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Species diversity and distribution of lizards in Montenegro

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Abstract. The southern part of Montenegro has been identified as an area with high diversity of herpetofauna. However, comprehensive studies of distribution and diversity patterns of reptiles on the country level are still missing. Such studies are essential in designating areas of special conservation importance and nature protection planning in a milieu of increased habitat loss and degradation due to rapid urbanization and tourism development in this small Mediterranean country. To make progress on this problem, we analyzed distribution and diversity patterns of the lizards in Montenegro using a large database consisting of literature data and our unpublished records. We found that fifteen lizard species inhabit Montenegro, and two additional species may be present. The lizards were most diverse in the Maritime biogeographic region of Montenegro, while low diversity was found predominantly along the state borders in the Mountain-valley region. The identified pattern of lizard diversity is at least partly influenced by sampling bias. The eastern mountainous subregion had a distinct species composition compared to all other parts of the country. The East-Mediterranean chorotype was the most dominant, represented by seven species. The great diversity of the lizard fauna of Montenegro can be attributed to its specific topographic position with great influence of Mediterranean climate, heterogeneity of biomes, complex geological history and diverse physiogeographic features. High lizard species richness in the Maritime region and a unique species composition in the eastern subregion of Montenegro indicate that these areas are of high conservation interest.

Keywords. Balkan Peninsula, distribution pattern, Lacertilia, species richness.

INTRODUCTION

The number of studies of herpetofaunal distribution and diversity patterns in the Balkan countries has increased over the last decade (Jablonski et al., 2012; Cogălniceanu et al., 2013; Tomović et al., 2014; Sterijovski et al., 2014; Uhrin et al., 2016; Mizsei et al., 2017). They have been driven not only by the creation of large distributional databases resulting from intensive biodiversity surveys for conservation purposes (such as implementation of the Natura 2000 network, preparation of national Red Lists and books of threatened species) and/or research of particular taxa, but also by the recognition that basic biogeographical studies have gained increased significance in ecological, evolutionary and systematic research (e.g., Jetz et al., 2011; Zachos and Habel, 2011). Such studies are especially important in areas of high conservation concern such as the Balkans, one of the main European centers of endemism and speciation within some herpetofaunal taxa (Džukić and Kalezić, 2004).

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The southern part of Montenegro lies within the Mediterranean belt, one of the globally recognized biodiversity hotspots (Myers et al., 2000). It has also been identified as an area of high concentration of reptile species (Crnobrnja-Isailović and Džukić, 1995; Džukić and Kalezić, 2004; Sillero et al., 2014). This has been further confirmed through studies on reptile distribution, intraspecific differentiation and speciation events in this area (Böhme et al., 2007; Ljubisavljević et al., 2007; Polović and Ljubisavljević, 2010; Polović and Čađenović, 2014; Jablonski et al., 2016). However, despite the evident importance of herpetofaunal diversity of Montenegro, there have been no comprehensive and detailed studies of distribution and diversity patterns of reptile species for the country as a whole.

The need for such studies is increasing due to newly described or discovered lizards in Montenegro (Ljubisavljević et al., 2007; Vergilov et al., 2016), recent nomenclatural (Sillero et al., 2014) and taxonomic changes (Jablonski et al., 2016; Marzahn et al., 2016) and the necessity of updating the national list of protected species and preparation of the Red Book of threatened species, bearing in mind the growing negative influence of habitat loss and degradation in recent years (Bataković et al., 2014).

In order to make progress and respond to these needs, we here present all available distribution data for lizards in Montenegro and analyze their patterns of diversity. In doing so, we provide the first zoogeographical analysis of the most numerous reptile group in this country. In this way, our study presents a starting point for the consideration of the distribution and diversity of all reptiles in the territory of Montenegro.

