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Earthworm community structure along altitudinal gradients on the western slopes of Kopaonik Mountain in Serbia

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Abstract: The aim of this study is to examine the altitudinal patterns of earthworm community structure at different habitat types on the western slopes of Kopaonik Mountain. In total, 30 plots between 420 and 1950 m a.s.l. were sampled within two years' fieldwork. Overall, 27 earthworm taxa belonging to 11 genera were found at the study sites. A combination of Pearson's correlation, polynomial regression, and cluster analysis (UPGMA) was used for determining the effects of altitude on the earthworm community structure. The earthworm abundance and species richness monotonically decreased with the increase in altitude, showing a significant negative correlation. Cluster analysis revealed two patterns of earthworm community composition, furthermore, there are taxa with a broad altitudinal range. The mean altitudinal range size of earthworms significantly increased along the altitudinal gradients, indicating that our results support the Rapoport's altitudinal rule. Secondly, we focused on the community of earthworms in different habitat types, analyzing species richness and community composition using nonmetric multidimensional scaling (nMDS) following by analysis of similarity (ANOSIM) and an analysis of similarity percentages (SIMPER). Both altitude and habitat type had strong effects on the community structure of earthworm.

Key words: Abundance, altitudes, earthworm, habitats, Rapoport's altitudinal rule, species richness

1. Introduction

In the early 1800s in the Andes Mountains and in the Southeast Asian islands, von Humbolt, Darwin, and Wallace first recorded nonrandom changes in community parameters along altitudinal and latitudinal gradients (Lomolino, 2001). Later, MacArthur (1972) indicated that there is a link between mountain ecology and the species-area relationship of island biogeography, given the similar conditions (small area, isolation, restricted spatial heterogeneity) of the previously mentioned ecosystems. However, Körner (2000) considered that the mountains are much easier to investigate in terms of scale than in terms of latitudinal bends, and thus suggested investigation of the distribution of biodiversity along altitudinal gradients as a good mediator for understanding distribution patterns along altitudinal gradients.

Two diversity patterns (hump-shaped and monotonic decrease) have been frequently observed along altitudes, but still, there is no unifying theory explaining those patterns. Stevens (1989) described the negative effect of latitude and altitude on species richness and called this phenomenon the Rapoport's rule. The Rapoport's rule was explained as a result of wider ecological tolerance among organisms at a higher altitude, a crucial feature, which they must possess in order to withstand wider climatic fluctuations. Respectively, species richness is higher at low altitudes because species from low altitudes cannot expand their upper limit of altitude range (Brown and Kodric-Brown, 1977). Overall, this rule is one of several species richness theories that explain the monotonic decrease in species richness that occurs as altitudes increase. Accordingly, few studies researched the Rapoport altitudinal rule for arthropods (Kwon et al., 2014; Meléndez-Jaramillo et al., 2019; Matevski et al., 2020). According to Lawton et al. (1987), harshness and unpredictability of the conditions prevailing at higher altitudes contribute to the decreased richness of species and reduction in resource diversity.

In addition to the previously mentioned effect, some studies showed that increased species richness has been observed at mid-altitudes (hump-shaped pattern). Colwell and Hurtt (1994) developed one-dimensional species richness stochastic models to explain the Rapoport's rule but unexpectedly found that the species richness pattern within the given domain produced a hump-shaped curve

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that declines symmetrically from the center towards the edges of the domain. This phenomenon was termed the mid-domain effect. This effect has been observed in land snails (Aubry et al., 2005), spiders (Chatzaki et al., 2005), and amphibian (Khatiwada et al., 2019).

So far, researches on earthworm fauna along the altitudinal gradients were conducted in Australia (Wood, 1974), South America (Gonzalez et al., 2007; Cardoso et al., 2014; González and Lodge, 2017) and Korea (Tsai et al., 2004). Regarding the ecological studies within which earthworm fauna along altitudinal gradients in Europe mountains were researched, they are scarce, mostly limited to the studies of the Alps (Martinucci and Sala, 1979; Salomé et al., 2011), Carpathians (Kasprzak, 1979; Rożen et al., 2013) and the Khibiny Massive (Zenkova and Rapoport, 2013).

In spite of a large number of studies on the community structure and the zoogeographical types of earthworm fauna in the mountains of Europe (Pop et al., 2010; Csuzdi et al., 2011; Stojanović et al., 2013; Popović et al., 2020), altitudinal patterns have not been sufficiently researched. Therefore, this study aims to examine the altitudinal patterns of earthworm community structure (total abundance, species richness, altitudinal range size, zoogeographical composition, and ecological categories) at different habitat types on the western slopes of the Kopaonik Mt. Specifically, we addressed the following questions: What are the patterns of total abundance and species richness along the altitudinal gradients? How altitude affects the zoogeographical composition and ecological categories? Are there Rapoport's altitudinal rules or mid-domain effect? As well as to determine species richness on investigated of habitats and the differences in the composition of the earthworm fauna between the investigated types of habitats.

2. Material and methods

2.1. Study area

The Kopaonik Mt. (43°16'N, 20°49'E) is the largest mountain in Serbia, it is situated between the central and southern part of Serbia and belongs to the Dinaric Mountain range (Figure 1). Geographical position and geomorphological characteristics give this mountain a unique climate, because there are maritime and continental climates. The Kopaonik Mt. is located in the zone which is influenced by the continental and maritime air masses. It is 150–220 km away from the Adriatic Sea and 290–375 km from the Aegean; there is a strong impact on the circulation of the air masses. Regarding the direction and altitude, it represents the climatic boundary between the Mediterranean climate in the southwest and the continental climate in the north and northeast, since it prevents the migration of warmer air masses from the southern part to the north (Smailagić, 1995).

