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Soil and habitat preferences of ground beetles (*Coleoptera, Carabidae*) in natural mountain landscape

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The distribution of ground beetle assemblages along an elevation gradient in the Bieszczady National Park (East Carpathians) was investigated. A principal component analysis of the spatial patterns of ground beetle assemblages clearly differentiated groups of species from various elevation zones. Forward selection of explanatory variables in redundancy analysis also indicated that the majority of the variation of species can be described by elevation and presence of vegetation zones (beech wood and alpine meadow). The close relationship between the empirical species richness and those predicted from a mid-domain effect proved the fit to the geometric null model, explaining 73% of the species variance.

Key words: *Carabidae*, soil decomposition, elevation, mid-domain, Bieszczadzki National Park

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INTRODUCTION

The potential influence of climate changes on terrestrial ecosystems has been recently taken into consideration by scientists (Walker & Steffen 1999). Temperature and precipitation have been shown to relate directly to soil organic matter content (Dai & Huang 2006), so this parameter is regarded as a good indicator of warming trends (Franz 1990). The dynamic of the soil carbon storage depends on the intensity of carbon input to soil by net primary production and carbon flow out by soil organic matter decomposition. A good model system reflecting the outcome of multiple interacting environmental factors combined in one local system, where the temperature and precipitation decrease simultaneously, is the elevation gradient (Gartenet al. 1999, Körner 2000).

Together with climatic changes, elevation diversity patterns can be distinguished (Lawton 1999, Whittacker et al. 2001). In one group of studies, the species richness declines along the elevational gradient (MacArthur 1972, Lawton et al. 1987, Stevens 1992, Rahbek 2005). However, hump-shaped distributions with the species richness peak at mid-elevations are pointed out as more common (Colwell & Less 2000, Zapata et al. 2003).

There are many mechanism responsible for such a distribution (for reviews see McCoy, 1990; Rahbek 1995, 2005, Sanders 2002), but climate and productivity (Grytnes 2003, Wang et al. 2009), area (Rahbek 1995, Sanders 2002, Bachman et al. 2004, Herzog et al. 2005) and geometric constraints (Sanders 2002, Bachman et al. 2004,) are the most important.

Hodkinson & Jackson (2005) suggested that terrestrial invertebrates are good tools for monitoring environmental changes in mountain ecosystems. Among them ground beetles play a very important role (Hodkinson 2005). They are usually regarded as bioindicators of broad scale of environmental changes (Rainio & Niemela 2003) and important elements of terrestrial ecosystems (Thiele 1977). There is however still literature concerning the altitudinal gradients of ground beetle diversity patterns. Climatic variables and altitude appear to be poor predictors of carabid distribution (Eyre et al. 2005). In alpine zones, species richness poorly described the deglaciated areas and the species composition depended indirectly on the age of the habitat (Gobbi et al. 2007).

However, first of all we must answer the question which factors and how they determinate ground beetle distribution under natural conditions. A good example of such an investigation may be the carabid assemblages occurring in the Bieszczady Mts (East Carpathians). This territory in the middle of Central Europe is very sparsely populated (no more than 2 people per sq km) with very well developed climatic zones. Moreover, in this region many endemic and relict species are concentrated (Rizun & Pawłowski 1998).

The aim of the presented study is to test community responses to habitat heterogeneity in a mountain landscape. We will try to extract environmental factors accounting for the distribution of particular species as well as community structure indices.

MATERIAL AND METHODS

Eight localities, differing in soil and vegetation properties were selected (table 1) along a transect between Mt Wielka Rawka and Mt Połonina Caryńska in the Bieszczadzki National Park (South-Eastern Poland) (fig. 1). The investigated transect lies within two climatic belts: the moderately cool one with the MAT between +6 °C and + 4 °C and the cool belt with the MAT from + 4 °C to + 2 °C (Hess 1965). The vegetation of the area also shows vertical variability connected with the climatic belts, though in many places its natural character has been significantly disturbed by human activity. To an altitude of 1150-1200 m a.s.l. grow lower mountain beech forests *Dentario glandulosae-Fagetum* and *Luzulo nemorosae-Fagetum*, above which the characteristic low shrubs of green alder (*Alnus viridis*) occur. Above, to an altitude of 1200-1220 m a.s.l., extend high-mountain meadows (połoninas) dominated by grass communities of *Calamagrostion* and blueberry communities of *Vaccinietum myrtylli gentianetosum*. In certain places, due to long-term human activity, (e.g. around Wyżniański Wierch) the former lower montane forest was transformed into arable land, now being a pastureland (*Campanulo serratae-Agrostietum capillaris*).

