

Distribution and diversity of reptiles in Albania: a novel database from a Mediterranean hotspot

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Abstract. Although Albania has a rich reptile fauna, efforts to reveal its diversity have so far been limited. To fill this gap, we collected available published and unpublished (museum collections, online sources) records of reptile occurrences and conducted several expeditions to search for reptiles in areas with few or no previous records. Our georeferenced database contains 3731 records of 40 species from between 1918 and 2015. Based on this comprehensive dataset, we prepared distribution maps for each reptile species of the country. Applying spatial statistics, we revealed that overall sampling effort was clustered, with hotspots associated with easily accessible areas and natural heritage sites. The maximum number of species per cell was 26 with an average of seven. Cells harbouring large reptile diversity were located along the Adriatic and Ionian coasts, on the western slopes of south Albanian mountains, i.e. in areas generally considered as Balkans biodiversity hotspots or potential historical refugia. We found that species presence and diversity is strongly influenced by landscape features. Diversity of land cover, altitudinal variation, temperature and precipitation variation explained the observed pattern in our models. Our study presents the largest database of reptile occurrences to date and is the first to analyse reptile diversity patterns in Albania. The database and the diversity patterns can provide a basis for future macroecological studies and conservation planning.

Keywords: Balkan Peninsula, BIOCLIM, biogeography, GLMM, range, species richness.

Introduction

The accelerating loss of biodiversity in the 20th century caused major environmental concern and is often referred to as the biodiversity crisis (Soulé, 1985). The decline of reptile populations has been reported worldwide and most often linked to habitat loss and degradation, unsustainable trade, expansion of invasive species,

pollution, disease, and climatic processes (Gibbons et al., 2000; Cox and Temple, 2009; Sineru et al., 2010; Todd, Willson and Gibbons, 2010). Extinction risk affects 20% of the reptile species globally (Böhm et al., 2013), thus knowledge on their distribution is essential for understanding biogeographic patterns and ecological processes that are fundamental to effective conservation (Zachos and Habel, 2011; Harnik, Simpson and Payne, 2012).

Mapping the distribution of reptiles and amphibians has a long history in Europe. After the emergence of national and regional atlases, the first European atlas of amphibians and reptiles was published in 1997 (Gasc et al., 1997). The subsequent increase in the number of records and further or more refined national atlas projects warranted a more recent, updated publication of the atlas (Sillero et al., 2014a). Unfortunately, the recent increase in information is spatially biased, and despite good knowledge of the distribution of most of the European reptile species, there are still regions or countries where data are missing, outdated or of poor

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quality. Although the Balkan Peninsula was traditionally among these regions, several comprehensive accounts of the distribution and diversity of reptiles have been published recently from this region. Updated distribution maps and patterns of reptile species richness were published in Bulgaria (Stojanov, Tzankov and Naumov, 2011), Greece (Valakos et al., 2008), Romania (Cogălniceanu et al., 2013), Republic of Macedonia (Sterijovski, Tomovič and Ajtič, 2014; Uhrin et al., 2016), Serbia (Tomovič et al., 2014), and a partial zoogeographical analysis of the herpetofauna was presented also for Bosnia and Herzegovina (Jablonski, Jandzík and Gvoždík, 2012).

One exception is Albania, which is an integral part of the globally important Mediterranean basin biodiversity hotspot (Myers et al., 2000). The exploration of the Albanian herpetofauna started in the early 20th century, when scientists from different countries visited Albania (e.g. Kopstein and Wettstein, 1920; Bolokay, 1921) but was mostly halted in the second half of the century due to the political, cultural and scientific isolation of Albania. Only a few works with reptile records were published from Albania from this period (e.g. Frommhold, 1962; see Haxhiu, 1998 and references therein). The last major updates provided a species list (Dhora, 2010) and coarse-scale distributional data (Bruno, 1989; Haxhiu, 1998) for the country. More recently, several short notes on the systematics, distribution and ecology of particular species or restricted regions provided more information (e.g. Farkas and Buzás, 1997; Haxhiu and Vrenozi, 2009; Oruçi, 2010; Jablonski, 2011). Despite the importance of Albania for understanding the biogeography of Mediterranean reptiles, none of these publications studied the reptile diversity of Albania in detail, resulting in this country being the herpetologically least explored country not only within the Balkans but probably in the whole of Europe (see Sillero et al., 2014a).

The few literature sources above suggest that Albania has a disproportionately large diversity of reptiles and habitats relative to its area. Forty-two terrestrial species and four species of sea turtles are known from the country (Bruno, 1989; Haxhiu, 1998; Jablonski, 2011). Albania has a high diversity of habitats which can host several species. This is related to the geological complexity and highly varied topography of the country (e.g. 70% of the terrain is mountainous) and the relative stability of a Mediterranean climate resulting from little influence of Pleistocene glaciations. There are indications that some of the Miocene-Pliocene speciation centre or Pleistocene glacial refugia of reptiles were located inside or in close vicinity of the territory of today's Albania (Médail and Diadema, 2009). For instance, the Hellenides range, where most of the Albanian mountains belong to, is probably one of the most important barriers in Europe that played a role in the allopatric speciation of many terrestrial reptiles (see Gvoždík et al., 2010; Psonis et al., 2017). The number of species endemic to this range (*Anguis graeca*, *Podarcis ionicus* complex, *Vipera graeca*) and recently detected patterns of hidden genetic diversity (e.g. for *Vipera ammodytes*, *Natrix tessellata*, *Lacerta viridis* complex, Ursenbacher et al., 2008; Guicking, Joger and Wink, 2009; Marzahn et al., 2016; Mizsei et al., 2017) also support the view that this country is highly important for understanding the historical biogeography, explaining the current diversity and designing the conservation of reptiles of the western Balkan region.

For the above reasons, a synthesis and an update of the knowledge on the distribution, species richness and biogeography of reptiles in Albania is highly warranted and timely. The aims of this study were to (i) present a complete and annotated checklist and updated distribution maps of reptile species in Albania, and (ii) analyse patterns in reptile diversity in relation to local environmental factors.

Materials and methods

Study area

Our study area was the terrestrial part of Albania including freshwaters but excluding marine areas (fig. 1). The area of the country is 28 748 km², and it has 362 km coastline. It has a large geomorphological complexity with 71 mountain peaks above 2000 m and 25 above 2500 m elevation. Mountains in the North and North-East belong to the Dinarides (Prokletije), while the others in the central and southern parts belong to the Hellenides (Korab, Tomorr, Pindos; e.g. Ostrovicë, Nemërckë). West Albania is mostly lowland with many lagoons on the seaside. Albania's territory partially covers the three largest lakes in the Balkan Peninsula, Shkodër, Ohrid and Prespa. As many mountains function as dividing ranges, there are 10 major rivers (e.g. Drin, Shkumbin, Vjosë) with 150 smaller ones. Climate is mostly warm Mediterranean and oceanic in lower altitudes while



Figure 1. Geographic map of the study area indicating toponyms mentioned in the text.

cold Alpine in higher altitudes. Vegetation is mostly macchia with karst forests and birch forests.

Collection and georeferencing distributional data

We used five sources of information to build a database on Albanian reptiles: published literature, personal communication with other researchers, museums and several online resources, and our own collection of data on reptile occurrences. First, we carefully searched the available primary scientific and grey literature for distributional data. If coordinates were available in these sources, we used the georeferenced coordinates as given (Petrov, 2006; Jablonski, 2011; Jablonski, Vági and Kardos, 2015; Mizsei et al., 2016a, 2016b). If maps were available, we georeferenced them using the GDAL plugin of QuantumGIS 1.8 (Bruno, 1989; Haxhiu, 1998). If geographical coordinates were missing or if we were unable to georeference maps from the literature sources (Chabanaud, 1919; Kopstein and Wettstein, 1920; Werner, 1920; Cabela and Grillitsch, 1989; Uhrin and Šíbl, 1996; Farkas and Buzás, 1997; Haxhiu, 2000a, 2000b, 2000c, 2000d; Korsós, Barina and Pifkó, 2008; Ursenbacher et al., 2008; Haxhiu and Vrenozi, 2009; Oruçi, 2010; Podnar, Mađarič and Mayer, 2014; Saçdanaku and Haxhiu, 2015), we attempted to identify localities using a combination of Google Maps (<http://www.maps.google.com>), the GeoNames database (<http://www.geonames.org>) and other websites and blogs. Second, we collected records from the database of the Hungarian Natural History Museum and the following online databases: Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>, which also contained museum records), Fieldherping.eu (<http://www.fieldherping.eu>), iNaturalist (<http://www.inaturalist.org>), and TrekNature (<http://www.treknature.com>). Finally, we conducted 20 expeditions to Albania between 2009 and 2015, to collect data on the occurrences of herpetofauna. These trips were specifically targeted (i) to survey areas of the country from where no records were previously available from the literature or from the other sources, and (ii) to detect rare species that had less than 10 records in other data sources. We visited all but two such areas at least twice to reduce the chances of missing species that are secretive, and whose activity depends on season and weather. We documented every field record by photographs of both specimens and habitats. We entered all records with reliable spatial reference into a GIS database. We stored the records from each of the three information sources in a point shape file. We also added the time period of the collection of the records, both for published and unpublished data sources, respectively.

Taxonomic considerations

We identified species based on Arnold and Ovenden (2002) and followed the taxonomy and nomenclature of Sillero et al. (2014a) with the consideration of the recent taxonomic change in *Xerotyphlops vermicularis* (from *Typhlops*, Hedges et al., 2014). In addition, we made four decisions based on more recent information. First, although *Anguis graeca* is the dominant species of slow worm in Albania

(Gvoždik et al., 2010), *A. fragilis* also occurs in the northern part of the country (Jablonski et al., 2016). As the identification of these two species is difficult due to little differences in their morphology, we merged these taxa as *Anguis fragilis/graeca* as area borders and overlaps are still unclear. Second, for similar reasons we did not differentiate between *Podarcis tauricus* and *P. ionicus*, we merged them as *Podarcis tauricus/ionicus* (Psonis et al., 2017). Third, we treated *Vipera ursinii graeca* as a separate species from *V. ursinii* as *V. graeca*, because recent phylogenetic studies supported its species status (Ferchaud et al., 2012; Mizsei et al., 2017). Finally, four sea turtles, *Caretta caretta*, *Dermochelys coriacea*, *Chelonia mydas* and *Eretmochelys imbricata*, which are known to occur in Albania, were excluded from our analyses because of their coastal and temporary appearance in the country (Casale and Margritoulis, 2010).

Spatial analyses

For spatial analyses, we aggregated point records into 10×10 km cells of the grid system of the European Environmental Agency (<http://eea.europa.eu/data-and-maps/data/eea-reference-grids>) in ETRS89 Lambert Azimuthal Equal Area projection (EPSG: 3035). The altitudinal range of the species was calculated using Shuttle Radar Topographic Mission (SRTM) 90 m Digital Elevation Database v4.1 (Jarvis et al., 2008) to uniformly identify elevations for all occurrence points. We calculated the Extent of Occurrence (EOO) of the species by fitting Minimum Convex Polygons to their point records and then intersected it with the territory of Albania using QuantumGIS 2.12. To evaluate whether sampling effort was spatially biased, we tested the pattern of records per cell for spatial autocorrelation using the global Moran's I spatial statistic, considering the null hypothesis that occurrence records are randomly distributed. We used the Moran's I Z-score to visualise and test deviations from the null hypothesis to evaluate if records are significantly ($P < 0.05$) spatially clustered ($Z > 0$) or dispersed ($Z < 0$) relative to the null hypothesis of random distribution. To assess the local patterns in sampling bias within Albania, we used the Getis Ord G_i^* spatial statistic (Ord and Getis, 1995) which estimates whether sampling effort was significantly lower (GiZ score < -1.96 indicates coldspot of sampling) or higher (GiZ score > 1.96 shows hotspot of sampling) than expected by chance. We used ESRI ArcGIS 10 in this analysis. Finally, we assessed reptile diversity by calculating Shannon's diversity index for each cell using the vegan package in the R statistical environment (R Development Core Team, 2015).

Environmental data and linear modelling

We selected several environmental variables which were expected to explain biodiversity patterns: climate, distance to sea, land cover diversity, altitude and altitudinal diversity. Climate data (all 19 variables available) were obtained from the WorldClim database (Hijmans et al., 2005). We reduced

the Bioclim variables in a principal component analysis to four components, which explained 98.9% of the total variance (table 1). For each cell, we measured the distances of their centroids from the Adriatic or the Ionian Sea shores with the NNJoin 1.2.2 Quantum GIS plugin. We calculated the Shannon-diversity of CORINE Land Cover categories (250 m resolution; European Environmental Agency) in all cells using the LecoS 1.9.8 plugin in Quantum GIS (Jung, 2012). We calculated mean and standard deviation (SD) of altitude in 10×10 km cells based on grid values of the SRTM in 90-m Digital Elevation Database v4.1 (Jarvis et al., 2008), using ZonalStatistics in Quantum GIS 2.12.

