REPTILES & AMPHIBIANS

Environmental Heterogeneity and Lizard Assemblages in Riparian Areas in Cyprus

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Abstract.—The island of Cyprus hosts a rich diversity of reptiles, including several endemic species. Reptiles are more common in Mediterranean-type shrublands and other open habitats in Cyprus, although riparian formations offer additional cover and food sources, especially during dry, hot summers. Riparian habitats are often very heterogeneous, an attribute that can be important for lizards since they can utilize a variety of microhabitats crucial for different aspects of their ecology. Nevertheless, reptilian diversity in riparian systems remains understudied and Cyprus is no exception. The aim of this study was to compare lizard diversity and abundance patterns across seasons and elevations, as well as their relationships with habitat heterogeneity and protected status of areas along riverbanks, as expressed by presence in or out of Natura 2000 sites. We examined the effects that these factors can have on lizard communities by studying three rivers that exhibit variations in environmental conditions. Additionally, we evaluated separately the abundances of four common species (Snake-eyed Lizard, *Ophisops elegans*; Troodos Rock Lizard, *Phoenicolacerta troodica*; Cyprus Rock Agama, *Laudakia cypriaca*; and Schreiber's Fringe-toed Lizard, *Acanthodactylus schreiberi*) while recording in riparian habitats seven of the 11 Cypriot species of lizards. Diversity and richness were not significantly associated with any of the explanatory variables examined (season, elevation, habitat heterogeneity, and protected status). Moreover, we found no relationship between the abundances of each of the four species and habitat heterogeneity, even though they responded differently to elevation, season, and protected status. Our results suggest that lizard diversity in riparian systems is high compared to the total number of lizard species found on Cyprus, reaching 60% of the overall richness.

The hypothesis that environmental heterogeneity promotes species richness as it increases opportunities for niche partitioning is fundamental in ecology (Stein et al. 2014). As a result, heterogeneity has been investigated at various levels (community, habitat types, landscape; Ben-Hur and Kadmon 2020) and components (i.e., spatial and structural; Fahrig et al. 2011; Bertrand et al. 2016). Numerous studies that have quantified the heterogeneity-diversity relationships (HDR) suggest complex patterns between them. Some authors have suggested that species richness may decrease at high levels of heterogeneity, in contrast to the usually expected positive relationship of the two factors (Yang et al. 2015; Ben-Hur and Kadmon 2020). Habitat heterogeneity is among the major drivers of diversity as it, when increased, provides a wider range of resources for more species to exploit, so it directly affects species population dynamics and community structure (Katayama et al. 2014; Souza Júnior et al. 2014; Yang et al. 2015). Therefore, understanding and maintaining habitat heterogeneity is fundamental for the conservation of many species (Barbaro et al. 2021; Schmidt et al. 2022).

Lizards occupy a variety of niches and perform a variety of valuable ecosystem services that include seed dispersal and pollination of plants (Valencia-Aguilar et al. 2013; Neghme et al. 2017). Also, lizards have been found to respond positively to the habitat clearing effects of fire by changing their diet during post-fire succession (Pianka and Goodyear 2012). Being quite variable, lizards exhibit a wide range of responses to variation in environmental heterogeneity, such as a higher mobility in heterogeneous than in homogenous environments (Hacking et al. 2014; Basson et al. 2017). Like other reptiles and despite numerous ongoing conservation efforts, such as the establishment of nature reserves, many lizard populations are declining due to factors including habitat loss and degradation, climate change, and invasive species (Gibbons et al. 2000; Stuart et al. 2004; Reading et al. 2010). Hence, evaluating the effects of protected sites on lizard diversity is important. Such studies are lacking in Mediterranean island systems (European Environment Agency 2020), so studying relationships of lizard diversity patterns with habitat heterogeneity is imperative.

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Riparian areas are characterized by microclimatic conditions and unique local habitats that provide increased humidity and food resources (e.g., increased densities of insects and other invertebrates and hygrophilous plants) for many organisms. Such areas may act as refugia for lizards, especially during dry, hot summer seasons when food is scarce (Ballouard et al. 2016). Even though riparian habitats cover only 1.4% of the global land surface, they contribute to more than 25% of all terrestrial ecosystem services, such as water and food for humans and animals (Millennium Ecosystem Assessment 2005; Vörösmarty et al. 2010).

Cyprus is a biodiversity hotspot due to its isolation and its location at the crossroads of Africa, Asia, and Europe (Delipetrou et al. 2008; Sparrow and John 2016). This eastern Mediterranean island (34.55–35.68°E, 32.28–34.58°N) is some 70 km from Turkey and 105 km from Syria (Makris 2003). Cyprus has a diversity of riparian landscapes, species, and habitats of European importance (Sparrow and John 2016). With a surface area of 9,251 km^2, the island supports 2,054 species and subspecies of plants, of which 182 are endemic, 398 species of birds, 30 species of mammals, 22 reptiles, and three amphibians (Tsintides et al. 2007; Sparrow and John 2016).

