IZVORNI I ZNANSTVENI ČLANCI – ORIGINAL SCIENTIFIC PAPERS
UDK 630* 114.6 + 411 (001)

Šumarski list br. 9–10, CXXXIV (2010), 475-486

VARIATIONS OF CARABID BEETLE AND ANT ASSEMBLAGES, AND THEIR MORPHO-ECOLOGICAL TRAITS WITHIN NATURAL TEMPERATE FORESTS IN MEDVEDNICA NATURE PARK

RAZLIKE U SASTAVU I MORFOLOŠKO-EKOLOŠKIM ZNAČAJKAMA MRAVA I TRČAKA U PRIRODNIM ŠUMAMA NA PODRUČJU PARKA PRIRODE MEDVEDNICA

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SUMMARY: The aim of this study was to investigate responses of ant and carabid assemblages and their morpho-ecological traits to habitat differences within natural temperate forests in Medvednica Nature Park. To quantify habitat differences in examined areas, both structural heterogeneity of the vegetation and taxonomic diversity of plants were measured on six plots.

Habitat complexity was quantified using four habitat characteristics within the site: tree canopy cover; shrub canopy cover; ground herbs and leaf litter cover. Ants and carabids were sampled using pitfall traps.

Ant species richness and abundance, unlike carabid species richness were positively correlated with habitat complexity, especially with leaf litter cover on plots. The responses of insects morpho-ecological traits to habitat were recorded, with more large bodied carabids present in more complex site and higher abundance of opportunist ant species in more open sites with low complexity of vegetation. Higher dominance of certain carabid species at the lower plots then those on the top of the mountain, suggest competitive exclusion, confirming lower areas as more stable. Species adapted to colder climate, that inhabit higher elevations such as flightless forest specialist Cychrus caraboides *and* Carabus irregularis*, and boreo-montane ant species* Camponotus herculeanus*, are less competent to colonize lower areas. Furthermore, they may not survive severe instability of their habitats, especially in a changing climate. Overall results suggest that conservation issues need to be focused on preserving stability and structural complexity of forest habitat in summit areas of the mountain.*

Key words: biodiversity, vegetation structure, litter, altitude, nature conservation, forest habitat

INTRODUCTION – Uvod

Mountain landscapes usually offer steep gradients for a wide range of environmental parameters (i.e. temperature, precipitation, etc.), what is reflected in the adaptation and distribution of different types of organisms and ecological communities that occupy different positions along these gradients (review in Hodkinson 2005). Many of these environmental factors are multifaceted and interlinked in defining overall structural complexity of insect habitats, which Hodkinson (2005) has found to decrease with increasing altitude. The latter affects not only the species richness but also the species composition of insect communities (Whittaker 1952

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in Hodkinson 2005). The physical structure of the environment, mediated by plant communities, can influence the distribution and interactions of species (review in Lawton 1983). "Structural heterogeneity hypothesis" assumes that structurally complex habitats may provide more niches and environmental resources for exploitation and thus increase species diversity, although empirical support for this relationship is biased towards studies of vertebrates and habitats under anthropogenic influence (Tews et al. 2004). Lassau and Hochuli (2004) and Lassau et al. (2005) showed that habitat complexity in forests may affect the composition of ant and beetles assemblages. Brose (2003b) showed that effects of habitat heterogeneity on ground beetle assemblages were positive on the micro- and meso-scale (0.25 and 500–1000 m^2, respectively), and were not significant on a macro-scale (10 km^2).

In "taxonomic diversity hypothesis" plant taxonomic diversity is positively correlated with the diversity of herbivore insects (Murdoch et al. 1972, Root 1973), and thus with predator diversity (Hunter and Price 1992). The importance of floristic richness for the ground beetle abundance was also reported by Baguette (1993).

Ants and ground beetles have been widely recommended as environmental, ecological and biodiversity indicators (e.g. Altegrim et al. 1997, Andersen 1997, Niemelä 2000, Szyszko et al. 2000, Andersen et al. 2002, Antonova and Penev 2006, Pearce and Venier 2006, Šerić Jelaska et al. 2007, Šerić Jelaska and Durbešić 2009). They respond well to natural and anthropogenic disturbances. Microhabitat characteristics, i.e. litter type, organic matter content, insolation, temperature fluctuation, are important for providing hunting, foraging niches and for protection of beetles from predators, ovipositioning, larval development, over wintering etc. (Thiele 1977, Pearce and Venier 2006). The use of carabids morpho-ecological traits like wing morphology, body size or diet are recommended in the evaluation of habitat quality (Blake et al. 1994, Gutiérrez et al. 2004, Gobbi and Fontaneto 2008). Brose (2003a) found that large carabids, as more preferable prey because of their higher nutritive value and reduced foraging time required, prefer dense vegetation plots as enemy-free spaces. According to Andersen et al. (2002), ant functional groups can be used as indicators of habitat quality and forest health under different management (Stephens and Wagner 2006).

Lassau and Hochuli (2004) suggested measurement of habitat complexity as a surrogate for the diversity of a range of arthropods including ants. Very often, different taxonomic groups indicate certain areas as important for protection or nature conservation, showing mutual positive correlations. Based on the existence of these correlations, the use of "surrogate species groups" for estimation of overall biodiversity has been reported (Garson et al. 2002; Sætersdal et al. 2003); being particularly useful where limited biodiversity data exist. Vascular plants have been reported by Sætersdal et al. (2003) as a good surrogate group, which also works for estimation of ground beetle diversity. Although, some habitat preferences are known for many species of ants and ground beetles, it is not always evident which environmental factors are the most responsible for species assemblage and distribution.