To evaluate the degree of association between either reptile presence/absence or reptile diversity and environmental predictors, we fitted Generalized Linear Mixed Models (GLMM) for all possible combinations of independent variables (Pinheiro and Bates, 2000). For presence/absence, we assumed binomial error distribution, whereas for reptile diversity, we assumed Poisson error distribution. To control for spatial autocorrelation, we included site as a random factor, whereas to control for sampling bias we included GiZ scores as a random factor. To minimize the effect of phylogenetic relatedness among species, we included species ID nested in order as an additional random factor. Because our dataset contained historical occurrence records from the period 1918-1950 and the climatic variables were from the period 1950-2000, it was possible that the differences in climatic conditions between the two periods could influence the results of the GLMM. To evaluate this potential bias, we ran the GLMMs both with all occurrence records included and with historical (pre-1950) records excluded. The two analyses provided qualitatively identical results, therefore, we decided to present analyses based on the entire dataset.

After fitting GLMs, the relative importance of environmental predictors was calculated using a model-comparison technique in an information-theoretic framework (Burnham and Anderson, 2002). In the first step, we calculated Akaike's information criterion corrected for small sample size (AICc) which is a metric of the trade-off between the goodness of fit of the model and its complexity, thus functioning as a measure of information entropy. Next, we assessed the corresponding Akaike weight of each model (ω) which represents the relative likelihood of a model later used to estimate model-averaged parameter values. In the third step, we selected models with substantial support: Akaike differences in the range 0-2 indicate substantial level of empirical support of a given model ($\Delta_i = AIC_i - AIC_{min} < 2.0$) (Burnham and Anderson, 2002). We calculated model-averaged parameter estimates (θ) and unconditional standard errors that controlled for model uncertainty (SEu; Burnham and Anderson, 2002) of each variable by the sums of their Akaike weights across all models with substantial support containing the given predictor. For all analyses, we used the R statistical computing environment (R Development Core Team, 2015). Model fitting and consequent model selection were performed by applying the MuMIn package (Bartón, 2011).

Table 1. Environmental variables used in the study.

Predictor	Description	Data source
BIO PC1	“Temperature” principal component BIO1 = annual mean temperature BIO6 = min temperature of coldest month BIO11 = mean temperature of coldest quarter	Hijmans et al., 2005
BIO PC2	“Precipitation” principal component BIO12 = annual precipitation BIO16 = precipitation of wettest quarter BIO19 = precipitation of coldest quarter	Hijmans et al., 2005
BIO PC3	“Temperature variation” principal component BIO2 = mean diurnal range [mean of monthly (max temp – min temp)] BIO4 = temperature seasonality (standard deviation × 100) BIO7 = temperature annual range (BIO5-BIO6)	Hijmans et al., 2005
BIO PC4	“Precipitation variation” principal component BIO9 = mean temperature of driest quarter BIO10 = mean temperature of warmest quarter BIO15 = precipitation seasonality (coefficient of variation)	Hijmans et al., 2005
CORINE DIV ALT MEAN	Shannon diversity of CORINE Land cover in 10 × 10 km cells Mean of altitude values in 10 × 10 km cells, calculated from the SRTM near 90 m data	European Environment Agency CGIA-CSI
ALT SD	Standard deviation of altitude values in 10 × 10 km cells, calculated from the SRTM near 90 m data	CGIA-CSI
SEA DIST	Min distance of 10 × 10 km cells centroids from the Adriatic Sea coast	present study

Results

Distributional evaluation

Our list of reptiles in Albania includes 40 species: 5 chelonians, 18 lizards and 17 snakes (table 2) and we present distribution maps for each species in the online supplementary material (figs S01-S40). We collected $N = 3731$ records from Albania. The earliest records were from 1918 and the latest from 2015 (fig. 2). The number of records started to increase in the 1990s, after the collapse of isolationist political system in the country (fig. 2). Of the $N = 3731$ records, 2706 (72.5%) were collected from the literature, 97 (2.6%) through personal communication with other researchers, 33 (0.9%) from internet sources, and 10 (0.3%) from museum collections. We collected $N = 885$ (23.7%) original observations (table 2, fig. 3A). Unpublished records (our own data, personal communications, internet sources and museum collections; $N = 1025$) made up 27.5% of the dataset. The number of records per species ranged from $N = 1$ (*Tarentola*

mauritanica) to $N = 379$ (*Testudo hermanni*). Minimum cell occupancy was 1 (*T. mauritanica*), while the maximum was 191 (*Vipera ammodytes*). The most widely distributed species were *T. hermanni*, *Lacerta trilineata*, *Lacerta viridis* complex, *Podarcis muralis*, *Anguis fragilis/graeca*, *Natrix natrix*, *N. tessellata*, *Dolichophis caspius*, *Zamenis longissimus* and *V. ammodytes*. Species with restricted distribution (<10% of the cells) were *Testudo graeca* (no recent records), *Testudo marginata*, *T. mauritanica* (no recent records), *Dalmatolacerta oxycephala*, *Dinarolacerta montenegrina*, *Lacerta agilis*, *Podarcis melisellensis*, *P. siculus*, *Zootoca vivipara*, *Eryx jaculus*, *Vipera berus*, *V. graeca* and *V. ursinii*. Seven species showed fragmented ranges (*Mediodactylus kotschyi*, *Algyroides nigropunctatus*, *Ablepharus kitaibelii*, *Xerotyphlops vermicularis*, *E. jaculus*, *Coronella austriaca* and *Platyceps najadum*) and 14 occurred at the margins of their overall range (*T. graeca*, *T. marginata*, *T. mauritanica*, *D. oxycephala*, *L. agilis*, *P. melisellensis*, *P. siculus*, *Z.*

Table 2. List of reptile species in Albania with their number of records, Extent of Occurrence (EOO) and global distribution type.

Species	Total records	Published records	Unpublished records	N of presence in 10 × 10 km cells	EOO (km ²)	Distribution type
1 <i>Ablepharus kitaibelii</i>	24	18	6	22	17 106	Eastern-Mediterranean
2 <i>Algyroides nigropunctatus</i>	105	80	25	81	24 713	Eastern-Mediterranean
3/4 <i>Anguis fragilis/graeca</i>	196	176	20	147	25 879	European/Eastern-Mediterranean
5 <i>Coronella austriaca</i>	39	30	9	33	22 170	European
6 <i>Dalmanolacerta oxycephala</i>	2	2	0	2	*	Eastern-Mediterranean
7 <i>Dinarolacerta montenegrina</i>	7	2	5	3	24	Eastern-Mediterranean
8 <i>Dolichophis caspius</i>	182	158	24	136	26 107	Eastern-Mediterranean
9 <i>Elaphe quatuorlineata</i>	98	87	11	75	21 633	Eastern-Mediterranean
10 <i>Enys orbicularis</i>	164	139	25	101	23 892	Turano-European-Mediterranean
11 <i>Eryx jaculus</i>	8	4	4	5	982	Turano-Mediterranean
12 <i>Hemidactylus turcicus</i>	47	39	8	32	11 307	Mediterranean
13 <i>Hierophis gemonensis</i>	78	50	28	65	23 582	Eastern-Mediterranean
14 <i>Lacerta agilis</i>	10	7	3	7	1647	Euro-Siberian
15 <i>Lacerta trilineata</i>	106	45	61	135	23 112	Eastern-Mediterranean
16 <i>Lacerta viridis</i> complex	182	134	48	70	25 737	Southern-European
17 <i>Malpolon insignitus</i>	132	101	31	97	21 709	Eastern-Mediterranean
18 <i>Mauremys rivulata</i>	68	54	14	44	10 253	Eastern-Mediterranean
19 <i>Mediodactylus kotschyi</i>	19	15	4	17	6112	Eastern-Mediterranean
20 <i>Natrix natrix</i>	241	192	49	173	25 986	Centralasiatic-European-Mediterranean
21 <i>Natrix tessellata</i>	157	129	28	118	24 339	Turano-European
22 <i>Platyceps najadum</i>	49	35	14	44	22 422	Turano-European
23 <i>Podarcis erhardii</i>	46	11	35	24	12 885	Eastern-Mediterranean
24 <i>Podarcis melisellensis</i>	10	7	3	8	1978	Eastern-Mediterranean
25 <i>Podarcis muralis</i>	298	218	80	186	26 273	Southern-European

Table 2. (Continued.)

Species	Total records	Published records	Unpublished records	N of presence in 10 × 10 km cells	EOO (km ²)	Distribution type
26 <i>Podarcis siculus</i>	3	1	2	2	14	Southern-European
27/28 <i>Podarcis tauricus/tonicus</i>	150	105	45	95	24 571	Eastern-Mediterranean/Eastern-Mediterranean
29 <i>Pseudopus apodus</i>	101	81	20	75	17 237	Turano-Mediterranean
30 <i>Tarentola mauritanica</i>	1	1	0	1	*	Mediterranean
31 <i>Telescopus fallax</i>	78	73	5	63	16 620	Turano-Mediterranean
32 <i>Testudo graeca</i>	2	2	0	2	*	Turano-Mediterranean
33 <i>Testudo hermanni</i>	379	238	141	186	25 583	Southern-European
34 <i>Testudo marginata</i>	22	15	7	8	1263	Eastern-Mediterranean
35 <i>Xerotyphlops vermicularis</i>	27	19	8	19	8037	Turano-Mediterranean
36 <i>Vipera ammodytes</i>	274	244	30	191	26 211	Eastern-Mediterranean
37 <i>Vipera berus</i>	19	13	6	13	2706	Euro-Siberian
38 <i>Vipera graeca</i>	208	1	205	11	2010	Eastern-Mediterranean
39 <i>Vipera ursinii</i>	18	14	4	14	3094	Southern-European
40 <i>Zamenis longissimus</i>	118	110	8	104	25 224	Southern-European
41 <i>Zamenis situla</i>	55	51	4	47	17 847	Eastern-Mediterranean
42 <i>Zootoca vivipara</i>	8	5	3	5	1155	Euro-Siberian
Total	3731	2706	1025	303		

*N of records is insufficient to calculate Extent of Occurrence.

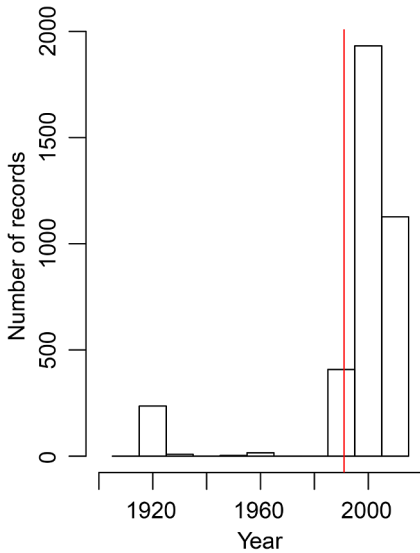


Figure 2. Number of records by year of publication (published sources) or year of data collection (unpublished sources). Vertical line indicates the year when the former isolationist political system ended in Albania (1991).

vivipara, *X. vermicularis*, *E. jaculus*, *V. berus*, *V. ursinii*). The number of unpublished records exceeded that of published records for all species, except for *L. trilineata* and *V. graeca*. It is likely that some species had been introduced in Albania outside of their native range by various human activities. One example is *Hemidactylus turcicus*, which occurs in towns far from its regular range in the Adriatic coast (e.g. Berat) or *T. mauritanica* (Mačát et al., 2014) and *P. siculus* (Podnar, Mayer and Tvrtković, 2005; Mizsei et al., 2016a). Based on previous zoogeographical literature, we classified the reptiles of Albania into 10 distribution types (table 2). The most frequent distribution type was Eastern-Mediterranean (20 species), followed by Southern-European (6 species) and Turano-Mediterranean (5 species).

Reptile diversity patterns

In our dataset, 303 out of 349 10×10 km cells contained at least one reptile species (fig. 3C). The maximum number of species per cell was 26 and 20 or more species were recorded in 12 cells, mostly in coastal and

southern Albania (fig. 3C). In contrast, zero or few (<5) species were recorded in many of squares in central Eastern Albania and border areas. The average number of species per cell was 7.0 ± 5.79 (mean \pm SD). Most of the cells with high reptile diversity were close to the Adriatic and Ionian coast in West Albania, while the Middle-East of Albania showed lower diversity levels (fig. 3C). However, lower diversity in Eastern Albania might also be a consequence of lower sampling intensity (fig. 3B). Global Moran's I values showed that overall sampling effort within Albania was spatially clustered ($Z = 6.6974$, $P < 0.0001$) (fig. 3B). The Getis Ord G_i^* metric identified no sampling coldspots in our dataset. In contrast, several sampling hotspots were identified (fig. 3B). Sampling hotspots were in the Prokletije Mountains, the Adriatic and Ionian coast, and the southern Albanian mountains (northern Pindos range) (fig. 3B).