MATERIAL AND METHODS

Study group

Lizards (Squamata: Lacertilia) comprise over 6000 species worldwide, with over 80 species in Europe. Thirty-six of these (belonging to six families) occur on the Balkan Peninsula and adjacent islands (excluding Crete) (Speybroeck et al., 2016). The lizards of the Balkans are quite diverse in terms of morphology and lifestyle. They include small to large taxa, normal-legged (true lizards), tiny-legged (e.g., *Ablepharus kitaibelii*) and legless forms (slow worms), diurnal to nocturnal species (geckos), and those with conspicuous or rather cryptic behavior (e.g., most skinks and slow worms). There are ground-dwelling (e.g., *Lacerta agilis* and *Zootoca vivipara*), saxicoulous (e.g., *Dalmatolacerta oxycephala* and *Dinarolacerta* spp.) to semi-arboreal lizards (e.g., green lizards) with oviparous (e.g., wall and green lizards) and viviparous reproductive modes (e.g., *Z. vivipara)*.

Study area

Montenegro is located in the west-central part of the Balkan Peninsula, bounded by the Adriatic Sea to the south and Dinaric Mountains to the north. The total land area of Montenegro is 13,812 km^2. Marković (1970) divided the territory of Montenegro into two main regions (Maritime and Mountain-valley) and six subregions (Fig. 1). The Maritime region is divided into Mediterranean and sub-Mediterranean subregions. The Mediterranean subregion of Montenegro is narrow coastal area (2–10 km wide), separated from the hinterland by the steep Dinaric Mountains (Orjen, Lovćen, Sutorman and Rumija). It is characterized by a typical Mediterranean climate with hot dry summers and mild wet winters (Matvejev, 1961). The sub-Mediterranean part of Montenegro includes valleys of the Zeta River and Skadar Lake, hilly areas in the western and central parts of the country and is bordered by high coastal mountains to the south. The climate in this subregion is modified Mediterranean with somewhat cooler and moister winters and long, dry and hot summers. The Mountain-valley region is divided into central, eastern, northern and western subregions according to geographic position. The Mountain-valley region is dominated by medium to high mountains intersected by deep canyons of the Tara and Piva Rivers in the northern subregion, the Morača River in the central and the valley of the Lim River in the eastern subregion. The western subregion is a largely high

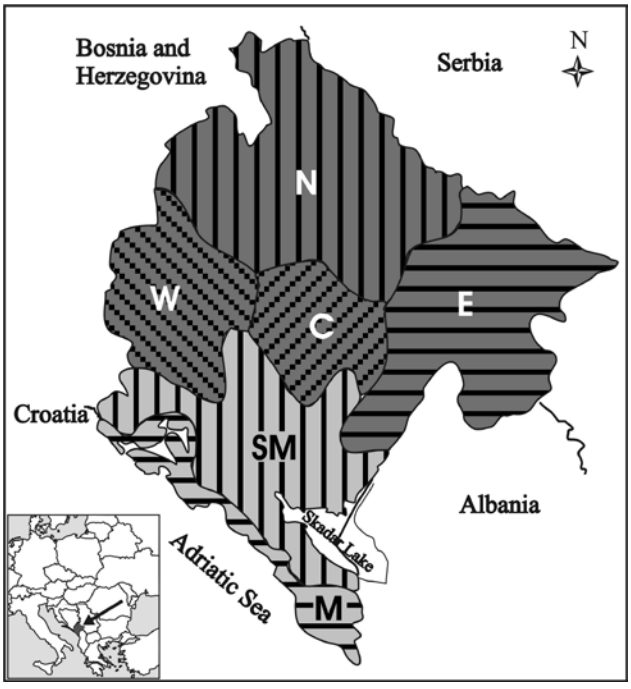

Fig. 1. Geographical regions and subregions of Montenegro (according to Stešević and Caković, 2013 and Vuksanović et al., 2016). Maritime region (in light grey) with Mediterranean (M) and sub-Mediterranean (SM) subregions. Mountain-valley region (in dark grey) with western (W), central (C), eastern (E) and northern (N) subregions.

dry karst area with scarce surface water bodies. The temperate continental climate in the Mountain-valley region, characterized by warm to hot summers and very cold winters, is often modified under the influence of high altitudes (mountain climate of the alpine type with short wet summers and long, cold snowy winters) or Mediterranean influence that spreads along the river canyons, gorges and valleys far inland (modified continental climate with milder winters) (Stevanović and Stevanović, 1995).

Methods

The dataset of locations in Montenegro where lizards were recorded consists of 1284 entries. The records were sorted by the year of observation (unpublished records), or the year of publication (literature records), and characterized as old or recent according to whether they were published/observed before or after 1990. This year was chosen in accordance with other similar studies of the Balkan herpetofauna (Cogălniceanu et al., 2013; Mizsei et al., 2017), and because more intense and systematic surveys of herpetofauna in certain areas of the country started after 1990.

