

The role of environmental heterogeneity on lizard assemblages along Cyprus riverbanks

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Abstract

Despite global efforts to halt biodiversity loss, it continues to decline due to a combination of unsustainable actions, increasing the urgency for measures to reverse this trend. A major constraint regarding efficient biodiversity management is the lack of knowledge on most species' population size and abundance patterns. Reptiles are used in ecological research as model organisms due to their ease in handling, and their diversity in behaviour and ecology. Reptile diversity of Cyprus is high and includes several endemic species. The aim of this study was to compare lizard diversity patterns along riverbanks within and around designated protected areas. Riparian habitats have received less attention in conservation-oriented studies in Mediterranean regions, despite their ecological significance and the distinct communities they host, or their vulnerability to climate change. The role of environmental factors, seasonality, and habitat heterogeneity for lizard assemblages in riparian areas was evaluated along three rivers that flow inside and outside protected areas. The abundances of the four more common species (*Ophisops elegans*, *Phoenicolacerta troodica*, *Laudakia cypriaca*, and *Acanthodactylus schreiberi*) were evaluated separately. We recorded most of Cyprus' lizard species in riparian habitats, but diversity and richness were not associated with any of the explanatory variables. The abundances of the four species exhibited different relationships each with elevation, season, and protection status, but not with habitat heterogeneity. The latter could be related to the fact that riparian habitat heterogeneity patterns are very similar throughout the study sites. Our results suggest that Cyprus' lizard diversity and riparian habitats have not been considered much in the design of protected areas.

Introduction

The Mediterranean basin is one of the globe's most important biodiversity hot spots, and it includes a large number of endemic species (Medail and Diadema 2009). The eastern Mediterranean area, in particular, is severely affected by the on-going climate change through changes in precipitation and temperature regimes that pose threats to biodiversity, both directly and indirectly, through interactions with land-use changes and habitat loss (Louca, Vogiatzakis and Moustakas 2015; Mantyka-Pringle, Martin and Rhodes 2012).

One of the most significant instruments for biodiversity conservation in the EU is the Habitats Directive on the conservation of natural habitats and wild fauna and flora (92/43/EEC) (Council of the European Community 1992), which has led, along with the Birds Directive (European Union 2010), 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 European Union's terrestrial land area and about 10% of its seas (European Environment Agency 2020). However, the effectiveness of the network in protecting biodiversity remains unknown, mostly due to the lack of systematic monitoring projects (European Environment Agency 2020).

Although riparian ecosystems 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 supply for humans and animals (Banville and Bateman 2012). Riparian habitats, especially those of intermittent streams on islands, are characterized by increased environmental heterogeneity, which is generally important for biodiversity (Katayama et al. 2014) as it influences population dynamics and community structure, and, in some cases, is a major determinant of species richness (Katayama et al. 201); Suza Junior, Ferreira and de Oliveira 2014).

Reptiles are considered useful indicators for ecosystem functions (Banville and Bateman 2012). Since reptiles are ectothermic and may be influenced by temperature variation, they are among the first priorities in studies on environmental heterogeneity related to temperature (Diele-Viegas, et al. 2020). Several factors have been shown to contribute to reptile richness decline, with habitat loss and degradation of aquatic habitats being among the most important (Todd, Willson and Gibbons 2010). Hence, an evaluation of the possible association between riparian habitats and reptile abundance, species richness, and diversity may also assist the protection of reptile communities themselves (Banville and Bateman 2012).

