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Distribution and diversity of amphibians in Albania: new data and foundations of a comprehensive database

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Full title: Distribution and diversity of amphibians in Albania: new data and foundations of a comprehensive database

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Key words: Balkan Peninsula, range, species richness, biogeography, BIOCLIM, GLMM

Introduction

Exploration and understanding the spatial distribution of biodiversity are one of the principal objectives of ecology (Gaston, 2000). Mapping species distributions and diversity also is a prime objective and tool in conservation (Pimm and Jenkins, 2005). However, the collection of records is often spatially biased, even in Europe.

Globally, amphibians are considered as one of the most threatened groups of animals (Gibbons et al., 2000, Alroy, 2015), where almost half of the species are declining (Stuart et al., 2004). The rapid decline of amphibians is explained by several factors such as fragmentation, degradation and complete loss of their habitats, global climate change, rapidly spreading diseases and synergies between these threats (Cushman, 2006; Sodhi et al., 2008). Rare species with restricted ranges and small populations are more likely to decline and to be affected by extinction risk (Harnik, Simpson and Payne, 2012). Moreover, some of amphibian species/endemic phylogenetic lineages are better adapted to past refugial regions and can survive better there than in current post-glacial ranges (Dufresnes and Perrin, 2015). Thus, information on species occurrences and their ranges are of key importance for conservation.

Albania is located in the western part of the Balkan Peninsula and is part of the Mediterranean hotspot of biodiversity (Griffiths, Kryštufek and Reed, 2004; Myers, 2000). The country covers 28,748 km^2 with an altitudinal range from sea level to 2764 meters. Collection of faunistic data on amphibians started in the early 20th century (Kopstein and Wettstein, 1920; Werner, 1920). This was followed by a long period when sampling lost its intensity until the next review on amphibians was published in the mid-nineties (Haxhiu, 1994). However, these data are more modest than those for reptiles from the same period (see Haxhiu, 1998; Jablonski, 2011; Mizsei et al., in press). After amphibians came into the spotlight of conservation from the early 1990s due to their rapid decline and after the former isolationist political system ended in Albania in 1992, the number of records on amphibian species from Albania started to increase again in the early 21th century. However, many of these records remained unpublished in scientific papers.

Related mainly to the north-south orientation of Albania, the country covers the distribution of a wide range of amphibian species occurring in the Balkan Peninsula. Moreover, despite its small area, Albania has a rather high geomorphological variety and highly varied topography, for example, 70% of its terrain is mountainous (Fig 1). These conditions, along with a favourable Mediterranean climate led to the formation of a diverse pool of amphibian species (Pabijan et al., 2015). Landscape topography is primarily explained by orogenic processes affecting Albania and its surrounding areas as a consequence of the collision of the Adria microplate with the Eurasian plate. During the last stage of the Neotectonic Pliocene-Quaternary period, from the Middle Pleistocene to the present times, local episodes of subsidence in Albania induced the formation of graben lakes such as Shkodra, Ohrid and Prespa, and the development of Quaternary graben plains (Aliaj, Baldassare and Shkupi, 2001). This land evolution, in combination with the later relative stability of the Mediterranean climate resulting from little influence of Pleistocene glaciations, led to allopatric speciation and differentiation of amphibians. There are strong indications that some of the Miocene-Pliocene speciation centres or Pleistocene glacial refugia of amphibians (and other taxa with limited dispersal ability) were located inside or in close to the current territory of Albania (Médail and Diadema, 2009). The Western Balkan is home to two endemic species of water frogs (Pelophylax epeiroticus, P. shqipericus), one endemic brown frog (Rana graeca), one endemic crested newt (Triturus macedonicus) and smooth newt (Lissotriton graecus) which are also part of the Albanian amphibian fauna (Sillero et al., 2014a; Pabijan et al., 2015; 2016). However, detailed data on the genetic diversity of amphibian species in Albania are still lacking. Current coastal and freshwater ecosystems include rivers, streams, lakes, swamps, estuaries, lagoons or drainage channels and all these represent suitable habitats for amphibians. To date, 16 species of amphibians have been detected in Albania (Haxhiu, 1994; Szabolcs and Mizsei, in press). Mainly due to the southern location and the landscape- and habitat-scale heterogeneity of Albania, this number of species is higher than in many other European countries covering a larger area (Haxhiu, 1994). Therefore, this region has central importance in understanding both the past and present patterns of amphibian diversity in Europe, which thus warrants a synthesis and an update of the current knowledge on amphibian species of the country.

The aims of our study were (i) to fill gaps in our knowledge on the distribution of amphibian species in Albania by collecting occurrence records from previous literature and supplementing them by our recently collected data into a single georeferenced database, (ii) to present up-to-date distribution maps for each species, and (iii) to analyse patterns in species diversity in order to find hotspots of amphibian diversity and to identify environmental factors explaining the distribution of amphibians in Albania. This study is complementary to our previous study on the distribution and diversity of reptiles in Albania (Mizsei et al., in press).

Materials and Methods

Data collection and processing

We used five sources of data to collate our database on the occurrences of amphibians in Albania. First, we collected records by searching the primary literature for studies and reports of amphibian species in Albania. Whenever it was possible, we georeferenced published maps in Quantum GIS 1.8.0 using the GDAL plugin (Bruno, 1989) or used the original field-collected coordinates (as in Bringsøe, 2011; Jablonski, 2011; Recuero et al., 2012; Pabijan et al., 2015; Szabolcs and Mizsei, in press). If maps or coordinates were not available (as in Kopstein and Wettstein, 1920; Werner, 1920; Frommhold, 1962; Schneider and Haxhiu, 1994; Haxhiu, 1994; 2000a; 2000b; 2000c; 2000d; Farkas and Búzás, 1997; Ragghianti et al., 1999; Haxhiu and Vrenozi, 2009; Shehu et al., 2009; Oruçi, 2010; Aliko et al., 2012; Denoël et al., 2012; Guignard et al., 2012; Aliko, Biba & Sula, 2013; Aliko, Qirjo & Nuna, 2014; Shkurti, 2013), we identified localities given in the studies using Google Earth 7.1.8, Google Maps (http://maps.google.com), the GeoNames database (http://geonames.org) and various other websites and blogs. Second, we processed records from the amphibian collection of the Hungarian Natural History Museum. Third, we added records from the Global Biodiversity Information Facility (GBIF, http://gbif.org, which includes records from several museums), iNaturalist (http://inaturalist.org) and TrekNature (http://treknature.com) databases with the permission of the data providers. Fourth, we obtained records from fellow scientists and citizen herpetologists with extensive knowledge of Albanian amphibians. The internet forum called Fieldherping.eu (http:// fieldherping.eu) was a major source to contact these experts. Fifth, we added our own unpublished data collected in a total of 21 expeditions to Albania. Most of these expeditions were conducted as part of studies on the Greek Meadow Viper (*Vipera graeca*, Mizsei et al. 2016), but we also visited areas from where we found no information in the above four sources during these trips to search for amphibians. We stored all records in point shapefiles in a GIS database.

