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Carabid beetles - their significance for bioindication of the landscape hydrological regimen

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Carabid beetles are characterized by a high species diversity and an enormous ecological differentiation enabling them to occupy almost all types of terrestrial ecosystems. These properties qualify them as an extraordinarily suitable animal groups for bioindication of environmental state and changes. The paper includes a brief general characteristics of their ecological differentiation, of their relations to main abiotic and biotic factors managing their distribution and community forming, some remarks to their use in bioindication and a generalised scenario of structural changes in Carabid communities in floodplain ecosystem with special regard to floodplain forests. Finally several illustrative examples of Carabid communities affected in different way by humidity changes are presented and commented.

Introduction

Carabid beetles (about 22,000 species in the world fauna, among them almost 600 species occur in Central Europe) exhibit excellent bioindicative abilities not only due to their large species diversity but especially due to their enormous autecological differentiation enabling them to form richly structured communities in all types of terrestrial ecosystems occurring in holarctic region. In addition, identification of most Central European Carabid species is relatively easy, knowledge of their ecological properties is good (especially when compared with many other groups of insects) and their can be easily collected by highly comparable quantitative methods (mostly pitfall trapping).

These properties make possible using the Carabids for bioindication of environmental changes not only on a purely theoretical level, but also for obtaining information for practical purposes in landscape planning or assessment of environmental impacts of various human activities.

When compared with plants especially with the edicator woody plants, the of Carabids, similarly as many other animal groups, often indicate different changes in the ecotope properties earlier. So they are more suitable for indication of short-term changes or make possible, to certain degree, a prognosis of next development of the ecosystem studied.

The use of Carabids for such purposes goes back to mid-1950-ies, but rather numerous carabidologic papers dealing directly with bioindication or focusing on community structure changes in spatial or temporal patterns began to appear as late as by turn of 1960- and 1970-ies. Since that time Carabids have become one of the most used animal groups in different monitoring projects and environmental studies.

Ecological requirements and differentiation of Central European Carabids

The Central European carabids are mostly soil surface dwelling beetles living in litter or in upper soil strata. Few species live on the or shrub leaves (*Lebia* spp., some *Dromius* spp.) and one species lives obligatorily under tree bark (*Tachyta nana*) and two species in decaying wood (*Rhyssodes* spp.). Most species are almost exclusively monovoltine (two major groups of species have been distinguished according to timing of egg laying - the spring breeders and autumn breeders) and predominantly carnivorous, but in mountain condition some species tend to prolong their larval development to two years. A considerable part of species is panthophagous (e. g. *Harpalus* spp.) or secondarily purely phytophagous (e. g. *Amara* spp. *Zabrus* spp.). Four species (*Brachynus* spp.) are parasitoids of insect larvae. Morphoecological adaptations to extremely variable scale of habitat types led to evolution of

various life forms characteristic of species occupying the same or similar ecological niches. Many species are fully wingless or have strongly reduced or polymorphic wings. However, even the flying species use the fly mostly only during reproduction period or during sudden changes of habitat (e. g. a flood, disturbance by man or large animals). So the moving activity of Carabids is considerably reduced and their bounding to their habitat is very close. On the contrary, the predominant carnivory or panthophagy make them relatively independent on a concrete food resource.

Most important natural factors influencing community structure of Carabids

Occurrence of Carabids in a habitat and structure of their community depend predominantly on the interactions between abiotic factors and ecological requirements of individual species, on their dispersal power and on competence between other equally sized Carabids or other, mostly evertbrate, carnivores. Influence of these factors is briefly characterized below. A schematic characteristic of ecological requirements and distribution of some selected species using the geobiocoenological units (Zlatník, Raušer 1966) is presented in table 1.

Humidity

Probably the most important factor influencing forming of Carabids communities in various ecosystem types is humidity (Tab. 1). In individual species, their relation to humidity is manifested directly by a clear habitat preference. In spite of the fact that each species has, of course, its characteristic preference of its own, the Central European Carabids can be roughly classified into five ecological groups - (1) polyhygrophilous (two species are able to hunt even in standing water), (in tables 2 - 5 additionally characterised by numbers 4 and 5), (2) hygrophilous (in tables 2 - 5 additionally characterised by numbers 1 - 3), (3) mesohygrophilous, (4) xerophilous and (5) extremely xerophilous. The three first groups are very reach in species, while the two former groups are relatively poor in species because of the predominance of humid oceanic climate in Europe.

Vegetation character

The relation of Carabids to humidity is indirectly reflected, to a considerable degree, in their relation to vegetation character. In this regard, three major groups of species can be distinguished.