The majority of our records were collected during field surveys in the last decade as results of independent projects or sub-projects on lizards (see Acknowledgements). A number of unpublished records came from the field databases of Dr. Miloš Kalezić, Dr. Georg Džukić and late prof. Dr. Gojko Pasuljević. All species were identified according to standard herpetological literature by visual inspection of diagnostic characters (Arnold and Ovenden, 2002). Regarding taxonomy and current nomenclature, we followed Sillero et al. (2014) and Speybroeck et al. (2016). Accordingly, *Anguis fragilis* and *A. graeca* were treated as a species complex, because the distinction between these two taxa and their precise distribution in Montenegro require further research (Sillero et al., 2014; Jablonski et al., 2016). The distinct lineages of *Lacerta viridis-bilineata* complex which, according to the newest study (Marzahn et al., 2016), occur in the Western Balkans including Montenegro but have not been taxonomically evaluated, were treated as *Lacerta viridis* complex following Marzahn et al. (2016) and Mizsei et al. (2017). The distributions of two species with doubtful old records (*Tarentola mauritanica* and *Podarcis tauricus*), the presence of which has not been confirmed during recent decades, are presented in Table 1 and Supplementary material, but excluded from further biogeographic analyses. The geographic distribution of every lizard species in Montenegro was presented on the country map overlain by a 10 × 10 km UTM (Universal Transverse Mercator) grid (see Figs. S3-S7). Doubtful findings were marked with a question mark (?). All georeferences are based on the WGS84 datum. The database includes the following locality information: site name, coordinates in decimal degrees, 10 × 10 km UTM square and data source type (see Table S1). A general distribution map of lizards in Montenegro (see Fig. S2 and supplementary data file) was constructed using the free DIVA-GIS 7.5.0 software (Hijmans et al., 2012), based on relationship between species records and the UTM 10 x 10 km grid using the grid cell code as a common attribute (Cogălniceanu et al., 2013).

Similarities among biogeographic subregions of Montenegro were evaluated using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). Chorotypes were determined according to Vigna Taglianti et al. (1999). For the analyses and designation of centres of lizard diversity in Montenegro, we used an application created in Visual Basic 6.1 in the program WinWord 2003 (Niketić, 1999), using the method of Walter and Straka (1970), at National Grid UTM Reference for Montenegro 10 × 10 km.

RESULTS

The dynamics of publications on and data collection for lizards in Montenegro from the end of the 19th century to 2017 are presented in Fig. 2. An increase in field research and publication effort is evident from the 1990s onwards. There were many more records dated after 1990 than before 1990 (Table 1). The majority of the published and unpublished data came from the last seven years, when field survey activities have intensified. The increase in published data during the nineties of the last century may be attributed to the systematic research on the herpetofauna, particularly lizards, of the Skadar Lake region. Unpublished records from the 1970s–1980s came from the unpublished notes of the late Prof. Dr. Pasuljević.

Fifteen lizard species from four families were confirmed to inhabit Montenegro (Table 2). The most diverse group were lacertid lizards (11 species). About 54 % of the UTM 10 × 10 km grid cells that cover the surveyed territory contained only recent records of lizards, 34% contained both old and recent records, whereas only 12 % of them contained only records from surveys performed prior to 1990 (Fig. S1). Roughly 63% of the total national UTM grid cells contained records of at least one lizard

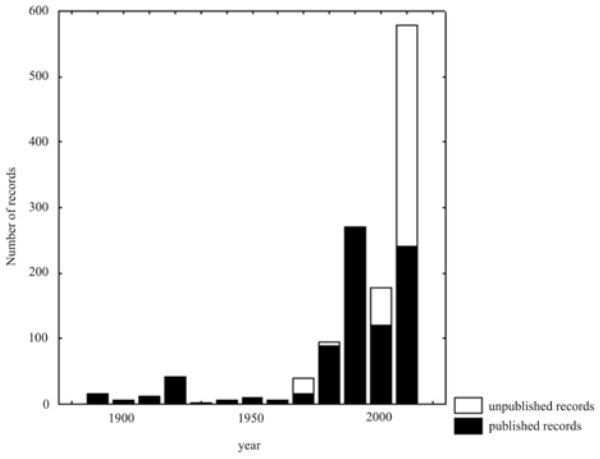

Fig. 2. Number of lizard records in Montenegro by year of collection (unpublished data) or publication (published data).