The Kopaonik Mt. has vegetation zones characteristic of the high mountains of the central Balkans, but there is a difference between the northern and the southern slopes of the massif (Mišić and Popović, 1954). According to Mišić and Popović (1954), this mountain has five forest belts: hilly, mountain, high mountain, subalpine, and alpine belts. Likewise, the vertical distribution of pedological soil types on the Kopaonik Mt. mostly coincides with the vertical zonation of vegetation. In the hilly belt up to 800 m, the oak forest dominates (thermophilic oak forest on alluvium), which is where sierozem on serpentines and humus silicate soil on serpentines occurs. From 800 to 1100 m, mesophilic oaks and beech forests occur mainly in brown soils on serpentine and acid brown soil on siliceous rocks. In the mountain belt from 1150 to 1500 m, the dominant are beech, beech and fir, spruce and fir

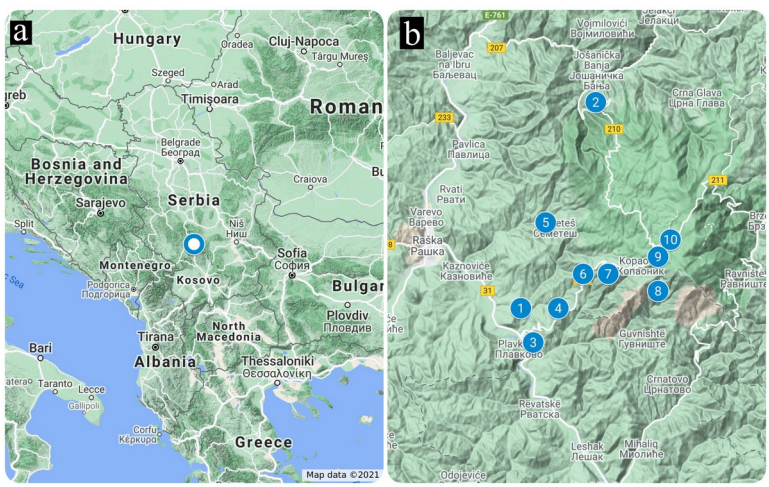


Figure 1. The geographic position of the Kopaonik Mountain on the Balkan Peninsula (a) and map of sampling sites (b) (seen localities in Table 1).

forests, and the soil types that appear are a humus variety of acid brown soil, brown soil on serpentine, and brown soil on limestone. The high mountain belt from 1500 to 1750 m is dominantly a mixed forest consisting of beech, fir and spruce, beech and spruce; the types of soil present are brown podzolic soil and acidic humus-silicate soils. The subalpine belt from 1750 m to 1950 m is comprised of shrubby formations of dwarf juniper and blueberry, with the occurrence of shrubs in spruce forms. In the alpine zone above 1950 m, the occurrence of spruce forests and high mountain pastures is often, while the soil types are brown podzolic soil and humus silicate soil.

2.2. Methods

Earthworm communities were sampled within four months in both 2018 and 2019 (from April to July, coinciding with the rainy season). A total of ten altitudinal transects were set ranging from a minimum of 420 to a maximum of 1950 m a.s.l. Altitude was recorded to the nearest meter by using an altimeter (Sun Altimeter). The transects cover different altitudinal ranges and, overall, they involve four vegetation belts (hilly, mountain, subalpine and alpine). By using land cover data derived from aerial photos and validated in the field, we classified each plot according to five categories of main habitat cover type: forests (oak, beech, spruce), meadows, humid meadows, pastures, and riverbanks. Each altitudinal transect was composed of three sampling units (plots) separated by an altitude range of ca. 200 m, to allow independence of sampled data, for a total of 30 plots. According to the protocol by Zicsi (1958), eight samples of 50 x 50 cm from each sampling unit were taken (plots). Sampling efforts were characterized by two consecutive years of sampling from the foothill to the highest parts of the mountain. In total, 480 samples for two years of fieldwork (Table 1).

The earthworms were sacrificed in 70% ethanol, immediately fixed in 4% formalin solution, and transferred and stored in 90% ethanol. Earthworms were identified to species level and only mature individuals were counted.

Table 1. Schedule of sampling along altitudinal transects for each plot, including species richness and total abundance of individuals.

Sites/altitude	Coordinates	Dates	Plots/abbreviations	Number samples	Taxa	Total number individuals
Rudnica (420 m)	43°14′07″N, 20°41′02″E	6–7 Apr. 2018. 7–8 Apr. 2019.	Meadow (M1), Oak forest (OF1), and Humid meadow (HM1)	48	15	118
Jošanička banja (550 m)	43°21′23″N, 20°45′08″E	27–28 Apr. 2018. 4–5 May 2019.	Meadow (M2), Beech forest (BF1), and River bank (RB1)	48	14	91
Mura (670 m)	43°14′01″N, 20°42′00″E	29–30 Apr. 2018. 7–8 May 2019.	Meadow (M3), Oak forest (OF2), and Humid meadow (HM2)	48	14	91
Novo selo (800 m)	43°14′19″N, 20°42′21″E	9–10 May 2018., 14–15 May 2019.	Meadow (M4), Oak forest (OF3), and Humid meadow (HM3)	48	13	84
Semeteš (1000 m)	43°17′45″N, 20°43′08″E	15–16 May 2018. 27–28 May 2019.	Pasture (P1), Beech forest (BF2), and Humid meadow (HM4)	48	12	73
Lisina (1250 m)	43°16′32″N, 20°45′06″E	3–4 June 2018. 4–5 June 2019.	Pasture (P2), Beech forest (BF3), and River bank (RB2)	48	12	64
Čajetina (1456 m)	43°16′28″N, 20°45′58″E	15–16 June 2018. 19–20 June 2019.	Pasture (P3), River bank (RB3), and Beech forest (BF4)	48	11	58
Treska (1622 m)	43°16′10″N, 20°48′54″E	28–29 June 2018. 4–5 July 2019.	Pasture (P4), Beech forest (BF5), and Beech-Air forest (BAF1)	48	9	50
Rtanj (1750 m)	43°17′26″N, 20°49′12″E	15–16 July 2018. 18–19 July 2019.	River bank (RB4), Pasture (P5), and Spruce forest (SF1)	48	6	40
Marine vode (1950 m)	43°17′34″N, 20°49′06″E	27–28 July 2018. 30–31 July 2019.	River bank (RB5), Spruce-Air forest (SAF1) and Spruce forest (SF2)	48	6	39
Total				480	27	708

Species identification was made according to the complex features provided in Mršić (1991), Csuzdi and Zicsi (2003), and Blakemore (2009). Vouchers were deposited at the Earthworm Collection of the University of Kragujevac, Serbia (CEKUS).