For species treatment, we used the most up-to-date nomenclature and taxonomy from Sillero et al. (2014a) and Speybroeck et al. (2016). Three species from the frog genus *Pelophylax* (*P. epeiroticus*, *P. ridibundus* and *P. shqipericus*) are difficult to identify based on external morphological characters, use similar habitats and are known to hybridise with each other. Although most of the *Pelophylax* species can be distinguished based acoustically (Schneider and Haxhiu, 1994, Lukanov, Tzankov & Simeonovska-Nikolova, 2015) we did not have this information in most cases, thus we merged these three species into

Pelophylax spp. to avoid the possibility of sampling bias to any of the three species (see e.g. Mester et al., 2015). According to recent taxonomical changes it seems that two species occur in Albania from the genus Bufotes (Özdemir et al., 2014). Because we could not differentiate them in the field we merged them under the name B. viridis/variabilis. We used the name Lissotriton graecus instead of L. vulgaris because recent molecular analyses are indicating the species status of this Balkan lineage (Pabijan et al., 2016).

For spatial visualisation and analyses, we aggregated point records into a 10×10 km grid system provided by the European Environmental Agency (http:/eea.europa.eu/data-and-maps/data/eea-reference-grids) in ETRS89 Lamberth Azimuthal Equal Area projection (EPSG: 3035). To identify the elevation of the localities in order to determine the altitudinal range of the species, we used the Shuttle Radar Topographic Mission (SRTM) 90-m Digital Elevation Database 4.1 (Jarvis et al., 2008). We also noted the year for every record.

Spatial analyses

Spatial autocorrelation among the records of the dataset and bias due to spatially uneven sampling are common biases in point occurrence data (Rocchini et al., 2011). We tested for spatial autocorrelation in the number of records per cell using the global Moran's I spatial statistic. This statistic tests the null hypothesis that the occurrence records are evenly distributed against the alternative hypothesis that the records are spatially either clustered ($Z > 0$) or dispersed ($Z < 0$). To analyse patterns in sampling bias, we used the Getis Ord Gi* spatial statistic (Ord and Getis, 1995), which informs whether sampling effort is significantly lower (GiZ score <-1.96, coldspot of sampling) or higher (GiZ score > 1.96, hotspot of sampling) than expected by chance. We used ESRI ArcGIS 10.0 in these analyses.

We calculated Shannon diversity for each 10×10 km cell and then visualised the occurrences of the species within the cells. Additionally, we calculated the Extent of Occurrence (EOO) for each species as the number by fitting a Minimum Convex Polygon to their point records and then dissected it with the territory of Albania to obtain the Albanian range of each species.

Environmental data and linear modelling

We obtained information on several environmental variables to test which factors correlate with patterns in amphibian presence/absence and diversity (Table 1). First, we obtained data on 19 Bioclim variables from the WorldClim database (Hijmans et al., 2005). We then applied a principal component analysis to extract four principal components, which explained 99% of the total variance. Second, to characterise habitat diversity, we calculated the Shannon-diversity of CORINE Land Cover (250 m resolution; European Environmental Agency) in each cell using the LecoS 1.9.8 plugin in QGIS (Jung, 2012). Third, to characterise elevation and altitudinal variation within the cells, we calculated the mean and standard deviation (S.D.) of altitude within each 10×10 km cell based on grid values of the Shuttle Radar Topographic Mission (SRTM) 90-m Digital Elevation Database 4.1 (Jarvis et al., 2008) using Zonal Statistics in QGIS 2.12. Finally, we calculated the distance between the centroid of each cell and the closest point to the sea shore using the NNJoin 1.2.2 plugin in QGIS.

To evaluate the effects of environmental variables on amphibian presence/absence, we applied a model selection approach by fitting generalized linear mixed models (GLMM) with binomial error distribution (Pinheiro and Bates, 2000) using the lme4 package in the R environment (R Core Team, 2015). We ran models for all possible combinations of the environmental variables. To evaluate the relation between Shannon diversity and environmental predictors, we fitted a GLMM using the Markov chain Monte Carlo (MCMC) routine of the MCMCglmm package with its default parameters (Hadfield, 2010). To control for spatial autocorrelation, we specified cell ID as a random factor, and to control for sampling bias, we included GiZ scores as a random factor in both modelling approaches. To minimise the influence of phylogenetic relatedness of the species, we included species ID nested in order as an additional random factor in the GLMM for amphibian presence.

After model selection, we calculated the relative importance of environmental predictors using model-comparison techniques in an information-theoretic framework (Burnham and Anderson, 2002). In the first step, we obtained the values of Akaike's information criterion corrected (AICc) for small sample sizes, 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) representing the relative likelihood of a model. 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 ($\Delta i = AICi - AICmin < 2.0$) (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 3.3.2 statistical computing environment (R Core Team, 2015). Model fitting and selection were performed applying the MuMIn package (Barton, 2011).

Results

Distributional evaluation

We collected a total of N = 1097 amphibian occurrence records. The earliest records were from 1920, and the rate of collection was slow until the mid-20th century (Fig. 2). After 1962, the number of records started to increase, with one large peak in 1994 (Haxhiu, 1994). Nearly half of the total number of occurrence records (N = 555) are published here for the first time, while the other half (N = 542) were published previously (Table 2, Fig. 3a). Of the unpublished records, we collected a total of N = 482 records during our expeditions, N = 18 from museum collection, N = 8 from internet sources and added N = 47 records from personal communication. The number of records ranged from three in the case of Pelobates syriacus to 339 in Pelophylax spp. For most species, half or nearly half of the records were unpublished, and we had at least one unpublished record for all species (except P. syriacus) (Table 2). In the database, P. syriacus was also the rarest species, present in only one grid cell, while Pelophylax spp. was the most widely distributed taxon, present in 181 grid cells. At least one species of amphibian occurred in 238 of the 349 grid cells covering Albania. Measurement of the EOO revealed that many species with only a few records had much larger possible range than expected. For instance, Lissotriton graecus was present in 47 or Rana graeca in 43 cells, however, their EOO was close to the total area of the country.

Amphibian diversity patterns

According to Global Moran's I spatial statistics, overall sampling effort in Albania was spatially clustered ($Z = 4.064$, $P < 0.0001$). Although Getis Ord Gi* statistics did not reveal coldspots of sampling effort, sampling hotspots were found (Fig. 3b), mostly in the Prokletije Mountains (Mts.), the vicinity of Ohrid and Prespa Lakes, Pindos Mts., coastal regions near Vlorë and around Butrint Lake in the south (Fig. 3c).

The mean number of species per cell was 1.8 ± (S.E.) 0.11, with a maximum of N = 10 in two cells. Cells with high amphibian diversity occurred in Prokletije Mts., Lura and Korab Mts., vicinity of Ohrid and Prespa Lakes, Grammos Mts., Çikës Mts. and coastal regions near Vlorë (Fig. 3c). Distribution maps of amphibians of Albania are presented in the Supplementary material S1-S16.

Most amphibians had a large altitudinal range between sea level to above 1500 m a. s. l., with the exception of a few, mostly mountain-dwelling species (e. g. Salamandra atra, Rana temporaria) which had lower sample sizes and/or narrower ranges (Fig. 4). GLMM models showed that the most important predictors for amphibian presence and diversity were land cover diversity (CORINE DIV) and precipitation (BIO PC2), whereas temperature variation (BIO PC3) was important for amphibian presence only (Table 3). Each of these variables was part of at least one of the best models for presence and diversity (Table 4). Model-averaged parameter estimates suggested that CORINE DIV (land cover diversity), BIO PC2 (precipitation) and BIO PC3 (temperature variation) significantly influenced amphibian presence, whereas diversity was influenced only by CORINE DIV (Table 5). The effect of CORINE DIV was positive for both presence and diversity, whereas that of BIO PC2 was negative for presence (Table 5, Fig. 5).