Soil properties (Table 1) were analyzed using common pedological methods. pH (in 1 M KCl) was determined on air-dried samples of fine earth using a soil/solution ratio of 1 : 2.5. The concentration of organic carbon (%C) was determined

Table 1. Habitat characteristics of the investigated localities

Locality	Soil unit	Vegetation	Succession stage	Ectohumus class	Altitude m a.s.l.	Exposure	Gradient of exposure	Slope (°)	pH (H_2O) in A	pH (KCl) in A	C/N in horizon A	% C org in horizon A	Decomposition rate
1	*Endoleptic Cambisol (Humic, Orthodystric, Skeletic)*	*Calamagrostion* with *Calamagrostis villosa*	2	2	1300	(N)	1	0	3,8	3,2	14	8,93	29,95
2	*Epileptic Folic Cambisol (Alumic, Humic, Skeletic)*	*Vaccinietum myrtylli gentianetosum*	3	3	1300	(N)	1	0	3,9	3,4	n.a.	4,4	32,43
3	*Endoleptic Cambisol (Humic, Orthodystric, Skeletic)*	*Luzulo nemorosae-Fagetum vaccinietosum*	4	1	930	(N)	1	5	3,6	2,9	15	17,9	21,78
4	*Endoleptic Cambisol (Humic, Epidystric, Skeletic)*	*Campanulo serratae-Agrostietum capillaris*	1	2	910	(E)	2	5	4,7	3,9	11	2,64	91,77
5	*Umbric Gleysol (Humic, Orthoeutric)*	*Dentario glandulosae-Fagetum allietosum*	4	1	1025	(S)	3	15	4,8	3,9	5	3,5	92,93
6	*Endoleptic Cambisol (Alumic, Humic, Skeletic)*	*Dentario glandulosae-Fagetum typicum*	4	1	1050	(S)	3	30	4,0	3,3	10	4,3	26,46
7	*Endoleptic Cambisol (Alumic, Humic, Skeletic)*	*Calamagrostion* with *Calamagrostis villosa*	2	2	1230	(S)	3	35	3,9	3,5	10	6,66	58,8
8	*Umbric Leptosol (Humic, Hyperdystric)*	*Vaccinietum myrtylli gentianetosum*	3	3	1250	(S)	3	10	4,2	3,8	9	7,93	30,6

using rapid dichromate oxidation techniques. Nitrogen determinations from samples were made using the Kjeldahl method (Bremner 1996). The measurements of the annual rate of cellulose decomposition were conducted using the cellulose filter method (Unger 1960 and Bieńkowski 1990). Cellulose filters were inserted vertically into the humus horizon at a depth of 0-8 cm. The measurements were conducted on cellulose filters (ø7 cm). The filters were boiled for 3 h in 2% KOH solution and rinsed to pH 7.0, dried at 105 °C, weighed and set on both sides of a glass plate in a bag made of polyethylene net mesh ø1 mm. After been taken out of the soil, the filters were boiled for 3 h in 2% KOH solution, rinsed to pH 7.0, dried at 105 °C, and weighed. Then the amount of ash was determined through combustion. The amount of decomposed cellulose was calculated from the difference between the net weight of the filter before insertion into soil and the filter net weight (ash considered) after the measurement (Drewnik 2006).

In the studied area, the soil cover (fig. 1) shows characteristics typical of mountain areas (Skiba et al. 1998), being controlled by bedrock as well as the vertical diversity of climate and vegetation. At the investigated localities soil profiles were exposed in pits and classified according to the WRB (IUSS Working Group WRB 2006).