Most species were recorded between 0 and 1000 m a.s.l., whereas mountain species were usually recorded at 1500 m and above (fig. 4). The most important predictor for reptile presence and diversity were altitudinal variation (ALT SD), land cover diversity (CORINE DIV), temperature (BIO PC1) and the precipitation variation (BIO PC4) principal components (table 3). Each of these variables were part of the five best models for both presence and diversity (table 4). Model-averaged parameter estimates suggested that ALT SD, CORINE DIV, BIO PC1 and BIO PC4 significantly influenced reptile presence, whereas reptile diversity was influenced only by ALT SD and CORINE DIV (table 5). The effects of ALT SD, CORINE DIV and BIO PC4 were positive, whereas that of BIO PC1 was negative (table 5, fig. 5).

Discussion

Our study presents the largest database of reptile occurrences in Albania to date and involves all

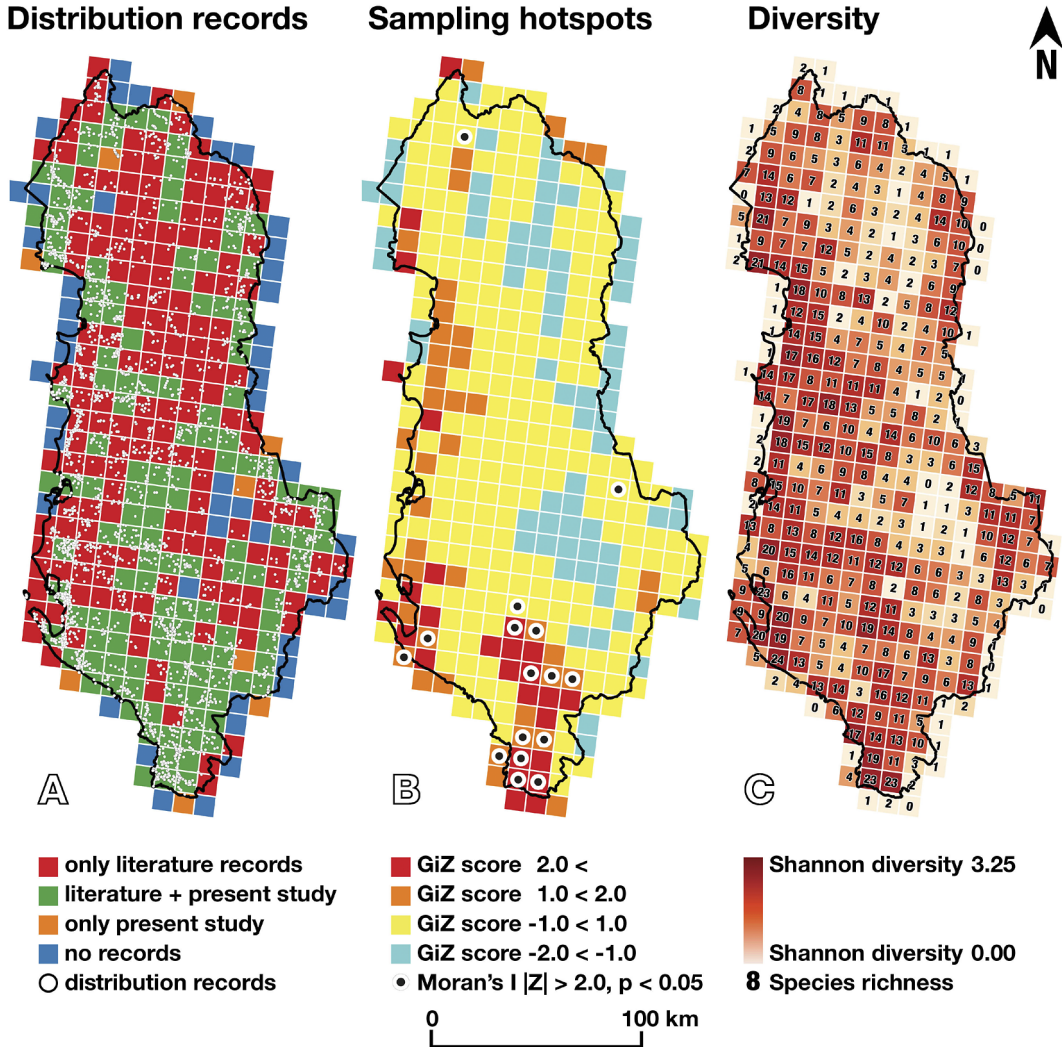


Figure 3. Sources of occurrence records of reptile species used in the present study (A), sampling hotspots (GiZ score > 1.0) and coldspots (GiZ score < -1.0), with significantly clustered or dispersed records based on Moran’s I values (dots) (B), and reptile species richness (numbers) with Shannon diversity (shading) (C) in Albania on a 10 × 10 km grid.

species currently known to occur in the country. In addition, our study is the first analysis of patterns in reptile diversity in Albania. Our database contains data from a large part of the country, i.e., 87% of the 10 × 10 km grid cells contained at least one occurrence point. In addition, our database now clarifies taxonomic allocations that were ambiguous in the few previous sources of available (see literature records at *L. trilineata*, *L. viridis* complex, *P. erhardii* or *P. melissellensis*).

We detected notable longitudinal differences between the western and the eastern parts of the country, with higher diversity in the West than in the East (fig. 3C). This finding evokes two mutually non-exclusive explanations. First, a large number species is found almost exclusively in the western part of the country along the Adriatic Sea, including *Mauremys rivulata*, *Elaphe quatuorlineata* or *H. turcicus*, for which the geographic range is well documented. In contrast, few species with large ranges occupy the east-

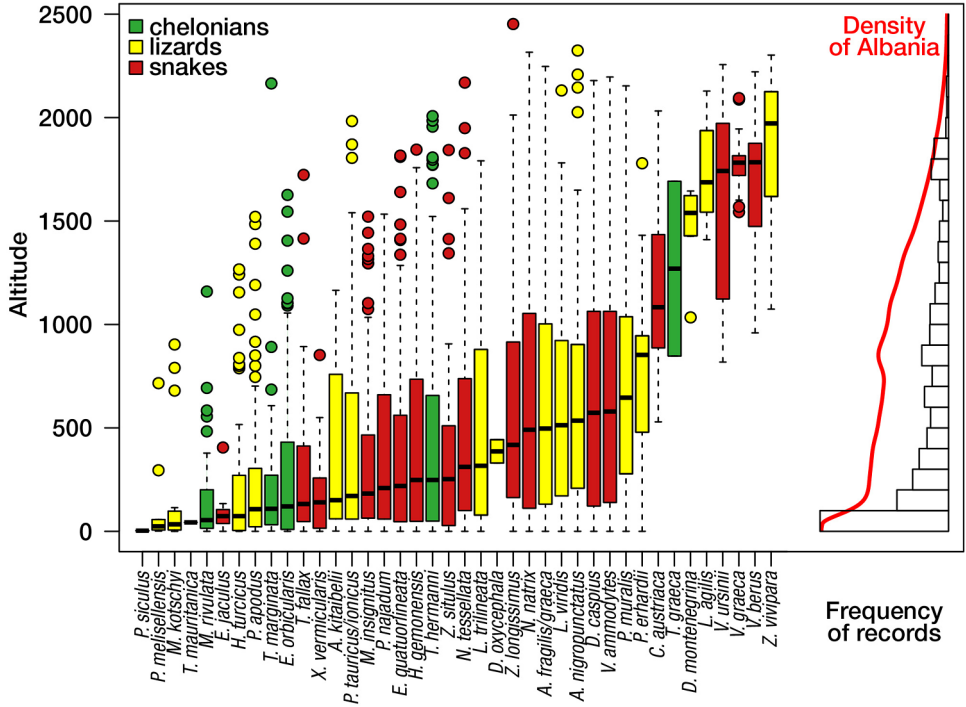


Figure 4. Altitudinal distribution of reptile species and frequency of occurrence records by altitude in Albania. Box-and-whiskers plots show the median (horizontal line), the 25th and 75th percentile (bottom and top of box, respectively), minimum and maximum values (lower and upper whiskers, respectively) and outliers (circles). The red line is the frequency distribution of altitudinal values in Albania.

Table 3. Predictor importance in the two GLMM models.

Presence		Shannon diversity	
Predictor	Importance	Predictor	Importance
ALT SD	1.000	ALT SD	1.000
CORINE DIV	1.000	CORINE DIV	1.000
BIO PC1	1.000	BIO PC1	1.000
BIO PC4	1.000	BIO PC4	1.000
BIO PC3	0.838	BIO PC3	0.577
SEA DIST	0.198	BIO PC2	0.241
BIO PC2	0.153	SEA DIST	0.203
ALT MEAN	0.140	ALT MEAN	0.000

ern areas almost exclusively, such as *P. erhardii*. In addition, some of the species distributed in the East exhibit narrower distribution, such as *T. graeca* (although it is possible that this species was historically misidentified with *T. hermanni* as continual areal of *T. graeca* is more eastward), and many species have restricted ranges, i.e. are found only in mountain habitats, such as *V. ursinii* and *Z. vivipara*. Second, our database also shows that sampling effort was higher in

the western than in the eastern part of the country (fig. 3B). The western part is more densely populated than the eastern part (CIA, 1990), resulting in a higher level of urbanisation and road density, increasing the chances of encountering reptiles, which may lead to a bias in sampling effort (Kadmon, Farber and Danik, 2004; Beck et al., 2010). Biases probably involve the region of Ohrid and Prespa Lakes and Prokletije Mountains, as these scenic landscapes are often visited by tourists and herpetologists. Another known sampling bias is in the Pindos Mountains in the south, a hotspot of sampling effort, which we visited frequently to conduct field studies on *V. graeca* (Mizsei et al., 2012, 2016b).

The specific behaviour and habitat requirement of reptiles can also lead to sampling biases. Species with the largest number of records are not just well distributed throughout the country, but they are often easily observable

Table 4. Parameter estimates and AIC values of the best ($\Delta AICc < 2$) GLMM models fitted on the presence and diversity of reptiles in Albania.

Variable	Model	ALT SD	CORINE DIV	BIO PC1	BIO PC4	BIO PC3	BIO PC2	SEA DIST	ALT MEAN	Df	AICc	$\Delta AICc$
Presence	1	0.00262	1.62607	-0.16322	0.23513	-0.09439	NA	NA	NA	10	8576.176	0.000
	2	0.00280	1.61176	-0.19995	0.24055	-0.12939	NA	0.00000	NA	11	8577.307	1.131
	3	0.00274	1.54686	-0.16413	0.24503	NA	NA	NA	NA	9	8577.708	1.531
	4	0.00267	1.62798	-0.16368	0.23726	-0.09342	-0.02202	NA	NA	11	8577.825	1.648
	5	0.00262	1.61655	-0.13999	0.20791	-0.09623	NA	NA	-0.00019	11	8578.002	1.826
Diversity	1	0.00121	0.69738	-0.08256	0.11718	NA	NA	NA	NA	7	1934.522	0.000
	2	0.00116	0.72704	-0.08166	0.11181	-0.03502	NA	NA	NA	8	1934.729	0.207
	3	0.00127	0.71770	-0.10660	0.11451	-0.05868	0.00000	0.00000	NA	9	1935.256	0.734
	4	0.00123	0.69929	-0.08282	0.11774	NA	-0.01274	NA	NA	8	1936.145	1.623
	5	0.00118	0.72806	-0.08189	0.11243	-0.03413	-0.01134	NA	NA	9	1936.464	1.942

Table 5. Model-averaged parameter estimates of GLMMs fitted on reptile presence and diversity. Parameter estimates with significant z -values are indicated in bold.