1. The first group (very rich in species) includes the species requiring habitat shadowing by a dense continuous tree vegetation. These species inhabit exclusively forests.
2. The second group (relative poor in species) includes species indifferent to shadowing.
3. The third group (relatively rich in species) consists of species preferring herbage vegetation, without presence of trees or shrubs, or even insolated places without any vegetation. These species inhabit, at present, almost exclusively fields, meadows, ruderals or river banks. The species of this group originate mostly from the narrow strips along water flows which were completely free of any vegetation or were grown only by high herbage vegetation. Occurrence of the most hygrophilous representatives of this groups, often also exhibiting other very specific ecological requirements, has been restricted on the immediate riparian strip. On the contrary, the less hygrophilous species inhabiting originally the drier tree-free, but herbage-covered parts of riverside terraces expanded enormously since the late Stone Age and agriculture beginning. The border between the s. c. forest and open-landscape species is, however, unsharp and strongly depends on the climate character of a landscape. E. g. the species behaving in Central Europe as characteristic and little tolerant forest species easily penetrate the large cities in Russia, open landscape in rainy North England or even in highlands of Central Europe, according to the landscape structure, may temporarily expand into the high grass stands of meadows before their mowing. These shifts in habitat preference confirm the primary role of humidity in preference for different vegetation formations.

Temperature (altitude and exposition climate)

Temperature is the third important factor determining distribution and community structure of Carabid communities. In the predominantly mountainous landscape of Central Europe (Alps, Hercynian)

Tab. 1
Schematic characteristic of ecological requirements and distribution of Central European Carabids according to vegetation tiers, trophical and hydric rows of the Zlatnikian geobiocoenological classification of natural forest geobiocoenoses.

Xero- or mesohygrophilous, steppiculous or silvicolous species	Vegetation tiers									Trophical rows				Hydric rows					
	1	2	3	4	5	6	7	8	9	A	B	C	D	1	2	3	4	5a	5b
<i>Ucinus cassideus</i> (Fabricius, 1792)																			
<i>Carabus hungaricus</i> Fabricius, 1792																			
<i>Zabrus spinipes</i> (Fabricius, 1798)																			
<i>Dyschirius rufipes</i> Dejean, 1825																			
<i>Cymindis exilis</i> (Fabricius, 1794)																			
<i>Carabus scabrinusculus</i> Olivier, 1795																			
<i>Platyderus rufus</i> (Duftschmidt, 1812)																			
<i>Carabus montivagus</i> Pallardi, 1825																			
<i>Ucinus depressus</i> Paykull, 1790																			
<i>Harpalus atratus</i> Latreille, 1804																			
<i>Leisidus rufomarginatus</i> (Duftschmidt, 1812)																			
<i>Carabus problematicus</i> Herbst, 1786																			
<i>Apinus bombarda</i> (Illiger, 1800)																			
<i>Carabus cancellatus</i> Illiger, 1798																			
<i>Abax parallelus</i> (Duftschmidt, 1812)																			
<i>Abax carinatus</i> (Duftschmidt, 1812)																			
<i>Pterostichus melas</i> (Creutzer, 1799)																			
<i>Carabus ulrichi</i> Germar, 1824																			
<i>Carabus nemoralis</i> O. F. Müller, 1764																			
<i>Carabus intricatus</i> Linnaeus, 1761																			
<i>Pterostichus ovoideus</i> (Sturm, 1824)																			
<i>Carabus convexus</i> Fabricius, 1775																			
<i>Carabus hortensis</i> Linnaeus, 1758																			
<i>Cymindis angulatus</i> (Gyllenhal, 1810)																			
<i>Carabus coriaceus</i> Linnaeus, 1758																			
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)																			
<i>Abax ater</i> (Villers, 1789)																			
<i>Abax ovalis</i> Duftschmidt, 1812																			
<i>Abax schweppeli</i> Germar, 1839																			
<i>Molops piceus</i> (Panzer, 1793)																			
<i>Molops elatus</i> (Fabricius, 1801)																			
<i>Carabus violaceus</i> Linnaeus, 1758																			
<i>Carabus scheideni</i> Panzer, 1799																			
<i>Carabus glabratus</i> Paykull, 1790																			