The aim of this study was to analyze ants and carabid species richness and abundance, carabids body size and ants functional groups, in different habitats within natural temperate mature forests, and to test whether higher habitat complexity and plant species richness support higher insect diversity along vertical gradient in Mt. Medvednica.

MATERIAL AND METHODS – Materijal i metode

Study Area – *Područje istraživanja*

Mount Medvednica is part of the Croatian continental karst, located north of Zagreb, the capital of Croatia. The great floristic diversity (Dobrović et al. 2006), due to the mosaic structure of forest communities, geographical position and geological structure make this area very interesting for biodiversity investigations. Dobrović et al. (2006) reported that the floristic richness and diversity of the mountain was higher than similar regions in Croatia and several European countries (Italy, Austria, Slovakia, Poland and Serbia). For protection of its valuable forest areas, the western part of Mt. Medvednica (228 km^2) was proclaimed a nature park by the Nature Protection Act in 1981. The highest peak of the mountain, named Sljeme, is placed 1035 m above sea level. Despite protection, anthropogenic pressures on Medvednica are constantly increasing (road construction, recreation, ski trails, logging, etc.), mainly at its upper elevations, changing the habitat quality. This can change structural complexity of forests, especially where trees and shrubs form part of the natural landscape.

Surveyed forests are natural temperate ones on brown acid soil with silicate parent rocks (Basch 1995). For this investigation, six plots (50 x 50 m) were selected along the central profile of Mt. Medvednica across a vertical gradient on both slopes of the mountain (Figure 1). They were placed in mature stands of five different forest communities, that account for 78% of the total forest cover of the nature park: *Querco–Castaneetum sativae* Ht. 1938, (plot 1); *Luzulo–Fagetum sylvaticae* Mausel 1937, (plot 2); *Lamio orvale–Fage-*

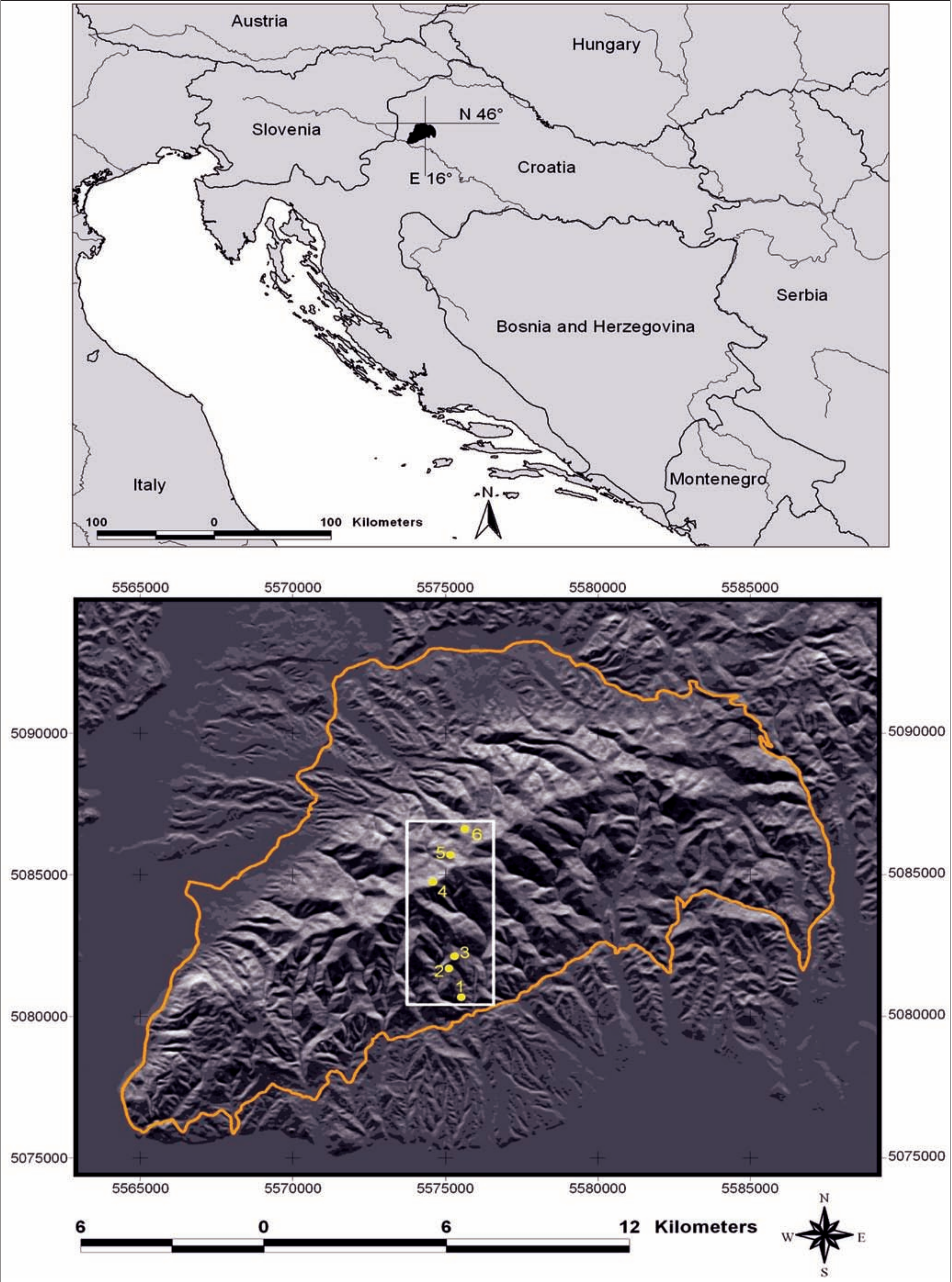

Figure 1 Position of the study area - Medvednica Nature Park (black polygon) and position of investigated plots in the Park
Slika 1. Područje istraživanja i položaj istraživanih ploha na području Parka prirode Medvednica