Cyprus is a biodiversity hotspot since it hosts a large number of species relative to its size (Delipetrou, et al. 2008) and hosts a variety of landscapes, species and habitats of European importance (Vogiatzakis et al. 2016). Natura 2000 sites cover 28.82% of the island's total area, representing one of the larger national covers in the EU (Tzirkalli et al. 2019). The high spatial heterogeneity of the biotic and abiotic environments of the island provides a mosaic of many different habitats suitable for different biological communities (Vogiatzakis et al. 2016). Lizards comprise a rich faunal group on the island, consisting of eleven species, all of which are protected under national legislation, and are listed in Appendices of the Habitats Directive (92/43/EEC) (Council of the European Community 1992) and the Bern Convention (Council of Europe 1979). Among these, *Phoenicolacerta troodica* and *Laudakia cypriaca* are endemic to the island, while *Mediodactylus kotschy fitzingeri*, *Ablepharus budaki budaki*, and *Acanthodactylus schreiberi schreiberi* are endemic sub-species (Baier, Sparrow and Wiedl 2013; Karameta et al. 2022). *Acanthodactylus schreiberi* is the only lizard in Cyprus listed as Endangered by IUCN (Cox and Temple 2009) due to a serious population decline, estimated to more than 50% over the last three generations (12 years) (Baier, Sparrow and Wiedl 2013). So far, research on the reptiles of Cyprus has focused on systematics and distribution (Baier, Sparrow and Wiedl 2013; Sparrow and Baier 2016), while there is little or no information regarding how environmental factors and habitat types affect lizard species and lizard assemblages. Therefore, this is the aim of this study, to look into the relationship between lizards and environmental factors, including also an evaluation of how sites under protection status, such as Natura 2000, affect lizard richness and abundance.

More specifically, we ask:

- a. How are lizard species diversity and species richness affected by environmental factors, habitat heterogeneity, and protection status along riverbanks?
- b. How is the abundance of common and endemic species, namely *Ophisops elegans*, *Phoenicolacerta troodica*, *Laudakia cypriaca*, and *Acanthodactylus schreiberi*, affected by environmental factors, habitat heterogeneity, and protection status along riverbanks?

Materials And Methods

Study area and sites

We sampled parts of the riverbanks along three rivers on the island of Cyprus, namely Alykos, Peristerona, and Mesa Potamos (Fig. 1), so as to include a variation in elevation, temperature regime, and habitat structure. All rivers were located at least 20 km apart from each other to ensure spatial independence. Sections of all three rivers were part of the Natura 2000 network. For each river, three transect lines were set (100 m long and 3 m wide) along the river banks within the Natura 2000 sites, and three same-sized transect lines were set outside Natura 2000 sites. Transect lines were at least 30 meters apart from each other, and in some cases, were located on different sides of the river.

Species richness and abundance

Field surveys of lizard species were carried out from May to September 2019 and from April to September 2020 to cover the spectrum of climatic conditions in two seasons and two consecutive years. In accordance with the biology of the species, we divided the surveys into 'summer' months (i.e., June, July, August) and 'non-summer' (April, May, September). Each transect was visited monthly. To record lizard species and abundance, the Visual Encounter Survey (VES) approach was employed. According to this method, the researcher actively walks slowly a specific distance and records each individual species spotted within the transect line. VES is commonly used to survey reptiles since most are found simply by walking and looking for refugia under rocks or fallen logs (Janiawati, Kusriani and Mardiasuti 2016).

Habitat heterogeneity

Vegetation, substrate type, and refugia across the transect lines were recorded. These included vegetation and soil cover categories (Janiawati, Kusriani and Mardiasuti 2016). In the absence of detailed habitat maps, the appropriate way for mapping the transect lines' habitats is to stratify the areas, i.e., by dividing the transects into different habitat types, such as bushes, rocks, trees, and so on (Sutherland 1996). The following habitat types were identified in our study sites based on vegetation and surface cover characteristics:

- (A) Dense tall shrubs, like reeds, bramble, herbs, and grasses
- (B) Low shrubs, like *Sarcopoterium spinosum*, *Cistus* spp., etc., without stones
- (C) Low shrubs with sparse stones
- (D) Stone shelters
- (E) Sparse trees
- (F) Bare soil with or without sparse grasses

In each transect line we used the DAFOR scale, i.e., Dominant, Abundant, Frequent, Occasional, and Rare, for estimating visually the habitat types presence. Habitat percentage was allocated as follows: Dominant (51–100%), Abundant (31–50%), Frequent (16–30%), Occasional (6–15%), and Rare (1–5%). Then, based on our experience and the literature on the ecology Cyprus lizards, we calculated a simple habitat diversity metric for each transect for each of the four commoner species (*Ophisops elegans*, *Phoenicolacerta troodica*, *Laudakia cypriaca*, and *Acanthodactylus schreiberi*) as follows: we ranked the habitats in every transect according to the species' preference from 1–5 in ascending order, and multiplied it with the mean percentage of each habitat type recorded in the transect. We followed the same approach to calculate a Habitat Diversity Metric (HDM) of each transect for total lizard diversity based on the ranking of habitat types when all species are taken into account (Table 3).