Sampling was carried out during the vegetation season from May till September in 1999. Because of non-harm effect of collection in protected areas, on each locality a minimum number of pitfall traps (five cups, 10 cm deep, 6 cm diameter) filled with ethylene glycol was established in one row at regular 5 meter intervals (Thiele 1977). Pitfalls were emptied monthly, and the collected beetles were preserved in ethylene alcohol. On each locality six samples were taken.

Patterns in the distribution of ground beetle assemblages among the sites were analysed using indirect ordination (principal component analysis). Subsequently, a redundancy analysis was performed to explain the pattern of variability of ground beetle abundance in environmental gradients. Forward selection of explanatory variables in the RDA (ter Braak & Prentice, 1988) was used to determine the relative importance of particular environmental parameters.

The multivariate analyses applied in the study were performed with the software Canoco for Windows Version 4.52 (ter Braak & Šmilauer, 2003).

The mid-domain effect (MDE) of empirical ground beetle distribution along the elevation gradient was compared with a null model generated in the RangeModel 5.0 program (1000 simulations) (Colwell 2006). A significant correlation between these two sets of distributions of species richness will indicate a similarity in patterns.

RESULTS

During the field studies a total of 1314 specimens of carabid beetles belonging to 21 species were collected (table 2).

The Principal Component Analysis of the ground beetle communities described 65% of the total variance for the first two axes (Fig. 2). The first factor of the PCA explained 36.5% of environmental variance. It clearly separates the assemblages along the altitude gradient, from those of seminatural subalpine meadows (Loc_4), beechwood assemblages (Loc_3, Loc_5, Loc_6) towards assemblages above the timberline (Loc_1, Loc_2, Loc_7, Loc_8). Close relationships between assemblages of particular habitat type, even from opposite slopes of the valley, indicate that its spatial distributions don't affect composition patterns. Habitat type is in that case more influential. The second factor explained 29% of variance, separating assemblages along a succession gradient from natural beechwood stands towards open seminatural alpine meadows.

Table 2. Ground beetle occurrences in the investigated gradient in the Bieszczady National Park.

	Species/Locality	Abbreviation	1	2	3	4	5	6	7	8	Total
1	*Abax parallelepipedus*	A_parall			X		X	X			14
2	*Carabus linnei*	C_linnei	X	X	X		X	X	X	X	119
3	*Carabus auronitens*	C_auron			X		X	X			47
4	*Carabus cancellatus*	C_cancel				X			X		2
5	*Carabus glabratus*	C_glab	X	X	X	X	X	X	X	X	22
6	*Carabus obsoletus*	C_obsole	X	X		X	X	X	X	X	147
7	*Carabus violaceus*	C_violac	X	X	X		X	X	X	X	43
8	*Cychrus caraboides*	Cy_carab	X	X	X		X	X	X	X	37
9	*Cychrus attenuatus*	Cy_atten			X						1
10	*Harpalus latus*	H_latus			X			X		X	5
11	*Pseudoophonus rufipes*	Ps_rufi				X					1
12	*Molops piceus*	Mol_pice			X						10
13	*Pterostichus fossulatus*	Pt_fossul	X	X	X		X	X	X	X	183
14	*Pterostichus foveolatus*	Pt_foveol	X	X	X		X	X	X	X	522
15	*Pterostichus jurinei*	Pt_jurin		X			X	X	X	X	52
16	*Pterostichus melanarius*	Pt_melan				X					2
17	*Pterostichus burmeisteri*	Pt_burm					X	X	X		6
18	*Pterostichus unctulatus*	Pt_unctu	X	X	X		X	X	X	X	58
19	*Amara lunicollis*	A_lunico	X			X			X	X	36
20	*Amara famelica*	A_fameli							X		1
21	*Trichotichnus laevicollis*	Tri_laev		X				X	X	X	6