2.3. Statistical analysis

Species richness was represented by the number of taxa on the altitudinal transects/habitat type, and total abundance by the total number of individuals of each taxa on the altitudinal transects. The categorization of earthworm taxa was based on their zoogeographic distribution, as proposed by Csuzdi and Zicsi (2003), Pop et al. (2010) and Csuzdi et al. (2011). Also, earthworm fauna was classified into three ecological categories (epigeic, anecic and endogeic species), based on their ecological behaviors (Bouché, 1977). The species richness, total abundance individuals, zoogeographical composition abundance, and ecological categories abundance were tested for the Pearson correlation with altitude. Cluster analysis (UPGMA) based on Jaccard's coefficient of similarity (Krebs, 1998) was performed for the comparison of community composition among altitudinal transects and in order to explore the altitudinal patterns of community composition. Note that the cluster analysis does not include species with a broad altitude range.

The altitudinal range size of each taxon was estimated by calculating the difference between the lowest and highest altitudes of its presence, that is, the so-called mean altitude range (Kim et al., 2019). Polynomial regression was used to assess whether earthworm fauna follows mean range size, as predicted by the Rapoport's rule. Before performing the ecological analysis, we tested the data for normal distribution with the Shapiro–Wilk test, respectively. Because of the fact that the distribution was not normal ($p < 0.05$), nonparametric methods were used for the further analysis of the data. The indirect ordination method, nonmetric multidimensional scaling (nMDS) (Taguchi and Oono, 2005), was used in order to visualize the similarities among a different habitat type (meadows, humid meadows, pastures, riverbanks and oak, beech, spruce forests) of the investigation based on the taxa recorded on them. The distance between two sampling points was estimated using the pairwise Bray-Curtis similarity index. Analysis of similarity (ANOSIM) relates the mean difference of ranks between and within groups, generating the Global statistic (R). The values of Global statistic (R) range from –1 to +1. Values near 0 and negative values demonstrate similarity among groups. Values impending +1 indicate a strong dissimilarity among groups. Similarity percentage (SIMPER) identifies the species that are most responsible for the observed patterns (e.g., the taxa which contributes to the intra-group similarity and those that contribute the most to the dissimilarity between groups) by disaggregating the Bray-Curtis similarities between samples. The more abundant a taxon is within a group, the more it contributes to the intra-group similarity, while a taxon with a consistently high contribution to the dissimilarity between groups is a good discriminating taxon (Clarke and Warwick, 2001). Paleontological statistics software (PAST) was utilized for calculating cluster analysis UPGMA, nMDS, ANOSIM, and SIMPER (Hammer et al., 2001), while for calculating Shapiro–Wilk test, polynomial regression, and Pearson's correlation, we used SPSS 20.0. (IBM Corp., 2011).

3. Results

A total of 708 earthworm individuals, of which 27 taxa (23 species and 4 subspecies) belonging to 11 genera were recorded in the study sites (Table 1). In four taxa (*Allolobophora* (*sensu lato*) *kosowensis*, *Allolobophora* (*s.l.*) *paratuleskovi*, *Allolobophora* (*s.l.*) *strumicae*, and *Allolobophora* (*s.l.*) *treskavicensis*), the taxonomic status, and the distribution needs to be revised. The most abundant taxa were *Dendrobaena octaedra* (N = 131; 19.4% of all observed individuals) and *Aporrectodea rosea* (N = 120; 17.7%). In contrast, *All. kosowensis*, *Aporrectodea handlirschi*, *Lumbricus castaneus* and *Octodrilus transpadanus* were rare taxa, occupying < 1% of the total number of individuals (Table S1). Total abundance of individuals and species richness per transect ranged from 39 to 118 and from 6 to 15. Both the total abundance and species richness of the earthworm fauna exhibited monotonically declining trends with the increase in altitude (Figure 2). The Pearson's correlation indicates a significant negative correlation between the altitude and species richness ($r = –0.96$, $p < 0.01$), as well as between altitude and total abundance ($r = –0.94$, $p < 0.01$). Also, species richness and total abundance individuals linear decrease after 670 m altitude, probably due to lower tolerance of tax to high mountain harshness, as well as due to changing habitat types. The cluster analysis showed that along the altitudinal gradients of the western slopes of the Kopaonik Mt., two main patterns of earthworm community structure are evident (Figure 3). Twelve taxa can be characterized as exclusive to the lower altitudes (*All. kosowensis*, *All. paratuleskovi*, *Allolobophora leoni*, *Allolobophora chlorothica chlorothica*, *Aporrectodea caliginosa trapezoides*, *Ap. handlirschi*, *Dendrobaena vejdovskyi*, *All. strumicae*, *Eisenia fetida*, *L. castaneus*, *Lumbricus polyphemus* and *Proctodrilus antipai*), given that their maximum activity is not up to 1000 m. In addition, we recorded taxa of middle-higher altitude (above 1000 m) in which tolerant taxa from the lower altitudes that can hardly reach higher altitudes, with their maximum activity being up to 1500 m (*Aporrectodea jassyensis* and *O. transpadanus*), as well as taxa from the higher