tum sylvaticae Ht. 1938, (plot 3), *Festuco drymeiae-Abietetum* ass. nova, Vukelić & Baričević 2007, (plots 4 and 6); *Chrysanthemo macrophylli–Aceretum pseudoplatani* (Ht. 1938) Borh. 1962 (plot 5), (Table 1). For each plot, altitude, slope and aspect were measured. Because of its circular nature, the terrain aspect was transformed into a continuous north-south gradient (northness) by calculating the cosine of aspect values (Guisan et al. 1999, Jelaska et al. 2003).

Table 1 Ecological variables and their values for six plots
Tablica 1. Vrijednosti ekoloških varijabli na šest istraživanih ploha

Variable/*plot* (50x50 m)	**1**	**2**	**3**	**4**	**5**	**6**
community/*zajednica**	qc	lf	lo	af	cm	af
Organic matter content/*udio org. tvari (%)*	8.99	16.36	15.96	21.47	18.82	13.28
Number of plant species/*br. biljnih vrsta*	62	19	41	43	36	39
Altitude/*visina (m)*	400	550	660	970	810	660
Slope/*nagib (º)*	21	18	17	28	21	7
Aspect/*aspekt (º)*	145	272	102	325	354	335
Northness/*sjevernost*	-0.819	0.035	-0.208	0.819	0.995	0.906
Canopy openness/*otvorenost sklopa (%)*	4.04	10.62	4.95	12.69	4.98	4.94
Leaf area index/*indeks lisne površine*	3.91	2.59	4.13	2.34	3.81	3.41
Soil type/*tip tla*	Brown acid/*kiselo smeđe*					

* *qc - Querco - Castaneetum sativae, lf - Luzulo - Fagetum sylvaticae, lo - Lamio orvale - Fagetum sylvaticae, af – Festuco drymeiae - Abietetum, cm - Chrysanthemo macrophylli – Aceretum pseudoplatani*

Habitat complexity was quantified using four habitat variables within the site: tree canopy cover; shrubs canopy cover; ground herb cover and amount of leaf litter.

Each variable was scored with 0, 1, 2 and 3 using an ordinal scale, where increasing scores indicate greater habitat complexity. This is modified version of the techniques used by Lassau and Hochuli (2004, 2008). Compared to the Lassau and Hochuli (2004) scoring method, there were no differences in two additional variables i.e. soil moisture and portion of logs, rocks and debris between investigated plots, hence we haven't used them in our analyses. Three characters (shrubs canopy cover; ground herb cover; amount of leaf litter) were visually quantified into four categories (from score 0 to score 3: low contribution to site complexity (score 0), the highest contribution to site complexity (score 3). Tree canopy cover was measured as Leaf Area Index (LAI) and classified into four categories with scores from 0 to 3. Summing up the scores for all quantified characters, habitat complexity range from 5 (lowest habitat complexity) to 10 (maximum habitat complexity) per plot (Table 2).

Table 2 Ecological variables used to derive measures of habitat complexity and their values for six plots
Tablica 2. Ekološke varijable korištene za određivanje kompleksnosti structure staništa na šest istraživanih ploha

Variable/*plot* (50x50 m)	**1**	**2**	**3**	**4**	**5**	**6**
Tree canopy cover (LAI)/*sklop krošnji (LAI)*	3 (3.91)	1 (2.59)	3 (4.13)	1 (2.34)	3 (3.81)	2 (3.41)
Shrub canopy cover/*pokrovnost grmlja*	2	0	1	0	0	2
Ground flora cover/*pokrovnost prizemnog bilja*	2	3	2	3	3	1
Leaf litter cover/*količina listinca*	3	3	3	1	2	1
Habitat complexity scores/*vrijednosti kompleksnosti staništa*	10	7	9	5	8	6

In each of the six plots, the number of vascular plants species was recorded on successive visits during the season (March – October). Data on canopy openness and LAI, as indirect estimators of available under story light, were measured using hemispherical photographs (as described in Jelaska 2004 and Jelaska et al. 2006) and analyzed with Gap Light Analyzer (GLA) software (Frazer et al. 1999).

Soil samples were collected twice during this investigation, at the beginning of the season in March 2001 and in May 2002. Four samples of the top 10 cm of soil were collected from each plot, after removal of the litter. Samples were diagonally placed across the plot, at 14 m intervals following general scheme in Scholz et al. 1994. To determine the percentage of organic matter, 10 g of soil was ashed at 400ºC. All environmental variables are displayed in Table 1.

Carabid Beetles and Ants Sampling – *Uzorkovanje trčaka i mrava*

Carabid beetles and ants were collected in 16 pitfall traps on each plot, placed in a regular rectangular net with cell size of 10 x 10 meters placed five meters from the edges of the plot. Altogether, 96 pitfall traps were exposed through the investigation period. Traps were filled with ethanol (96%), acetic acid (9%) and water in equal proportions and emptied every two to three weeks from March 2001 to April 2002. Carabids and ants were identified using specialized keys (Collingwood 1979, Agosti and Collingwood 1987, Trautner and Geigenmüller 1987, Hůrka 1996, Freude et al. 2004 and Seifert 2007). According to Andersen et al. (2002) ants were classified in four functional groups. Based on personal measurements of carabid specimens and data from Hůrka (1996) and Freude et al. (2004), average body size for analyzed species were classified into three categories: (1) small (4–8 mm); (2) medium (8–21 mm); and (3) large (22–40 mm) using a size distribution graph.