Table 1. continuation

Xero- or mesohygrophilous, steppiculous or silvicolous species	Vegetation tiers									Trophical rows				Hydric rows					
	1	2	3	4	5	6	7	8	9	A	B	C	D	1	2	3	4	5a	5b
<i>Cychrus caraboides</i> (Linnaeus, 1758)																			
<i>Carabus obscurus</i> Sturm, 1815																			
<i>Carabus irregularis</i> Fabricius, 1792																			
<i>Pterostichus bumelsteni</i> Heer, 1841																			
<i>Trichostichus laevicollis</i> (Duftschmidt, 1812)																			
<i>Carabus arcensis</i> Herbst, 1784																			
<i>Cychrus attenuatus</i> (Fabricius, 1792)																			
<i>Pterostichus foveolatus</i> (Duftschmidt, 1812)																			
<i>Pterostichus pilosus</i> (Host, 1789)																			
<i>Carabus auronitens</i> (Fabricius, 1792)																			
<i>Trechus pulchellus</i> Putzeys, 1846																			
<i>Trechus pilosus pilosus</i> Csiki, 1918																			
<i>Carabus innai</i> Panzer, 1810																			
<i>Trechus latus</i> Putzeys, 1847																			
<i>Leisidus piceus</i> Frölich, 1825																			
<i>Pterostichus unctulatus</i> (Duftschmidt, 1812)																			
<i>Pterostichus puniceus</i> (Dejean, 1828)																			
<i>Calathus metallicus</i> (Dejean, 1828)																			
<i>Nebria rufescens</i> (Stroem, 1768)																			
<i>Nebria jockischii</i> Hoepfner, 1826																			
<i>Carabus sylvestris</i> Panzer, 1796																			
<i>Pterostichus ruficornis</i> (Dejean, 1828)																			
<i>Pterostichus morio carpathicus</i> Kull, 1944																			
<i>Pterostichus neglensis</i> (Sturm, 1824)																			
<i>Deltomerus carpathicus</i> L. Miler, 1868																			
<i>Deltomerus tatricus</i> (L. Miler, 1869)																			
<i>Nebria tatrica</i> L. Miler, 1859																			
<i>Duvallius microphthalmus</i> Miler, 1859																			
<i>Pseudanopthalmus pilosellus</i> L. Miler, 1859																			

Symbols:

- rare occurrence
- ▒ subrecent (<1%)
- ▒ recent (1-2%)
- ▒ subdominant (2-5%)
- ▒ dominant (5-10%)
- ▒ eudominant (>10%)
- R - descends along rivers
- A - penetrates alluvia
- N - man-disturbed habitats
- Z - enormously strong population in 2dátse vřchy hills
- bold - Carpathian endemics

Vegetation tiers: 1 - oak, 2 - beech-oak, 3 - oak-beech, 4 - beech, 5 - fire-beech, 6 - spruce-fire-beech, 7 - spruce, 8 - mountain pine, 9 - alpine meadows.

Trophic rows: A - acid, B - normal, C - nitrophilous, D - calciphilous

Hydric rows: 1 - extremely xerophilous, 2 - xerophilous, 3 - mezoglyophilous (normal), 4 - rarely flooded, 5a - polyhygrophilous, flooded with stagnant water, 5b - polyhygrophilous, flooded with flowing water, 6 - polyhygrophilous oligotrophic (montane peat bogs).

system, Carpathians), it is manifested by a clear zonation of vertical distribution of species. Principally, three major groups of species can be defined (Tab. 1).

1. The species having their the existence optimum in lowlands in the beech-oak vegetation tier (RAUŠER & ZLATNÍK 1966), hence in the altitudes of about 200 m a. s. l.
2. The species having their distribution optimum in the areas of fire-beech vegetation tier, hence in the altitudes of about 800-900 m a. s. l. Some of these species are endemic of Central European mountain ranges.
3. The species having their optimum in the mountain pine vegetation tier, hence in the altitudes of about 1900-2000 m a. s. l. Most of these species are endemic.

Within all three groups, subgroups of the forest and ripicolous species exist. On the contrary, the typical open-landscape species are represented by a large number species only in the first group and by a considerably limited number in the second group.

Out of the above three groups of species, there is also a very limited number of thermophilous species in lowlands, which reach here their northern border of their geographic distribution or occurs here in extrazonal enclaves (e. g. the typically steppicolous *Carabus hungaricus* having a continuous distribution in steppes of South Ukraine and Russia). Their actual existence optimum lies in similar altitudes in South-East Europe.

Geological substrate

The fourth very important factor is geological substrate. It influences the Carabid communities in two ways.