Table 1. The list of lizard species in Montenegro with number of records. Old and recent records correspond to the publication/collection dates before and after 1990. (*) species with doubtful old records, the presence of which has not been confirmed in recent times.

Species	Total records	Published records	Unpublished records	Old records	Recent records
Hemidactylus turcicus	45	20	25	12	33
*Tarentola mauritanica**	1	1	0	1	0
Algyroides nigropunctatus	44	30	14	4	40
Dalmatolacerta oxycephala	139	99	40	39	100
Dinarolacerta montenegrina	14	13	1	0	14
Dinarolacerta mosorensis	123	119	4	37	86
Lacerta agilis	54	36	18	7	47
Lacerta viridis complex	90	58	32	9	81
Lacerta trilineata	112	66	46	18	94
Podarcis melisellensis	137	72	65	24	113
Podarcis muralis	240	166	74	34	206
*Podarcis tauricus**	2	2	0	2	0
Podarcis siculus	8	8	0	5	3
Zootoca vivipara	22	19	3	7	15
Ablepharus kitaibelii	1	1	0	0	1
Anguis fragilis complex	118	70	48	22	96
Pseudopus apodus	134	77	57	14	120
Total	1284	857	427	235	1049

Table 2. List of confirmed lizard species in Montenegro with endemicity status for the Balkans, marginality and range fragmentation on the territory of Montenegro, extent of their occurrence in subregions, and UTM squares and chorotype classification.

Family	Species	Marginal zone	Balkan endemic	Fragmented range	Subregion	N of UTMs	Chorotype
Gekkonidae	*Hemidactylus turcicus*				M,SM	14	Mediteranean
Lacertidae	*Algyroides nigropunctatus*		+		M,SM,C	22	E-Mediterranean
	Dalmatolacerta oxycephala	+	+		M,SM,C,N,W	40	E-Mediterranean
	Dinarolacerta montenegrina	+	+		E	4	E-Meditrranean
	Dinarolacerta mosorensis	+	+	+	M,SM,C,N,W	21	E-Mediterranean
	Lacerta agilis	+		+	C,E,N,W	21	Euro-Siberian
	Lacerta viridis complex				M,SM,C,E,N,W	39	S-European
	Lacerta trilineata		+		M,SM	31	E-Mediterranean
	Podarcis melisellensis		+		M,SM,W	38	E-Mediterranean
	Podarcis muralis				M,SM,C,E,N,W	70	S-European
	Podarcis siculus	+		?	M	1	S-European
	Zootoca vivipara	+		+	E	9	Euro-Siberian
Scincidae	*Ablepharus kitaibelii*	+		?	E	1	E-Mediterranean
Anguidae	*Anguis fragilis* complex				M,SM,C,E,N,W	45	Euro-Siberian
	Pseudopus apodus				M,SM	38	Turano-Mediterranean

species, of which 22% were located in areas not covered by previously published surveys. Consequently, 37% of the UTM grid cells were without records (Fig. S2).

Only potentially introduced species or those with doubtful records (*Tarentola mauritanica, Podarcis tauricus, P. siculus*) had more old than recent records (Table 1). Nearly all species, with the exception of *Hemidactylus turcicus*, had more published than unpublished records. The species with the highest number of records was *Podarcis muralis* (240), followed by *Dalmatolacerta oxycephala* (139), *Podarcis melisellensis* (137) and *Pseudopus apodus* (134). *Ablepharus kitaibelii* (1), *Dinarolacerta*

montenegrina (14) and *Zootoca vivipara* (22) had the lowest number of records for the confirmed and native species (Table 1).

Almost half of the confirmed species (47%) reaches the edge of their distribution in Montenegro, while 40% of them are endemic to the Balkan Peninsula (Table 2). Most of species that inhabited medium to high-altitude areas of Montenegro (*Dinarolacerta mosorensis, Lacerta agilis* and *Z. vivipara*) had fragmented ranges (Table 2, Figs. S4 and S5). Recent discovery (*A. kitaibelii*) and/or low number of confirmed records (*P. siculus*) precluded evaluation of range fragmentation in these species (Table 2).

