P. siculus* is distributed across the entire island of Menorca, and its presence on Menorca has been documented since the early 20th century (Müller, 1905).

The satellite islets of Menorca represent a particularly valuable system for assessing the potential for interspecific competition through the evaluation of habitat-use overlap. These islets have remained free from allochthonous predators and competitors, and therefore constitute the last refuges for *P. lilfordi*. Currently, all known populations of *P. lilfordi* on Menorcan islets persist in allopatry with the two introduced lacertid species; however, *P. siculus* has already demonstrated the capacity to colonise nearby islets (Illa Plana and Illot Llatzeret; Pérez-Cembranos and Pérez-Mellado, 2023). As a result, the risk of future contact is plausible. At present, concerns about competitive displacement rely on indirect evidence, including inferred ecological overlap based on habitat use patterns and the documented replacement of endemic insular lizard species (e.g., *Podarcis raffonei* by *P. siculus* in the Aeolian Islands; Capula, 1992).

In this study, we evaluated the habitat use of these three species in the Balearic Islands. We hypothesised that, because *P. siculus* is a generalist species (Rugiero et al., 2021; Romano et al., 2023), it may exhibit habitat-use patterns similar to those of the other two lacertid species. In contrast, due to its more rupicolous habits (Perera, 2015), *S. perspicillata* is expected to differ from *P. lilfordi* in habitat use. These patterns provide useful information for evaluating scenarios of potential *P. siculus* expansion to the satellite islets of Menorca, and for guiding the management of the two non-native lacertid species.

MATERIALS AND METHODS

Study system and surveys

The study primarily focused on Menorca and its adjacent islands and islets (Fig. 1). Since large islands are absent around Menorca, two additional islands (Sa Dragonera and Cabrera, situated near Mallorca) were included to broaden the range of the environments available for analysis (Fig. 1). These islands share similar Mediterranean climate, vegetation structure, and host the same focal species, *Podarcis lilfordi*, ensuring ecological comparability. Furthermore, their larger size provides a greater diversity of vegetation types than the smaller Menorcan islets, allowing a more comprehensive characterisation of the species' habitat-use patterns. Surveying was conducted between March and September during the period 2022–2025 (18 campaign days). Sampling sessions were conducted in the morning, with a standardised effort of four hours per day: 07:00–11:00 in summer (July–September) and 10:00–14:00 in March–April. Although survey time was fixed, the distance covered within transects varied depending on lizard encounter rates and terrain complexity, as expected for visual detection methods in

structurally diverse Mediterranean landscapes. Surveys were conducted under sunny or partly cloudy skies, as rainy days significantly reduced surveying efficiency.

All surveys were conducted by the same observer (first author). Transects were randomly placed across various sectors of each island and islet, covering the full spectrum of available land-cover types, including forests, shrublands, agricultural areas, wetlands, and beaches, with a minimum distance between transects of 1.5 km. The number of sampling sites depended on island size, ranging from 3 sites on islets smaller than 1 acre to 13 sites on larger satellite islands. In Cabrera, access to certain areas was restricted due to national park conservation regulations, which limited sampling coverage on that island. For *Scelarcis perspicillata*, surveys were concentrated in the western sector of Menorca, as this species is exclusively distributed in this part of the island (Perera, 2015). Lizards were identified visually to species level, with binoculars (Celestron Nature 8×32 mm) used when necessary. Habitat features were recorded for all lizards detected within 2 meters on either side of the transect. The perch was defined as the site where the individual was initially observed, since this position could shift as the observer approached. No lizards were handled during the surveys.

Niche characterisation

The ecological niche of each species was described along three axes: 1) the abiotic niche, including air temperature, humidity, cloud cover, and topography; 2) vegetation, encompassing plant community structure and land cover types; and 3) perch features (Van Damme et al., 1989; Capula and Luiselli, 1994; Vanhooydonck et al., 2000) (Table 1). Air temperature and relative humidity were recorded in situ adjacent to the perches using a UT330 Digital Hygrometer (±1.0ºC/ ±5% RH; UNI-T Ltd., Dongguan City, China). Cloud cover was obtained from freely available meteorological websites (Ventusky,

2025). Topography was characterised by elevation and slope extracted from a 30 m resolution digital elevation model (Kovács et al., 2026).