Discussion

Our study presents a spatially explicit database containing the largest amount of amphibian records from Albania to date and a fine-scale analysis of patterns in amphibian occurrence and diversity involving all known species in the country.

The relatively low species richness in many cells indicates that most of the country is still data deficient (Fig. 3b). Amphibian biodiversity hotspots were found where sampling effort was higher than average (i.e., in protected areas or popular tourist destinations such as Theth and Prespa National Parks, Butrint World Heritage Site). These results are similar to those of Cogălniceanu et al. (2013) from Romania, a country also characterized by uneven sampling mainly due to high altitudinal complexity and uneven road density. Because amphibian species richness per cell was relatively low in our study (c.f. mean number of species per cell: 1.68), rare species exerted a large impact on the designation of amphibian hotspots. Among them we found Pelobates syriacus which reaches its westernmost distribution in a single cell in the southeast (Szabolcs & Mizsei, in press), and montane species Ichthyosaura alpestris, Rana temporaria and S. atra with a relatively restricted altitudinal distribution (Table 1; Fig.4). These results imply that the low number of records for some rare species cannot be expanded by further sampling due to biogeographic constraints determining their range (Bruno, 1989). Although we found no evidence of sampling coldspots and the altitudinal distribution of records corresponded well with the frequency distribution of altitudinal values of Albania (Fig. 4), it was clear from the generally low species richness that there is a need to add more data on the occurrences of species other than these rare specialists.

The temporal distribution of our records showed that data collection was almost halted during the Communist era (1946-1992), then restarted during the 1990s, and more recently it has yielded an unprecedented amount of records. This corresponds to the abandonment of the political and economic isolation of the previous regime, which also resulted in higher standards of living and a dynamically growing GDP (http://imf.org). However, economic development also leads to the abandonment of traditional land uses and an increasing rate of habitat alterations, both of which usually have a negative impact on amphibian diversity (Scribner et al., 2001; Hartel et al., 2009). Examples are shown by an increasing number of road constructions and large-scale hydropower projects for example in the valleys of Vjosë or Valbona rivers (Freyhof, 2010; http://balkanrivers.net), which may lead to the devastation of important wetland habitats (Cushman, 2006).

Our analysis of the data currently available showed that the diversity of land cover was the most important factor affecting both the occurrence and the diversity of amphibian species in Albania. These results agree well with those of several previous landscape-scale studies (e.g. Van Buskirk, 2005; Denoël and Ficetola, 2008; Hartel et al., 2009; Vági et al., 2013) and can be explained by two mutually non-exclusive hypotheses. First, most amphibians are characterised by a complex life cycle and they use different environments during their larval and adult life, thus, most species are expected to require complex habitats. Second, those species which use aquatic habitats all year round even as adults can mainly spread along aquatic habitats (Ficetola and De

Bernardi, 2004), thus their occurrence is primarily related to local hydrological factors rather than to climate or land use and they can occur under various climatic conditions and land use types. Indeed, in our study, the species with the largest amount of records were Pelophylax spp. and Bombina variegata (Table 2.). Both of these anurans are associated with freshwater habitats all year round (Arnold and Ovenden, 2002). The relatively large number of records for these two species can also be explained by their high detectability: these anurans are frequent in several types of waters due to their wide ecological tolerance, are often active in daylight, and calling males can be easily detected acoustically even in the hottest summer months due to their prolonged breeding season (Arnold and Ovenden, 2002). All these factors can lead to sampling bias in mapping surveys (Cogălniceanu et al., 2013).

In contrast, other amphibians are mostly terrestrial throughout the year, are often active only in rainy and moist weather, mainly at night, thus are more difficult to detect in the field. These terrestrial, but still widespread species can be characterized by a large, country-wide EOO often with a wide altitudinal range, even if they were detected only in a small fraction of cells. Species in this group included Bufo bufo, Bufotes viridis/variabilis, Hyla arborea, Lissotriton graecus, Rana dalmatina and Triturus macedonicus (Table 2.). Two other species, Rana graeca and Salamandra salamandra also showed large EOO because these species are mostly associated to mountain habitats, and can thus be widespread in Albania (Table 2.). Adequate sampling of these species requires surveys during the breeding season in spring, when most amphibians stay in and around water bodies all day. The detection probability of individuals in various life stages can be further increased by a combination of newt traps, dip-netting and visual or acoustic surveys (Ficetola and De Bernardi, 2004; Van Buskirk, 2005; Mattfeldt, 2007; Vági et al., 2013; Mester et al., 2015).

We did not distinguish between the three *Pelophylax* species occurring in Albania, as they are hard to identify based only on morphological characters. *P. ridibundus* is capable of hybridisation with the two other species (Schneider and Haxhiu, 1994; Ragghianti et al., 1999; 2004) which also makes their identification difficult. *P. epeiroticus* is found between the extreme south-western Albania to southern Greece along the Ionian coast and is genetically related to *P. ridibundus* (Lymberakis et al., 2007). *P. shqipericus* lives in southern Montenegro from Lake Shkodra to Vlora Bay in western Albania along the Adriatic coast. This species is genetically related to *P. lessonae* (Ragghianti et al., 2004). *P. ridibundus* has a country-wide distribution and is common in the Balkans and Europe (Sillero et al., 2014a). The latter species may co-occur with the two former ones although we found no evidence for habitat overlap between the three species. Little is known about the ecology of the two Balkan species and their coexistence with *P. ridibundus*, therefore, further research is highly necessary as both are threatened with extinction. IUCN Red List category of *P. epeiroticus* is Vulnerable (Uzzell, Lymberakis & Haxhiu, 2009) and of *P. shqipericus* is Endangered (Uzzell and Crnobrnja-Isailović, 2009).

Besides habitat alteration (loss, fragmentation, degradation), other threats to amphibians include climate change and spread of diseases. Climate change can alter the amount and distribution of precipitation, which was among the most important factors governing amphibian occurrences (Table 5). Finally, the chytrid fungus *Batrachochytrium dendrobatidis* (Fisher, Garner and Walker, 2009) has been also detected in eight species of Albanian amphibians (Vojar et al., 2017), although we are not aware about any outbreak of the disease chytridiomycosis in the East Mediterranean. In conclusion, a detailed assessment of the distribution of amphibian species and diversity and an evaluation of the efficiency of protected and properly managed areas is urgently needed in Albania. We hope that our work will be an important starting point toward this aim. To facilitate future work, the spatially explicit database and methodological approaches presented here provide important baseline information. Our results can be integrated to larger databases such as the NA2RE – New Atlas of Amphibians and Reptiles of Europe (Sillero et al., 2014a; 2014b; http://na2re.ismai.pt).