1. Its direct influence is mediated by character of its weathering products. There are species obviously preferring the rough gravel or sandy substrates and species requiring fine sandy, loamy or even marshy substrates. Such a specialisation is especially typical of many ripicolous species, where a striking differences may occur between two close places. This specialisation may reach such a degree that a protective colouring imitating colour pattern of the rough sand produced by igneous rocks, in which they live, can arise (some East-Asian *Bembidion* species).
2. Its indirect influence is mediated by the substrate trophicity (Tab. 1). When compared with the poor acid or neutral rocks, the basic or nitrophilous rocks make possible a higher primary production of plants, herbivores, and consequently of carnivores, inclusively of the most Carabids. The substrate trophicity may have an enormous influence of population size of each species. The number of individuals may be several times higher on a lime stone or dolomite substrate than on a granite substrate. At the contact of land patches with basic and acid a sharp border between carabid communities may exist (e. g. ŠUSTEK & ŽUFFA 1986).

Dispersal power

The dispersal power of Carabids strongly varies according to the total or facultative reduction of wings or their full development. The wingless species are characteristic first of all of the stable conditions in oligo- and mezohygrophilous forests. Their re-immigration into a disturbed mezohygrophilous forests community strongly depends on presence of suitable biocorridors, or distance from suitable immigration sources or on a sufficient time for community reestablishment. On the contrary, the flying species predominate in unstable conditions in any wetland or floodplain ecosystem as well as in the man made arable land, city interiors, ruderals etc. The carabid communities in wetland ecosystems are very sensitive on small changes in humidity and they often leave them after small humidity fluctuation, but on other hand just the hygrophilous carabids, due to their ability to fly, are able to rapidly (re)constitute their communities in a newly arisen wetland ecosystem even in a very isolated position. An extreme example of such ability are communities of hygrophilous species at shores of small temporary lakes dispersed in Central Asian deserts. A similar situation can be observed in communities of the s. c. field or open landscape species which, however, originate mostly from the dry zones of riverside terraces.

Predation and competition

Some carabid species (e. g. *Abar* spp.) are known to have developed a kind of primitive maternal care at their eggs, but they are generally supposed to be unable to recognise their larvae. Therefore their larvae may become a prey not only of other predators, but even of the conspecific adults or mature larvae. So the population size of individual species may be considerably reduced. Mutual predation pressure may be observed between Carabids and small insectivores (*Sorex*, *Crocidura*), spiders, ants or staphylinids.

At the same time, populations of similarly sized Carabid species with similar ecological requirements may exhibit considerable fluctuations during several years, whereas their cumulative abundance and biomass are remarkably stabilised. This phenomenon reflects changes in food source repartition among individual species and the actual carrying capacity of the respective ecosystem.

General remarks to bioindication based on community structure

The proportion in which representatives of individual ecological groups form community in a concrete place depends on the altitude, exposition, geological substrate and degree of natural character and spatial parameters of an ecosystem and competition pressure of other species of similar size and trophic relations. Community in a natural, homogenous and sufficiently extensive area consist usually of representatives of species with similar ecological requirements or of species with a wide ecological tolerance. On the contrary, in a disturbed (irrespectively whether the disturbance is of natural or anthropogenous nature) ecosystem or in a heterogeneous patchy environment, the community(ies) consist(s) of representatives of a species mixture with very different ecological requirements. This mixture includes as the species preferring the original state or habitat conditions characteristic for one type of patches as the species preferring the probable final state of succession or conditions dominating on other type of patches. In addition representation of tolerant (indifferent) species may increase under such circumstances. Proportion in which representatives of one or other ecological group of species coexist reflect position of a community along the transition (succession) trajectory from one state to other. According to the local conditions, the same community structure may be interpreted as a degree of community degradation or regeneration. This interpretation depends only on the knowledge of the original and desired state of the community studied. In this situation, the role of the original state may be played as by a natural as by a man-made ecosystem. On the contrary, the desired state should converge to the potential natural state, which results (would result) from the pertinence to a biogeographical area and permanent ecotopic properties like altitude and exposition climate and geological substrate.

The natural character of a community structure can be determined only on the base of comparison of many communities in similar conditions, their gradual typification and, if possible, also analysis of their development in the past. In botany, several classification systems of plant communities have been developed. They supply a more or less reliable basis for bioindication studies. On the contrary, in zoology only attempts at community typification exist within the framework of individual animal groups and with a territorially limited validity. Elaboration of a general zoocenological classification systems is extremely difficult, because of very different methods of studying (collecting) representatives of individual animal groups, their migration and often hidden mode of life.