Vegetation characteristics, including plant community structure and land cover, were assessed at two scales. First, three orthogonal transects of 30 m were established, intersecting at the perch. Along these transects (1 m on either side), the abundance of plant species was recorded (Guénnette and Villard, 2005). Species identification of trees, shrubs, and perennial grasses followed Castroviejo (2014) and Thorogood (2018). These data were used to compute a Shannon-Wiener diversity index (Shannon, 1948) using the *BiodiversityR* package (Kindt and Coe, 2005) in R (R Development Core Team, 2025). Second, within 3 × 3 m plots centred on the perch where each lizard was initially detected, the percentage cover of water, rock, bare ground, litter, shrubs, grasses, trees, and canopy was estimated visually. Vegetation height was measured with a tape measure. The proportion of rocks with blocks larger than 50 cm was recorded, following Vanhooydonck et al. (2000). Perch characteristics were recorded at the exact point where each lizard was first observed. Perch height and distance to the nearest rock fissure or vegetation cover (potential refuges) were measured with a tape measure. Perch angle was measured with a clinometer. Substrate type was classified as rock, ground, trunk, or sand, following Vanhooydonck et al. (2000).

Data analysis

The study assessed (i) the position of each species within a multidimensional niche space and niche breadth, and (ii) the environmental variables underlying differences in environmental niche among species (Capula et al., 1993; Vanhooydonck et al., 2000). All analyses were carried out in R.

The relative positions of *P. lilfordi*, *Podarcis siculus*, and *S. perspicillata* along each niche axis were visualised using Outlying Mean Index (OMI) ordination (Dolédec et al., 2000), implemented with the *ade4* package (Dray and Dufour, 2007). The OMI method estimates the mean niche position of each species relative to the overall assemblage centroid and provides a measure of species marginality. Prior to OMI ordination, all environmental variables were standardised. For each species, niche breadth was estimated along each niche axis using the nichevar() function from the *indicspecies* package (De Cáceres and Legendre, 2009), following De Cáceres et al. (2011). A Euclidean similarity matrix was then computed among resource states, and niche breadth was calculated as the weighted variance of species occurrence across the resource space, accounting for the similarity among resource states.

To identify the environmental variables most strongly associated with interspecific differences in habitat use, redundancy analyses (RDA) were conducted for each niche dimension. Each RDA used a binary presence-absence matrix of two species as the response variable. Variable selection was performed via forward selection using the ordiR2step() function from the *vegan* package (Oksanen et al., 2026), with the adjusted R^2 of the full model as the stopping criterion (Blanchet et al., 2008). This procedure retains only predictors that contribute independent explanatory variance, implicitly reducing multicollinearity among selected variables.

Species differences were further examined using a Bayesian spatial autoregressive probit model, fitted separately for each pairwise species comparison and niche dimension using the sarprobit() function from the *spatialprobit* package (Wilhelm and Godinho de Matos, 2024). The model was fitted on the subset of predictors selected by the RDA forward selection. Diffuse priors were specified for all parameters: $\beta \sim N(0, 10^{12})$ for regression coefficients and $\rho \sim \text{Uniform}(-1, 1)$ for the spatial autocorrelation parameter.

To account for spatial dependence among sampling sites, a spatial weights matrix W was constructed using the k-nearest neighbours method (k = 5), with inverse-distance weighting and a distance threshold set at twice the median inter-neighbour distance. The resulting matrix was row-standardised (LeSage and Pace, 2009). MCMC sampling was run for 10,000 burn-in iterations followed by 10,000 retained draws. Convergence was assessed using the effective sample size (ESS) and Geweke z-scores; ESS > 200 and $|z| < 2$ were used as thresholds for adequate mixing and chain stationarity (Gelman et al., 1995). Bayesian regression models produce 95% credible intervals for each parameter; when these intervals do not include zero, there is sufficient posterior evidence to consider the variable a relevant predictor in the model (Gelman et al., 1995).

RESULTS

A total of 18 transects encompassing 150 sampling sites were surveyed across three lizard species: 30 *Podarcis lilfordi* (20%), 67 *Podarcis siculus* (44.7%), and 53 *Scelarcis perspicillata* (35.3%). *Scelarcis perspicillata* was found only at the western tip of the island, *P. lilfordi* was restricted to the satellite islands and islets, and *P. siculus* occurred throughout the island of Menorca (Fig. 1 Supplementary Material 1). The mean values and the range for the variables and species are shown in Supplementary Material 1.

Results from the OMI analysis indicate substantial similarities in habitat use among the three species (Fig. 2). *Podarcis siculus* occupied a more central position (OMI = 4.1, p = 0.0001) than *P. lilfordi* (OMI = 7.4, p = 0.0043), whereas *S. perspicillata* occupied the most marginal niche (OMI = 13.2, p = 0.0001). *Podarcis siculus* also tended to exhibit the broadest niche (Fig. 2), particularly along the vegetation dimension (Table 2), while *S. perspicillata* was the most specialised species (Table 2).