Data Analyses – *Analiza podataka*

The total abundance and species richness of ants and carabids was determined for each habitat (i.e. plot). The Shannon-Wiener and Sørensen indices (Krebs 1989) were calculated for all plots to assess ground beetles and ants' diversity and similarity using Programs for Ecological methodology Ver. 5.2 (15-III. 2000). Sørensen similarity values between plots were used in cluster analyses with the Euclidean distance as distance measure and single linkage as linkage rule for constructing dendrograms using STATISTICA 6.1 (StatSoft Inc. 2003). We compare habitat complexity scores, plant species richness and measured environmental variables (soil organic matter, slope, aspect and elevation) with data about richness and abundance of ants and carabids, ant functional groups and carabids body size distribution patches using Pearson Product Moment correlations in STATISTICA 6.1 software.

RESULTS – Rezultati

A total of 9288 beetles and 2958 ants belonging to 43 and 20 species, respectively, were trapped (Table 3). The number of captured species per plot varied from 17 to 27 for carabids, and from 5 to 14 for ants. *Abax parallelepipedus*, *Abax paralellus, Aptinus bombarda*, *Carabus violaceus* and *Cychrus attenuatus* were carabids found at all surveyed plots (Table 3). Only one ant species *Myrmica ruginodis* was found at all plots, unlike *Crematogaster schmidti*, *Camponotus herculeanus*, *Formica gagates* and *Formica rufa* recorded at single plot (Table 3). Ant species richness was negatively associated with carabid richness per plot (r = -0.86; *p* = 0.029), opposite to the trend for their abundance (r = 0.85; p = 0.031).

Table 3 Carabid and ant species with number of specimens per plot. Plot number corresponds to those in Figure 1
Tablica 3. Vrste i brojnost jedinki trčaka (Carabid) i mrava (Ant) na istraživanim plohama. Broj plohe odgovara onome na slici 1.

Carabid species/*Plots*	**1**	**2**	**3**	**4**	**5**	**6**
Abax carinatus (Duftschmid 1812)	156	23	2		1	26
Abax ovalis (Duftschmid 1812)			1	3	37	1
Abax parallelepipedus (Piller & Mitterpacher 1783)	654	89	328	5	61	50
Abax parallelus (Duftschmid 1812)	498	2	283	1	145	136
Agonum gracilipes (Duftschmid 1812					1	
Platynus scrobiculatus (Fabricius 1801)					1	19
Amara aenea De Geer 1774	3	2	1	1		
Aptinus bombarda (Illiger 1800)	1108	4	11	3	213	45
Bembidion lampros (Herbst 1784)			1			
Bembidion deletum Audinet-Serville 1821				1		
Carabus convexus Fabricius 1775	445	343	362	1		
Carabus coriaceus L. 1758	34	23	82	2		10
Carabus gigas Creutzer 1799	16	5				1
Carabus intricatus L. 1761	132	49	78		1	3
Carabus irregularis Fabricius 1792				72	85	12
Carabus nemoralis O. F. Müller 1764	636	379	52		15	6
Carabus praecellens Palliardi 1825	18	3	2	24	35	
Carabus ulrichii Germar 1824	548	29	100		52	8
Carabus violaceus L. 1758	23	168	43	29	35	63

Cychrus attenuatus (Fabricius 1792)	43	221	70	44	99	43
Cychrus caraboides (Linnaeus 1758)				5	1	
Dromius fenestratus (Fabricius 1794)					3	
Harpalus atratus Latreille 1804			1			
Harpalus marginellus Dejean 1829		2				
Harpalus laevipes Zetterstedt 1828				1		
Harpalus dimidiatus (P. Rossi 1790)						1
Leistus piceus Frölich 1799				5	3	1
Leistus rufomarginatus (Duftschmid 1812)	3		1	1	62	67
Licinus hoffmannseggii (Panzer 1803)			2	23	83	3
Molops elatus (Fabricius 1801)				9	27	4
Molops piceus (Panzer 1793)	20		27	5	1	37
Nebria brevicollis (Fabricius 1792)						1
Notiophilus biguttatus (Fabricius 1779)				1	5	1
Notiophilus rufipes Curtis 1829	23	3	1			
Platyderus rufus (Duftschmid 1812)				4	24	
Pseudoophonus rufipes (De Geer 1774)	1					1
Pterostichus anthracinus (Illiger 1798)						1
Pterostichus fasciatopunctatus (Creutzer 1799)				2		11
Pterostichus oblongopunctatus (Fabricius 1787)				121	120	
Pterostichus transversalis (Duftschmid 1812)				5	7	79
Stomis rostratus (Sturm in Duftschmid 1812)			1	1		
Synuchus vivalis (Illiger 1798)		1		4		1
Trechus cardioderus Putzeys 1870				1		
Number of species/*broj vrsta*	18	17	21	27	26	26
Number of specimens/*broj jedinki*	4350	1346	1449	374	1117	631
Ant species/*Plots*	**1**	**2**	**3**	**4**	**5**	**6**
Aphaenogaster subterranea (Latreille 1798)	57		4			9
Camponotus fallax (Nylander 1856)	2					
Camponotus herculeanus (Linnaeus 1758)				2		
Camponotus ligniperda (Latreille 1802)		11	144	4	7	
Crematogaster schmidti (Mayr 1853)	26					
Dolichoderus quadripunctatus (Linnaeus 1771)	8	1	1			1
Formica fusca Linnaeus 1758	14	18	1			
Formica gagates Latreille 1798	22					
Formica polyctena Förster 1850		154				1
Formica rufa Linnaeus 1758			2			
Lasius brunneus (Latreille 1798)	14	65	11		2	91
Lasius citrinus Emery 1922					1	1
Lasius emarginatus (Olivier 1792)	629	180	4	1		3
Lasius fuliginosus (Latreille 1798)	1			3		1
Myrmecina graminicola (Latreille 1802)	28	16				
Myrmica ruginodis Nylander 1846	50	244	127	199	54	156
Myrmica sabuleti Meinert 1861		4	2			
Prenolepis nitens (Mayr 1853)	135	11				
Stenamma debile (Förster 1850)	6	10	17			35
Temnothorax crassispinus (Karavajev 1926)	134	44	165		2	20
Number of species/*broj vrsta*	14	12	11	5	5	10
Number of specimens/*broj jedinki*	1126	761	478	209	66	318