Eleven species of lizards are known to occur in Cyprus, seven of which are protected by national legislation (Law No. 153(I)/2003, for the Protection and Conservation of Nature and Wild Life), and are listed in the Appendices of the Habitat Directive (92/43/EEC) and the Bern Convention. Of these, the Troodos Rock Lizard (*Phoenicolacerta troodica*) and Cyprus Rock Agama (*Laudakia cypriaca*) are endemic, as are subspecies of the Mediterranean Thin-toed Gecko (*Mediodactylus kotschyi fitzingeri*) and Schreiber's Fringe-toed Lizard (*Acanthodactylus schreiberi schreiberi*) (Baier et al. 2013; Karameta et al. 2022). *Acanthodactylus schreiberi* is the only Cypriot lizard listed as Endangered on the IUCN Red List (Hraoui-Bloquet et al. 2009), although it is locally abundant and can be found all over the island (Baier et al. 2013).

Most of the research on the reptiles of Cyprus has focused on systematics, phylogeography, and/or distribution (Baier et al. 2013; Sparrow and John 2016), and little or no information addresses how environmental factors and habitat heterogeneity affect the presence of lizards and lizard assemblages, especially in riparian habitats. Therefore, the principal aim of this study was to investigate the roles of season, elevation, environmental and habitat heterogeneity, and protected status (i.e., inclusion in the European Natura 2000 reserve system; see also below) on lizard diversity in riparian habitats of Cyprus, with an emphasis on the four most frequently encountered species (*Ophisops elegans*, *Phoenicolacerta troodica*, *Laudakia cypriaca*, and *Acanthodactylus schreiberi*).

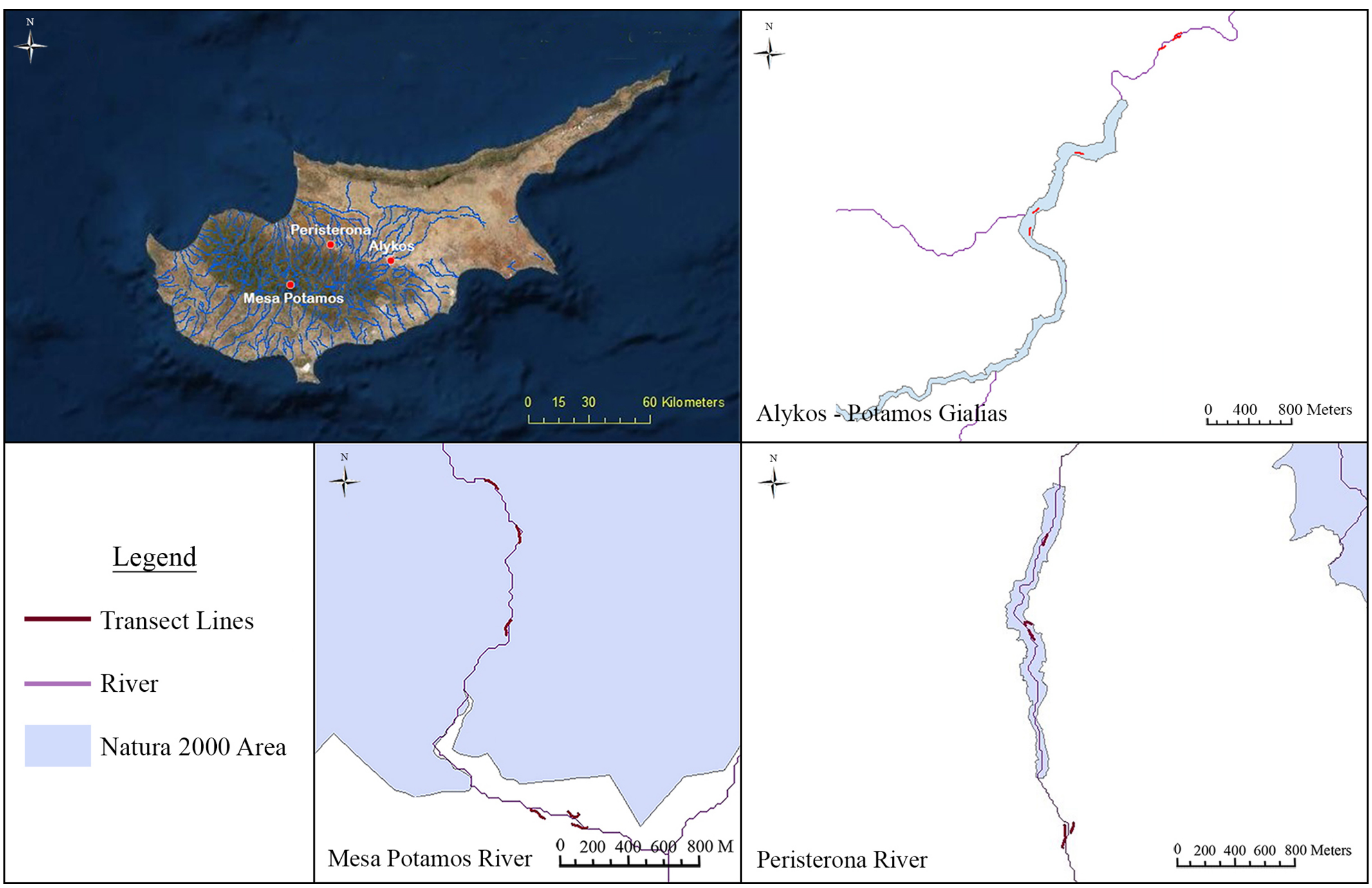

Fig. 1. Topography and river systems in Cyprus and the location of the three rivers studied and the positions of transect lines in each river.