Response	Main effect	Estimate	S.E.	z value	P
Presence	(Intercept)	-6.228	0.674	9.232	0.000
	ALT SD	0.007	0.000	3.542	0.000
	CORINE DIV	1.609	0.203	7.926	0.000
	BIO PC1	-0.167	0.043	3.921	0.000
	BIO PC3	-0.102	0.054	1.885	0.059
	BIO PC4	0.234	0.074	3.150	0.001
	SEA DIST	0.000	0.000	0.994	0.320
	BIO PC2	-0.022	0.037	0.599	0.549
	ALT MEAN	-0.000	0.000	0.424	0.671
Diversity	(Intercept)	-1.320	0.807	-1.635	0.102
	ALT SD	0.002	0.000	2.226	0.026
	CORINE DIV	0.689	0.213	3.227	0.001
	BIO PC1	-0.074	0.085	-0.867	0.385
	BIO PC4	0.094	0.105	0.898	0.368
	BIO PC3	-0.049	0.080	-0.616	0.537
	BIO PC2	-0.011	0.057	-0.201	0.840
	SEA DIST	0.000	0.000	0.366	0.713
	ALT MEAN	-0.000	0.000	-0.350	0.726

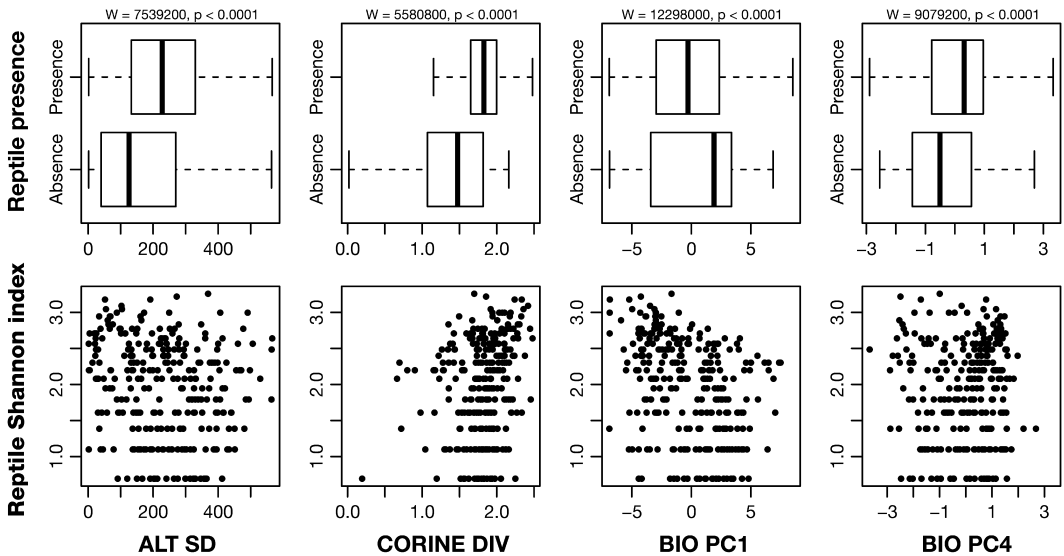


Figure 5. Species presence and Shannon diversity as a function of the most important predictors identified by GLMM model selection (for abbreviations, see table 1).

during their daytime activity. It is not surprising that *T. hermanni* has the largest number of records in the dataset (table 2), as this species has a wide range, is active during the day, and it is easy to observe. A subset of species occupy a wide range of habitats and altitudes, such as *Dolichophis caspius*, *N. natrix* and *V. ammodytes* (fig. 4), while others colonize ur-

ban areas, such as the *Lacerta viridis* complex or *Podarcis muralis* (Arnold and Ovenden, 2004). Species with special habitat or climatic requirements are represented in our database by fewer records, and include *D. montenegrina*, *V. berus*, *V. ursinii* and *Z. vivipara*, which inhabit hardly accessible high-altitude montane habitats (fig. 4). Other species are difficult to record as

a result of their secretive behaviour. For example, *E. jaculus* and *Telescopus fallax* are mostly nocturnal, while *X. vermicularis* has a fossorial lifestyle (Arnold and Ovenden, 2004). Some of these secretive species have a large extent of occurrence (EOO, table 2) but the occurrence records are very scarce and dispersed, as in the case of *A. kitaibelii* or *C. austriaca*. In addition, a number of reptiles reach the edge of their range and are only marginally present in Albania, such as *D. oxycephala*, *P. melisellensis*, *T. graeca* (dubious, see above) and *T. marginata*. Two species, *P. siculus*, known from a few localities in northern Albania, and *T. mauritanica*, present only in Sazan Island, are possibly of introduced origin. Both species are highly capable of establishing new populations and are known to be picked up accidentally e.g. by merchant ships both in ancient and recent times (Podnar, Mayer and Tvrtkovič, 2005; Mačát et al., 2014).

The importance of mountains has been detected through screening the altitudinal distribution of the species presented here. The majority of reptile species in a Mediterranean landscape inhabit lower elevations, and only a few cold-tolerant species occur up at alpine meadows. That pattern was explained by the analyses of environmental factors affecting species presence and diversity, which identified the “temperature variation” principal component (BIO PC1) as a key climatic explanatory variable, because these ectotherms cannot reproduce on cold temperatures, except the viviparous species (e.g., *Zootoca vivipara*, *Coronella austriaca*, *Vipera* spp.). Elevation diversity on mountains is strongly correlated with temperature, but these altitudinal gradients usually increase the availability of niches on smaller spatial scales (Schall and Pianka, 1978). This effect was mediated by the “precipitation variation” principal component (BIO PC4), which was an important variable in our modelling, in accordance with other studies (Rodríguez, Belmontes and Hawkins, 2005; McCain, 2010). In addition to elevational and climate factors, diversity of land cover (CORINE DIV) has strong explanatory

power on diversity as expected (Keil et al., 2012), where the presence of remnants of natural habitats can be explained by the variation of altitude (ALT SD).

According to recent molecular biogeographical analyses the number of reptile species in Albania will likely increase in the future. Several studies showed hidden diversity of evolutionary distinct lineages in the Balkan Peninsula which facilitates new description of species. In the recent past the *Anguis fragilis* complex was divided into five distinct species whereby *A. fragilis* and *A. graeca* lives in Albania (Gvoždík et al., 2010; Jablonski et al., 2016). The Dinaric endemic *Dinarolacerta* was also divided with *D. montenegrina* in the Prokletije Mountain and *D. mosorensis* in the Montenegrin, Croatian and Bosnian karst range (Ljubisavljević et al., 2007; Podnar, Mađarič and Mayer, 2014). There are probably distinct lineages within *Natrix tessellata* (Guicking, Joger and Wink, 2009) and *Lacerta viridis* complex (Marzahn et al., 2016) which are not taxonomically evaluated. The *Podarcis tauricus* complex was yet divided to two species, *P. tauricus* and *P. ionicus* complex, both present in Albania, but the latter are also a composition of five distinct lineages where new species descriptions are possible (Psonis et al., 2017). The territory of Albania is located on two main mountain systems of the Balkans, on the Dinarides in the north and on the Hellenides in the centre and south. These mountains can serve as a barrier for migration and thus they can facilitate population divergence and speciation (Joger et al., 2007; Jablonski et al., 2016).

It seems that range size has the strongest effect on extinction risk beyond other factors with a smaller chance of survival in less widespread species (Harnik, Simpson and Payne, 2012). Thus, our dataset could serve as an important basis for conservation interventions in Albania and this knowledge can also be applied to other countries or regions (Ribeiro et al., 2016). Further, it might also be feasible to create gap-analysis with existing protected areas either

with or without the involvement of species distribution modelling (Carvalho et al., 2010; de Pous et al., 2011; de Novaes e Silva et al., 2014). The database could be also integrated into larger areas such as the European continent and thus will fill an important gap for macroecological studies (Sillero et al., 2014a, 2014b; Estrada et al., 2015).

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Distribution and diversity of reptiles in Albania: a novel database from a Mediterranean hotspot