No significant correlations were found between plant richness and arthropod diversity. Habitat complexity scores were positively correlated with carabid and ant abundances and ant species richness, but negatively correlated with carabid species richness (Table 4). Of the four environmental variables assessed by scoring method, shrub and leaf litter cover were positively correlated with ant species richness and carabid abundance. Large negative correlations were found between carabid richness and litter cover (-0.90, $p = 0.015$).

Table 4 Correlation coefficients between ant and carabid assemblages and habitat variables
Tablica 4. Koeficijenti korelacije između sastava mrava i trčaka sa stanišnim čimbenicima

Habitat variables / *stanišne varijable* Community features / *osobine zoocenoza*	Habitat complexity score / *kompleksnost staništa*	Plant richness / *broj biljnih vrsta*	Altitude / *visina*	Aspect (northness)	Organic matter / *organska tvar (%)*
Ant richness / *broj vrsta mrava*	r=-0.59 p=0.220	r=0.20 p=0.701	*r=-0.95* *p=0.004*	*r=-0.85* *p=0.033*	*r=-0.86* *p=0.029*
Carabid richness / *broj vrsta trčaka*	r=-0.62 p=0.192	r=0.04 p=0.946	*r=0.84* *p=0.035*	*r=0.87* *p=0.024*	r=0.57 p=0.239
Ant abundance/ *abundancija mrava*	r=0.60 p=0.211	r=0.34 p=0.503	*r=-0.89* *p=0.017*	*r=-0.92* *p=0.010*	r=-0.78 p=0.068
Carabid abundance / *abundancija trčaka*	*r=0.82* *p=0.044*	r=0.66 p=0.157	r=-0.80 p=0.058	*r=-0.85* *p=0.031*	r=-0.80 p=0.057
Ant Shannon indeks / *Shannon indeks mrava*	r=0.42 p=0.407	r=-0.05 p=0.918	*r=0.87* *p=0.024*	r=-0.70 p=0.122	r=-0.74 p=0.095
Carabid Shannon indeks / *Shannon indeks trčaka*	r=-0.25 p=0.637	r=0.15 p=0.780	r=0.44 p=0.388	r=0.73 p=0.102	r=0.14 p=0.788

There was no correlation between the heterogeneity of vegetation structure and plant species richness. Habitat complexity was negatively correlated with altitude ($r = -0.70; p=0.12$) and with aspect ($r = -0.77; p = 0.074$). The same trend was found for ant richness, abundance and diversity indices for ants' communities (Table 4). Carabid species richness was positively correlated with altitude and aspect, opposite to carabids abundance and ant assemblages (Table 4). Large and small bodied species showed opposite trends in their distribution across investigated sites. Large carabids were positively correlated with leaf litter cover ($r = 0.81$, $p = 0.05$). Small carabids positively correspond with higher altitude ($r = 0.89$, $p = 0.018$).

The most abundant carabids were *A. parallelepipedus*, *A. paralellus, A. bombarda*, *C. nemoralis* and *C. ullrichi* (Table 3) respectively, accounting for 37.16% of the total catch. The highest number of specimens, comprising 47.11% of all specimens, was captured in the most complex site (plot 1), though this plot recorded almost the lowest number of species (i.e. 18, as compared to the minimum of 17 on plot 2). On the contrary, the highest number of carabid species (27) was recorded on plot 4 (with the lowest habitat complexity score) but with the lowest abundance making only 4% of captured specimens.

The highest number of ant species (14) and abundance (1126 specimens) was recorded on plot 1. The lowest number of ant species and their abundance was recorded on plots 4 and 5. 45% of them are woodland species and only 10% of sampled species prefer open habitats. The rest of them occur in both woodland and open habitats. Analyzing the functional groups, according to Andersen (1997), 65% of recorded species (13 species) are cold climate specialists (CCS), 3 species are opportunists (O), 3 of them are subordinate camponotini (SC) and 1 species belong to generalized Myrmecinae (GM). Presence of species representatives of all four groups were recorded on plot 1, only. *M. ruginodis* (opportunist) that was found on all plots had the highest abundance in the low complexity areas (plots 2 and 5). The abundance of opportunist ants was negatively correlated with canopy cover ($r = -0.91$, $p = 0.05$). High correlations were found between ant abundance and richness with the amount of organic matter in the soil (Table 4). Organic matter content in the soil rise with higher altitude ($r = 0.9$, $p = 0.012$).