The Habitats Directive (92/43/EEC) (Council of the European Community 1992) is the most significant instrument in the EU that addresses the conservation of natural habitats and wild fauna and flora. Together with the relevant Birds Directive (2009/147/EC) (European Parliament and the Council of the European Union 2010), it has led to the establishment of the Natura 2000 Network of protected areas. Today, the Natura 2000 Network includes 27,852 sites, covering almost one-fifth of the EU's terrestrial land area and about 10% of its seas (European Environment Agency 2020). In compliance with the Habitats and Birds Directives, the Republic of Cyprus has designated 69 Natura 2000 sites that protect habitats and species of community importance.

Materials and Methods

Study area and sites.—In order to include variation in elevation, seasonality, and habitat structure, we sampled riparian sections of riverbanks along three rivers on Cyprus: Alykos-Potamos Gialias, Peristerona, and Mesa Potamos (Fig. 1 and Table 1). These rivers are located at least 20 km from each other, ensuring independence. Since 2004, sections of all three rivers are part of the Natura 2000 Network of protected habitats and species (CY2000007, CY2000011, and CY5000004, respectively), although less than 50% of their combined lengths are in Natura 2000 areas.

Table 1. List of the transects surveyed in this study. Locations are indicted by the coordinates (WGS84) of the transect midpoint. The "In" or "Out" in the name of each transect indicates whether they were inside or outside a Natura 2000 site. Elevations are in meters above sea level (m asl).

Transect	Location	Elevation
Alykos-In-01	35.00103, 33.34101	290
Alykos-In-02	34.99527, 33.33591	300
Alykos-In-03	34.99197, 33.33449	305
Alykos-Out-01	35.01344, 33.35366	270
Alykos-Out-02	35.01393, 33.35417	270
Alykos-Out-03	35.01279, 33.35246	270
Peristerona-In-01	35.06015, 33.08012	350
Peristerona-In-02	35.05229, 33.07806	375
Peristerona-In-03	35.05101, 33.07798	370
Peristerona-Out-01	35.03633, 33.08210	415
Peristerona-Out-02	35.03524, 33.08137	405
Peristerona-Out-03	35.03624, 33.08122	400
Mesa Potamos-In-01	34.88554, 32.90971	890
Mesa Potamos-In-02	34.89037, 32.91018	950
Mesa Potamos-In-03	34.89229, 32.90901	980
Mesa Potamos-Out-01	34.87485, 32.91473	710
Mesa Potamos-Out-02	34.87605, 32.91094	730
Mesa Potamos-Out-03	34.87590, 32.91372	720

The Alykos-Potamos Gialias site (CY2000007) is about 20 km south of Nicosia. Its elevation is 266–430 m (elevations of our transects ranged from 270 to 305 m). Habitats in the Natura 2000 area have not been extensively transformed by human activities and they include different kinds of wetlands, phrygana (or garrigue) with *Sarcopoterium spinosum*, two priority habitats (*Ziziphus lotus* matorral-5220* and xerophilous grasslands-6220*), and six endemic plant taxa. Also, the area is home to the Western Caspian Turtle (*Mauremys rivulata*), which is rare in Cyprus, and the Common Grass Snake (*Natrix natrix*), the Cypriot population of which was until recently considered an endemic subspecies (*N. n. cypriaca*). Several small patches of cultivated cereal grains and trees (olives and almonds) were within 200–300 m of our transects.

The Peristerona River (CY2000011) is located in the northern foothills of the Troodos Mountain Range at elevations of 340–1,280 m (elevations of our transects ranged from 350 to 415 m). The Natura 2000 area includes various wetland habitats and cultivated sites that support populations of several Cypriot endemics, including *Phoenicolacerta troodica*, *Laudakia cypriaca*, Cyprus Whipsnake (*Hierophis cypriensis*), Cypriot Mouse (*Mus cypriacus*), and Cyprus Long-eared Hedgehog (*Hemiechinus auritus dorotheae*), along with additional species of amphibians, reptiles, and mammals. The ecological importance reflects the presence of priority habitats, such as the *Zizyphus lotus* mattoral, and seven endemic plant species. Human activity and cultivated areas are within 200–300 m of our transect lines.

Part of Mesa Potamos River is in the Natura 2000 area 'Ethniko Dasiko Parko Troodous' (= National Troodos Forest Park) (CY5000004). The elevational range of the river is 650–1,500 m (elevations of our transects ranged from 710 to 980 m). The National Troodos Forest Park is in the center of the Troodos Massif, which extends from northwestern to southcentral Cyprus. It is home to more endemic plants than any other site on the island along with a variety of habitats, including pine forests, juniper shrubs, and serpentinophilous grasslands. No human activities occur within 200–300 m of our transects.

Transects in and outside Natura 2000 areas (100 x 3 m) were at least 30 m apart and elevations of individual transects varied less than 5 m. All were monitored by the lead author.

Species richness and abundance.—We conducted field surveys of lizard species from May to September 2019 and from April to September 2020 to cover the spectrum of climatic conditions during two seasons and two consecutive years. In accordance with the biology of the species, we divided the surveys into 'summer' (i.e., June, July, August; mean = 29.5 ± 5.1

Table 2. Numbers of each species recorded at each transect inside (In) and outside (Out) Natura 2000 sites along each river (All), and the total number at all sites (TOTAL). Species: ***Oe*** = Snake-eyed Lizard (*Ophisops elegans*); ***Pt*** = Troodos Rock Lizard (*Phoenicolacerta troodica*); ***Lc*** = Cyprus Rock Agama (*Laudakia cypriaca*); ***As*** = Schreiber's Fringe-toed Lizard (*Acanthodactylus schreiberi*); ***Cc*** = Common Chameleon (*Chamaeleo chamaeleon*); ***Ab*** = Cyprus Snake-eyed Skink (*Ablepharus budaki*); ***Co*** = Ocellated Skink (*Chalcides ocellatus*).