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Table 1.Environmental variables used in this 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	Shannon diversity of CORINE Land cover in 10×10 km cells	European Environment Agency
ALT MEAN	Mean of altitude values in 10×10 km cells, calculated from the SRTM near 90 m data	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

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

Species	**Total records**	**Published records**	**Unpublished records**	**N of presence 10×10 km cells**	**EOO (km^2)**	**Distribution type**
Bombina variegata	136	46	90	67	24457	Southern-European
Bufo bufo	70	27	43	50	25977	European
Bufotes viridis/variabilis	96	36	60	53	25945	Turano-Europeo-Mediterranean
Hyla arborea	48	26	22	33	21559	Europeo-Mediterranean
Ichthyosaura alpestris	63	43	20	31	12047	European
Lissotriton graecus	55	34	21	47	25065	European
Pelobates syriacus	3	3	0	1	1	Eastern-Mediterranean
Pelophylax spp.	399	221	178	181	26010	Eurasian
Pelophylax epeiroticus	8	5	3	6	597	Eastern-Mediterranean
Pelophylax ridibundus	59	54	5	41	23735	Turano-European
Pelophylax shqipericus	25	21	5	19	7028	Eastern-Mediterranean
Rana dalmatina	54	28	27	35	22938	Southern-European
Rana graeca	69	16	53	43	23250	Eastern-Mediterranean
Rana temporaria	16	15	1	14	6536	European
Salamandra atra	6	2	4	3	335	Central-European
Salamandra salamandra	42	31	11	40	24424	Europeo-Mediterranean
Triturus macedonicus	39	14	25	29	21279	Eastern-Mediterranean
Total	**1097**	**539**	**558**	**238**		

Table 3.Predictor importance in the two GLMM models.

Presence		**Shannon diversity**	
Predictor	**Importance**	**Predictor**	**Importance**
CORINE DIV	1.000	CORINE DIV	1.000
BIO PC2	0.903	BIO PC2	0.427
BIO PC3	0.756	BIO PC4	0.291
BIO PC1	0.217	ALT SD	0.181
SEA DIST	0.204	ALT MEAN	0.087
ALT SD	0.122	BIO PC3	0.069
ALT MEAN	0.095	SEA DIST	0.000
BIO PC4	0.000	BIO PC1	0.000

Table 4.Parameter estimates and AIC values of the best (ΔAICc< 2) GLMM models fitted on the presence and diversity of amphibians in Albania.

Variable	**Model**	**CORINE DIV**	**BIO PC2**	**BIO PC3**	**BIO PC1**	**SEA DIST**	**ALT SD**	**ALT MEAN**	**BIO PC4**	**df**	**AICc**	**ΔAICc**
Presence	1	1.37504	-0.08859	-0.10412						8	2890.266	0.000
	2	1.29567	-0.08835							7	2891.487	1.222
	3	1.38543	-0.09603	-0.10198			0.00052			9	2891.656	1.391
	4	1.37858	-0.14665		0.08909	-0.00001				9	2891.834	1.568
	5	1.38769	-0.08935	-0.10471	0.01423					9	2891.945	1.679
	6	1.35787		-0.10515						7	2892.121	1.856
	7	1.38320	-0.08723	-0.10331				0.00006		9	2892.161	1.896
	8	1.37949	-0.08434	-0.11082		0.00000				9	2892.204	1.939
Diversity	1	0.31683								4	632.902	0.000
	2	0.31918	-0.02937							5	633.056	0.154
	3	0.32254							-0.04277	5	633.357	0.455
	4	0.32408	-0.03133						-0.04564	6	633.641	0.739
	5	0.29448	-0.03213				0.00037			6	634.041	1.139
	6	0.32376						0.00008		5	634.095	1.193
	7	0.29240					0.00032			5	634.563	1.661
	8	0.33340		-0.02531						5	634.663	1.761

Table 5.Model averaged parameter estimates of GLMM fitted on amphibian presence and MCMCglmm fitted on Shannon diversity of amphibians. Significant parameter estimates are indicated in bold.

Response	**Main effect**	**Estimate**	**S.E.**	**z value**	**P**
Presence	(Intercept)	-5.172	0.804	6.428	0.000
	CORINE DIV	**1.367**	**0.227**	**6.015**	**0.000**
	BIO PC2	**-0.096**	**0.046**	**2.093**	**0.036**
	BIO PC3	-0.105	0.053	1.982	0.047
	BIO PC1	0.053	0.049	1.072	0.284
	SEA DIST	0.000	0.000	0.766	0.444
	ALT SD	0.001	0.000	1.109	0.267
	ALT MEAN	0.000	0.000	0.326	0.745
	BIO PC4	0.000	0.000	-0.191	0.848

Response	**Main effect**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**P**
Diversity	(Intercept)	0.224	-0.636	1.001	0.558
	CORINE DIV	**0.325**	**0.175**	**0.495**	**0.001**
	BIO PC2	-0.048	-0.101	0.004	0.078
	BIO PC4	-0.056	-0.145	0.028	0.228
	ALT SD	0.000	-0.001	0.001	0.772
	ALT MEAN	0.000	-0.001	0.000	0.606
	BIO PC3	-0.001	-0.069	0.063	0.962
	SEA DIST	0.000	0.000	0.000	0.474
	BIO PC1	0.037	-0.046	0.108	0.302

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

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).

Figure 3. Sources of occurrence records of amphibian species used in the present study (A), sampling hotspots (GiZ score > 1.0) and coldspots (GiZ score < -1.0) (B), and amphibian species richness (numbers) and Shannon diversity (shading) (C) in Albania on a 10×10 km grid.

Figure 4. Altitudinal distribution of amphibian 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). Grey line (red in the colour version) is the frequency distribution of altitudinal values in Albania.

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).