Cluster analyses of species composition on plots revealed differences in carabid assemblages between the southern (plots 1, 2, 3) and northern slopes (plots 4, 5, 6) of Mt. Medvednica (Figure 2). Some species such as *Carabus convexus*, *Notiophilus rufipes* and *Carabus intricatus* were found exclusively on the southern slope of mountain, unlike *Carabus irregularis*, *Notiophilus biguttatus*, *Molops elatus*, *Platyderus rufus* and all of the collected species of the genus *Pterostichus,* which were recorded exclusively on northern slope of the mountain. There was also a significant difference in number of collected ants on southern and northern slopes (2365 on south, 593 on north). Cluster analyses using Sørensen indices based on ants' species composition, separate the two highest plots, 4 and 5, from others (Figure 3). An ant species *C. herculeanus* is recorded for plot 4, which is 970 m high and has northern exposure. *C. herculeanus* has altitudinal range from 1000–1700 m, and boreal mountain distribution, with a very restricted area. It prefers coniferous mountain forests and can withstand very low temperatures, 38.5 ºC below zero (Seifert 2007).

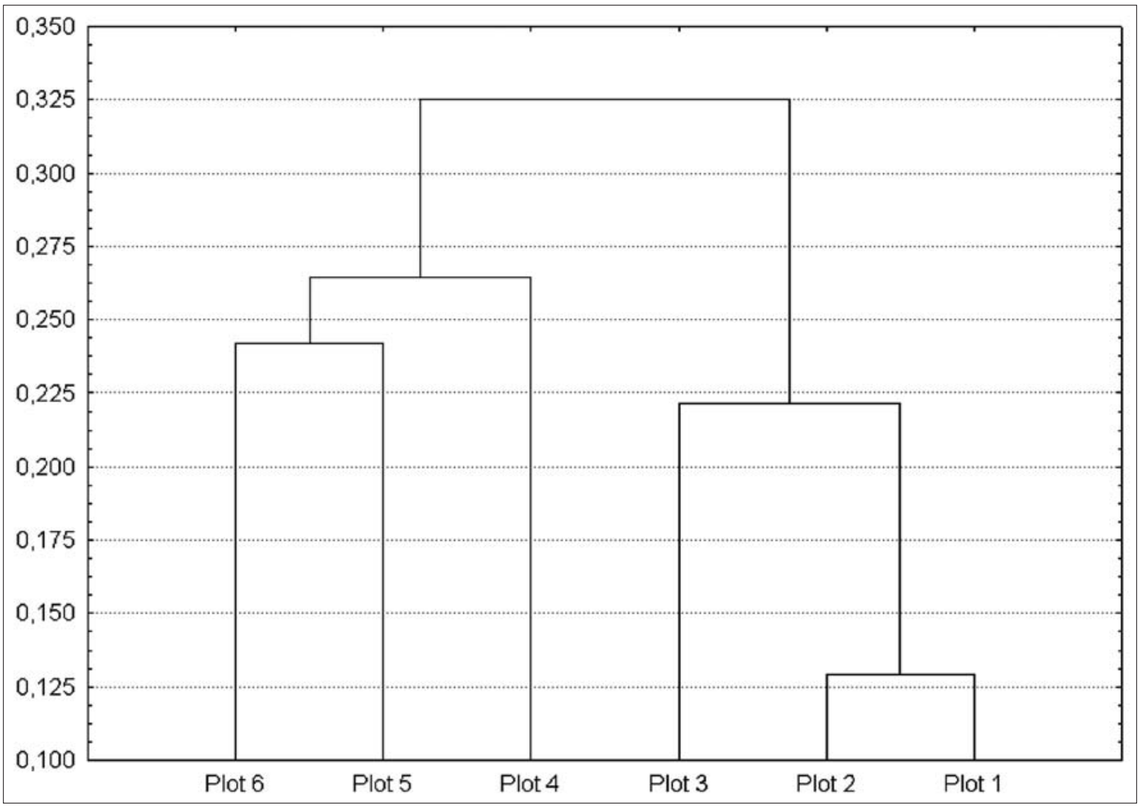

Figure 2 Tree diagram of cluster analyses using Sørensen indices based on carabid species composition in investigated plots as similarity measure. Numbers on X axes denote investigated plots

Slika 2. Dendrogram sličnosti istraživanih ploha koristeći Sørensen indeks ovisno o prisutnosti vrsta trčaka tijekom razdoblja uzorkovanja. Broj na osi X označava plohe