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Supplementary material

Figures S01-S40. Distribution maps of reptile species in Albania

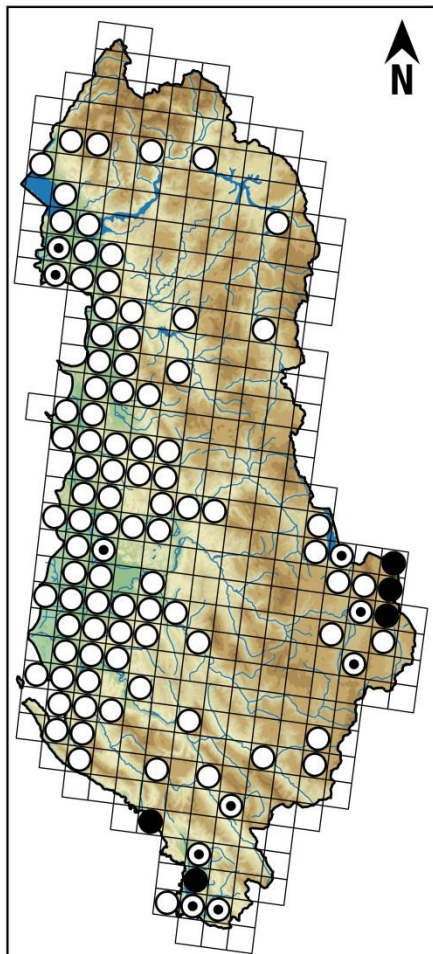


Fig. S01. *Emys orbicularis*

○ literature records
 ● literature + new records
 ● new records

0 50 km

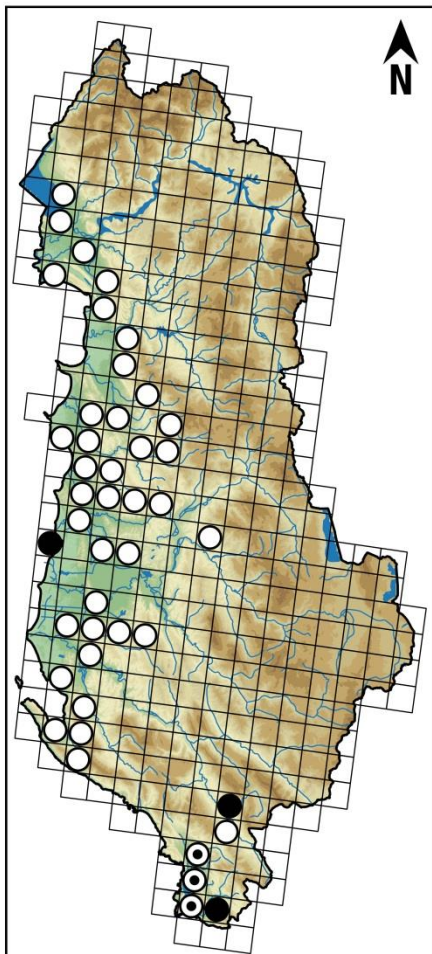


Fig. S02. *Mauremys rivulata*

○ literature records
 ● literature + new records
 ● new records

0 50 km

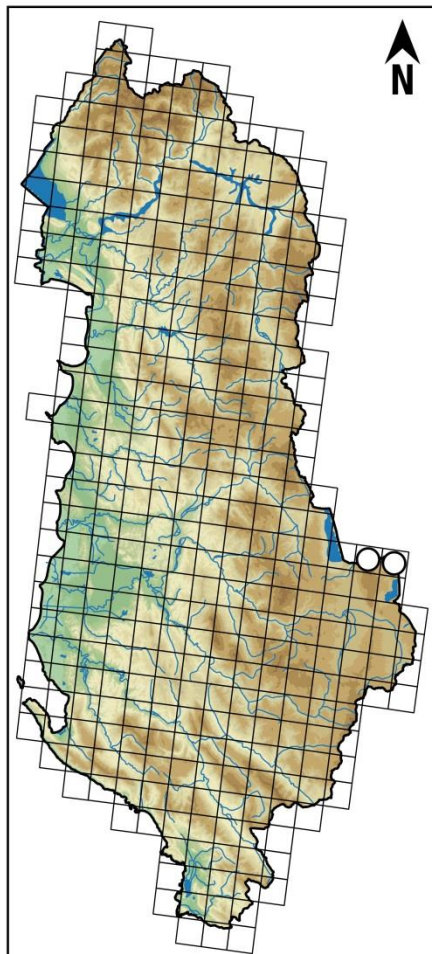


Fig. S03. *Testudo graeca*

○ literature records
 ● literature + new records
 ● new records

0 50 km

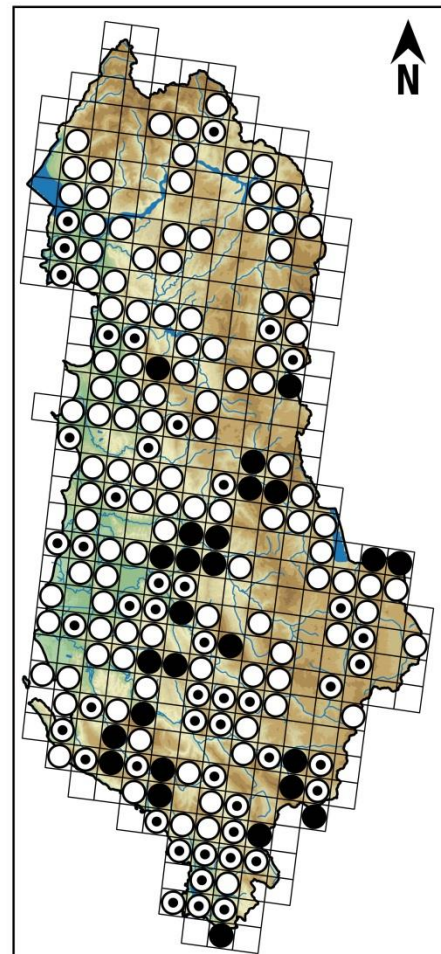


Fig. S04. *Testudo hermanni*

○ literature records
 ● literature + new records
 ● new records

0 50 km

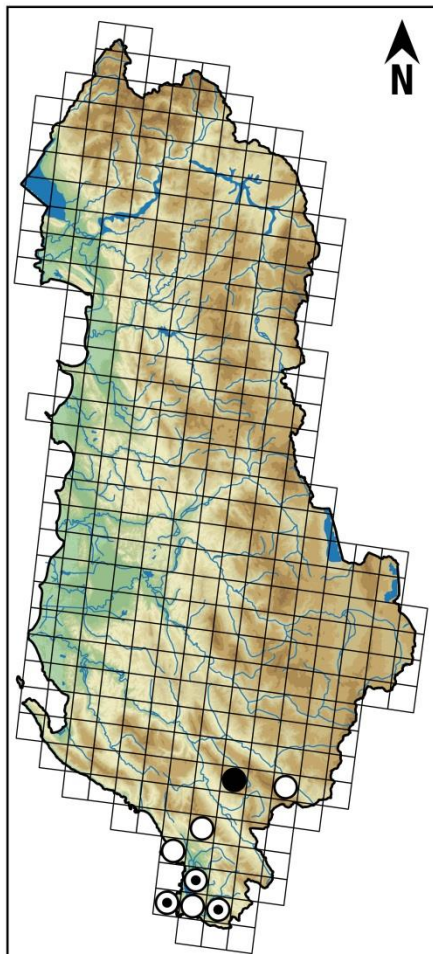


Fig. S05. *Testudo marginata*

○ literature records
 ● literature + new records
 ● new records

0 50 km

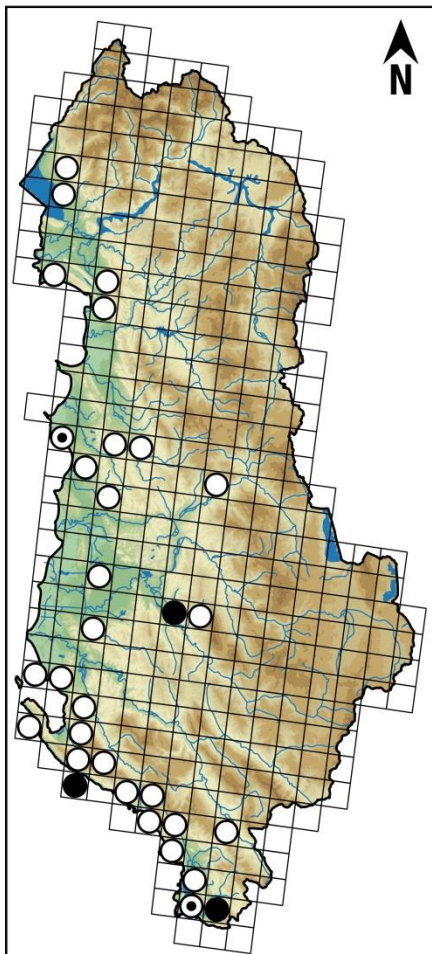


Fig. S06. *Hemidactylus turcicus*

○ literature records
 ● literature + new records
 ● new records

0 50 km

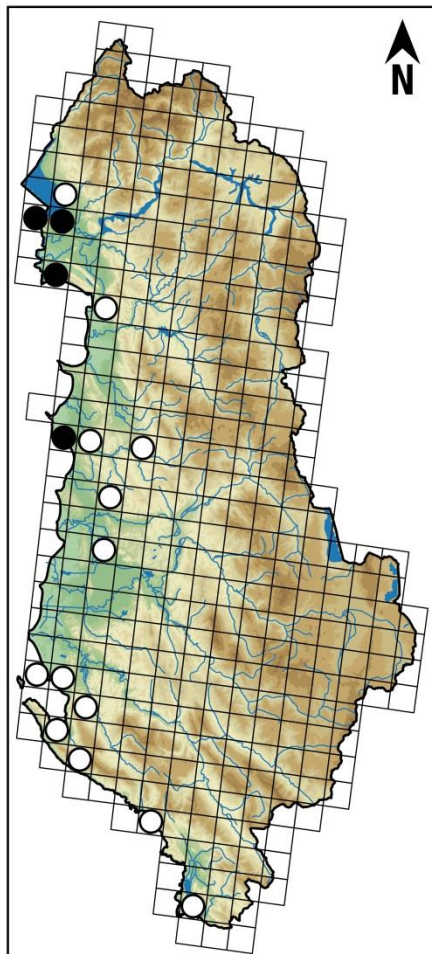


Fig. S07. *Mediodactylus kotschy*

○ literature records
 ● literature + new records
 ● new records

0 50 km

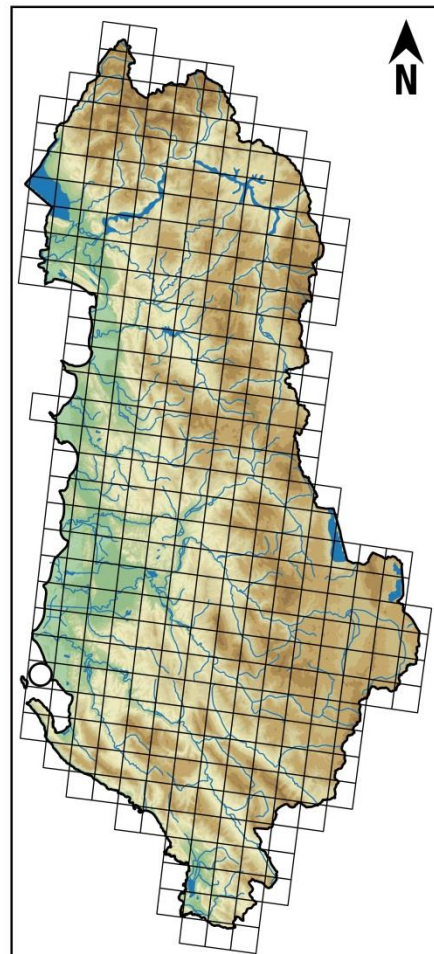