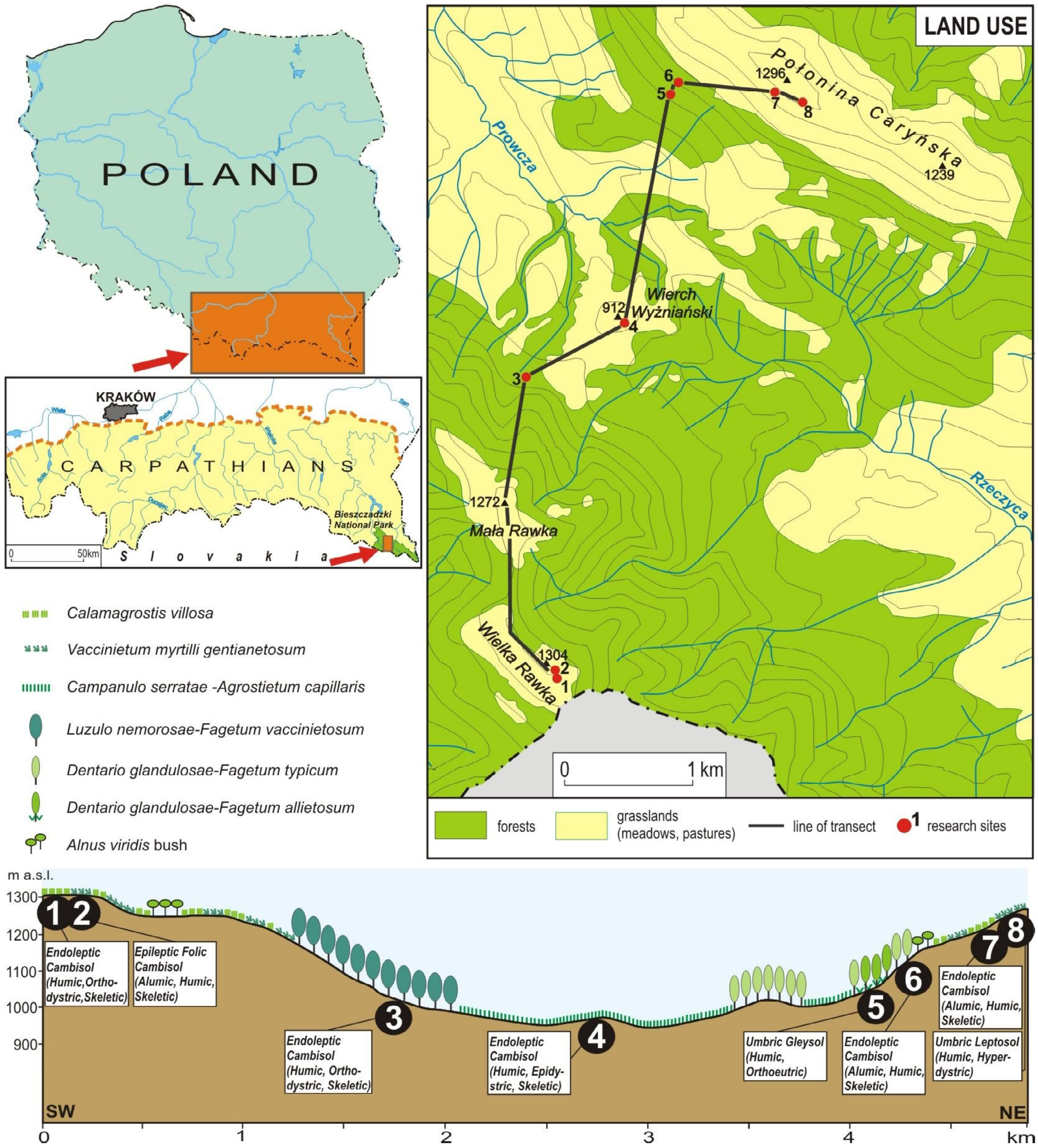

Fig. 1. Location, land use structure and transect line of study area in the Bieszczadzki National Park (*Source: based on Skiba et al. 1998, Drewnik et al. 1999*).