Podarcis muralis was the most widely distributed lizard in Montenegro, inhabiting the territory covered by 39% of the national UTM grid cells, followed by *P. melisellensis*, *P. apodus, L. viridis* complex, *D. oxycephala* and *A. fragilis* complex which occurred in 21% to 25% of UTM grid cells (Figs. S4-S7). *Podarcis siculus*, *A. kitaibelii* and *D. montenegrina* were the rarest species, confined to fewer than 3% of the UTM cells covering the Montenegrin territory (Figs. S4, S6 and S7).

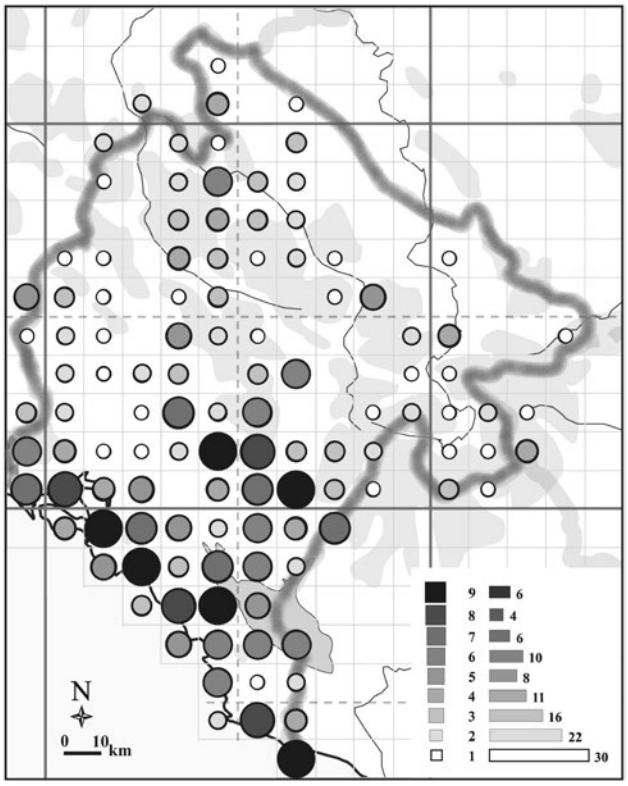

Fig. 3. Diversity of lizard species in Montenegro in the 10 × 10 km UTM grid. Colours and sizes of squares present numbers of lizard species per UTM cell (left-hand side of the legend), and colours and sizes of the rectangles present numbers of UTM squares with corresponding numbers of lizard species (right-hand side of the legend).

The highest numbers of species (eight to nine) were recorded in 10 UTM squares located along the Adriatic coast, in the Skadar Lake region, the Zeta River plain and around the capital of Montenegro (Podgorica). However, a great number of UTM squares (30) contained only one lizard species, while nearly one third of UTM squares that cover the territory of Montenegro were without any records. Most of the squares with no lizard species or low lizard diversity were located in the north-eastern border area and western part of the country (Figs. 3, S1 and S2).

In line with these results, species diversity was greater in the Maritime than in the Mountain-valley region. Mediterranean and sub-Mediterranean subregions were inhabited by 11 and 10 species, respectively, whereas central, eastern and western subregions had seven species each (Table 2). The lowest number of species (six) was found in the northern, high mountain subregion. Three taxa (*L. viridis* complex, *P. muralis* and *A. fragilis* complex) with both wide geographic and altitudinal ranges were distributed in all subregions.

According to our cluster analysis Mediterranean and Sub-Mediterranean subregions were the most similar to one another (Fig. 4). They formed a distinct cluster due to identical composition of 10 lizard species, with only one additional species (*P. siculus*) found in the Mediterranean subregion. Northern, central and western parts of the Mountain-valley region formed another cluster, differing mutually by no more than one species. The eastern subregion was the most distinct due to the presence of three species (*A. kitaibelii*, *D. montenegrina* and *Z. vivipara*) that were not found in other subregions.