Statistical analysis

Data from each season were pooled at the transect level to avoid issues with pseudoreplication. For each transect and season ($n = 36$), we estimated (a) species diversity, using the Shannon-Wiener index (Price, Kutt and McAlpine 2010), and (b) species richness. Additionally, we calculated the abundance of the following four species, for which we had enough sightings (≥ 5) across all study sites: *Ophisops elegans*, *Phoenicolacerta troodica*, *Laudakia cypriaca*, and *Acanthodactylus schreiberi*. We then developed a linear mixed model for each of the six response variables (i.e., species diversity and species richness and the abundances of the four species). We used the ID of the river as a random effect to account for the fact that there were multiple transects at each monitoring area. We assessed the distribution of the response variables using histograms. Species diversity and species richness were normally distributed, and therefore for those two variables, we used a General Linear Mixed Model with a Gaussian distribution. The abundances of the four species followed a Poisson distribution, and therefore for those variables, we used Generalized Linear Mixed Models.

In all six models, we included the following fixed effects (a) habitat heterogeneity based on results of the DAFOR scale, (b) protection status, i.e., whether the transect was situated inside or outside the respective Natura 2000 site, (c) elevation, and (d) season (Table 1). 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. The marginal value corresponds to the variance explained by the fixed effects, while the conditional 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 were not violated (i.e., that there were no significant deviations from the expected distributions and no dispersion issues). Moreover, to confirm that there were no 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. In all cases, VIF was < 2 , therefore, we retained all four variables in the analyses. To verify that our data were not spatially

autocorrelated, we used the "ape" package in R (Paradis and Schliep 2019) to calculate the Moran's I value of each model's residuals. In all cases, the p-value was > 0.05, confirming the absence of spatial autocorrelation.

To assess whether our final results were sensitive to the method used to calculate habitat heterogeneity, we recalculated the index by (a) switching the rankings between the habitats, and (b) by using the baseline percentage of each DAFOR category rather than its mean. Our results were qualitatively the same in all cases; hence, we only report the results of the original index. Lastly, to confirm that habitat heterogeneity and elevation did not differ significantly between the transects located inside vs outside the Natura 2000 sites, we tested each variable using an ANOVA and the Natura 2000 sites as the predictor. In all cases, the p-value was > 0.05, confirming no statistically significant differences.

Results

(a) Richness and abundance

We recorded 613 individual lizards belonging to seven species (individuals in brackets), i.e., *Ophisops elegans* (462), *Phoenicolacerta troodica* (55), *Laudakia cyprica* (19), *Acanthodactylus schreiberi* (69), *Chamaeleo chamaeleon* (3), *Ablepharus budaki* (4), and *Chalcides ocellatus* (1). Alykos river hosted the highest overall abundance, i.e., 241 individuals, followed by Peristerona river with 212 individuals, and Mesa Potamos river with 160. The population size of *O. elegans*, which is the most common lizard in Cyprus, was 164, 180, and 118 individuals in Alykos, Peristerona, and Mesa Potamos, respectively. Abundance per species and transect line is given in Table 2.

(b) Abundance inside vs outside Natura 2000 areas

Highest total abundance was found inside Natura 2000 areas, with 351 individuals, in contrast to 262 individuals outside Natura 2000 areas. Alykos river hosts 167 individuals inside Natura 2000 areas compared to 74 individuals outside. The numbers of individuals inside and outside the Natura 2000 site at Mesa Potamos were almost the same, i.e., 81 and 79 outside, while in Peristerona river, individuals outside Natura 2000 areas were higher than those inside, i.e., 103 vs 109 individuals, respectively. Results on each species' abundance inside vs. outside Natura 2000 sites in each river can be seen in Table 2.

(c) Effects of environmental heterogeneity on diversity and richness

The Habitat Diversity Metric (HDM) described in Methods, exhibited extensive variance among transect lines regardless of their location inside or outside Natura 2000, even among lines of the same river (Table 3).

Species diversity and richness were not associated with any of the explanatory variables used in the analysis (Table 4). The variance explained by these two models was low (10% and 7% respectively).