Figure1bw

Click here to download Figure Fig-1_bw.jpg

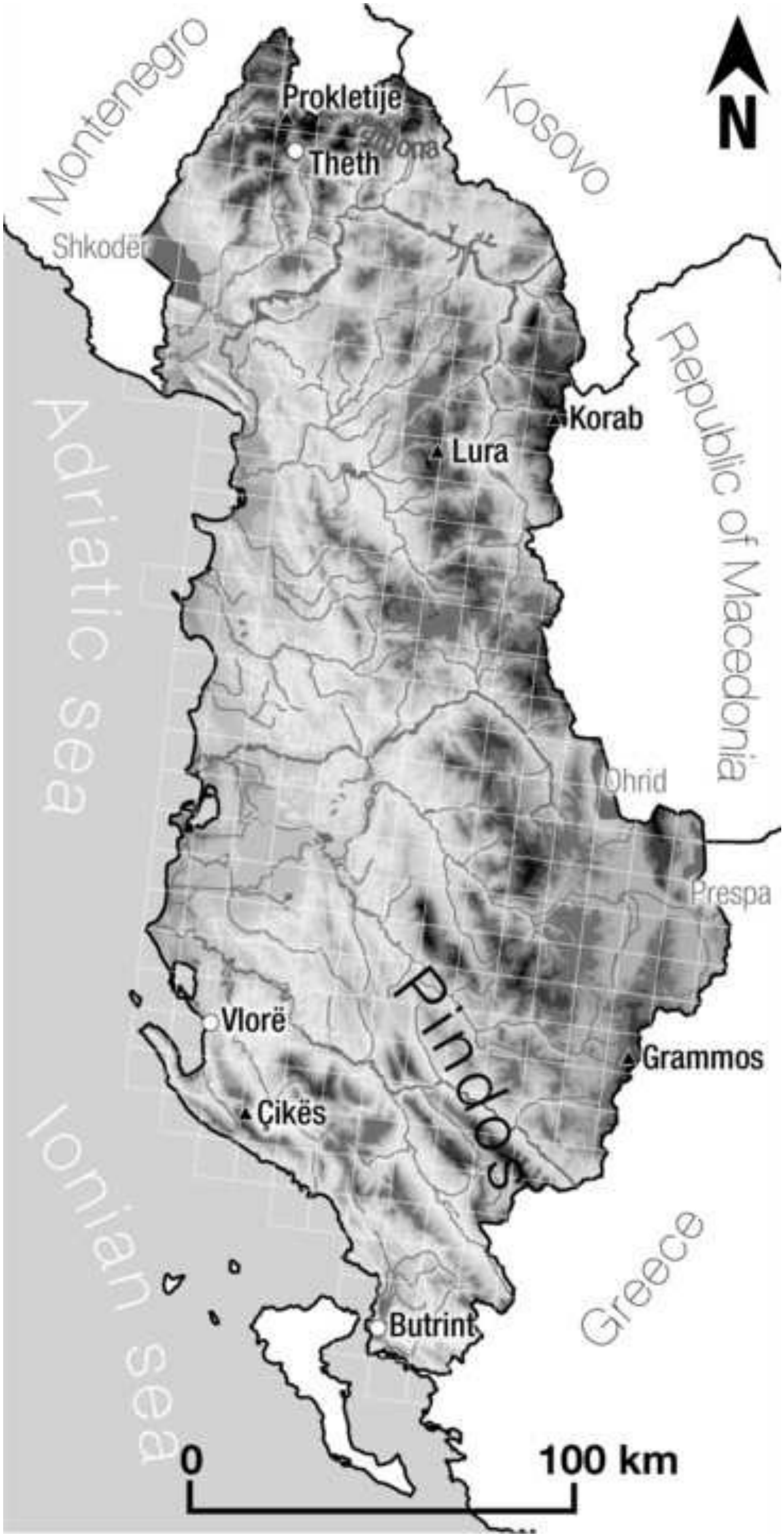

Figure1col

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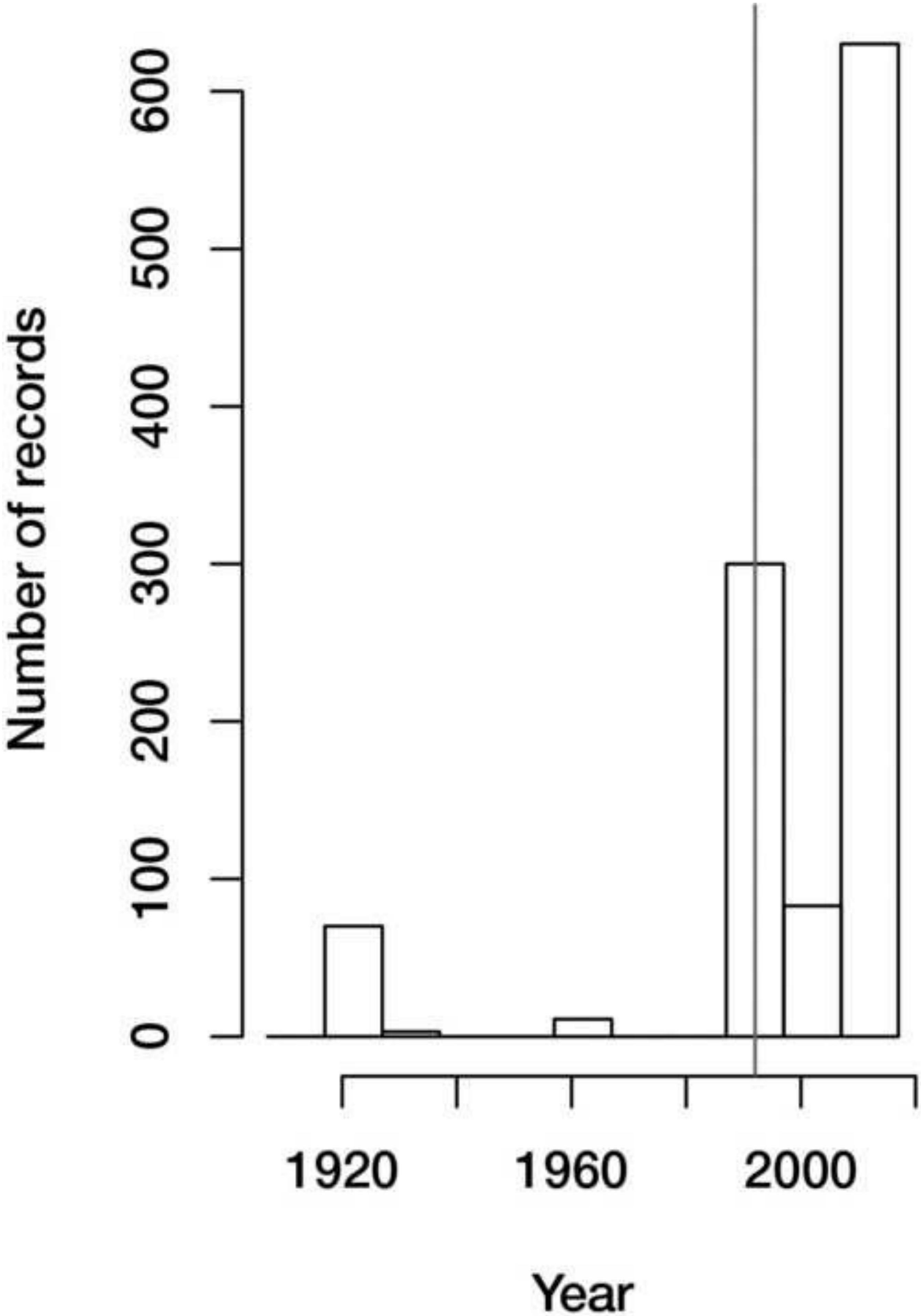