The lizards of Montenegro were classified into five chorotypes (Table 2). The most common chorotype was East-Mediterranean, represented by seven species. The Euro-Siberian and South-European chorotypes were rep-

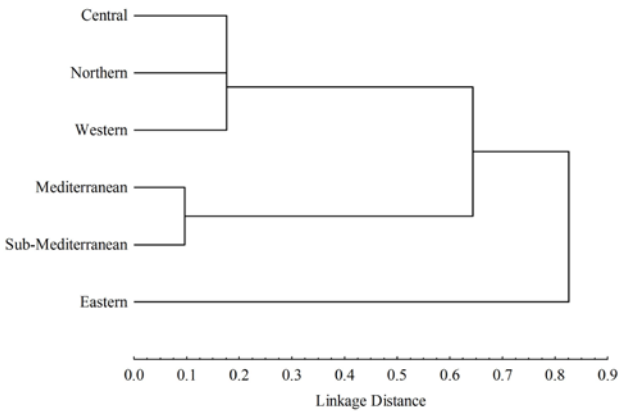

Fig. 4. Cluster diagram of Bray-Curtis similarity index of lizard fauna for biogeographic subregions in Montenegro.

resented with three species each. The rarest chorotypes were Mediterranean and Turano-Mediterranean, represented with one species each.

DISCUSSION

With 15 species confirmed, Montenegro is amongst the countries with the highest diversity of lizards in the Balkans (e.g., Petrov, 2007; Krofel et al., 2009; Jablonski et al., 2012; Cogălniceanu et al., 2013; Sillero et al., 2014; Tomović et al., 2014; Uhrin et al., 2016; Mizsei et al., 2017). Furthermore, 10 recorded species are regional endemics, having marginal ranges in Montenegro or a fragmented range in it (Table 2), contributing to a high potential for further evolutionary diversification of the lizard fauna (Džukić and Kalezić, 2004).

A comparative analysis of the diversity of lacertid lizards among the Balkan countries showed a clear distinction between the western and eastern countries, with Montenegro grouping together with Bosnia and Herzegovina, Croatia and Slovenia within the western Balkan cluster (see Urošević et al., 2015). This pattern remained the same when we included all lizards (results not shown). The lizard fauna of Montenegro is most similar to those of Bosnia and Herzegovina and Croatia, mostly owing to the presence of the western Balkan endemic lacertids *Dalmatolacerta oxycephala* and *Dinarolacerta mosorensis* in these three countries. Actually, the only difference in lizard fauna between Montenegro and Bosnia and Herzegovina is the presence of the endemic *Dinarolacerta montenegrina* in Montenegro. This points out the important impact of landscape features of the Dinaric Mountains in shaping biodiversity of the western Balkans (e.g., Redžić et al., 2011; Ivković and Plant, 2015).

A great diversity of lizard fauna inside the smallest Balkan country can be attributed to its specific geographic position with great influence of Mediterranean climate, heterogeneity of biomes, complex geological history and diverse physiogeographic features ranging from high mountains in the north, through deep river canyons and valleys to the broad plain in the south (Matvejev, 1961; Matvejev and Puncer, 1989). Macroevolutionary events, such as speciation within the genus *Dinarolacerta* (Ljubisavljević et al, 2007), or division of the "mainland clade" of *Dalmatolacerta oxycephala* (Podnar et al., 2014) took place in the Montenegrin mountains. Furthermore, heterogeneous mountain topography and proximity to the Mediterranean were important factors in shaping genetic diversity of two species complexes of lizards, the *L. viridis* complex and the *A. fragilis* complex (Böhme et al., 2007; Jablonski et al, 2016; Marzahn et al., 2016). Marzahn et al. (2016) revealed the existence of two distinct lineages of *L. viridis* complex in Montenegro, while Jablonski et al. (2016) identified contact zones between two lineages of Slow worms (*A. fragilis* complex) in southernmost part of the country.

Although the presence of five chorotypes points out the variability of zoogeographical links, the predominance of Mediterranean chorotypes clearly indicates a dominant influence of the Mediterranean. Higher lizard diversity in areas under the influence of Mediterranean climate is not surprising and is evidenced in other studies of reptile diversity of the Balkan countries (e.g., Jablonski et al., 2012; Urošević et al., 2015; Mizsei et al., 2017).