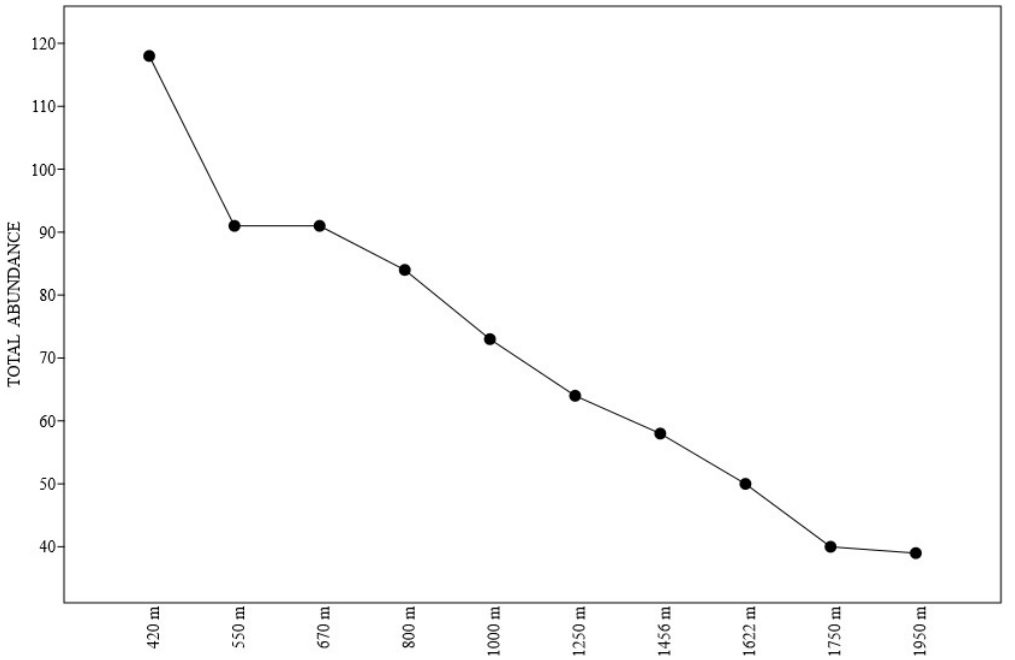


Figure 2. Relationship between earthworm abundance, species richness, and altitudes.

altitudes zone, which are better adapted to the mountain's conditions, with their maximum activity being above 1500 m (*All. treskavicensis* and *Dendrobaena alpina alpina*), were present. Eleven taxa that have broader altitudinal range (*Aporrectodea caliginosa caliginosa, Ap. rosea*, *Bimastos rubidus*, *Dendrobaena byblica*, *Dendrobaena illyrica*, *D. octaedra*, *Eisenia lucens*, *Eiseniella tetraedra*, *Lumbricus rubellus*, *Lumbricus terrestris* and *Octolasion lacteum*) were recorded in total. Polynomial regression is represented by a significant relationship ($R^2 = 0.68$, $p < 0.01$, Figure 4). The patterns in mean altitudinal range-size distributions showed a tendency of broader range-size distribution, with increasing altitudes. This is the result of higher ecological tolerances of the earthworm fauna, which mainly favored the formation of the high-altitude taxa in comparison to the tolerance of taxa originating in the lower altitudes. Also, our results showed that taxa from lower altitudes cannot be found at higher altitudes, as well that taxa covering broader altitude range are mostly of a higher abundance at a lower altitude.

The autochthonous earthworm fauna of this mountain includes 15 taxa belonging to zoogeographic types: endemic (*All. kosowensis*, *All. paratuleskovi*, *All. strumicae* and *All. treskavicensis*), Balkanic-Alpine (*D. alpina alpina* and *D. vejdovskyi*), Ilyric (*D. illyrica*), Trans-Aegean (*All. leoni*, *Ap. jassyensis*, *Ap. handlirchi* and *P. antipai*), Central-European (*E. lucens*, *L. polyphemus* and *O. transpadanus*) and not so numerous Circum-Mediterranean (*D. byblica*). However, 12 taxa (*All. chlorotica chlorotica, Ap. caliginosa caliginosa*, *Ap. caliginosa trapezoides*, *Ap. rosea*, *B. rubidus*, *D. octaedra*, *E. fetida*, *Ell. tetraedra*, *L. castaneus*, *L. rubellus*, *L. terrestris* and *Oc. lacteum*) along the mountain have peregrine distribution. The Pearson's correlation showed a significant negative correlation between the abundance of peregrine taxa and the increase in altitude ($r = –0.87$, $p < 0.01$), while it did not show a significant correlation between the abundance of autochthones taxa and the increase in altitude ($r = 0.26$, $p > 0.05$).

The abundance of ecological categories of earthworms showed a different relationship with the increase in altitude. Namely, the abundance of anecic and endogeic taxa showed a negative correlation with increased altitude ($r = –0.75$, $p < 0.05$, $r = –0.88$, $p < 0.01$), while the abundance of epigeic taxa increased with the increase in altitude ($r = 0.85$, $p < 0.01$).

The species richness per of habitats ranged from two to seven taxa. The highest species richness was recorded on the M3 (7 taxa) in the lowest altitude, while SF1 and SFF1 on the highest altitude had the lowest species richness among all sites (2 taxa) (Table 2). Ordination of habitat using Bray–Curtis distance on binomial data is seen in Figure 5 (stress = 0.17). The ANOSIM showed significant differences between earthworm communities of habitat type ($R = 0.707$, $p < 0.001$), and the pairwise comparisons indicated significant the difference between the earthworm communities of meadows/oak forests/riverbanks and spruce forests ($R = 1$, $p < 0.05$), then in between meadows/oak forests and beech forests ($R = 0.99$, $p < 0.05$) and between oak forests and riverbanks ($R = 0.80$, $p < 0.05$). The SIMPER analysis identified the taxa