Fig. S08. *Tarentola mauritanica*

○ literature records
 ● literature + new records
 ● new records

0 50 km

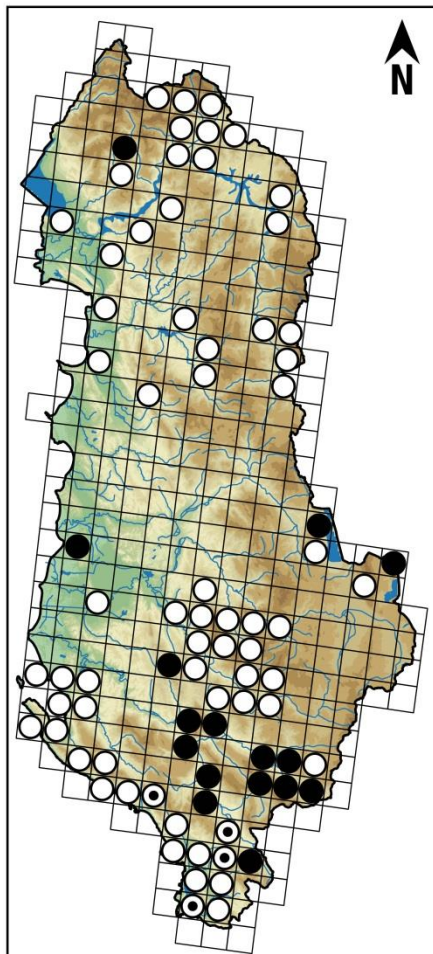


Fig. S09. *Algyroides nigropunctatus*

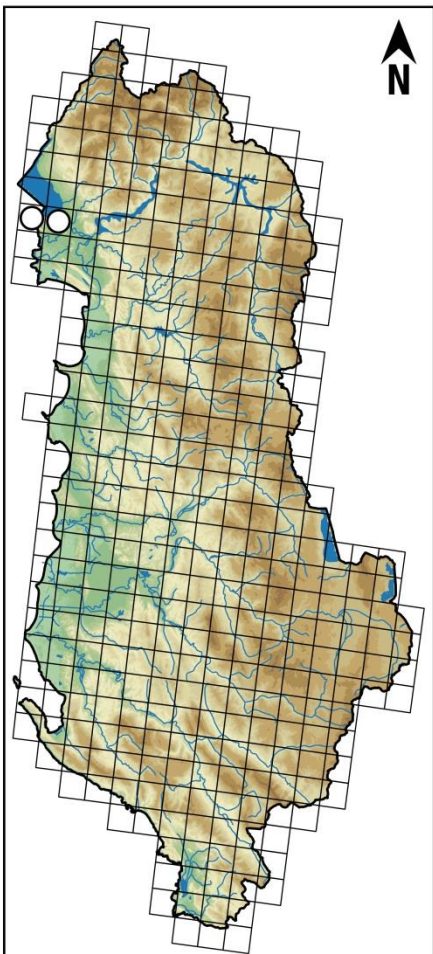


Fig. S10. *Dalmatolacerta oxycephala*

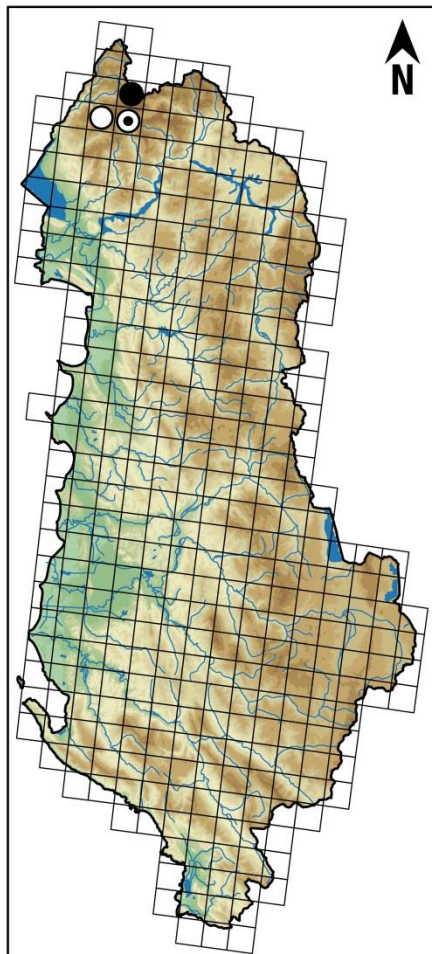


Fig. S11. *Dinarolacerta montenegrina*

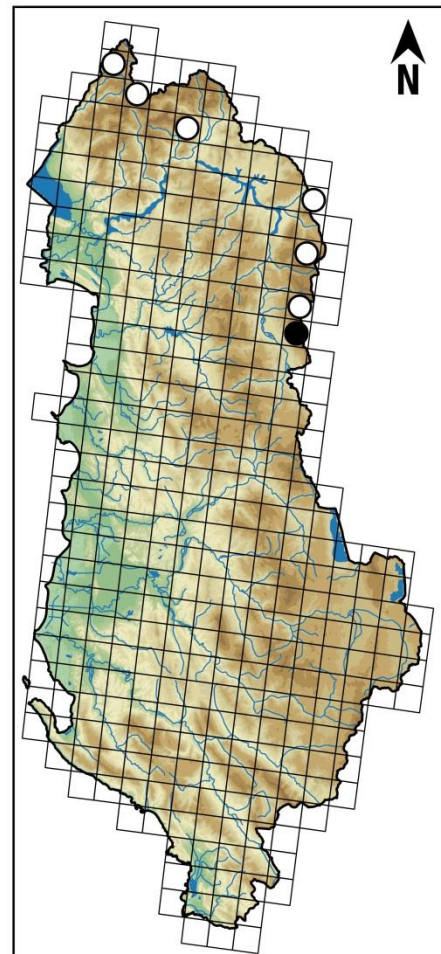


Fig. S12. *Lacerta agilis*



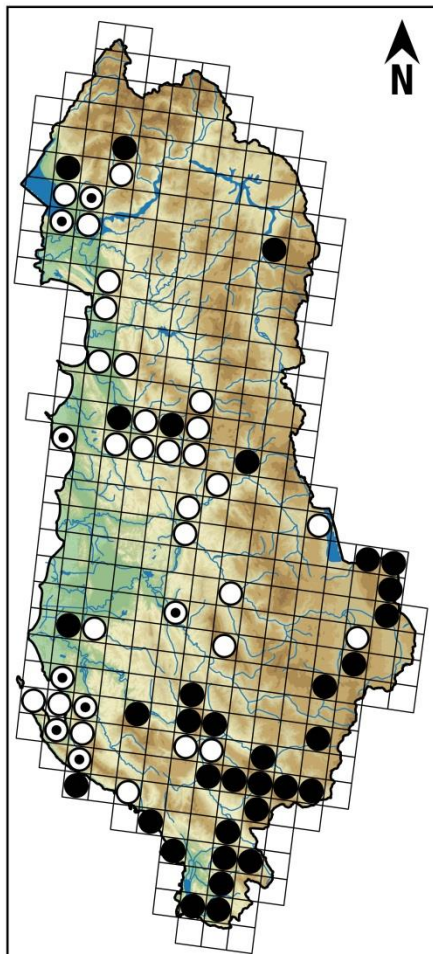


Fig. S13. *Lacerta trilineata*

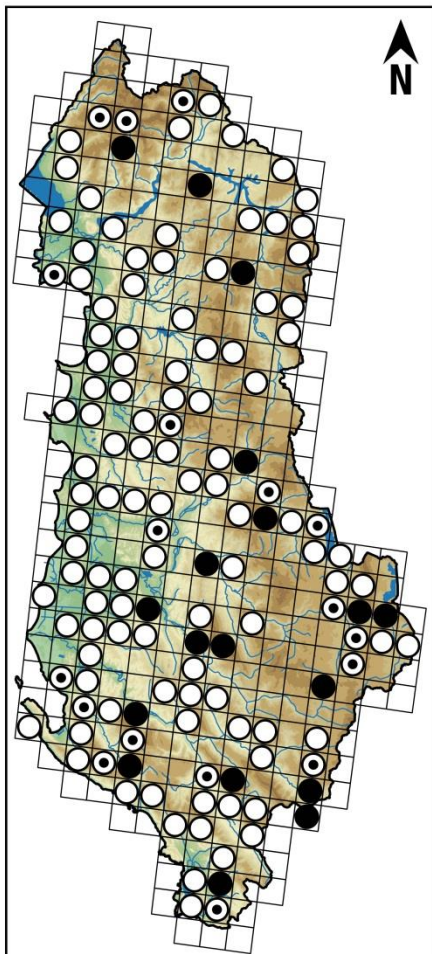


Fig. S14. *Lacerta viridis*

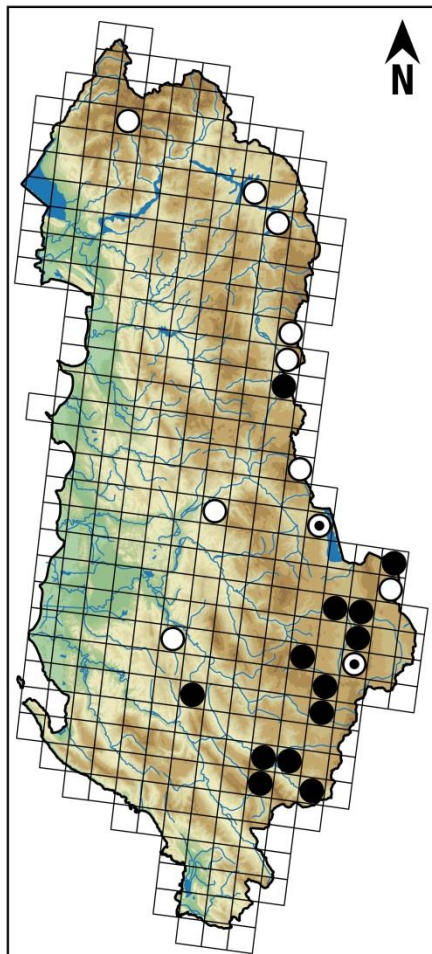


Fig. S15. *Podarcis erhardii*

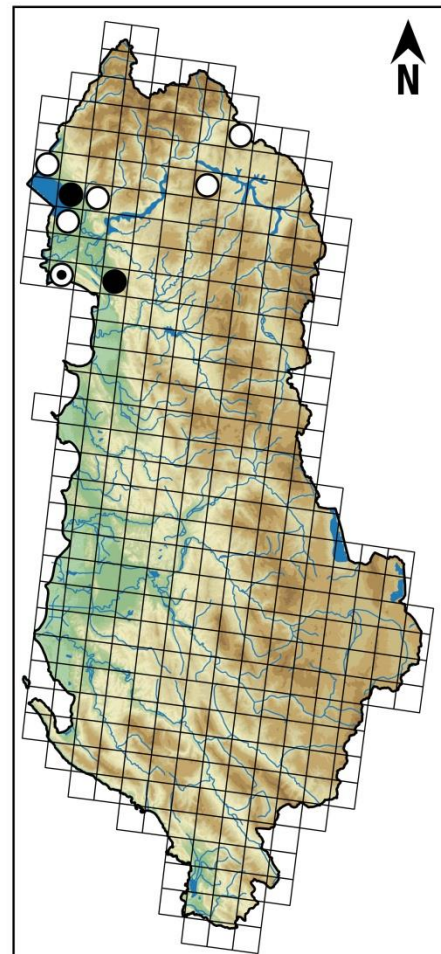


Fig. S16. *Podarcis melisellensis*



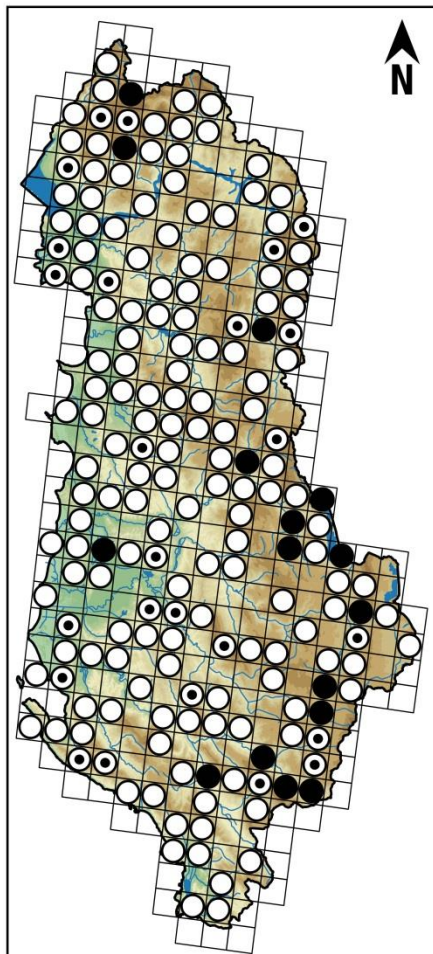


Fig. S17. *Podarcis muralis*

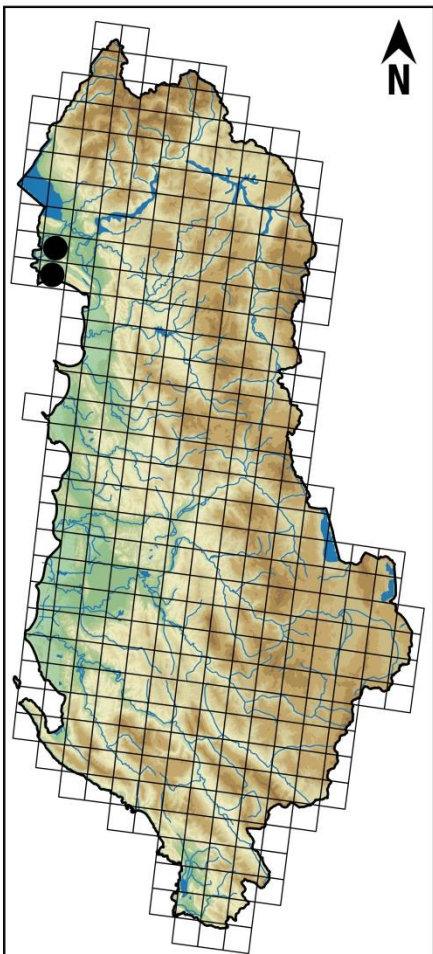


Fig. S18. *Podarcis siculus*

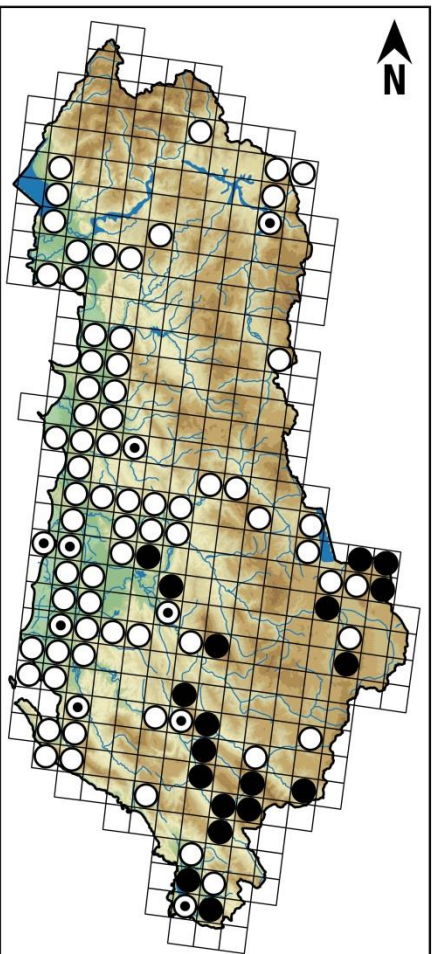


Fig. S19. *Podarcis tauricus/ionicus*

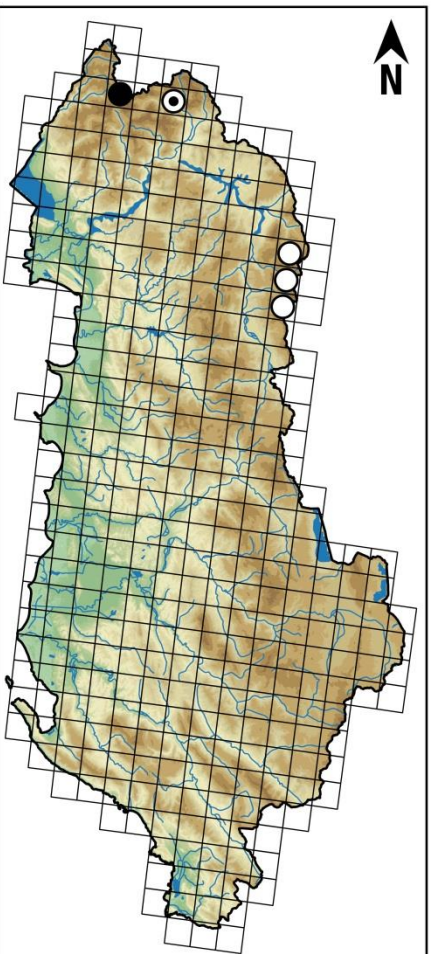


Fig. S20. *Zootoca vivipara*



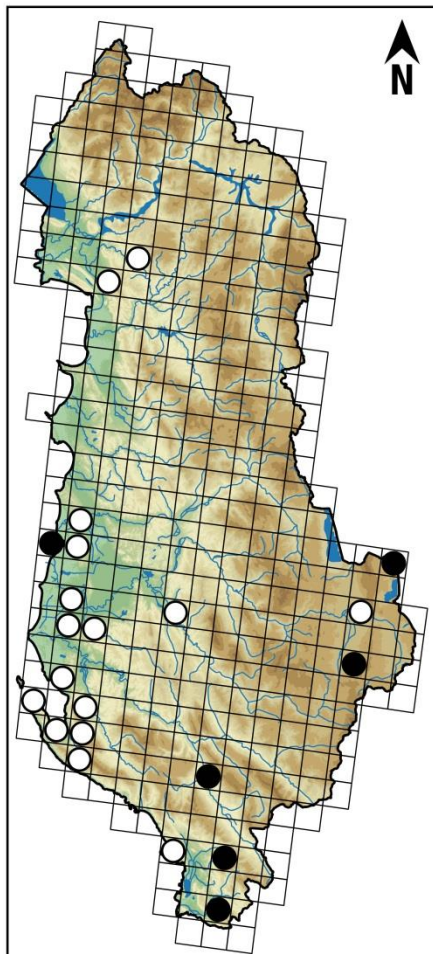


Fig. S21. *Ablepharus kitaibelii*

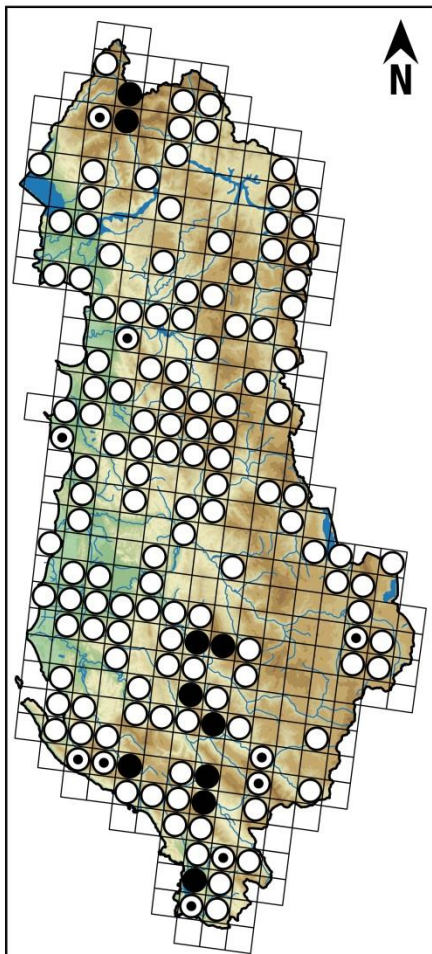


Fig. S22. *Anguis fragilis/graeca*

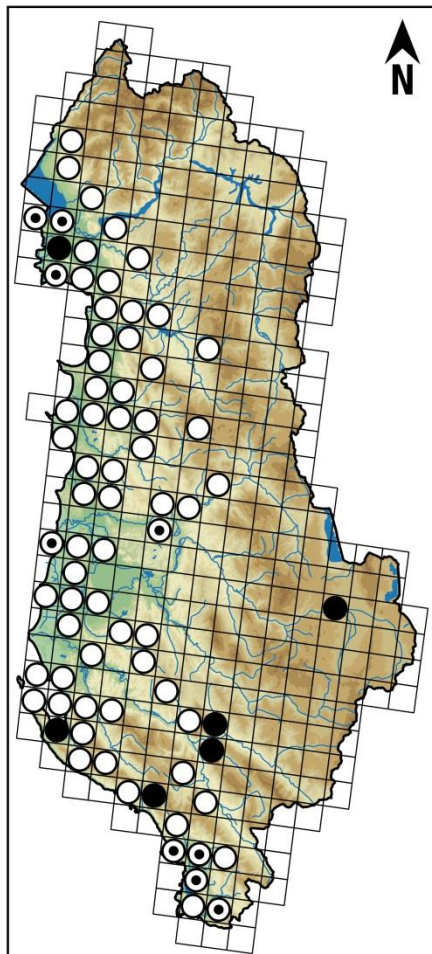