A great diversity of lizards, and herpetofauna in general, in the Skadar Lake region and coastal zone (Crnobrnja-Isailović and Džukić, 1995; Džukić and Kalezić, 2004; Polović and Ljubisavljević, 2010; Polović and Čađenović, 2014; this study) indicates that these areas are of particular conservation interest, especially bearing in mind the trend of rapid urbanization and development of touristic infrastructure in recent years. Although a wide range of EU policies and legislation which address specific problems evidenced in coastal environments were adopted in Montenegro, their implementation has been slow and represents a significant challenge for future conservation initiatives (Knežević et al., 2015). Furthermore, the presence of some endemic species (*D. montenegrina*) and species with scarce records at the periphery of their distribution (*A. kitaibelii*, *Z. vivipara*) in the eastern mountainous subregion indicate that this area should be also considered during conservation planning.

Observed patterns of lizard diversity in Montenegro could be influenced by the elevational gradient, which is correlated with temperature and mediated by precipitation (McCain, 2010; Mizsei et al., 2017), but also by the so-called "Linnean shortfall" (the knowledge gap of the number of existing species) and "Wallacean shortfall" (incomplete knowledge about the geographical distribution of species, which is usually related to variation in survey effort) (Lomolino, 2004; Hortal et al., 2015). The relatively recent discovery of *D. montenegrina* (Ljubisavljević et al., 2007) and the possible existence of still unidentified or undescribed taxa, e.g., within *L. viridis* complex (Böhme et al., 2007; Marzahn et al., 2016), *A. fragilis* complex (Jablonski et al., 2016) or *D. oxycephala* mainland clade (Podnar et al., 2014), may indicate that lizard diversity is subject to the Linenan shortfall. Large area without lizard distributional data in the Mountain-valley region suggests that this pattern may be also affected by the Wallacean shortfall. For example, UTM squares that cover the areas of Durmitor Mt., Bjelasica Mt. and Krnovo mountain plateau have the highest number of

species in the Mountain-valley region and, at the same time, are hotspots of sampling effort. These mountains have been surveyed frequently during the course of different herpetological studies (Džukić, 1991; Tomović et al., 2004; Polović and Čađenović, 2013).

Nevertheless, considerably higher sampling effort during the recent period has contributed to reduce gaps in the knowledge of the distribution of lizards in Montenegro. New records extended national ranges for many species. The ranges of *L. agilis*, and the *L. viridis* and *A. fragilis* complexes were extended to the east and west, while the ranges of *P. melisellensis* and *P. muralis* were extended to the central and western part of the country. New data also helped to fill in some distribution gaps for *H. turcicus, Algyroides nigropunctatus* and *D. oxycephala*.

Among the confirmed species, only *P. siculus*, represented by the stenoendemic subspecies *P. s. cattaroi* could have anthropochorous origin (Ljubisavljević et al., 2005; Podnar et al., 2005). The Moorish gecko (*T. mauritanica*), a species with a doubtful record in Montenegro (Bruno, 1988), is also easily transported by humans and considered to be introduced to the Adriatic coast and Greece (Krofel et al., 2009; Speybroeck et al., 2016).

Our results showed that distribution gaps still remain for most species, especially in the north-eastern and north-western parts of Montenegro. Survey efforts should be focused on lizards with high conservation concern such as *Dinarolacerta* spp. (Ljubisavljević et al., 2017). Distribution gaps in areas with suitable habitats for at least some of the wide-ranging species (e.g., *L. viridis* complex, *P. muralis*, *A. fragilis* complex) suggest that a scattered distribution pattern is rather a result of a lack of systematic field surveys than a consequence of specific ecological demands. Perhaps the best example of this is the recent discovery of *A. kitaibelii,* a species known from neighboring countries, in eastern Montenegro (Vergilov et al., 2016).

Other species, such as *Mediodactylus kotschyi* and *Podarcis tauricus*, known from border regions of north-western Albania (Haxhiu, 1998; Mizsei et al., 2017), are also likely to be discovered in Montenegro in upcoming years, due to the presence of suitable habitats in south-eastern Montenegro and lack of barriers to dispersal of these species. Furthermore, northern, western and north-eastern areas of Montenegro should be of high priority for future systematic reptile field research.

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SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found at <http://www.unipv.it/webshi/appendix> manuscript number 21327.

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