(d) Effects of environmental heterogeneity on the abundance of four species

The HDM varied also widely among species, as expected by the different ecological features of each species. For *Ophisops elegans* the highest HDM was observed in Mesa Potamos river, in the first transect line inside Natura 2000 (i.e. 771.5), while the smallest in the same river, in the third transect line, outside Natura 2000 (i.e. 285.5). For *Phoenicolacerta troodica* the highest value was found in Mesa Potamos river's first transect line, outside Natura 2000 (i.e. 771.5), while the lowest in Peristerona river, in the third transect line, outside Natura 2000 (i.e. 341.5). *Laudakia cyprica* exhibited its highest value in Peristerona river, third transect line, outside of Natura 2000 (740.5) and its lowest in Alykos river, second transect line, again outside of Natura 2000 (257). Finally, for *Acanthodactylus schreiberi*, the highest value was found in Mesa Potamos river, third transect line, inside Natura 2000 (722.5), while the lowest in Peristerona river, third transect line, inside Natura 2000 (377).

The abundance of *Ophisops elegans* was negatively associated only with elevation (Table 5, Fig2A). *Phoenicolacerta troodica* was not associated with any of the variables included in the analysis. The abundance of *Laudakia cyprica* was associated with Natura 2000 sites, elevation, and season (Table 5). On average, there were more individuals outside Natura 2000 sites (Fig2B), in sites at higher elevations (Fig2C), and during the summer months (Fig2D). These three variables together explained ca. 45% of the variation in the abundance of *L. cyprica* across all sites. Lastly, the abundance of *Acanthodactylus schreiberi* was associated with Natura 2000 sites and with elevation (Table 5). There were more individuals inside the Natura 2000 sites (Fig2E) and at sites at lower elevations (Fig2F). The amount of variance explained by the model was ca. 98%.

Discussion

We present the first comparative account on lizard populations inside and outside protected areas of Cyprus, focusing on the generally understudied riparian habitats, such as the banks of intermittent rivers, which are more common on the island. These habitats are of particular significance for the arid eastern Mediterranean region in view of the on-going climate change because of the severe decrease in precipitation predicted for this area (Lelieveld et al. 2012). In addition, we still lack a robust, data-based evaluation of the region's protected areas' effectiveness in preserving biodiversity. Therefore, in situ field survey projects like the one presented herein, can provide crucial information for future improvement of conservation practices.

We found no evidence for an association of species diversity or richness with elevation, season, protection status, or habitat heterogeneity. Even though lizards may respond to aspects of environmental heterogeneity not included in the present study, our results are in accordance with certain studies that have questioned the relationship between environmental heterogeneity and species diversity or richness (Zhiyong et al. 2015).

On the other hand, the abundance of the three out of four most common species has been found to be associated either with elevation, and/or season (more individuals during summer), and/or protection status (inside Natura 2000 site or not). In particular: *Ophisops elegans* was associated negatively with

elevation, as expected for such a thermophilic Mediterranean species, which prefers open lowland. This is one of the most common species on the island, and it doesn't seem to be affected by the Natura 2000 network. *Phoenicolacerta troodica*, on the other hand, was not affected by any of the factors examined. The species is known to prefer areas with dense vegetation cover and large stones (Nicolaou, Lymperakis and Pafilis 2014), which can be found in many sites, regardless of the habitat type recorded in our study. *Laudakia cypriaca* was associated positively with elevation and season. According to the literature, this endemic species is found up to 1,900 m and exhibits physiological and behavioral adaptations that help it avoid the high-temperature regime of Cyprus' summers, particularly in open lowlands (E. Karameta 2018), despite being more active during summer. Also, more individuals were found outside Natura 2000 sites, probably due to the species' association with human constructions and presence, as well as to its preference for a wide range of habitats not particularly associated with rivers (Nicolaou, Lymperakis and Pafilis 2014). Lastly, *Acanthodactylus schreiberi* was positively associated with the protection status of the areas and negatively with elevation, which is in agreement with what we know about its ecology (Savvides et al. 2019). *Acanthodactylus schreiberi* is a thermophilic species that prefers areas with thin soil to dig in, such as sand dunes, and banks where sandy soils are common (Savvides et al. 2019). This species has been declining in population size, thus listed as «Endangered» in the IUCN Red List. The positive effect of Natura 2000 sites is encouraging towards its effective conservation.