217 The RDA and regression analyses assessed the factors contributing to differences
218 in habitat use among species pairs (Tables 3, 4, and 5). *Podarcis lilfordi* and *P. siculus*
219 did not differ along the abiotic or perch dimensions (Table 3), but they did segregate in
220 terms of vegetation (adj. $R^2 = 0.321$). The features contributing to this separation were
221 the association of *P. siculus* with higher ground cover and greater plant diversity
222 (Shannon-Wiener index) (Table 3). *Podarcis lilfordi* and *S. perspicillata* differed in both
223 the vegetation (adj. $R^2 = 0.404$) and perch dimensions (adj. $R^2 = 0.226$) (Table 4).
224 *Podarcis lilfordi* occurred more often in simplified communities dominated by bushes
225 and used ground perches in closer proximity to vegetation than *S. perspicillata* (Table 4).
226 Finally, *S. perspicillata* and *P. siculus* were segregated by vegetation (adj. $R^2 = 0.316$)
227 and perch characteristics (adj. $R^2 = 0.192$) (Table 5). *Scelarcis perspicillata* was
228 associated with areas characterised by a lower proportion of ground substrate and low-
229 growing plants, as well as perches on more vertical rocky surfaces, and away from refuge
230 plants (Table 5). MCMC convergence diagnostics (effective sample size and Geweke z-
231 scores) for the Bayesian spatial autoregressive probit models are provided in
232 Supplementary Material 1.

233

234 ## DISCUSSION

235 This study investigated patterns of habitat use among the three lacertid species
236 inhabiting Menorca and its surrounding islets. The results indicate that *Podarcis siculus*
237 exhibits high habitat versatility, suggesting that it could potentially occupy a substantial
238 portion of the habitat suitable for the insular endemic, *Podarcis lilfordi*. In contrast,
239 similarity in habitat use between *P. lilfordi* and the other introduced species, *Scelarcis*
240 *perspicillata*, was comparatively lower. The three species showed similar responses to
241 meteorological conditions, remaining active under comparable temperature, humidity,

and cloudiness levels. Such convergence was expected, as all are fundamentally heliothermic and the introduced taxa originate from regions with Mediterranean climates closely resembling that of the Balearic Islands. Likewise, they showed no differential responses to topographic variation, including terrain, elevation, terrain slope, and terrain aspect.

Both *P. siculus* and *P. lilfordi* display broad ecological flexibility in vegetation types and perch use, suggesting the potential to occupy a wide range of insular environments. Despite this, *P. lilfordi* is absent from the main island of Menorca and currently persists only on surrounding islets, most likely as a consequence of the historical introduction of non-native predators on the larger islands (Pérez-Mellado et al., 1997; Carretero and Pinya, 2011). Ecological similarity between *P. siculus* and *P. lilfordi* is further supported by the lack of significant differences in perch attributes. However, the two species differ in their association with plant community structure, with *P. lilfordi* more frequently occurring in areas characterised by higher shrub cover and lower plant diversity. This pattern likely reflects the simplified vegetation typical of small rocky islets (Cardona et al., 1998; Llorens et al., 2021), where relict populations of *P. lilfordi* persist, rather than true interspecific differences in responses to vegetation structure. Consistently, on larger islands with more developed arboreal cover, such as Sa Dragonera and Cabrera, *P. lilfordi* occupies a broader range of vegetation types, including *Pinus halepensis* groves.

One limitation of our study is the lack of geographic overlap among the species compared. Consequently, some of the observed variation in habitat use, particularly in relation to vegetation structure, may be partly driven by environmental differences between main islands and satellite islets. This confounding effect is difficult to fully disentangle without experimental or reintroduction data. Nevertheless, the inclusion of Sa

Dragonera and Cabrera partially mitigates this limitation by extending the environmental gradient sampled for this species beyond the depauperate conditions typical of smaller islets.

Ecological differences between *P. lilfordi* and *S. perspicillata* are evident in vegetation and perch use. *Podarcis lilfordi* is more often found in shrub-rich areas, and it relies more heavily on ground substrates and positions near vegetation, reflecting a more terrestrial than rupicolous habit. Because rocky areas are also present on the smaller islets, these patterns suggest that the two species exhibit differential use of available perch types.