	Alykos									Peristerona									Mesa Potamos									
Species	**1**	**2**	**3**	**In**	**4**	**5**	**6**	**Out**	**All**	**7**	**8**	**9**	**In**	**10**	**11**	**12**	**Out**	**All**	**13**	**14**	**15**	**In**	**16**	**17**	**18**	**Out**	**All**	**TOTAL**
Oe	16	30	51	**97**	23	38	6	**67**	**164**	25	35	25	**85**	38	12	45	**95**	**180**	43	11	10	**64**	11	25	18	**54**	**118**	**462**
Pt	0	1	5	**6**	0	0	2	**2**	**8**	8	1	1	**10**	8	3	2	**13**	**23**	11	1	1	**13**	3	7	1	**11**	**24**	**55**
Lc	0	0	0	**0**	0	0	0	**0**	**0**	0	1	1	**2**	0	0	1	**1**	**3**	3	0	0	**3**	2	5	6	**13**	**16**	**19**
As	1	7	53	**61**	0	4	0	**4**	**65**	4	0	0	**4**	0	0	0	**0**	**4**	0	0	0	**0**	0	0	0	**0**	**0**	**69**
Cc	1	0	1	**2**	0	0	1	**1**	**3**	0	0	0	**0**	0	0	0	**0**	**0**	0	0	0	**0**	0	0	0	**0**	**0**	**3**
Ab	0	1	0	**1**	0	0	0	**0**	**1**	0	1	0	**1**	0	0	0	**0**	**1**	0	1	0	**1**	1	0	0	**1**	**2**	**4**
Co	0	0	0	**0**	0	0	0	**0**	**0**	0	1	0	**1**	0	0	0	**0**	**1**	0	0	0	**0**	0	0	0	**0**	**0**	**1**
	18	39	110	**167**	23	42	9	**74**	**241**	37	39	27	**103**	46	15	48	**109**	**212**	57	13	11	**81**	17	37	25	**79**	**160**	**613**

°C) and 'non-summer' (April, May, September; mean = 25.4 ± 5.6 °C). We visited each transect monthly at 0700–1100 h, when lizards are most active. Monitoring once a month was considered adequate, since the parameters examined (i.e., temperature) did not change considerably within shorter periods. We used Visual Encounter Surveys (VES) (McDiarmid et al. 2012) and recorded each lizard encountered along the transect (Table 2). One person visited transects at a site, starting at a different transect each time. Although we did not mark individuals, we avoided double-counting by tracking each lizard observed. Because this research did not involve collecting or capturing animals for measurements, tagging, or tissue sampling, we did not need permits from the responsible government authorities.

Habitat heterogeneity.—We recorded vegetation, substrate type, and refugia along transects (Janiawati et al. 2016). In the absence of detailed habitat maps, we divided the transects into different types of structural habitat, such as bushes, rocks, and trees (Sutherland 1996). The following structural habitat categories were identified in our study sites based on vegetation and surface-cover characteristics (Fig. 2): (A) dense tall, reed-like shrubs, brambles, herbs, and grasses; (B) low shrubs, including *Sarcopoterium spinosum*, *Cistus* spp., etc., without stones; (C) low shrubs with sparse stones; (D) stone piles; (E) sparse trees; (F) bare soil with or without sparse grasses.

Using visual surveys supplemented by photographs and drone (DJI Mavic 2 Pro) images, we applied the DAFOR scale, (i.e., dominant, abundant, frequent, occasional, and rare) (Hill et al. 2005) to quantify habitat types present along each transect, assigning percentages to each category: dominant (51–100%), abundant (31–50%), frequent (16–30%), occasional (6–15%), and rare (1–5%). We then calculated a simple Habitat Diversity Metric (HDM) for each of the four most common species along each transect by ranking from one to six in ascending order the habitats according to the abundance of each species and multiplying each value with the mean percentage of each habitat type along that transect. We used the same approach to calculate the HDM of each transect for total lizard diversity based on the ranking of habitat types and the abundance of all species (Table 3). An example using *Ophisops elegans* is illustrated in Fig. 3.

Statistical analysis.—We first used paired t-tests to examine potential differences in lizard abundances between transects located in and outside of Natura 2000 sites along each river. We then used linear mixed models to evaluate the potential effects of season, elevation, habitat heterogeneity, and protected status on species diversity, richness, and the abundances of the four most frequently encountered species (*O. elegans*, *P. troodica, L. cypriaca*, and *A. schreiberi*). To avoid pseudoreplication, we pooled data at the transect level (n = 18), with seasons (n = 2) kept separate to account for seasonal variations in temperature, rainfall, and other climatic factors. For each season and each transect (n = 18 x 2 = 36), we estimated species diversity using the Shannon-Wiener index (Price et al. 2010) and also species richness. Additionally, we estimated abundance (i.e., total number of individuals recorded along each transect during each season) of the four most abundant species for which we recorded at least five sightings across all study sites. We then developed a linear mixed model for each of the six response variables (i.e., species diversity, species richness, and the abundance of each of the four species). To identify the most appropriate type of model for each response variable, we assessed visually its distribution using histograms as recommended by Zuur et al. (2010). Species diversity and species richness were normally distributed; therefore, we used general linear mixed models with a Gaussian distribution to model those two variables. Abundances of the four species followed Poisson distribu-