The Natura 2000 network is one of the main instruments for protecting European biodiversity, even if there is a debate about whether protected areas achieve this goal (Spiliopoulou et al. 2021; Lison and Sanchez-Fernandez 2015; Abellan and Sanchez-Fernandez 2015). Our results did not demonstrate a general association of lizard diversity and richness with the conservation status of the study areas, besides certain individual species, but this could be attributed to the lack of specific management practices inside the Natura 2000 sites studied. A simple mental border-line that separates the 'inside' from the 'outside' of a protected site cannot per se affect the diversity of species unless the internal part comes under an effective management plan. Even if the lizard species recorded herein are not listed in Annex II of the European Directive 92/43/EEC (Council of the European Community 1992) or the corresponding national law behind the Natura 2000 network, we might expect these sites to host a higher overall biodiversity, at least in terms of abundances. Of course, several studies have shown that not all protected areas are effective in conserving biodiversity (Anderson and Mammides 2020).

Conclusions: Management Implications

The current study is among the few that investigate the role of habitat heterogeneity on lizard biodiversity in riparian habitats and the first to explore the association of such habitat types with faunal elements in Cyprus. Riparian systems include complex habitats which are particularly important for ectothermic terrestrial species, like lizards, but also for other taxa (Merritt and Bateman 2012; Bateman and Merritt 2020). The fact that seven out of the eleven lizard species occurring in Cyprus have been found within the sampling sites, despite the fact that the habitat types included therein represent a very small percentage of the country's terrestrial habitat coverage, highlights the significance of these rivers for local biodiversity.

Knowledge of species ecology, distribution, and the threats they face is of utmost importance in order to establish effective conservation strategies. Some studies suggest that Natura 2000 areas are more heterogeneous and comprise higher number of species (Nuneza, Ates and Alicante 2010). It is self-evident that in order to optimize the conservation of species and habitats, the special environmental conditions of particular areas must be taken into account, and each area must be managed under specific plans (Spiliopoulou et al. 2021). For reptiles, as well as many other taxa, it is essential to consider correlations of their abundance with aspects of habitat heterogeneity, as well as their sensitivity to habitat degradation due to their low dispersal ability and generally small home ranges (Bohm et al. 2013).

Globally, the effectiveness of protected areas is a prerequisite to successful conservation (Mammides 2020). Literature indicates that reptiles are underrepresented in the Natura 2000 sites and other protected areas (Abellan and Sanchez-Fernandez 2015). Despite the fact that several studies have shown that Natura 2000 sites offer little protection to species (Jantke, Schlepner and Schneider 2011) and the network doesn't meet Europe's biodiversity conservation goals (Ayllon, Baquero and Nicola 2022), the inclusion of riverbanks in protected areas networks can have a positive effect on some lizard species abundance. The need to establish robust management plans by authorities responsible for biodiversity conservation in European countries in order to optimize the protection of species inside Natura 2000 sites is indisputable, and field studies such as this can provide a valuable tool towards that end.

Declarations

The authors have no relevant financial or non-financial interests to disclose.

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Tables

Table 1. Positional characteristics of the transect lines.

	Transect	Coordinates (N, S)	Natura 2000 In/Out	Elevation (m)
1	Alykos-In-01	35.001035, 33.341019	In	290
2	Alykos-In-02	34.995278, 33.335911	In	300
3	Alykos-In-03	34.991972, 33.334492	In	305
4	Alykos-Out-01	35.013444, 33.353669	Out	270
5	Alykos-Out-02	35.013934, 33.354176	Out	270
6	Alykos-Out-03	35.012797, 33.352468	Out	270
7	Peristerona-In-01	35.060152, 33.080127	In	350
8	Peristerona-In-02	35.052294, 33.078064	In	375
9	Peristerona-In-03	35.051011, 33.077983	In	370
10	Peristerona-Out-01	35.036336, 33.082107	Out	415
11	Peristerona-Out-02	35.035242, 33.081378	Out	405
12	Peristerona-Out-03	35.036246, 33.081223	Out	400
13	Mesa Potamos-In-01	34.885547, 32.909711	In	890
14	Mesa Potamos-In-02	34.890375, 32.910183	In	950
15	Mesa Potamos-In-03	34.892292, 32.909011	In	980
16	Mesa Potamos-Out-01	34.874858, 32.914732	Out	710
17	Mesa Potamos-Out-02	34.876052, 32.910942	Out	730
18	Mesa Potamos-Out-03	34.875994, 32.913717	Out	720

Table 2: Abundance of species at each transect line, inside and outside of Natura 2000 and total in each river.