The abiotic and biotic factors described above may act in a very variable ways in relation to expected influence of different anthropogenous factors, whose impacts are mostly the objective of bioindication studies. They can weaken the anthropogenous factors or strengthen them. This fact is to be carefully taken in account when evaluating samples collected for bioindicative purposes, because a superficial analysis of data may give very misleading conclusion.

Brief characteristics of Carabid communities in natural floodplain forests and scenarios of their anthropogenous degradation

The Carabid communities in natural floodplain forests fluctuate between three theoretical states.

1. The first state is characteristic of the extensive habitats (stands of group of geobiocoens *Salici-Alneti*) with constantly high level of ground water where the flooding water intensively flow through the forests, transforms the soils surface and takes or transfers the litter and other organic materials. In such oligotrophic and mechanically disturbed, places the Carabid communities usually consist of about 30 species and their cumulative abundance moves from 300-1000 individuals per vegetation season and ten pitfall traps. The species spectrum is characterised by presence of a large spectrum of hygrophilous species, but the abundance of such species like *Pterostichus nigrita*, *Pterostichus antracinus*, *Platynus krynickii* and *Agonum moestum* (s. lat.) is very low or these are absent.
2. The second state is characteristic of the extensive habitats (stands of groups of geobiocoens *Ulm-Fraxineta populnea*, *Ulm Quercera* etc.) with constantly high level of ground water where the flooding water stagnates in forests during the flood and sedimentation processes enrich the soil by nutrients. In such eutrophic and disturbed habitats, the Carabid communities usually consist of 30-50 species and their cumulative abundance moves within a wide range of about 300 - 4000 individuals per vegetation season and ten pitfall traps. The species spectrum is characterised by presence of a large spectrum of hygrophilous species, the species like *Pterostichus nigrita*, *Pterostichus antracinus*, *Platynus krynickii* and *Agonum moestum* (s. lat.) are always present and occur as subdominant or dominant species.

The concrete composition of communities in these two states is, however, very richly structured (c. f. ŠUSTEK 1984).

3. The third state is characteristic of the habitats (stands of group of geobiocoens *Ulm-Fraxineta carpinea*) with decreased level of ground water and facultative incidence of short termed floods. Such communities are characterise by penetration of tolerant mesohygrophilous forest species like *Carabus coriaceus*, *Carabus ulrichi*, *Carabus violaceus*, *Abax parallelipipedus*, *Pterostichus oblongopunctatus*, surviving of the hygrophilous species like *Platynus assimile*, *Agonum obscurum* and absence of the very hygrophilous species like *Europhilus nivic*, *Europhilus fuliginosus*, *Agonum moestum*, *Pterostichus nigrita*, *Pterostichus antracinus* etc.

Within this state, several community types also can be distinguished (c. f. ŠUSTEK 1984).

They reflect, to a considerable degree, the competition between large species of the genus *Carabus*, and the habitat position along the humidity gradient. With increasing distance from the water flow the proportion of mesohygrophilous species increases. The borders between the alluvial and adjacent mesohygrophilous ecosystems is very flexible and changes even within one vegetation period.

The degradation of floodplain communities of Carabids runs according three generalised scenarios.

1. In the habitats like large urban parks (e. g. Sad Janka Kráľa in Bratislava, Lužánky in Brno), where the humidity relations and stand structure are more or less preserved, but the ecosystem is exposed to various anthropic pressures, the relative and absolute abundance of few (1-2) species strongly increases and the community stabilises in this state (Fig. 1).
2. In the habitats, where the humidity has been artificially decreased, but stand structure has been more or less preserved and a suitable immigration source of the mesohygrophilous forests is in nearness, the proportion of hygrophilous species decreases in favour of more tolerant or less hygrophilous species and mesohygrophilous immigrants may become predominant. In this way arise a community, which in other places could be considered to be natural.
3. In the habitats, where the humidity has been artificially decreased and, at the same time, the stand structure and integrity has been damaged (drying or selective cutting of trees etc.), the proportion of hygrophilous species strongly decreases of this species disappear at all., only the most tolerant hygrophilous or mesohygrophilous forest species survive and invasion of the open landscape mesohygrophilous species (e. g. *Pseudoophonus rufipes*, *Poecilus cupreus*, *Trechus quadristriatus*, *Harpalus* spp., *Ophonus* spp.) begins. Result of such a man-initialised succession is a community of

an indeterminate ecotonal character, usually with low abundance of all species, but sometimes with a remarkably high number of species of very different ecological character (Fig. 1).

In concrete cases, the succession trajectory may, however, run somewhere between all three scenarios.