Figure 2. Structural habitats: (A) Dense tall, reed-like shrubs, brambles, herbs, and grasses; (B) low shrubs, including *Sarcopoterium spinosum*, *Cistus* spp., etc., without stones; (C) low shrubs with sparse stones; (D) stone piles; (E) sparse trees; (F) bare soil with or without sparse grasses.

tions, so we used Generalized Linear Mixed Models to model those variables (Zuur et al. 2010). All analyses were conducted using the R programming language (R Core Team 2023).

We included the following independent variables in all six models: (a) habitat heterogeneity calculated using the DAFOR scale, (b) protected status (i.e., whether a transect was in or outside a Natura 2000 site), (c) elevation, and (d) season (Table 1). We used river as a random effect to account for multiple transects in each monitoring area (river). We used the *r.squaredGLMM* function in the "MuMIn" package (Barton 2022) in R to measure the models' marginal and conditional pseudo-R^2 values (Nakagawa and Schielzeth 2013). The marginal value corresponds to the variance explained by the fixed effects (independent variables), whereas the con-

Table 3. Habitat Diversity Metric (HDM) calculated for each transect for each of the four most common species and for total lizard diversity based on the ranking of habitat types when all species are taken into account. Species: ***Oe*** = Snake-eyed Lizard (*Ophisops elegans*); **Pt** = Troodos Rock Lizard (*Phoenicolacerta troodica*); **Lc** = Cyprus Rock Agama (*Laudakia cypriaca*); **As** = Schreiber's Fringe-toed Lizard (*Acanthodactylus schreiberi*).

	Alykos-In			Alykos-Out			Peristerona-In			Peristerona-Out			Mesa Potamos-In			Mesa Potamos-Out		
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Oe	612.0	383.0	747.0	360.0	526.5	463.5	632.5	446.0	617.0	712.0	629.5	561.0	771.5	721.0	429.0	607.0	667.5	285.5
Pt	746.5	528.5	596.5	505.5	493.0	700.0	767.0	542.5	726.5	526.5	764.0	341.5	600.0	647.5	467.5	771.5	682.0	436.0
Lc	448.5	405.5	586.0	497.5	257.0	360.0	381.5	377.5	391.0	673.5	378.5	740.5	467.0	407.5	429.5	356.0	354.0	500.5
As	419.5	623.0	637.0	646	575.0	469.0	390.0	696.5	377.0	619.5	402.0	464.5	612.5	616.5	722.5	424.5	467.5	600.5
All	694.5	390.0	769.5	413.0	448.0	526.5	680.0	439.0	639.5	734.5	677.0	498.0	713.5	689.0	396.0	662.0	622.5	295.0

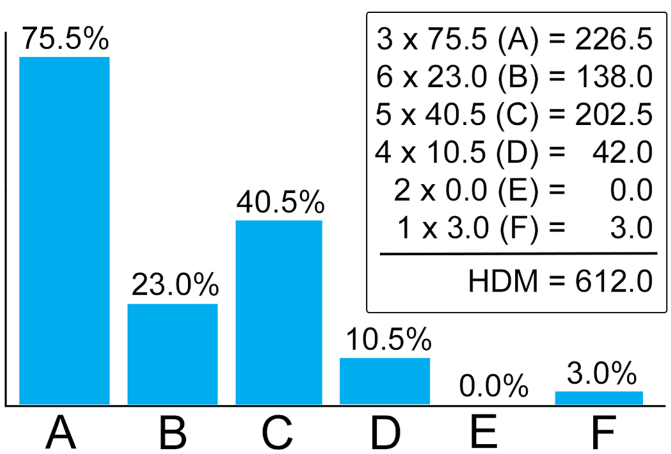

Figure 3. An example of the Habitat Diversity Metric (HDM) calculated for *Ophisops elegans* at Alykos-Potamos Gialias (Transect Line 1) within the Natura 2000 site. Percentages are those of each structural habitat along this transect. Structural habitats (A–F) are as in Fig. 2 (see also text).

ditional value corresponds to the variance explained by the whole model, including the random effects (Barton 2022).

We assessed the residuals of all six models using the "DHARMa" package (Hartig 2022) to ensure that regression assumptions (i.e., no significant deviations from expected distributions and no dispersion issues) were not violated. Moreover, to confirm the absence of any issues with collinearity, we used the "vif" function in the "car" package (Fox and Weisberg 2019) to measure the Variance Inflation Factor (VIF) of each of the four explanatory variables in our models. Since VIF was <2 in all cases, we retained all four variables in the analyses (Zuur et al. 2010). Finally, to verify that our data were independent and not spatially autocorrelated, we used the "Moran.I" function in the "ape" package in R (Paradis and Schliep 2019) to calculate the Moran's I value of each model's residuals.