Number of records
0
100
200
300
400
500
600
1920
1960
2000
Year

Figure2col

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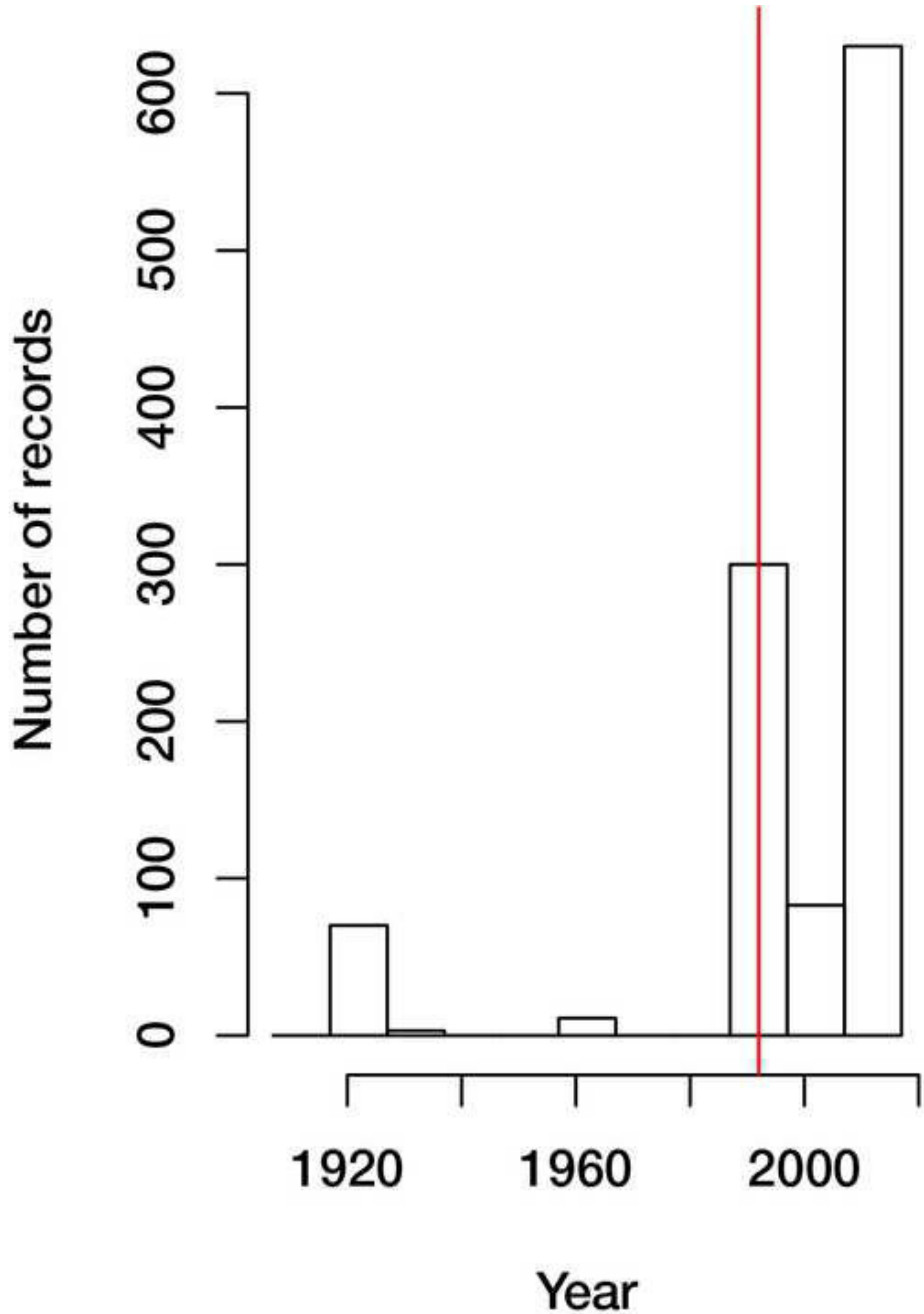

Figure3bw

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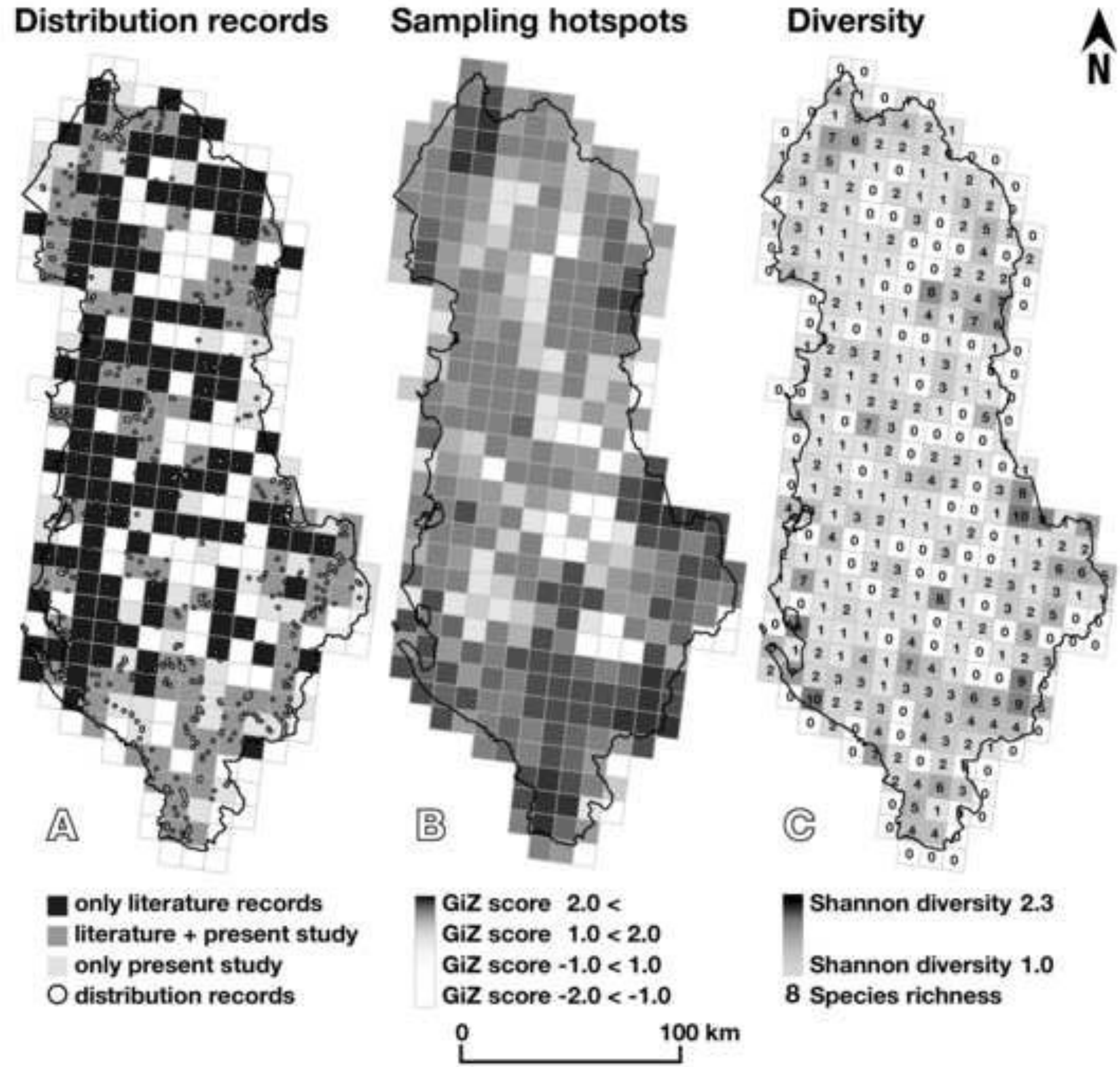