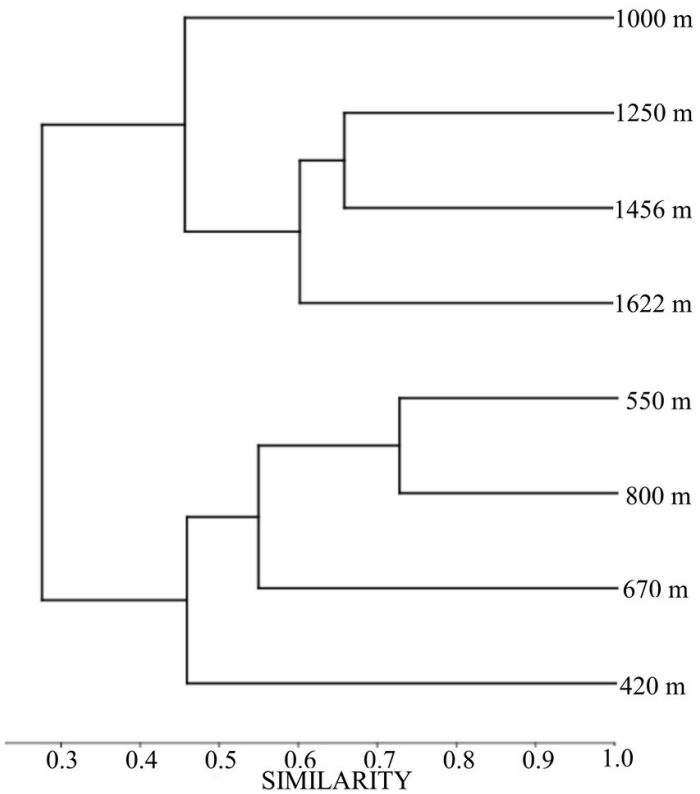


Figure 3. Cluster analysis (UPGMA) using the Jaccard's index of similarity among the altitudinal transects.

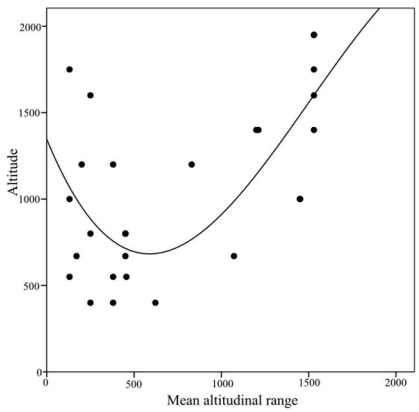


Figure 4. The altitudinal pattern of mean altitudinal range in altitudes.

contributing most to average similarity intra-investigated habitat types as well as dissimilarity between habitat types. *Dendrobaena octaedra*, *Ap. rosea* and *Oc. lacteum* consistently contributed the most to within-habitats similarity. On the other hand, mostly autochthones taxa consistently contributed the most between-habitats dissimilarities (see Table 2).

4. Discussion

Understanding how community structure change along altitudinal gradients have been a central topic in modern ecology, biogeography, and conservation (Körner, 2007). According to our data were detected of 27 earthworm taxa within the studied area, which covered more than 35% of the total earthworm taxa in Serbia (Stojanović et al., 2018). This fact indicates the high earthworm species richness on the western slopes of the Kopaonik Mt. Particularly, we found monotonically declining relationships between total abundance/species richness and altitudinal gradients (from 15 to 6 taxa, and from 118 to 39 individuals), indicating that more earthworms prefer low altitude climates as their habitat. During researching the invertebrate diversity (including earthworm) at the altitudes of the Western Carpathians, Rozen et al. (2013) reported a decline in species richness at higher altitudes. Also, the study conducted by Cardoso et al. (2014) provided an account of the distribution of earthworm fauna along an altitudinal gradient of the Caratuva Massif (Brazil) and showed that the abundance and species richness were not positively correlated with altitude, as well that peregrine taxa were present only at the lowest altitudes. Contrary to previous studies, González and Lodge (2017) indicated

Table 2. Similarity percentages (SIMPER) across the seven habitat type and similarity percentages highlighting the most influential taxa per habitat comparison (Legend; average abundance values ranking 1-rare; 2-common; 3-very common; >4-dominant; Av. Diss. = Average dissimilarity; Contrib. = Contribution (%) to the within-group similarity; Cumulative total (%) of contributions).

Average dissimilarity = 78.41%										
Taxon	Av. Dissim	Contrib. %	Cumulative %	Meadows	Oak forests	Beech forests	Humid meadows	Pastures	River banks	Spruce forests
D. octaedra	16.34	20.84	20.84	0	8.33	13.20	2.50	4.60	1	20.70
Ap. rosea	9.81	12.51	33.36	11.80	9.33	0	4	6.40	4.20	0
Oc. lacteum	4.76	6.08	39.43	0	0	0	4	2.20	4.40	0
B. rubidus	3.91	4.99	44.42	2.50	0	1.50	0.50	0.80	3	0
Ell. tetraedra	3.71	4.73	49.15	0	0	0	3.50	0	3.40	0
L. rubellus	3.61	4.60	53.75	1.50	7.67	1	0	0	0	0
Ap. caliginosa caliginosa	3.43	4.38	58.12	5.25	0	0	0	2.60	0	0
L. terrestris	3.18	4.06	62.18	1.75	0	0	4.25	0	1.2	0
D. illyrica	3.18	4.05	66.23	0	0	4	0.50	0.80	0	0
D. vejdovskyi	3.05	3.89	70.12	0	1.67	2.50	2	0	0	0
E. lucens	2.95	3.77	73.89	0	0	4.50	0	0	0	0
D. alpina alpina	2.57	3.28	77.17	1.50	0	2.17	0	1.40	0	0
Ap. caliginosa trapezoides	2.22	2.83	80.00	1	0	0	3	0	1.20	0
D. byblica	1.96	2.49	82.49	0	0	1.50	0	0	0	2.67
L. polyphemus	1.85	2.36	84.85	1.75	0	0	2	0.40	0	0
All. chlorotica chlorotica	1.57	2.00	86.85	3.25	1.33	0	0	0	0	0
All. (*s.l.*) *paratuleskovi*	1.50	1.92	88.77	3.25	0	0	0	0.40	0	0
All. (*s.l.*) *strumicae*	1.50	1.91	90.68	2	2	0	0	0	0	0
Ap. jassyensis	1.07	1.37	92.05	0	0	0	0	1.80	0	0
E. fetida	1.03	1.32	93.36	0	3.33	0	0	0	0	0
P. antipai	1.01	1.29	94.65	0	3	0	0	0	0	0
O. transpadanus	1.00	1.28	95.93	0	0	1.50	0	0	0	0
All. (*s.l.*) *treskavicensis*	0.80	1.02	96.95	0	0	0	0	1.20	0	0
All. leoni	0.67	0.85	97.80	0.75	1	0	0	0	0	0
L. castaneus	0.60	0.77	98.57	0	0	0	0.75	0	0.60	0
All. (*s.l.*) *kosowensis*	0.60	0.77	99.33	1.50	0	0	0	0	0	0
Ap. handlirschi	0.52	0.67	100.00	1.25	0	0	0	0	0	0

that the total abundance and abundance of autochthonic taxa increases with the increase in altitudes on the Luquillo Mts. in Puerto Rico, due to decreased air temperature and increased annual rainfall.