To assess whether our results were sensitive to the method used to calculate the Habitat Diversity Metric (Fig. 3), we recalculated the metric after switching the rankings (1 to 6) between similarly ranked habitats (e.g., between 1 & 2, 3 & 4, and 5 & 6) and also after using the baseline percentage of each DAFOR category mentioned in the methods rather than its mean (e.g., 51% for the dominant category rather than 75.5%). Finally, to confirm that habitat heterogeneity and elevation did not differ significantly between each river's transects located in versus outside Natura 2000 sites, we tested each variable using ANOVA with the Natura 2000 sites as the predictor.

Results

Richness and abundance.—We recorded 613 individuals belonging to seven species (Table 2). The highest abundance (241 individuals) was at Alykos, followed by Peristerona (212), and Mesa Potamos (160). The abundance of *O. elegans*, the most abundant lizard on Cyprus, was 164 individuals in Alykos, 180 in Peristerona, and 118 in Mesa Potamos.

Abundance inside vs outside Natura 2000 areas.—Abundance was higher in Natura 2000 areas (351 individuals) than outside Natura 2000 areas (262) (Table 2). At Alykos, 167 individuals were in Natura 2000 areas compared to 74 individuals outside (paired t-test: $t = 2.15$, $df = 61$, $p = 0.04$). The numbers of individuals inside and outside the Natura 2000 site at Peristerona (103 vs. 109 individuals, paired t-test: $t = -0.16$, $df = 55$, $p = 0.87$) and Mesa Potamos (81 vs. 79 individuals, paired t-test: $t = 0.07$, $df = 62$, $p = 0.95$) were nearly equal.

Effects of environmental heterogeneity on the overall diversity and richness.—The Habitat Diversity Metric (HDM) varied considerably among transects regardless of whether they were in or outside Natura 2000 areas, even along the same river (Table 3). Species diversity and richness were not associated with any of the explanatory variables used in the analysis (Fig. 4). The variance explained by these two models was low, 10% and 7%, respectively (Table 4). Models based on the two alternative methods used to calculate habitat heterogeneity produced the same results (i.e., confirming that lizard species diversity and richness at the three rivers examined were not associated with habitat heterogeneity or any other variables examined).

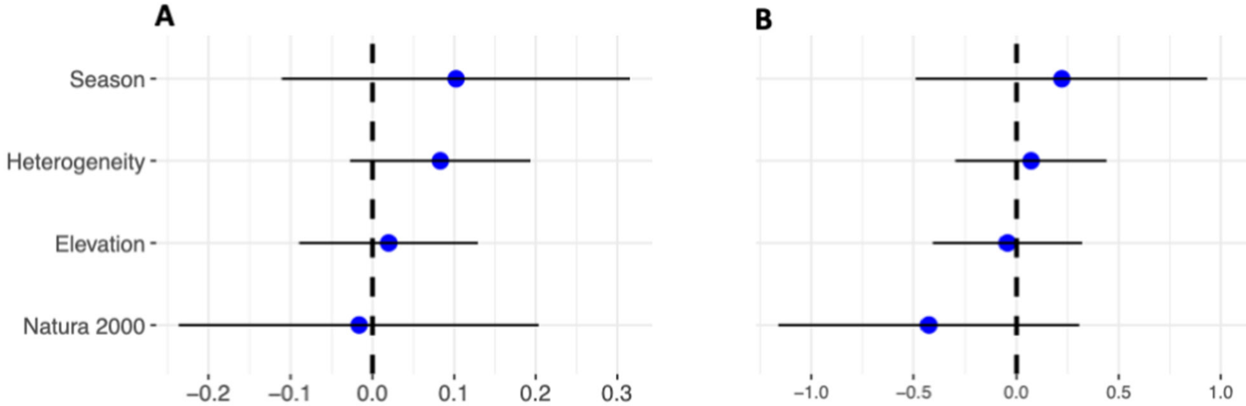

Figure 4. The relationship between (A) species diversity, (B) species richness, and the four independent variables examined using general linear mixed models: (1) season, (2) habitat heterogeneity, (3) elevation, and (4) protected status (inside vs. outside Natura 2000 sites). No relationship was statistically significant.

Table 4. Results of the general linear mixed models showing the relationship between the four explanatory variables and species diversity and richness. Statistically significant effects are in bold.

	Species Diversity			Species Richness		
Predictors	**β**	**SE**	**P**	**β**	**SE**	**P**
Intercept	0.40	0.09	**<0.001**	2.32	0.30	**<0.001**
Natura 2000 (Out)	-0.02	0.11	0.879	-0.43	0.36	0.244
Elevation	0.02	0.05	0.714	-0.04	0.18	0.806
Habitat heterogeneity	0.08	0.05	0.136	0.07	0.18	0.696
Season (summer)	0.10	0.10	0.334	0.22	0.35	0.528
$R^2_{Marginal}$ / $R^2_{Conditional}$	0.097 / 0.097			0.061 / 0.061		

Effects of environmental heterogeneity on the abundance of four species.—HDM varied widely among species and transects (Table 3). The abundance of *O. elegans* was negatively associated only with elevation (Table 5, Fig. 5A), whereas the abundance of *P. troodica* was not associated with any of the variables examined (Table 5, Fig. 5B). The abundance of *L. cypriaca* was associated with protected status (Natura 2000 designation), elevation, and season (Table 5), with more individuals encountered outside Natura 2000 sites (Fig. 5C), in sites at higher elevations (Fig. 5C), and during summer months (Fig. 5C). Finally, the abundance of *A. schreiberi* was associated with protected status and elevation (Table 5), with more individuals in Natura 2000 sites (Fig. 5D) and sites at lower elevations (Fig. 5D). As in the cases of species diversity and richness, models based on the two alternative methods used to calculate habitat heterogeneity produced the same results regarding which variables were associated with the abundance of each species.