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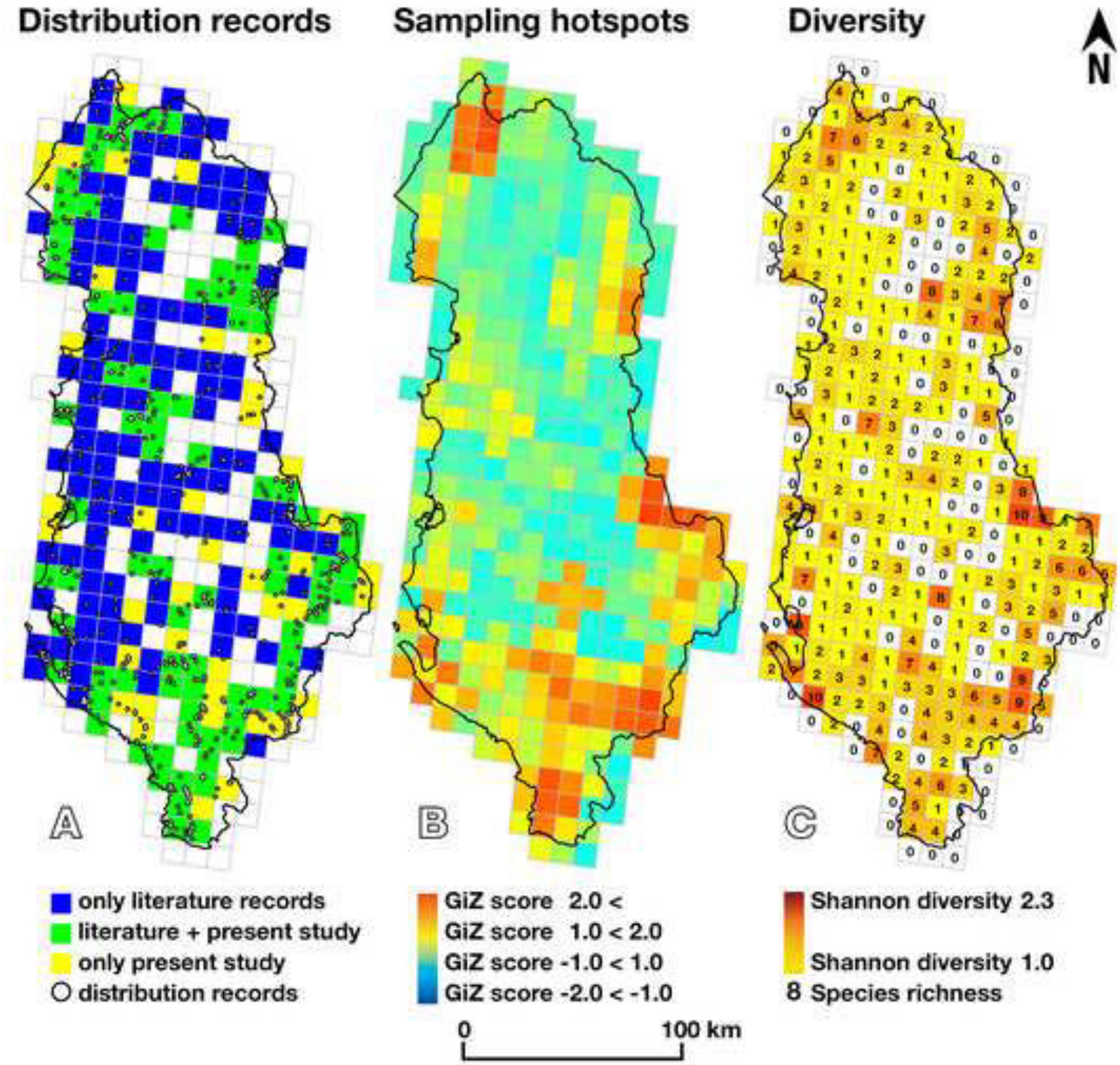

Figure4bw

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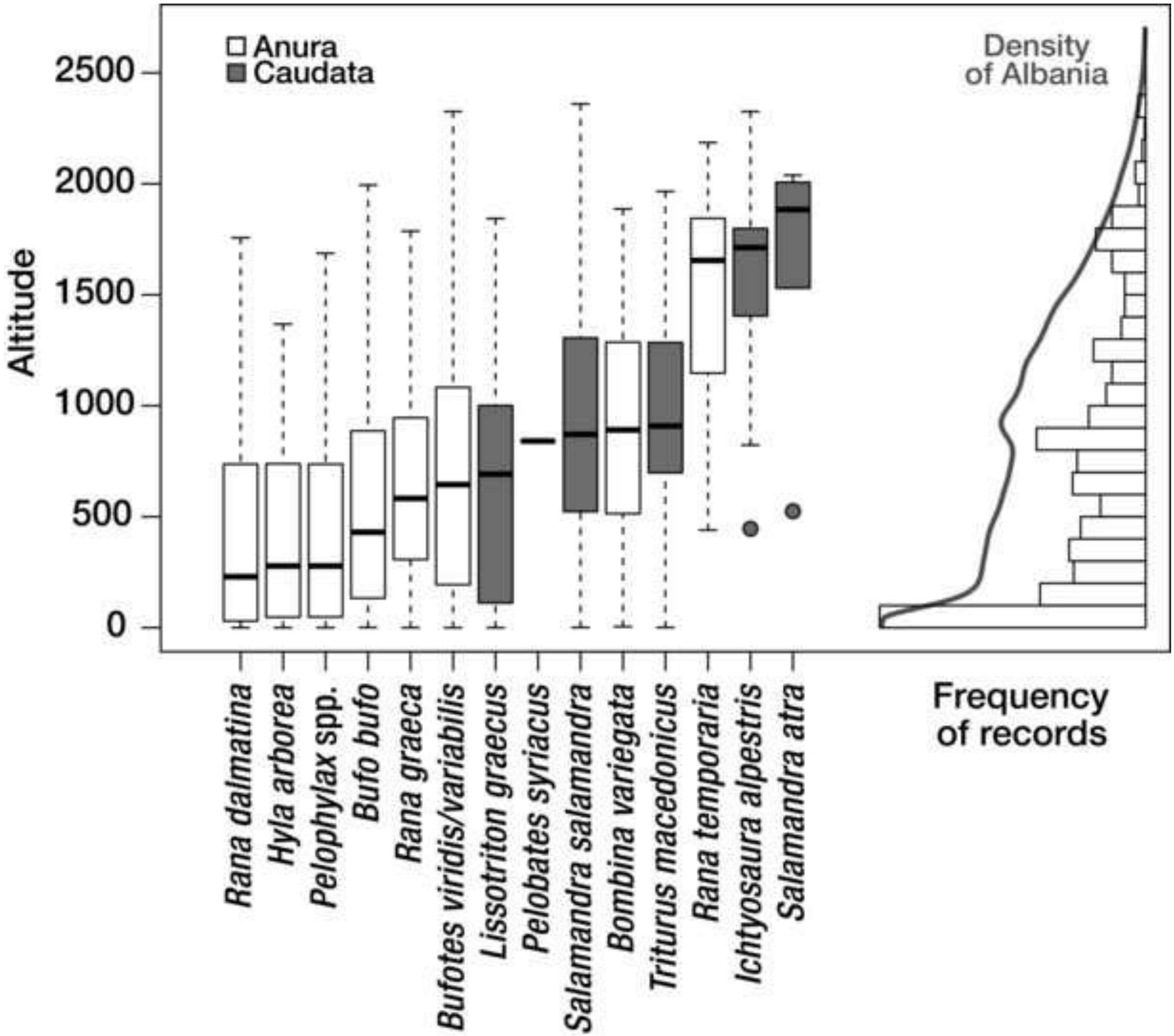