The two introduced species (*P. siculus* and *S. perspicillata*) coexist sympatrically in the western tip of Menorca (Mayol, 2003). As reported by Perera (2015), we did not detect *S. perspicillata* beyond the western region of Menorca. Its most northeastern population was found in Cala Morell, whereas similar environments located a few kilometres further east (e.g., Biniatram or Algaiarens) were occupied solely by *P. siculus*. The observed distribution suggests that *S. perspicillata* occurs in isolated colonies, with populations that can be highly abundant and conspicuous in some areas while completely absent just a few hundred meters away. Although our sampling does not entirely preclude the presence of very low-density groups outside these colonies, such patchy distributions are consistent with limited invasive potential, but may also reflect introduction history or propagule pressure (Alexander and Edwards, 2010; Stringham and Lockwood, 2021). Our analyses suggest that syntopic coexistence between the two alien species may be favoured by differences in perch use. *Scelarcis perspicillata* predominantly occupies rocky areas with sparse vegetation and favours vertical perches. Although *P. siculus* can use the same perches, it does not show a particular pattern of utilisation for them, whereas *S. perspicillata* seldom uses ground perches distant from rocky walls.

Overall, our results underscore the potential risk associated with the presence of *P. siculus* in Menorca, as its high colonisation ability could allow it to reach the satellite islets and potentially affect the native lacertid species. Its recent expansion into Mallorca illustrates this capacity for rapid spread (Zawadzki and Seemann, 2009). In a broader context, biological invasions often feature species established in anthropogenically modified environments expanding into adjacent natural areas (Liu et al., 2024). Although the present study did not explicitly analyse human disturbance as a predictor variable, the known synanthropic affinities of *P. siculus* and its current distribution in Menorca provide a relevant backdrop. These contextual factors suggest that a progressive expansion toward the satellite islets, where *P. lilfordi* currently persists, represents a plausible future conservation risk for this endemic species.

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AUTHORIZATIONS

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Table 1. Niche parameters evaluated to characterize the niche properties of three species of lizards in the Balearic archipelago (Menorca, satellite islets, Cabrera, and Sa Dragonera).

Dimension	Explanation	Variables	Source
Abiotic	Weather	Air temperature, air humidity, cloud cover	In situ
	Topographic	Terrain elevation, slope	30 m (GIS model)
Vegetation	Plant community	Vegetation stems and diversity	30 m transects
	Land cover	Cover categories (water, rock, ground, litter, bush, grass, tree), canopy cover and vegetation height	3 m plots
Perch	Perch properties	Perch height, perch angle, substrate type (rock, ground, trunk, sand), nearest rock/vegetation	In situ

Table 2. Niche breadth of each lizard species, controlling for the similarity between resources (De Cáceres et al., 2011).

	Dimension	Niche breadth
Podarcis lilfordi	Abiotic niche	96.046
	Vegetation	169.272
	Perch	141.342
Podarcis siculus	Abiotic niche	96.499
	Vegetation	191.419
	Perch	145.665
Scelarcis perspicillata	Abiotic niche	95.267
	Vegetation	148.087
	Perch	118.541

Table 3. Results of the Bayesian autoregressive probit model, estimating the effect of environmental variables on the presence of *P. lilfordi* (positive) vs. *P. siculus* (negative). Adj. R^2 represents the proportion of explained variance. CI: Credible Interval (2.5% and 97.5% percentiles).

	Adj. R^2	Variables	Estimate	CI 2.5	CI 97.5
Abiotic niche	0.021	–	–	–	–
Vegetation	0.321	Bush%	0.568	–0.044	1.087
		Ground%	–0.820	–1.625	–0.238
		Plant stems	–0.567	–1.177	–0.047
		Shannon-Wiener index	–0.611	–1.088	–0.139
Perch	– 0.020	–	–		

Table 4. Results of the Bayesian autoregressive probit model, estimating the effect of environmental variables on the presence of *P. lilfordi* (positive) versus *S. perspicillata* (negative). Adj. R^2 represents the proportion of explained variance. CI: Credible Interval (2.5% and 97.5% percentiles).

	Adj. R^2	Variables	Estimate	CI 2.5	CI 97.5
Abiotic niche	0.092	–	–	–	–
Vegetation	0.404	Bush%	0.483	0.050	1.476
		Litter%	0.953	0.333	2.127
		Shannon-Wiener index	–0.383	–1.229	–0.006
Perch	0.226	Ground base	0.505	0.019	1.091
		Nearest cover:plant	0.347	–0.136	0.816

Table 5. Results of the Bayesian autoregressive probit model, estimating the effect of environmental variables on the presence of *S. perspicillata* (positive) vs. *P. siculus* (negative). Adj. R^2 represents the proportion of explained variance. CI: Credible Interval (2.5% and 97.5% percentiles).