Table 5. Results of the generalized linear mixed models showing the relationship between the four explanatory variables and species abundance of *Ophisops elegans*, *Phoenicolacerta troodica, Laudakia cypriaca*, and *Acanthodactylus schreiberi*. Statistically significant effects are in bold.

	O. elegans			***P. troodica***			***L. cypriaca***			***A. schreiberi***		
Predictors	β	SE	P	β	SE	P	β	SE	P	β	SE	P
Intercept	2.41	0.16	<0.001	-0.06	0.39	0.886	-3.30	0.85	<0.001	-9.62	4.71	0.041
Natura 2000 (Out)	-0.14	0.19	0.484	0.05	0.41	0.903	1.93	0.64	0.003	-4.81	1.91	0.012
Elevation	-0.23	0.10	0.022	0.27	0.21	0.189	1.22	0.37	0.001	-11.49	5.84	0.049
Habitat heterogeneity	0.17	0.10	0.088	0.22	0.22	0.298	0.11	0.27	0.692	0.83	0.61	0.174
Season (summer)	0.13	0.19	0.485	0.19	0.41	0.648	1.32	0.56	0.019	2.47	1.32	0.061
$R^2_{Marginal}$ / $R^2_{Conditional}$	0.203 / 0.793			0.073/ 0.461			0.452 / 0.452			0.978/ 1.000		

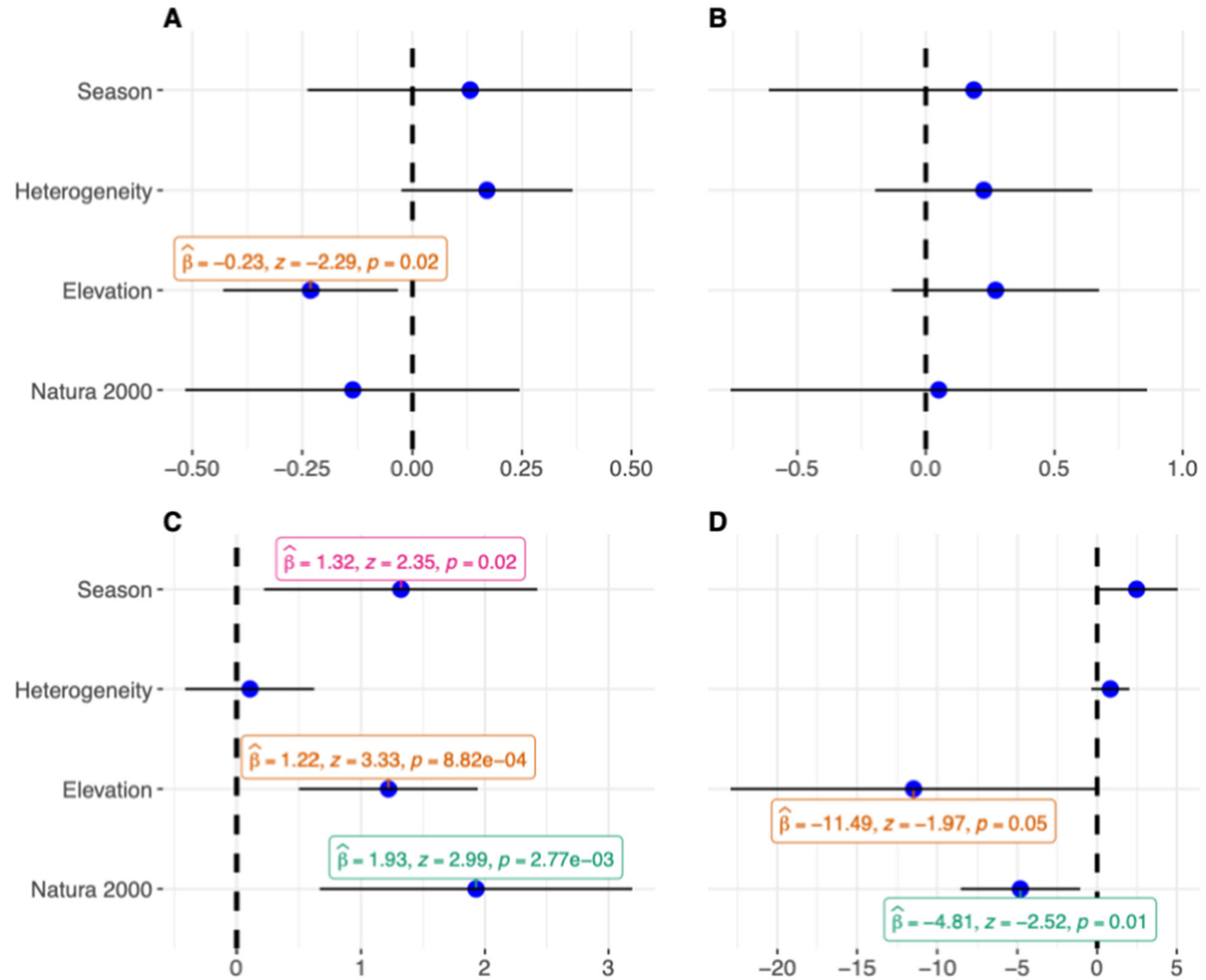

Figure 5. The relationship between the abundances of the four most common species of reptiles (A) Snake-eyed Lizard (*Ophisops elegans*), (B) Troodos Rock Lizard (*Phoenicolacerta troodica*), (C) Cyprus Rock Agama (*Laudakia cypriaca*), and (D) Schreiber's Fringe-toed Lizard (*Acanthodactylus schreiberi*), and four independent variables examined using generalized linear mixed models: (1) season, (2) habitat heterogeneity, (3) elevation, and (4) protected status (inside vs. outside Natura 2000 sites). Statistically significant relationships are indicated by the corresponding regression coefficient and p-value.