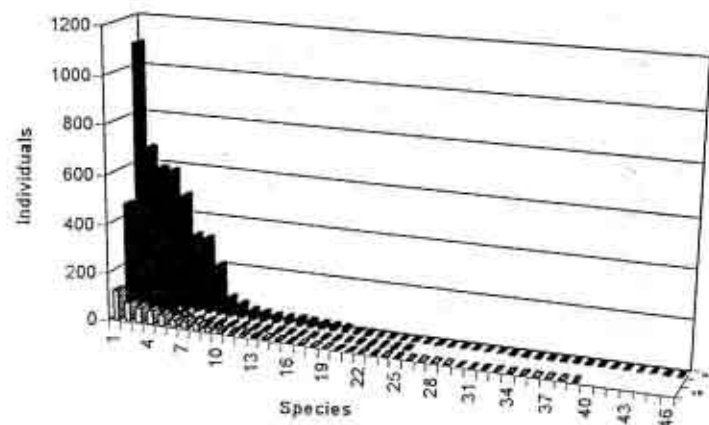


Fig. 1. Sequence of species ranked according to decreasing number of individuals in a very rich community in a natural floodplain forest (ML - Malé Levčre, 46 species, diversity index $H' = 2.36$, equitability 0.62), in a disturbed rich community in an urban alluvial park (LŽ - Lužánky, Brno, 24 species, $H' = 1.26$, equitability 0.39) and in a strongly affected desintegrated floodplain forests (VR - Vrakúša, Bratislava, 39 species, $H' = 2.68$, equitability 0.73).

Examples of reactions of Carabid communities on humidity changes in floodplain forests and reed swamps

The first example (Tab. 2) describes succession of carabids in the forest Ranšpúrk at the confluence of the Morava and Dyja rivers affected by regulation of both rivers during late 1970-ies and early 1980-ies. The ground water level was reduced by ca. 1.5 m and the regular spring floods were stopped. The regular monitoring was started as late in 1993 when a considerable degradation had already been reached and continued during next two years.

The polyhygrophilous species, which would have best correspond to the local conditions, were absent or represented by a few individuals. Similarly even the very tolerant species like *Carabus granulatus* exhibited a low abundance or their abundance was decreasing from year to year (*Nebria brevicollis*). On the contrary, the abundance of mesohygrophilous forest species (e. g. *Abax carinatus*, *Carabus ulrichi*) increased and, beside this, open landscape species (the expansive *Pseudoophonus rufipes*, *Poecilus cupreus*) penetrated the community. The degradation processes culminated in 1995.

Tab. 2. Example of a Carabid community strongly affected by river regulation causing a decrease of ground-water level and prevention of flood and since 1996 passing through a renaturation process after an enormous flood and adoption of measures moderating impact of river regulation (Moravia, Rantpurk), rare species omitted.

Species	Degree of hygrophily	Years						
		1993	1994	1995	1996	1997	1998	1999
Species of mezohygrophilous forests								
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)		2	7	16	22	11	3	2
<i>Abax carinatus</i> (Duftschmidt, 1812)		20	98	139	86	25	12	31
<i>Carabus ulrichi</i> Germar, 1824		59	51	113	73	146	61	77
<i>Leistus rufomarginatus</i> (Duftschmidt, 1812)		5	9	16		2	3	3
Hygrophilous forest or hygrophilous eurytopic species								
<i>Carabus violaceus</i> Linnaeus, 1758	1	11	113	47	80	31	150	131
<i>Pterostichus melanarius</i> (Illiger, 1798)	2	40	80	55	28	17	20	85
<i>Pterostichus niger</i> (Schaller, 1783)	2	9	33	39	87	121	810	664
<i>Nebria brevicollis</i> (Fabricius, 1792)	3	101	84	35	37	17	192	442
<i>Pterostichus strenuus</i> (Panzer, 1797)	3	1				5	1	6
<i>Platynus assimilis</i> (Paykull, 1790)	4	6	1	1		4	2	
<i>Carabus granulatus</i> Linnaeus, 1758	4	2	11	18	67	46	104	132
<i>Psotrus atrorufus</i> (Stroem, 1768)	4	19	20	8	20	9	80	154
<i>Epaphys secalis</i> (Paykull, 1790)	3	2	1		4		6	73
Polyhygrophilous species								
<i>Pterostichus anthracinus</i> (Illiger, 1798)	5	2	5	3	2		14	10
<i>Agonum moestum</i> (Duftschmidt, 1812)	5	5	5	1	1	7	16	5
<i>Bembidion mannerheimi</i> C. R. Sahlberg, 1827	5	1	19	5	2	39	3	24
<i>Dyschirius globosus</i> (Herbst, 1783)	5	2	6			1		
<i>Oxytelus obscurus</i> (Herbst, 1784)	4		1				1	3
<i>Bembidion biguttatum</i> (Fabricius, 1779)	5					5	18	22
<i>Pterostichus nigrita</i> (Paykull, 1790)	5				1	6		
<i>Europhorus micans</i> (Nicolai, 1822)	4					1	3	3
<i>Bembidion dentellum</i> (Thunberg, 1787)	5						2	1
<i>Platynus krynickii</i> (Sperk, 1835)	5							4
Mesohygrophilous "field" species								
<i>Poecilus cupreus</i> (Linnaeus, 1758)		14	29	31	23	53	7	18
<i>Pseudophonus rufipes</i> (De Geer, 1774)		1	20	48	16	6	3	
<i>Pseudophonus griseus</i> (Panzer, 1797)				2				
<i>Harpalus latus</i> (Linnaeus, 1758)				1	2	1	2	
Total of individuals		327	527	460	480	583	1526	1907
Total of species		29	31	28	29	33	31	31