Fig. S23. *Pseudopus apodus*

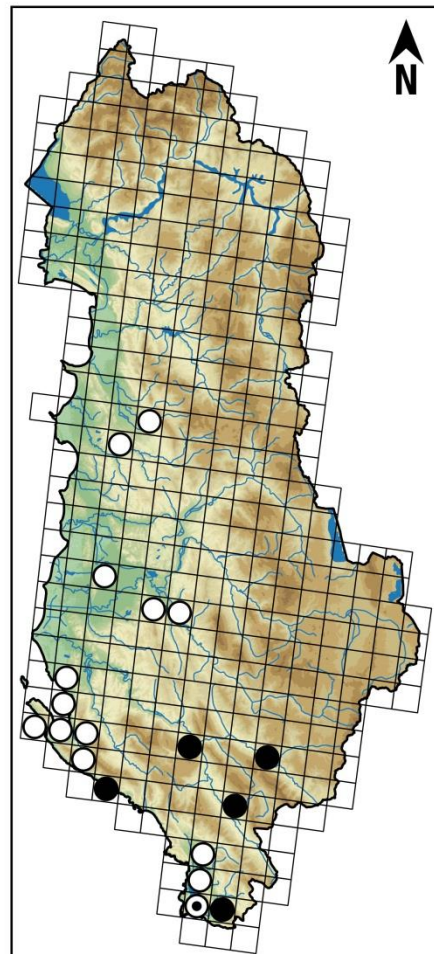


Fig. S24. *Xerotyphlops vermicularis*



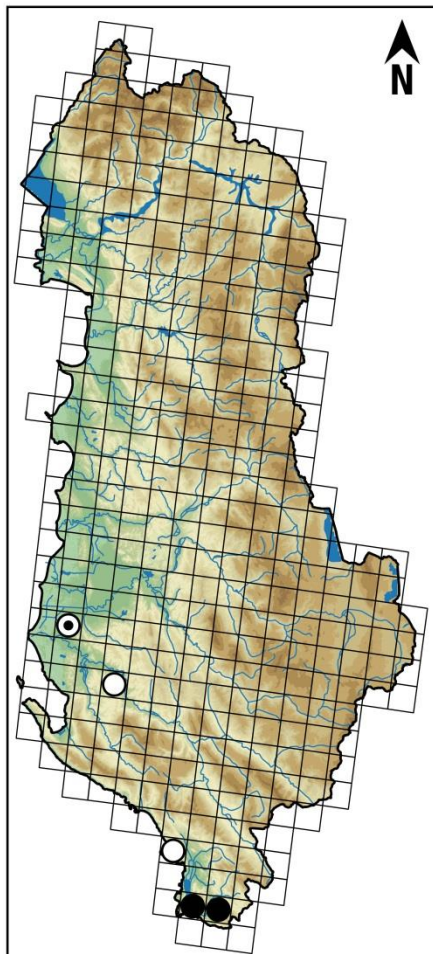


Fig. S25. *Eryx jaculus*

○ literature records
 ● literature + new records
 ● new records

0 50 km

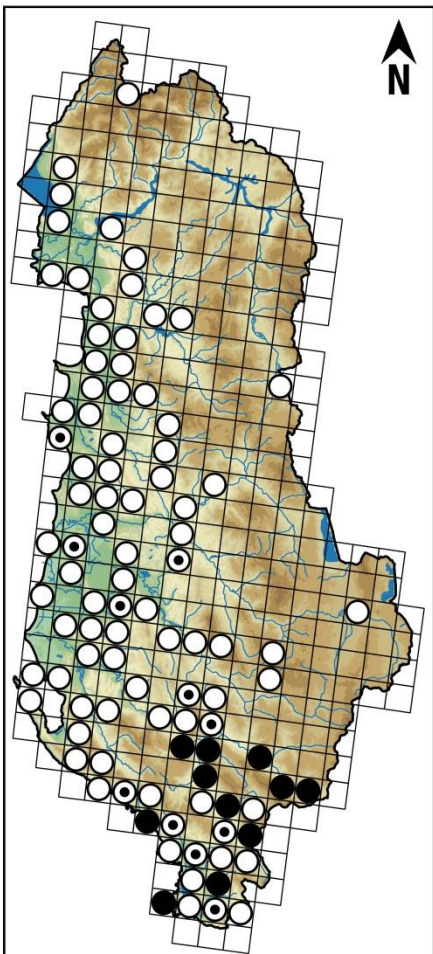


Fig. S26. *Malpolon insignitus*

○ literature records
 ● literature + new records
 ● new records

0 50 km

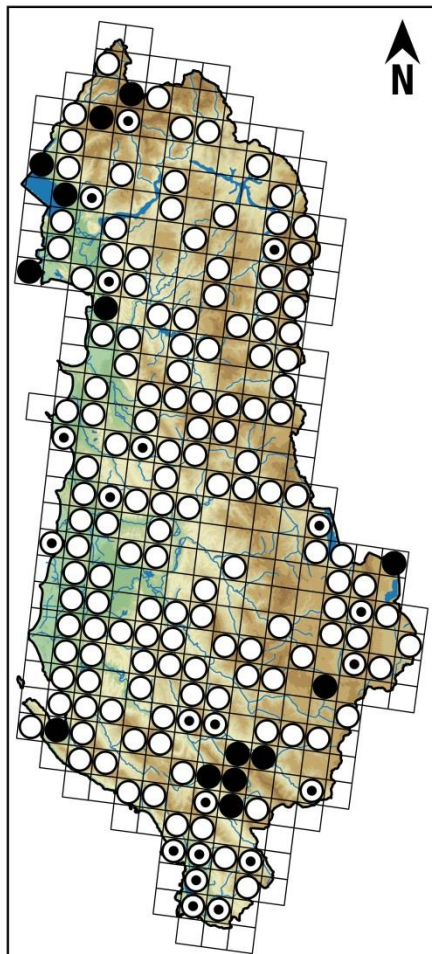


Fig. S27. *Natrix natrix*

○ literature records
 ● literature + new records
 ● new records

0 50 km

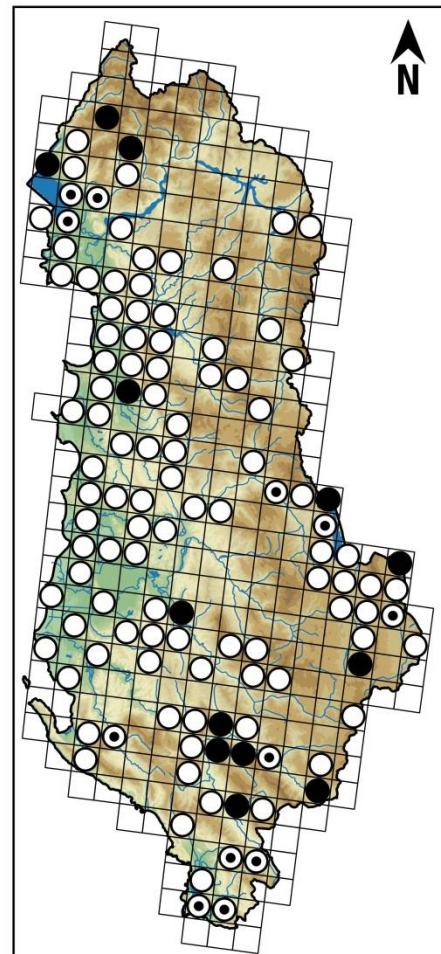


Fig. S28. *Natrix tessellata*

○ literature records
 ● literature + new records
 ● new records

0 50 km

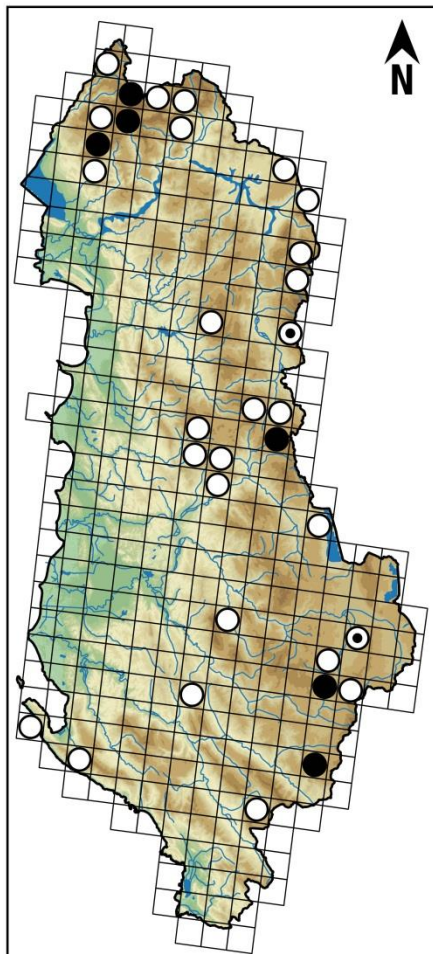


Fig. S29. *Coronella austriaca*

○ literature records
 ● literature + new records
 ● new records

0 50 km

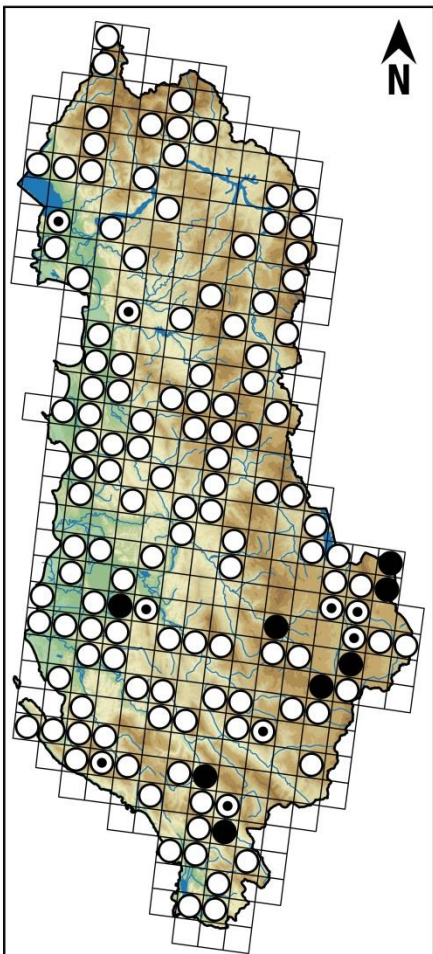


Fig. S30. *Dolichophis caspius*

○ literature records
 ● literature + new records
 ● new records

0 50 km

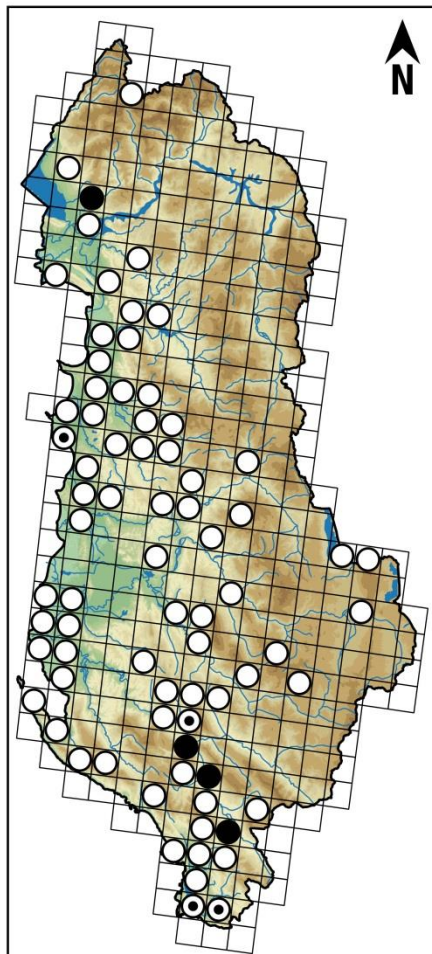


Fig. S31. *Elaphe quatuorlineata*

○ literature records
 ● literature + new records
 ● new records

0 50 km

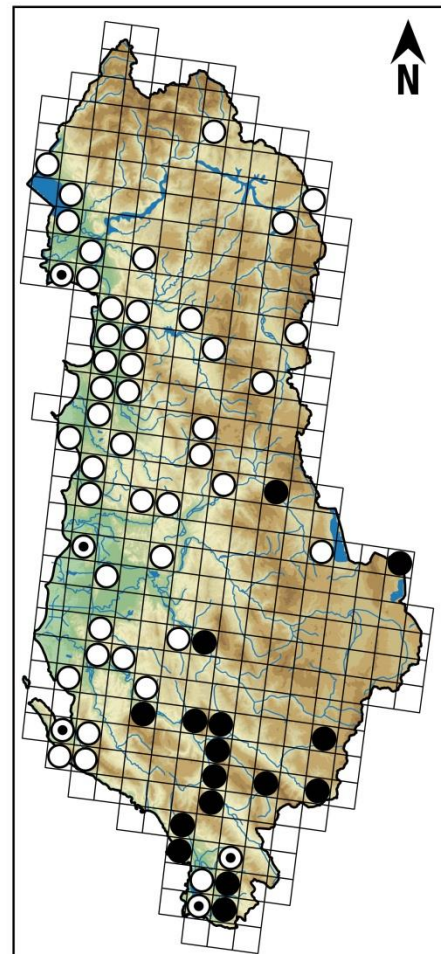


Fig. S32. *Hierophis gemonensis*