The altitudinal range size of taxa is an important component of community structure. In this study, the mean altitudinal range size of earthworms did increase with the increase in altitude and, thus, supporting the Rapoport's altitudinal rule. According to Webb and Gaston (2003), the range of taxa is the result of many complex interaction factors, including physiological properties, history of specification, and expansion and constraints of continental shape. Cooper et al. (2008) believed that size of the range of species is a major factor that correlates with the extinction of the risk to organisms and is also critical for the study of biotic responses to an environmental factor. Taxa which are of a small range of distribution will be more compromised (Whitton et al., 2012). Interestingly, McCain and Knight (2013) stated that, on mountains above 23˚N latitude, significantly stronger support for the altitudinal Rapoport's rule was detected. The area we studied was located above 23˚N latitude, thus the above-mentioned geographical features were influential.

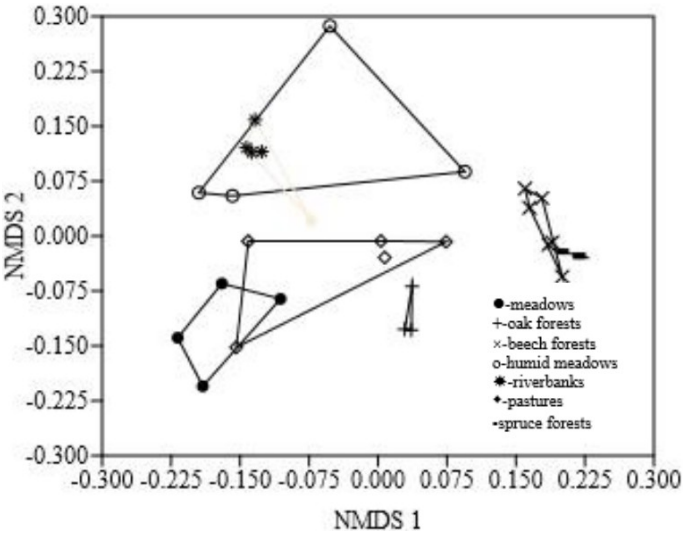


Figure 5. Nonmetric multidimensional scaling (nMDS) ordination plots based on Bray Curtis dissimilarities of earthworm communities by habitat types.

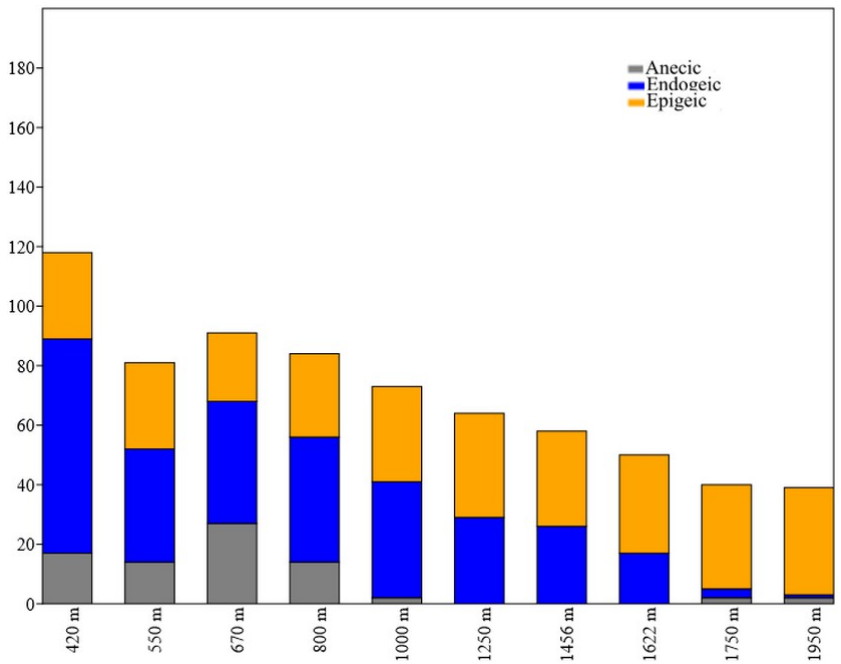


Figure 6. Altitude effect on the abundance of ecological categories.

We suppose that rich zoogeographical composition of earthworm fauna depends largely on specific climatic factors, the history of a region, and on the special characteristics of each taxon. The rich content of the zoogeographic composition results from the following two influences: continental and Mediterranean elements. The influence of the huge Kopaonik mass (continental element) comprising of endemic, Balkanic-Alpine, Iliric and Central-European types, is also noted, as well as the Mediterranean influence, entering through the Ibar Valley and comprising of Trans-Aegean and Circum-Mediterranean types. We suppose that the higher abundance of peregrine taxa at a lower altitude can be explained by the fact that anthropogenic impacts were more pronounced on the lower altitudes. According to Tóth et al. (2020), peregrine taxa are restricted to human-modified habitats, due to the natural vegetation of coniferous forests and low pH value, impedes the spread

of these taxa. Nonetheless, future changes in climatic conditions, as well as uncontrolled land use, may facilitate earthworm colonization from densely populated areas to wildlands (Moore et al., 2018; Tóth et al., 2020). Also, most earthworms are autochthonous, present high tolerance to the environmental conditions of the mountain. Although, Salomé et al. (2011) did not present a zoogeographic analysis in their paper, we analyzed the data presented in Table 2 and found that, at higher altitude, the species richness of autochthonous taxa was lower and that the highest richness was observed in the lowest region.