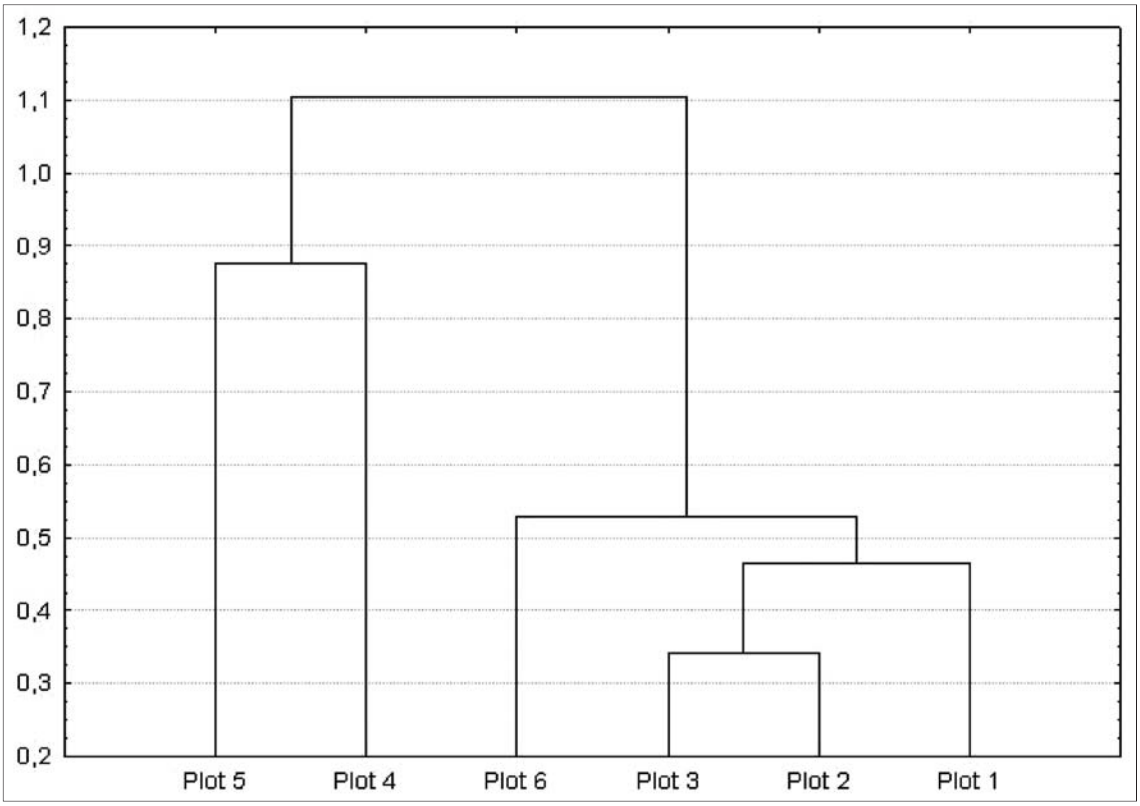

Figure 3 Tree diagram of cluster analyses using Sørensen indices based on ant species composition as similarity measure. Numbers on X axes denote investigated plots

Slika 3. Dendrogram sličnosti istraživanih ploha koristeći Sørensen indeks ovisno o prisutnosti vrsta mrava tijekom razdoblja uzorkovanja. Broj na osi X označava plohe

DISCUSSION – Rasprava

The relationship between habitat features and diversity of ants and carabid beetles was analyzed. We recorded great differences in carabid species composition and abundance among plots, where carabid abundance, but not the richness, was significantly higher in habitats with higher complexity scores. Brose (2003a) showed that an experimental reduction of vegetation complexity reduced the activity-abundance of large carabid species. Our results supports "enemy-free space hypothesis" (Lawton, 1983) that prey species have more chances of escaping from natural enemies in dense vegetations. We found that large carabids prefer dense vegetation plots covered with leaf litter as enemy-free space.

Furthermore, carabid species richness was negatively correlated with ant species richness. The results of ant richness analyses differ from those of Lassau and Hochuli (2004), but not those analyzing functional groups where they also found the largest abundance of opportunist species in low complexity sites. Stephens and Wagner (2006) have found that species richness, diversity, and dominance were a less satisfactory measure of various forest management impacts on ants than functional group analysis.

The highest number of ant species (14) and abundance (1126 specimens) was recorded on plot 1, and the lowest number of the species and their abundance on plots 4 and 5. This result was in accordance with their habitat preferences. Ants in general, with exception of a few cold-temperate species, are thermophilic animals, and function poorly below 20 ºC and not at all below 10 ºC (Hölldobler and Wilson, 1994). Greater abundance and species number in lower altitudes can be explained, in addition to temperature, with precipitations, thickness and volume of leaf litter and available food resources (Brühl et al. 1999).

The highest Shannon-Wiener index for carabid diversity (Table 5) was recorded on plot 5, situated in the *Chrysanthemo macrophylli–Aceretum pseudoplatani* forest, with high concentration of soil organic matter as a consequence of the longer persistence of snow-cover and hence higher soil humidity and a shorter micro-organism activity period. The herbaceous layer of this forest is characterized by nitrophilous plant species e.g. *Lunaria rediviva* L.*, Urtica dioica* L.*, Corydalis solida* (L.) Swartz, etc. The impact of leaf litter origin on carabids has also been reported by Niemelä et al. (1992), Koivula et al. (1999) and Magura et al. (2005), in which the latter two authors observed significant impact of leaf litter on certain species e.g. *Pterostichus oblongopunctatus* and *C. caraboides.* In this study, both above mentioned species were found only on plots 4 and 5, which had the highest soil organic matter content. Soils in cooler climates commonly have more organic matter because of slower decomposition rate (Bot and Benites 2005).

Table 5 Shannon-Wiener (H') indices, numbers of equally common species (N) and Smith & Wilson evenness (S&W) for investigated plots

Tablica 5. Shannon-Wiener (H') indeksi raznolikosti, broj zajedničkih vrsta (N) te Smith & Wilson jednolikost (S&W) trčaka (carab.) i mrava (ants) na istraživanim plohama

Plots /	1		2		3		4		5		6	
Indices	carab.	ants	carab.	ants	carab.	ants	carab.	ants	carab.	ants	carab.	ants
H'	3.049	2.262	2.724	2.585	2.951	2.074	3.201	0.366	3.711	0.977	3.625	1.936
N	8.27	4.80	6.61	6	7.73	4.21	9.19	1.29	13.10	1.97	12.34	3.83
S&W	0.138	0.26	0.153	0.39	0.128	0.322	0.291	0.22	0.182	0.293	0.218	0.295

On plots 1, 2 and 3, smaller number of species was recorded, while plots 4, 5 and 6 had a higher number of species with a low abundance, indicating less structured arthropods communities without dominant species. Also, cluster analyses of species composition on six plots divided carabids based on aspect and ants species based on elevation of investigated plots.