Results of Moran's I test confirmed the absence of spatial autocorrelation in all six models ($p > 0.05$). Additionally, ANOVA test results indicated that habitat heterogeneity and elevation did not vary significantly between transects along each river located in or outside Natura 2000 sites ($p > 0.05$).

Discussion

We found no evidence of a relationship between overall lizard species diversity or richness and elevation, season, protected status, or habitat heterogeneity. Lizards might respond to aspects of environmental heterogeneity not considered in this study or show other responses to heterogeneity constrained by resource availability (e.g., Yang et al. 2015). Similarly, Moreno-Rueda and Pizzaro (2009) found no association of reptilian species richness with habitat heterogeneity, whereas Atauri and de Lucio (2001) identified effects only of certain land-use types. Hence, the heterogeneity-richness relationship in reptiles remains unclear.

The abundance of three out of four of the most commonly found lizard species has been linked to different factors, such as elevation, season (with more individuals being present in 'summer'), and whether the area is located in a Natura 2000 site or not. In particular, *O. elegans* was associated negatively with elevation, as expected for a thermophilic Mediterranean species most frequently found in open lowlands. This is one of the most common species on the island, and our results suggest that its abundance is not affected by the Natura 2000 network. *Phoenicolacerta troodica* was not affected by season and elevation, habitat heterogeneity, or site protection. This species is known to prefer areas with dense vegetation cover and large stones (Nicolaou et al. 2014), a combination of factors that is common throughout study sites, regardless of dominant habitat type. The three variables (i.e., protected status, elevation, and season) together explained about 45% of the variation in abundance of *L. cypriaca* across all sites, with abundance associated positively with elevation and season (this species occurs at elevations to 1,900 m and, although more active during summer, exhibits physiological and behavioral adaptations that help it avoid the high temperatures of Cypriot summers, particularly in open lowlands; Karameta 2018). That more individuals were found outside Natura 2000 sites probably is attributable to the species' association with humans and an ability to exploit a wide range of habitats not necessariy associated with rivers (Nicolaou et al. 2014). Finally, abundance of *A. schreiberi* was positively associated with the protected status and negatively with elevation. This is a thermophilic species typically found in areas with thin soil (e.g., sand dunes) and banks where sandy soils are common (Savvides et al. 2019). Many of the protected areas have such soils. The positive effect of Natura 2000 sites is suggestive of effective conservation.

The Natura 2000 network is one of the main instruments for protecting European biodiversity (Bastian 2013; Abellan and Sanchez-Fernandez 2015; Lison and Sanchez-Fernandez 2015; Spiliopoulou et al. 2021). However, our results did not demonstrate an association of lizard diversity and richness with protected status of the study areas. Similarly, van der Sluis et al. (2016) concluded that presence of amphibians and reptiles in and outside Natura 2000 sites had a negligible effect on species richness. The latter might reflect a lack of specific management practices inside the Natura 2000 sites studied; also, those studies did not examine riparian habitats. Protected Natura 2000 riparian sites on Cyprus have been found to be important for the conservation of wildlife, including reptiles (Zotos et al. 2021), but evidently this is scale-related and such an effect could not be detected at the local level of our study.

That seven of the eleven lizard species known to occur on Cyprus were found within the few riparian habitats studied, even if the habitat types included therein represent a very small percentage of the country's terrestrial habitats, highlights the importance of such habitats for the maintenance of local reptilian diversity. Riverbanks are particularly important for foraging, nesting, and finding shelter, and riparian habitats generally because they provide water, food resources, and connectivity of habitats (Faria et al. 2019). Consider also that the studied systems are banks of intermittent rivers (i.e., those with temporally irregular water flow), which are much more common on the island than perennial rivers (i.e., those with permanent and usually regular water flow). These habitats are particularly important in the arid eastern Mediterranean in light of ongoing climatic changes resulting in predictions of dramatic decreases in precipitation for the region (Lelieveld et al. 2012).

Given that we still lack a robust, data-based evaluation of how effectively the region's protected areas contribute to biodiversity conservation, field surveys like those in the present study can provide information crucial for improving conservation practices. Some studies have shown that Natura 2000 sites offer little protection to some species (Jantke et al. 2011) and that the network does not fully meet Europe's biodiversity conservation goals (Ayllon et al. 2022) established in the EU's new Biodiversity Strategy (i.e. at least 30% of the EU's land and seas protected; European Commission 2020). Given that one of Europe's conservation goals include the restoration of rivers, expressed also within the Water Framework Directive (European Parliament and the Council of the European Union 2000), the inclusion of riverbanks in protected area networks can have a positive effect on the abundance of reptiles, including at least some species of lizards, that exploit riparian habitats (Bohm et al. 2013).

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