Looking at the ecological groups (Figure 6), we observed the dominance of epigeic tax in higher altitudes; they were most dominant in beech and coniferous forests. Also, the optimum environmental conditions at lower altitudes can provide suitable habitats for the anecic and endogeic taxa. This fact especially applies for anecic taxa, which are almost exclusively dependent on easily palatable leaf-litter (except a few like *L. terrestris*) and so the deciduous forest belt. The ecological study of the earthworm fauna along altitudinal gradients on the Khibiny Massive in Russia showed the persistence of epigeic taxa at high altitudes (Zenkova and Rapoport, 2013). Namely, beech and conifer forests are responsible for notable acidification of the upper soil layer, decreasing the pH value influence of the dominant epigeic taxa (Vahder and Irmler, 2018). Besides, in temperate soils, epigeic taxa are also abundant in acid soils. According to Edwards (2004), the reduced abundance of anecic taxa at the subalpine level leads to accumulation of organic matter over the soil surface in the most developed forest stages, thus, maintaining favorable habitats for epigeic taxa. Holmstrup (2007) proved that *D. octaedra* has higher freeze resistance than endogeic taxa. The freeze-hardiness, the high degree of reproduction (parthenogenesis), as well as the ability of taxon *D. octaedra* to tolerate acid soils and exploit poor quality litter, are seemingly the major reasons for the frequency of this species in beech and spruce forests (Tiunov et al., 2006; Terhivuo and Saura, 2008). This fact indicated the tolerance of this species to harsh climate. Salomé et al. (2011) presented the altitudinal variation of earthworm fauna in the Swiss Alps, reporting that maximum density and biomass were observed at the hill level mainly due to the contribution of anecic taxa, while no earthworm was found at the alpine level. The anecic taxa are sensitive towards acidic soil (Schelfhout et al., 2017), and, therefore, they are mainly closely associated with meadows and eutrophic deciduous forests (Jänsch et al., 2013). *Lumbricus terrestris* was found to be the only anecic taxa present in the highest altitudes. Essentially, the presence of taxon *L. terrestris* is not surprising, because it tolerates alkaline soils. However, this species is not frost-tolerant, indicating that it hibernates in deep soil layers during the winter (Tiunov et al., 2006). Also, this species one of the few anecic species, which does not bound exclusively to the forests, but it can live in meadow habitats as well behaving as an endogeic species (Zicsi et al., 2011).

Further, it is known that the earthworm species richness as well as the relative significance of different ecological categories of a region, is determined by climatic factors, phylogenetic and biogeographic history, and regional parameters such as vegetation type or soil characteristics (Lavelle and Spain, 2001). So, in our study, altitude is not the only factor that affects the structure of earthworm. In fact, habitat type plays an important role in determining distribution patterns of earthworm. However, as altitude increases, habitat conditions become less favorable. For that, significant differences are observed in species richness between different habitats at lower (seven taxa in meadow) and higher altitudes (two taxa in spruce forest). Namely, according to Pop (1997), the complexity of plant cover on the lower altitudes increases the diversity of earthworm fauna. In general, earthworm communities are reported to have from two to five taxa (Lee, 1985). Nevertheless, research on earthworm community structure in pasture habitats in the region of the Kapela Mountain, which was conducted by Hackenberger and Hackenberger (2014), indicated earthworm communities are reported to be able to have from one to 11 taxa. The ordination (nMDS) and ANOSIM showed a low level of similarity between the earthworm composition and investigation habitats. The main factors inducing faunal dissimilarity among habitats are the dissimilar altitudes, distance, and heterogeneity of habitats. The SIMPER analysis reveals that *D. octaedra*, *Ap. rosea* and *Oc. lacteum* contributed a much greater value than the other taxa when it comes to contributing the most to within-habitats similarity. This result is not surprising, considering that these species are common in Serbia (Stojanović et al., 2018). In addition, autochthonous taxa contributed the most to between-habitats dissimilarities. Few "archaic" taxa (*All.* (*s.l.*) *kosowensis*, *All.* (*s.l.*) *paratuleskovi*, *All.* (*s.l.*) *strumicae* and *All.* (*s.l.*) *treskavicensis*) have a narrower, more specialized niche. Besides, archaic taxa evolved historically under local environmental conditions, where taxa respond differently to them, deploying various adaptations. Therefore, we conclude that the mountain ecosystems are particularly sensitive to changes in climate and land cover, but, at the same time, they can offer important refuges for taxa on the opposite of the more altered lowlands.

Overall, due to the high diversity of earthworm fauna and the fact that they occupy a broader altitudinal range in the areas where they occur, as well as due to the important roles these organisms have in the functioning of a variety of ecosystems, earthworms have a high potential as model organisms for this type of a study. However, there cannot exist a single model for describing how earthworm fauna

reacts to the change in altitude, owing to the fact that further work is needed in order to test this controversial rule. We must mention that the altitudinal Rapoport's rule has not yet been fully supported due to the following reasons: the differences in sampling effort, habitat type, methodology, geographical scale, and the mechanism used (McCain and Bracy Knight, 2013). Thus, in our study, we conducted a field survey that utilized identical sampling intensity. Moreover, we performed a field survey in heterogeneous mountainous habitats.

The pattern of distribution of earthworms is explained by the fact that, with increase in altitude, habitat conditions become less favorable that establishes a broad range of environmental barriers and leads to a limitation of taxa spread. Even though our results could provide important baseline information on altitudinal patterns of earthworm community structure, further work is needed in order to understand if our observed patterns represent only transient changes or are the first signals of the mentioned trend. Therefore, we, thus, encourage other lumbricologists and ecologists to carry out similar studies in order to increase our limited understanding of the Rapoport's altitudinal rule of the earthworm fauna.

Conflict of interest

The authors declare that there's no conflict of interests.

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Table S1. (Supplementary material) Earthworms taxa with their number of individuals observed on altitudinal transects/habitat types on western slopes Kopaonik Mt. Numbers refer to the total percentage contribution of each species to the total sample.