A redundancy analysis was subsequently used to determine the explanation of variation in the species distribution and environmental variables (Fig. 3). While all the variables characterising habitat conditions along the elevation gradient were considered in the analysis, the statistical procedure eliminated the former as having no significant influence on the observed variation of dependent variables. Forward selection of explanatory variables in the RDA identified three environmental factors that were significant in explaining a portion of the variation in species data. Namely, altitude ($\lambda = 0.29$), succession stage ($\lambda = 0.27$) and gradient of exposure ($\lambda = 0.15$), in consecutive three steps explained significantly 72% of species variance. The first ordination axis

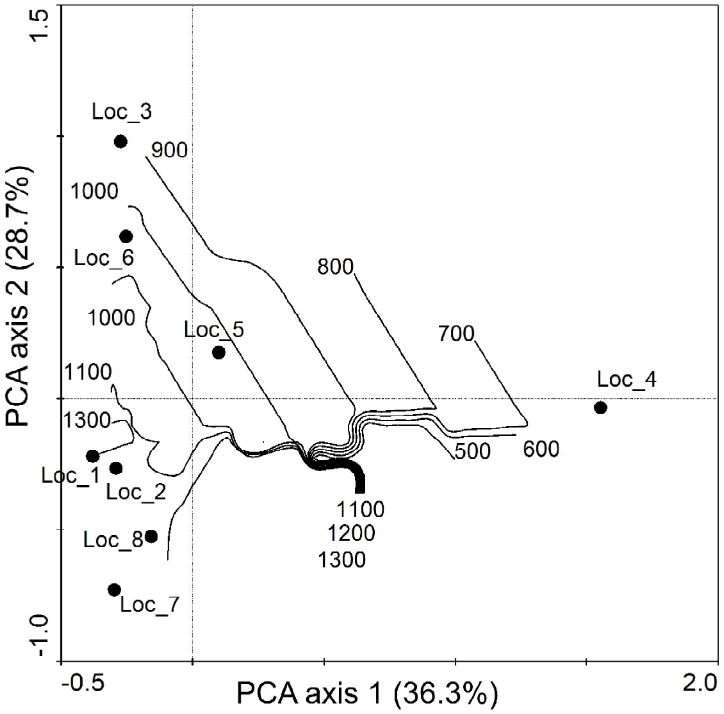

Fig. 2. Data attribute plot of ground beetle assemblages in respect to elevation ordinated by principal component analysis

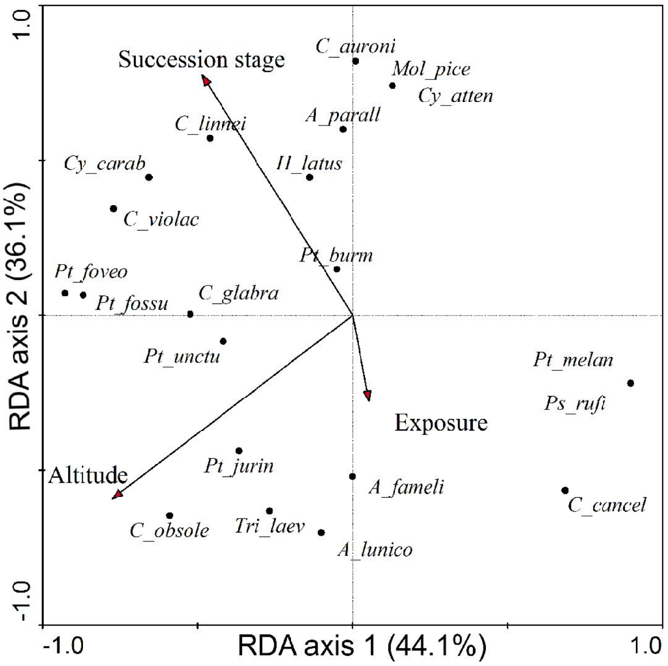

Fig. 3. Biplot of redundancy analysis with forward selection of explanatory variables , indicating the distribution of particular species along significant environmental factors (abbreviations of species names as in table 2)