In 1996, the stand was flooded artificially in spring. It was immediately reflected by a moderate decrease of abundance of some mesohygrophilous forests species and of the open-land invaders. On the contrary, abundance of more tolerant hygrophilous species considerably increased.

In 1997, out of simulated flood, an enormous unexpected summer flood wave flooded the whole area for about one month. The populations of species whose seasonal activity culminates in late summer and autumn (*Carabus violaceus*, *Abax carinatus*, *Pseudophonus rufipes*) were considerably reduced without respect to their relations to humidity and vegetation character and in addition further invading of *Pseudophonus rufipes* prevented. The destructive influence of flood lasted, however, very shortly. Already in September and October 1997 the community structure on one-months samples was considerably restituted and, in addition, some polyhygrophilous species (e. g. *Bembidion mannerheimi*) reappeared in this locality.

In two next years, abundance of majority of tolerant hygrophilous species considerably increased and occurrence or reappearance of the polyhygrophilous species continued. The colder rainy seasons in 1996 xenocous *Pseudophonus rufipes* disappeared. The community considerably approximated to the state which is natural in such condition. This process also was supported by a series of several - 1999. As a result of the partial renaturation, the cumulative abundance of carabids increased 4-6-times.

Tab. 3. Abundance changes of most frequent species in a Carabid community in the within-dike area moderately affected by the changed hydrological regimen after putting the Gabčíkova barrage system into operation (Slovakia, Šulany), rare species omitted.

Species	Degree of hygrophily	Years						
		pre-dam		post-dam				
		1991	1992	1993	1994	1995	1996	1997
Polyhygrophilous species								
<i>Bembidion femoratum</i> Sturm, 1825	5	2	11	20				
<i>Badister sodalis</i> (Duftschmidt, 1812)	4	29	15	2	1	7	10	
<i>Agonum moestum</i> (Duftschmidt, 1812)	5	4	16	1	4	2		6
<i>Bembidion dentellum</i> (Thunberg, 1787)	5	13	70	6	2	2		2
<i>Pterostichus strenuus</i> (Stroem, 1768)	4	135	56	58	14	18	9	5
<i>Platynus assimilis</i> (Paykull, 1790)	4	141	129	106	55	5	62	6
<i>Civina fossor</i> (Linnaeus, 1758)	4	47	21	2	5	7	9	3
<i>Europhorus micans</i> (Nicolai, 1822)	5	15	13	4	14	2	2	6
Hygrophilous forest and hygrophilous eurytopic species								
<i>Asaphidion flavipes</i> (Linnaeus, 1761)	4	331	154	171	88	156	110	28
<i>Carabus granulatus</i> Linnaeus, 1758	4	88	272	206	169	29	22	67
<i>Oxytelus obscurus</i> (Herbst, 1784)	4	38	84	64	80	47	70	135
<i>Pterostichus melanarius</i> (Illiger, 1798)	2	54	74	480	115	11	18	19
<i>Pterostichus niger</i> (Schaller, 1783)	2	31	208	446	67	20	14	73
<i>Pterostichus strenuus</i> (Panzer, 1797)	3	105	131	99	124	111	144	126
<i>Stomis pumicatus</i> (Panzer, 1796)	3	13	19	72	15	11	25	16
Mesohygrophilous eurytopic "field" species								
<i>Trechus quadristriatus</i> (Schränk, 1781)		14	12	69	75	190	165	140
Total of individuals		1088	1348	1853	870	640	728	680
Total of species		28	37	33	28	22	29	31

The second and third examples (Tab. 3 and 4) show reaction of Carabid communities on the Danube by-passing in autumn 1992. Their reactions were very differentiated the whole affected area over. They depended on the draining effect of the old Danube river bed and on the degree to which the arms supplied by water from the intake structures or back-water in the downstream part of the affected area were able to compensate the effect of absence of periodical floods. As an illustration of these different reactions, two communities were chosen in this paper.