	Adj. R^2	Variables	Estimate	CI 2.5	CI 97.5
Abiotic niche	0.077	–	–	–	–
Vegetation	0.316	Rock%	0.100	–0.235	0.462
		Ground%	–0.325	–0.671	–0.026
		Plant height	–0.605	–1.233	–0.156
Perch	0.192	Rock base	0.507	0.186	0.871
		Perch angle	0.453	0.113	0.837
		Nearest cover:plant	–0.521	–0.919	–0.164

Figure 1. Study area (Balearic archipelago), showing the level of forestation of the terrain as a background (greater green intensity indicates higher tree density; Tuanmu and Jetz, 2014). A) *Podarcis lilfordi* red circles; B) *Podarcis siculus* green triangles; C) *Scelarcis perspicillata* sky blue squares. Symbols represent individual sampling sites. The red circles show the number and location of the sampling transects. Photo credits: Daniel Escoriza.

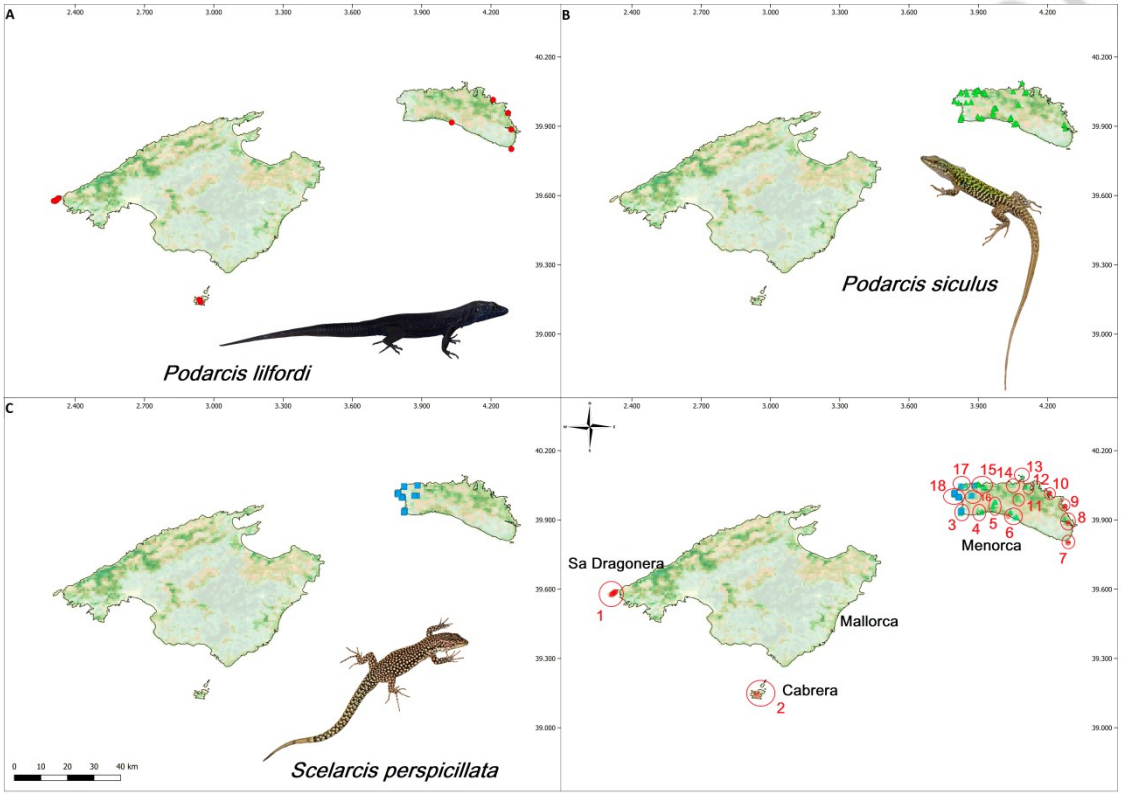

Figure 2. OMI scatterplot showing the relative position of the three Menorcan lacertid species in the multidimensional niche. The top figure shows the sites encompassed by a minimum convex hull; the bottom figure shows the environmental variables represented as vectors. In both panels, the origin represents the average environmental conditions. Red circles, *Podarcis lilfordi*; green circles, *Podarcis siculus*; sky blue circles, *Scelarcis perspicillata*.