○ literature records
 ● literature + new records
 ● new records

0 50 km

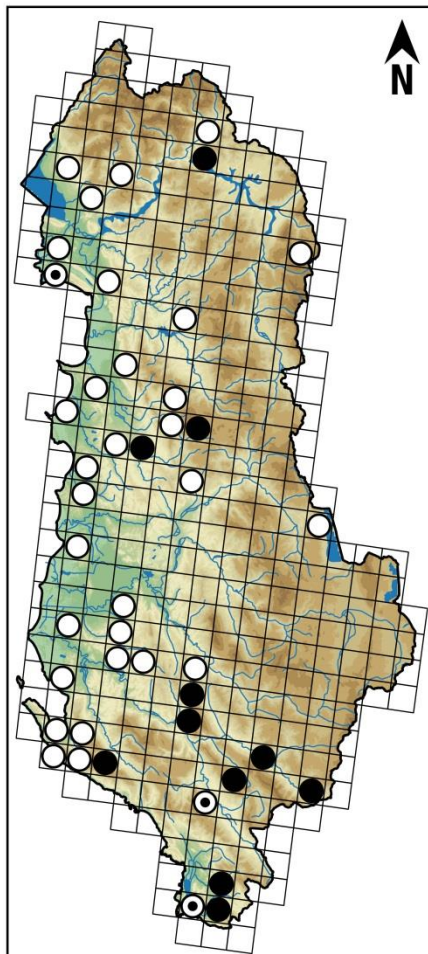


Fig. S33. *Platyceps najadum*

○ literature records
 ● literature + new records
 ● new records

0 50 km

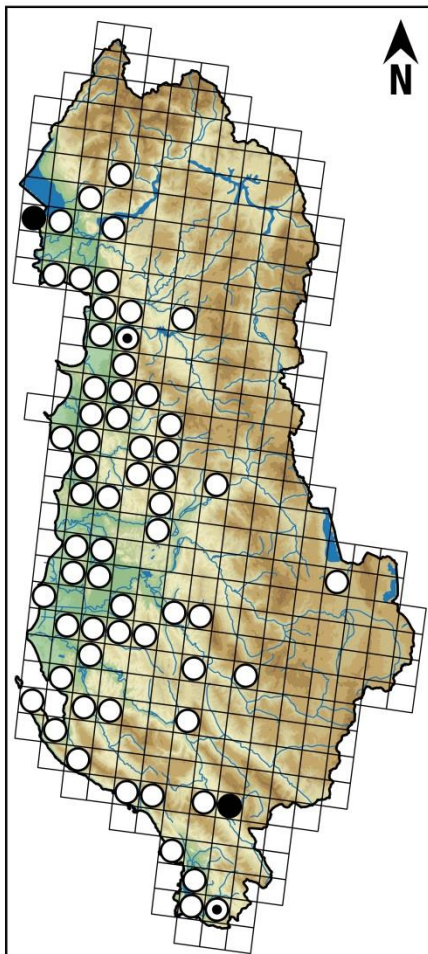


Fig. S34. *Telescopus fallax*

○ literature records
 ● literature + new records
 ● new records

0 50 km

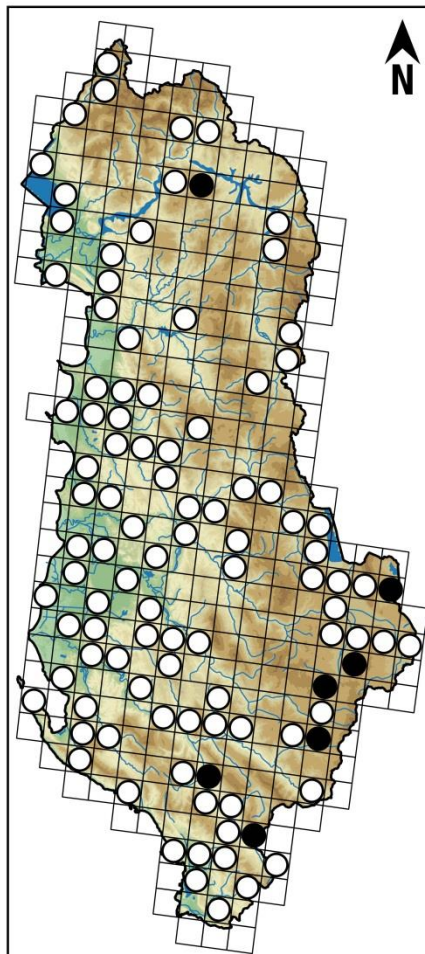


Fig. S35. *Zamenis longissimus*

○ literature records
 ● literature + new records
 ● new records

0 50 km

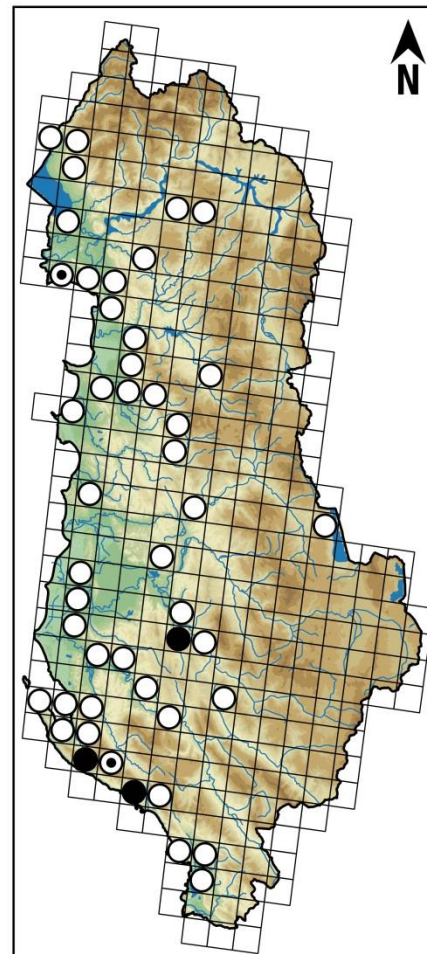


Fig. S36. *Zamenis situla*

○ literature records
 ● literature + new records
 ● new records

0 50 km

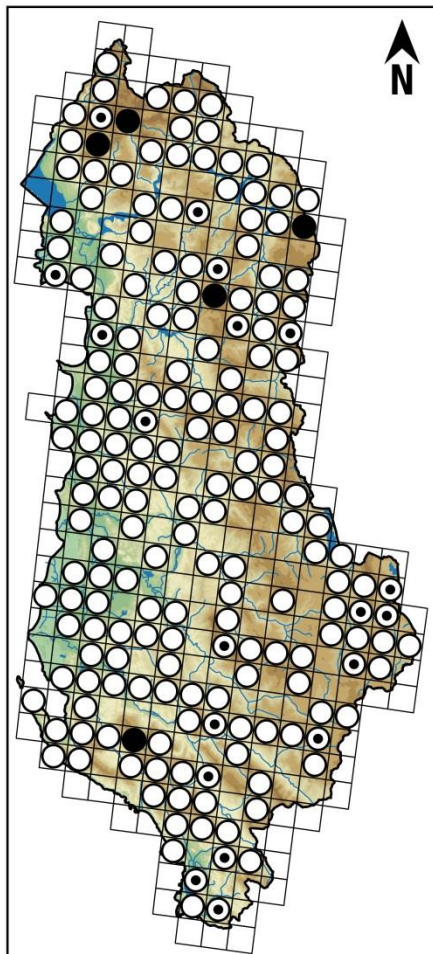


Fig. S37. *Vipera ammodytes*

○ literature records
 ● literature + new records
 ● new records

0 50 km

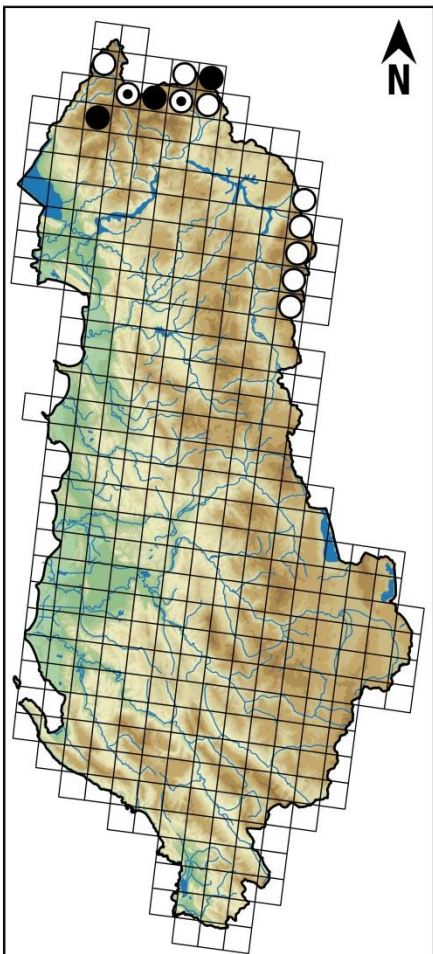


Fig. S38. *Vipera berus*

○ literature records
 ● literature + new records
 ● new records

0 50 km

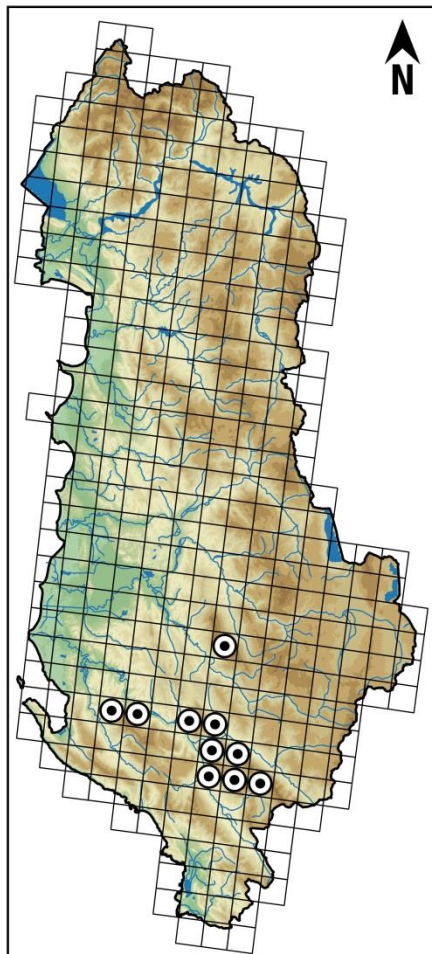


Fig. S39. *Vipera graeca*

○ literature records
 ● literature + new records
 ● new records

0 50 km

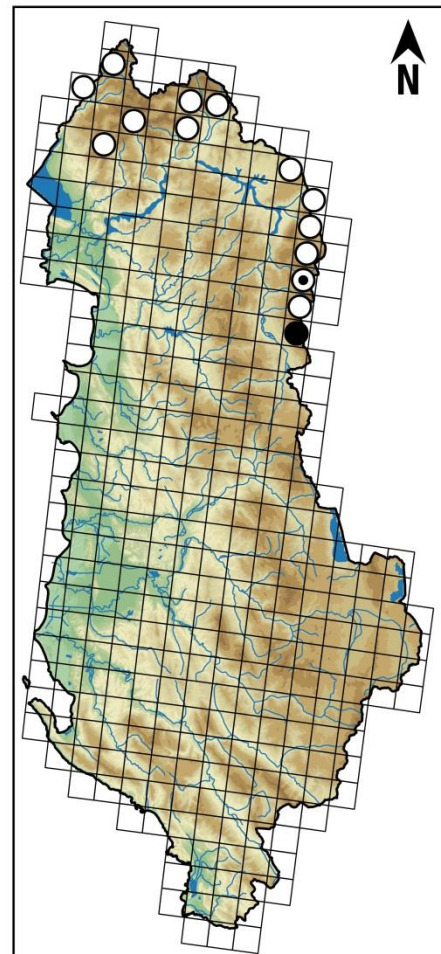


Fig. S40. *Vipera ursinii*

○ literature records
 ● literature + new records
 ● new records

0 50 km