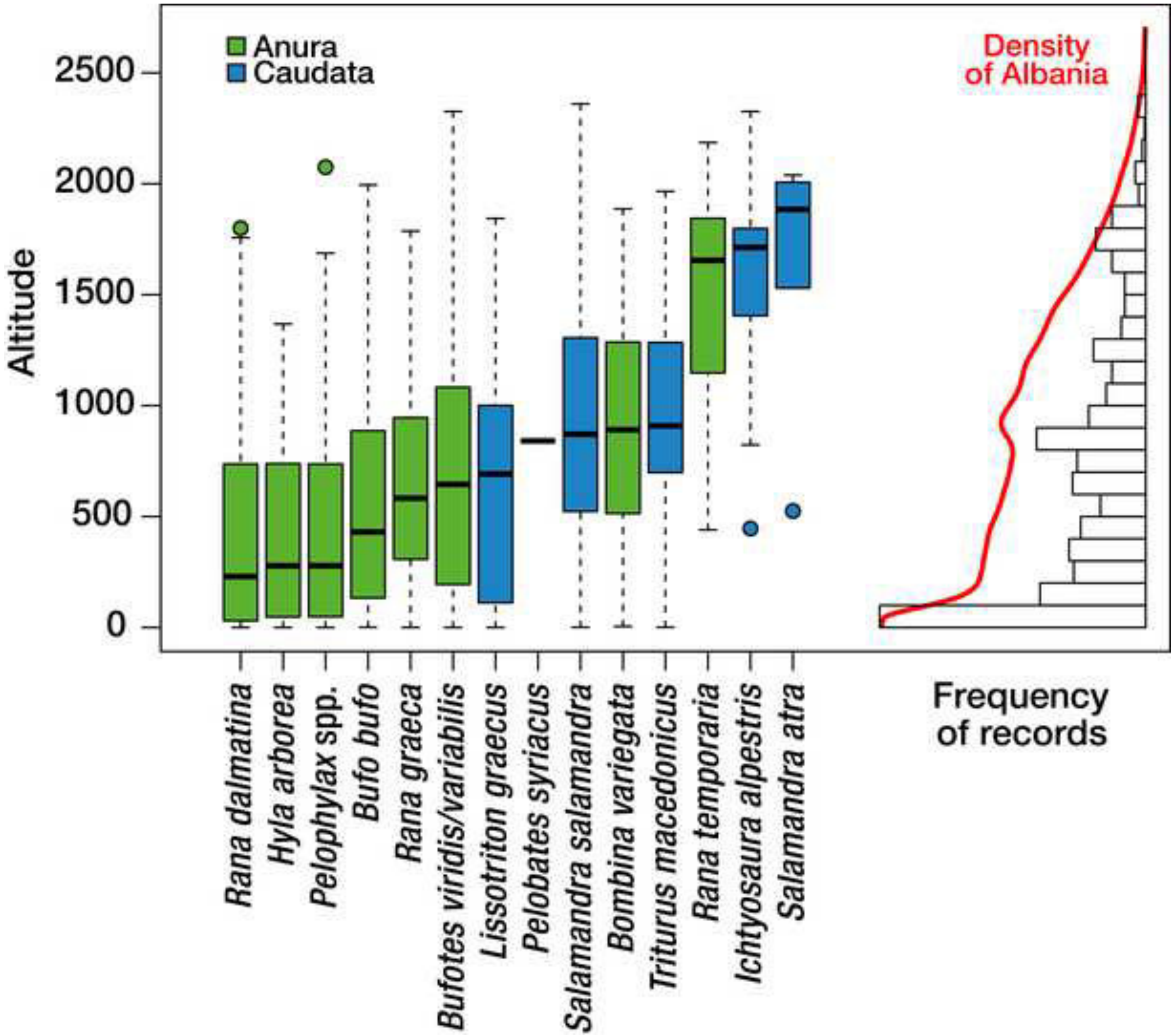
Anura
Caudata
Density
of Albania
Altitude
2500
2000
1500
1000
500
0
Rana dalmatina
Hyla arborea
Pelophylax spp.
Bufo bufo
Rana graeca
Bufotes viridis/variabilis
Lissotriton graecus
Pelobates syriacus
Salamandra salamandra
Bombina variegata
Triturus macedonicus
Rana temporaria
Ichtyosaura alpestris
Salamandra atra
Frequency
of records

Figure5

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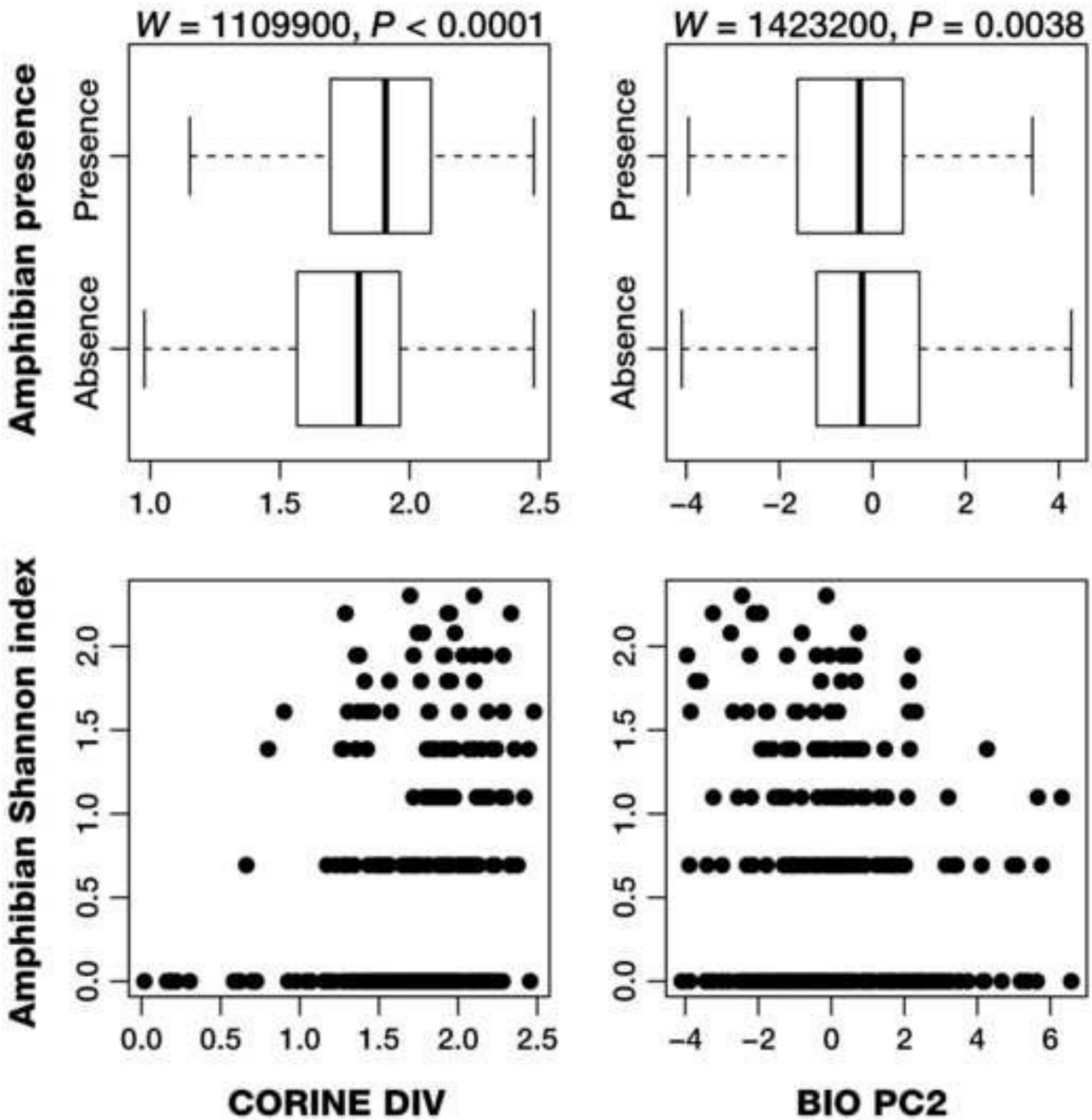

Supplementary File