Ant and carabid diversity and species body size distribution highly correlate with altitude and aspect (expressed as northness). On warmer, more south exposed plots (plots 1, 2 and 3) smaller number of carabid species was recorded. On the contrary, plots on northern slopes (plots 4, 5 and 6) had a higher number of species with a smaller number of specimens. Salgado et al. (1997) reported similar findings in their research of deciduous oak forests, where 10 of 42 species represented 90% of the total catch on five plots. They recorded a smaller number of species on plots with higher abundance of specimens and those with smaller abundance and larger number of species, the latter having unstable climatic conditions. In this study, plot 1, with recorded capture of 47.11% of the total catch, is situated at the lowest altitude with southern exposure, thereby ensuring more stable and warmer climate conditions that enable formation of ground beetle communities with the dominant and co-dominant species present (e.g. *A. bombarda, A. parallelus, A. parallelepipedus, C. ullrichi, C. nemoralis, C. convexus* and *C. intricatus*; Table 3). The highest number of carabid species, but the lowest abundance was recorded at the highest altitude (plot 4) with the lowest habitat complexity score. Flightless forest specialist such as *C. caraboides* that preferred higher elevations and lower temperatures and *C. irregularis* are distributed on top of the mountain with a small number of individuals on the northern plots. Geomorphologic and climatic conditions, large habitat complexity and very low disturbances in plot 1, contribute in forming more stable carabid and ant communities. Community composition can be used to indicate broader aspects of habitat quality and more general changes (i.e. degradation and recovery following stress or disturbances), (Hodkinson and Jackson 2005). High abundance of carabids but low richness at the warmer plots could suggest competitive exclusion confirming that habitat stability may have unimodal effect on richness. The intermediate disturbance hypothesis predicts that diversity will be greatest when physical disturbances prevent competitively dominant species from excluding other species from the community. At the low level of disturbances, diversity is low because only the best competitors persist and competitive exclusion leads to species loss at either end of the disturbance continuum (Death and Winterbourn 1995). Stephens and Wagner (2006) found that different ant functional groups were dominant under different levels of disturbance intensity.

Data about species richness and habitat complexity within undisturbed forest systems with low direct anthropogenic impacts can be used as reference data for environmental monitoring of changes in temperate forests. Knowledge on how management of forests relates to forest carabids and ants diversity is poorly documented in Croatia. We found that ant functional groups and carabids body size analyses respond well to differences in habitat complexity. These results confirm the need for sustainable forest management that will preserve higher level of habitat complexity that provide more niches and environmental resources for exploitation and thus support dominance of larger carabids and high animal biomass. Furthermore, carabids and ants may serve as target groups in climate change risks assesment in mountain ecosystems.

ACKNOWLEDGEMENTS – Zahvala

Grateful thanks to Gregor Bračko for helping us in species determination. This study was financed by Croatian Ministry of Science, Education and Sports (Grants 0119-123, 119-1193080-1206 and 119-0000000-3169).

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SAŽETAK: Ovim istraživanjem željeli smo utvrditi razlike u sastavu te morfološkim i ekološkim značajkama trčaka i mrava u različitim šumskim staništima na području Parka prirode Medvednica. Kako bi kvantificirali razlike između istraživanih područja, odredili smo raznolikost strukture prisutne vegetacije te raznolikost biljnih vrsta na šest ploha. Značajke kao što su pokrovnost drveća, grmlja, prizemnog bilja te listinca na svakoj plohi, koristili smo u mjerenju kompleksnosti strukture staništa. Strukturna kompleksnost staništa opadala je s nadmorskom visinom. Mravi i trčci uzorkovani su metodom lovnih posuda.

Bogatstvo vrsta mrava pozitivno je korelirano s kompleksnošću staništa, posebice s količinom listinca, za razliku od trčaka. Veći udio mrava koji su ekološki oportunisti zabilježen je u otvorenijim staništima sa slabije izraženom heterogenom strukturom staništa, za razliku od trčaka kod kojih veličina tijela korelira s kompleksnošću staništa. Stabilnija struktura zajednica trčaka s većom brojnosti dominantnih vrsta na plohama smještenim na nižoj nadmorskoj visini može se objasniti kompetitivnim isključivanjem, kao posljedicom stabilnijih ekoloških uvjeta u odnosu na plohe smještene na vrhu planine. Vrste koje su prilagođene hladnijim klimatskim uvjetima te nastanjuju zasjenjena područja na višim nadmorskim visinama, kao što su beskrilne vrste trčaka, specijalisti Cychrus caraboides *i* Carabus irregularis*, te boreo-montana vrsta mrava* Camponotus herculeanus*, zabilježene su na najvišim nadmorskim visinama i sjevernim ekspozicijama Medvednice. Neke od ovih vrsta ne nastanjuju niža područja, te u slučaju uništavanja povoljnih staništa njihov opstanak na Medvednici može postati ugrožen. Jedan od razloga može biti i uslijed klimatskih promjena koje utječu na visokoplaninske vrste hladnijih područja. Sveukupni rezultati ovog istraživanja ukazuju na potrebu očuvanja složene strukture šumskih staništa, posebice na vršnim dijelovima Medvednice.*

Ključne riječi: biološka raznolikost, struktura vegetacije, listinac, nadmorska visina, očuvanje prirode, šumsko stanište