Taxa			*All. chlorotica chlorotica* (Savigny, 1826)	*All. (s.l.) kosowensis*,Karaman, 1968	*All. (s.l.) paratuleskovi* (Šapkarev ,1975)	*All. (s.l.) strumicae* (Šapkarev, 1973)	*All. (s.l.) treskaviciensis* (Mršić, 1991)	*All. leoni* Michaelsen, 1891	*Ap. caliginosa caliginosa* (Savigny, 1826)	*Ap. handlirschi* (Rosa, 1897)	*Ap. jassyensis* (Michaelsen, 1891)	*Ap. rosea* (Savigny, 1826)	*Ap. caliginosa trapezoides* (Duges, 1828)	*B. rubidus* (Savigny, 1826)	*D. alpina alpina* (Rosa, 1884)	*D. byblica* (Rosa, 1893)	*D. illyrica* (Cognetti, 1906)	*D. vejdovskyi* (Černosvitov, 1935)	*D. octaedra* (Savigny, 1826)	*E. fetida* (Savigny, 1826)	*E. lucens* (Waga, 1857)	*Ell. tetraedra* (Savigny, 1826)	*L. castaneus* (Savigny, 1826)	*L. polyphemus* (Fitzinger, 1833)	*L. terrestris* (Linnaeus, 1758)	*L. rubellus* (Hoffmeister, 1843)	*Oc. lacteum* (Örley, 1881)	*O. transpadanus* (Rosa, 1884)	*P. antipai* (Michaelsen, 1891)
Altitude (meters above sea level)/habitat types	420	M1	1.55	0.28	0.7	0	0	0	1.55	0	0	1.97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9
		OF1	0.84	0	0	0	0	0.42	0	0	0	1.83	0	0	0	0	0	0	0.84	0.98	0	0	0	0	0	0.98	0	0	0
		HM1	0	0	0	0	0	0	0	0	0	0.98	0.59	0	0	0	0	0	0	0	0	0.98	0.42	0	0.48	0	0.98	0	0
	550	M2	0	0	0	0	0	0	0	0	0	0	0	0.7	0	0	0.7	0.84	1.55	0	0.7	0	0	0	0	0	0	0	0
		BF1	0	0	0	0	0	0	0.7	0	0	1.41	0	0.42	0.7	0.42	0	0	0	0	0	0	0	0.56	0.7	0	0	0	0
		RB1	0	0	0	0	0	0	0	0	0	0.7	0.56	0	0	0	0	0	0.7	0	0	0	0.14	0	0.42	0	0.84	0	0
	670	M3	0	0.56	1.12	0.84	0	0	0.7	0.7	0	1.12	0.59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		OF2	0	0	0	0.56	0	0	0	0	0	0.98	0	0	0	0	0	0	0.42	0.42	0	0	0	0	0	0.84	0	0	0.98
		HM2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0.98	0	0	0	0	0.7	0	0	0.56	0	0
	800	M4	0	0	0	0.29	0	0.42	0	0	0	1.12	0	0.84	0	0	0	0	0	0	0	0	0	0.42	0	0.84	0	0	0
		OF3	0	0	0	0.29	0	0	0	0	0	0.84	0	0	0	0	0	0.7	1.12	0	0	0	0	0	0	0.56	0	0	0.28
		HM3	0	0	0	0	0	0	0	0	0	0.98	0.84	0	0	0	0	0	0	0	0	0.56	0	0.28	0.7	0	0.7	0	0
	1000	P1	0	0	0	0	0	0	1.12	0	0.56	0.84	0	0	0.7	0	0	0	0	0	0	0	0	0.28	0	0	0	0	0
		BF2	0	0	0	0	1.97	0	0	0	0.29	0.42	0	0.29	0	0	0	0	0	0	0	0	0	0	0	0	0.28	0	0
		HM4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.84	0.56	1.83	0	0	0	0	0	0.28	0	0	0	0
	1250	P2	0	0	0	0	0.28	0	0.7	0	0	0.98	0	0.28	0.28	0	0	0	0	0	0	0	0	0	0	0	0.58	0	0
		BF3	0	0	0	0		0	0	0	0	0.56	0	0.14	0	0	0	0	0	0	0	0.88	0	0	0	0	0.7	0	0
		RB2	0	0	0	0	0	0	0	0	0	0	0	0	0.42	0.42	0.42	0	1.55	0	0.56	0	0	0	0	0.56	0	0	0
	1456	P3	0	0	0	0	0.28	0	0	0	0	0	0	0.56	0.42	0	0.56	0	0.98	0	0.42	0	0	0	0	0	0	0.42	0
		RB3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.28	0	0.56	0	0	0	0	0	0	0	0.42	0.28	0
		BF4	0	0	0	0	0	0	0	0	0.56	1.41	0	0	0.28	0	0	0	0.42	0	0	0	0	0	0	0	0.28	0	0
	1622	P4	0	0	0	0	0	0	0	0	0	0	0	0	0.42	0.42	0	0	1.12	0	0.98	0	0	0	0	0	0	0	0
		BF5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0	0	0	0	0	0	0	0.28	0	0.56	0	0
		BFF1	0	0	0	0	0.42	0	0	0	0	0.88	0	0	0	0	0.28	0	0.88	0	0	0	0	0	0	0	0.14	0	0
	1750	RB4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0	0	0	0	0.88	0	0	0.29	0	0.28	0	0
		P5	0	0	0	0	0	0	0	0	0	0	0	0	0	0.28	0	0	0.98	0	0	0	0	0	0	0	0.42	0	0
		SF1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.56	0	0	1.27	0	0	0	0	0	0	0	0	0	0
	1950	RB5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.28	0	0	0	0	0	0	0	0.28	0	0.14	0	0
		SFF1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.28	0	0	3.53	0	0	0	0	0	0	0	0	0	0
		SF2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.28	0	0	0	0	0.42	0	0	0.28	0	0	0	0
Relative abundance			2.39	0.84	1.92	1.82	3.1	2	5.03	0.74	1.48	17.7	2.6	2.2	3.4	2.5	5.3	2.96	19.4	1.48	2.81	3.7	0.44	2.22	4.44	4	7.25	0.74	1.33