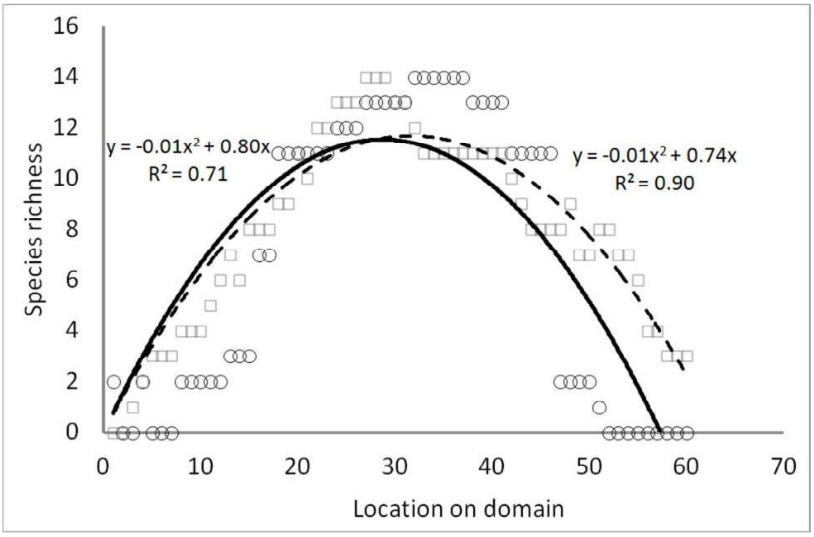

Fig. 4. Relationship between species richness, the mid-domain effect and elevation. Open circle and solid line show the number of species located in the domain, open squares and broken line show the expected number of species by the mid-domain effect.

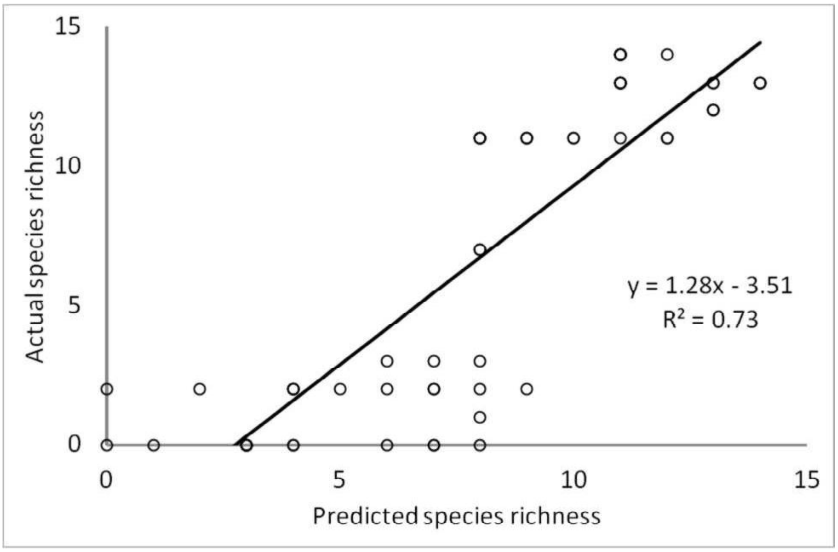

Fig. 5. Relationship between species richness predicted from mid-domain effect and actual species richness

explained 44.1% of variance of species-environment relationship, meanwhile the second one 36.1%. Altitude correlated significantly with the first axis (r = -0.77), and succession stage, reflecting woody habitats correlated with the second one (r = 0.78). Three groups of species could be distinguished (Fig. 3). The first one consisted of species from the highest elevations, mostly east carpathian endemits (C*arabus obsoletus*, *Pterostichus jurinei*), the second consisted mostly of woodland species from genus *Carabus* and *Pterostichus* with broader geographic distribution, the third one consisted of three species preferring open seminatural conditions (*Pt. melanarius, Pseudoophonus rufipes and Carabus cancelatus*). Surprisingly there wasn't any soil parameter which could significantly describe the ground beetle distribution.