Sites/Rivers	Alykos Inside N2000				Alykos Outside N2000				Peristerona Inside N2000				Peristerona Outside N2000				Peristerona	Me N2	
	1	2	3	Pooled	4	5	6	Pooled	7	8	9	Pooled	10	11	12	Pooled			
Tran. Lines Species	1	2	3	Pooled	4	5	6	Pooled	7	8	9	Pooled	10	11	12	Pooled		13	
<i>Oele</i>	16	30	51	97	23	38	6	67	164	25	35	25	85	38	12	45	95	180	43
<i>Ptro</i>	0	1	5	6	0	0	2	2	8	8	1	1	10	8	3	2	13	23	11
<i>Lcyp</i>	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	1	1	3	3
<i>Asch</i>	1	7	53	61	0	4	0	4	65	4	0	0	4	0	0	0	0	4	0
<i>Ccha</i>	1	0	1	2	0	0	1	1	3	0	0	0	0	0	0	0	0	0	0
<i>Abud</i>	0	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0
<i>Coce</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0
	18	39	110	167	23	42	9	74	241	37	39	27	103	46	15	48	109	212	57

Oele: *Ophisops elegans* Ménériés, 1832; *Ptro*: *Phoenicolacerta troodica* (Werner, 1936); *Lcyp*: *Laudakia cypriaca* (Daan, 1967); *Asch*: *Acanthodactylus schreiberi* Boulenger, 1878; *Ccha*: *Chamaeleo chamaeleon* (L., 1758); *Abud*: *Ablepharus budaki* Göçmen, Kumlutas & Tosunoglu, 1996; *Coce*: *Chalcides ocellatus* (Froskall, 1775).

Table 3. The Habitat Diversity Metric calculated for each species and total diversity of each transect. For its calculation see text.

Sites/Rivers	Alykos Inside N2000			Alykos Outside N2000			Peristerona Inside N2000			Peristerona Outside N2000			Mesa Potamos Inside N2000			Mes Outs
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
<i>O. elegans</i>	612	383	747	360	526.5	463.5	632.5	446	617	712	629.5	561	771.5	721	429	607
<i>P. troodica</i>	746.5	528.5	596.5	505.5	493	700	767	542.5	726.5	526.5	764	341.5	600	647.5	467.5	771.
<i>L. cypriaca</i>	448.5	405.5	586	497.5	257	360	381.5	377.5	391	673.5	378.5	740.5	467	407.5	429.5	356
<i>A. schreiberi</i>	419.5	623	637	646	575	469	390	696.5	377	619.5	402	464.5	612.5	616.5	722.5	424.
<i>HDM all</i>	694.5	390	769.5	413	448	526.5	680	439	639.5	734.5	677	498	713.5	689	396	662

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 shown in bold.

Predictors	Species Diversity			Species Richness		
	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		

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 in bold.

Predictors	<i>O. elegans</i>			<i>P. troodica</i>			<i>L. cyprica</i>			<i>A. schreiberi</i>		
	β	SE	<i>p</i>	β	SE	<i>p</i>	β	SE	<i>p</i>	β	SE	<i>p</i>
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		

Figures

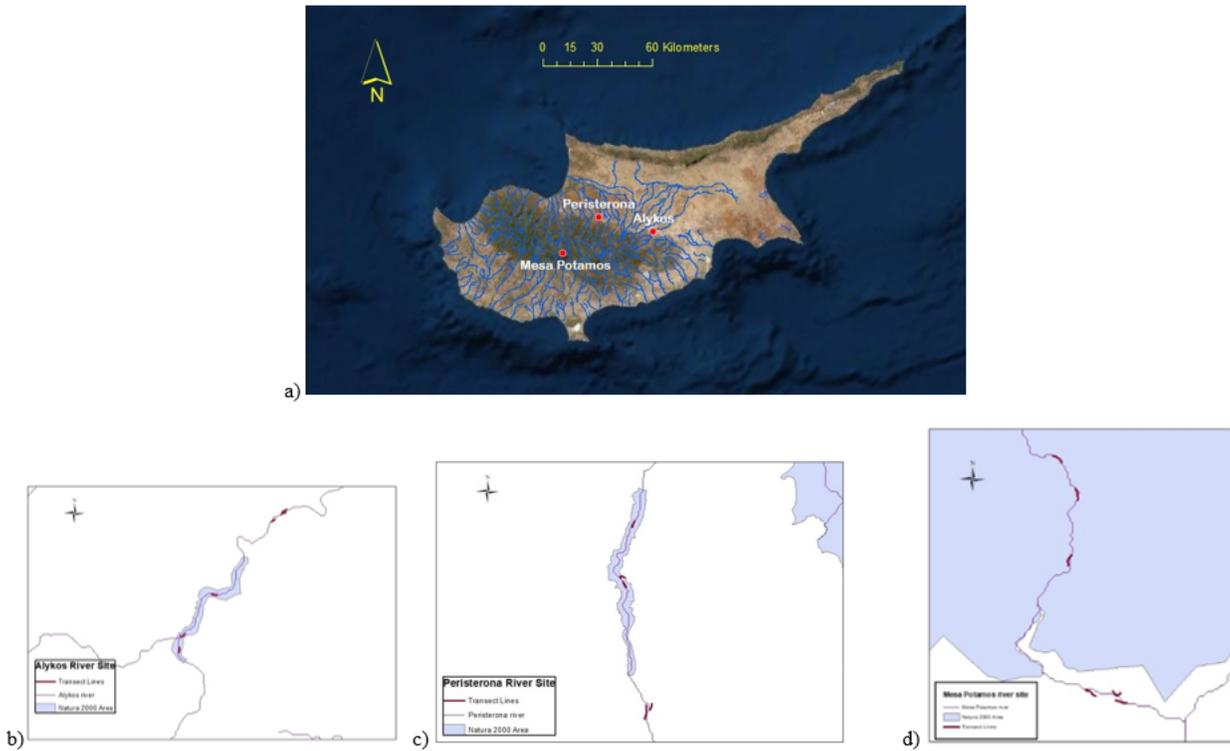


Figure 1

a) Topography and river systems in Cyprus and the location of the three rivers studied. b-d) The position of transect lines at each site.

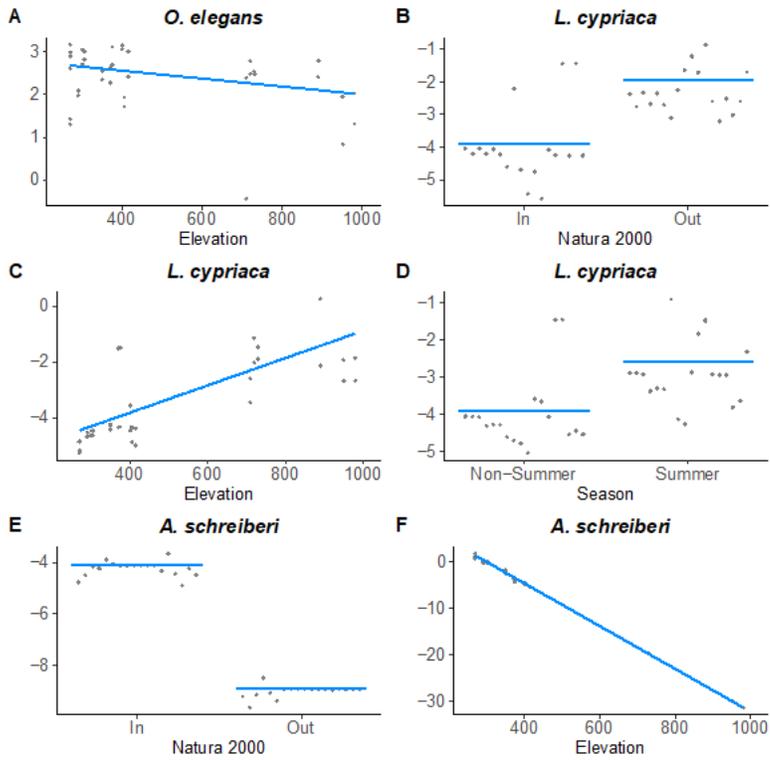


Figure 2
 The relationship between species abundance and elevation, season, and occurrence inside/outside Natura 2000 sites for the three common species that showed statistically significant effects.