The altitudinal gradient of species richness is typically hump-like. The interpolated line of empirical species richness distribution showed the maximum at mid-domain level (solid line) and explained 71% of species distribution variance (Fig. 4). The predicted species richness under the assumption of random range placement (mid-domain effect) showed a similar pattern of distribution (broken line). The close relationship between the empirical species richness and those predicted from a mid-domain effect proved the fit to the geometric null model, explaining 73% of the variance (Fig. 5).

DISCUSSION

The spatial pattern of species richness along an elevation gradient has long been known and is typical for many terrestrial taxa (Stevens 1992, Mc Coy 1990, Rahbek 1995, Fleishmann et al. 2000, Stevens 1992, Brehm et al. 2006, Colwell et al. 2009). Most frequent is a tendency for species richness to reach the maximum at mid-elevation (Colwell, Less 2000, Rahbek 2005). In the present study , a similar pattern of ground beetle distribution is visible (Fig. 4). The mid-domain effect is deffined as an increasing species ranges overlap towards the center of an elevation domain. Each domain has limits which can be physiographical or biological. In the present study the biological limits of two climatic belts reflecting a tree line zonation can be distinguished. These zones reflect quaternary glacial-interglacial cycles and dynamic of various biomes migration to this territory (Ralska-Jasiewiczowa et al. 206). The pollen analyses from theBieszczady Mts, show the phases of meadows created one group of assemblages. If the distribution of ground beetles will be gradual with decline of some species towards the top, we will have two patterns of elevations from different slopes. This thesis is also supported by forward selection of redundancy analysis (Fig. 3). The significant influence of altitude and succession stage, which reflects climatic changes from colder towards warmer climate and colonization by beech wood, explains the presence of different species groups. The species which are positively correlated with altitude (e.g. *Carabus obsoletus* or *Pterostichus jurinei*) are mostly endemic for alpine meadows located above the timber line (Rizun & Pawłowski 1998). They are relics of former colder climates which were pushed up by new colonizers from warmer periods (e.g. typical forest species as *Carabus linnei* or *Carabus auronitens*). If the amplitude of climatic changes will be higher, the forest species will colonize also the tops of the ridges.

The importance of the amplitude of climatic oscillations was emphasized by Dynesius & Janson (2000). They indicated that the amplitude of climatic changes, which depends also on latitude, is a main force of latitudinal gradients of diversity. The areas of higher amplitude have a higher rate of extinctions and more recent colonizers, however lower variation in the amplitude of climatic changes causes higher numbers of range-restricted endemic species (Jansson 2003). We also may expect that, if the climate will change and the temperature will increase, the forest line will also increase and entirely cover the summits. It will cause the extinction of alpine species preferring open habitats.

Recent stochastic models for species range shifts along elevation gradients are linked with climatic cycles and various rates of extinctions (Colwell & Rangel 2010). Mountain top extinctions during interglacials and lowland extinctions at glacial maxima favor mid-elevation lineages and the mid-domain effects becomes more realistic.

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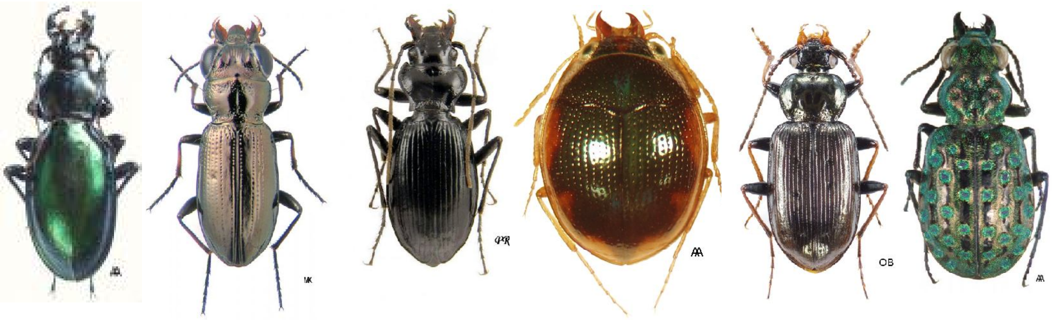
Welcome to amazing world of

Ground-Beetles (Carabidae, Coleoptera)!



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