The community in the monitoring plot at the Šulany village (Tab. 3) was in the area which was partly in reach of influence of rest of arms systems and the lower parts were even flooded for a short time during the "simulated floods" (fact is that the "simulated floods" were represented only by a moderately increased discharge in the remnants of the arm system). In spite of this, abundance of all polyhygrophilous suddenly decreased in 1994 with an one-year delay after the Danube damming (1992) and, until 1997, some of them disappeared in this locality. On the contrary, the less hygrophilous species were even favoured by this change for about two years (1993-1994), but then they abundance also began to decline. In 1997, however a colder and rainier weather made possible a small re-increase of abundance of all hygrophilous species. The obvious draining of this locality caused a sudden increase of population of the xenocous *Trechus quadristriatus*. It is obvious that even a relatively favourable position of this locality and artificial simulated floods were not able to fully compensate the effect caused by the Danube damming.

A fully different situation was recorded in the community on the monitoring plot near the Dobrohošť village (Tab. 4). This locality was situated upstream of the intake structure supplying the remnants of the arm system with water from the by-pass canal. It was out of reach of any arm and of the "simulated floods". This was reflected even visually in a complete destruction of the tree layer, drying on many trees, first of all of willows.

Tab. 4. Abundance changes of most frequent species in a Carabid community in the within-dike area strongly affected by the changed hydrological regimen after putting the Gabčíkovo barrage system into operation in autumn 1992 (Slovakia, Dobrohošť), rare species omitted.

Species	Degree of hygrophily	Years									
		pre-dam					post-dam				
		1989	1990	1991	1992	1993	1994	1995	1996	1997	
Polyhygrophilous species											
<i>Platynus krynickii</i> (Sperk, 1835)	5	1									
<i>Platynus livens</i> (Gyllenhal, 1810)	5	1		3							
<i>Europhilus micans</i> (Nicolai, 1822)	4	3		4					1		
<i>Pterostichus anthracinus</i> (Illiger, 1798)	5	8	2	3			2	1			
<i>Pterobius atrorufus</i> (Stroem, 1768)	4	40	28	23	30	8	12	1			
<i>Oxytelaphus obscurus</i> (Herbst, 1784)	4	75	25	15	41	9	5	1	3	3	
<i>Agonum moestum</i> (Duftschmidt, 1812)	5	45	12	33	51	15	10	5	3	6	
<i>Badister laetitosus</i> (Sturm, 1815)	4	27	17	5		14	3	2	2	3	
<i>Stomis pumicatus</i> (Panzer, 1796)	3	37	23	15	25	21	6	12	2	13	
Moderately hygrophilous but temporarily favored species											
<i>Epaphius secalis</i> (Paykull, 1790)	3		1	10	2	3	3				
<i>Carabus granulatus</i> Linnaeus, 1758	4	4	5	12	21	49	39	4	1		
<i>Pterostichus niger</i> (Schaller, 1783)	2	8	17	16	121	13	67	14	1		
<i>Platynus assimilis</i> (Paykull, 1790)	4	12	6	3	28	24	1	5	3		
<i>Asaphidion flavipes</i> (Linnaeus, 1761)	4	7	2	4	44	11	11	12	15		
A mezohygrophilous eurytopic, but finally also affected species											
<i>Trechus quadristriatus</i> (Schrank, 1781)		21	17	32	17	8	6	17	3	2	
Xero- or mesohygrophilous open landscape species											
<i>Calathus fuscipes</i> (Goeze, 1777)							2		1	3	
<i>Lichius depressus</i> (Paykull, 1790)			1		2	2	4	4	4	1	
<i>Pseudophonus rufipes</i> (De Geer, 1774)		6			2	1	15	25	12	10	
Total of individuals		337	187	233	474	227	231	146	71	38	
Total of species		32	28	29	32	28	30	26	20	23	

Similarly as in Šul'any, a decline of abundance of the polyhygrophilous species and a short period of favouring the less hygrophilous or more tolerant species started in 1993/1994. In contrast to Šul'any, both groups of species with different requirements to humidity were equally strongly affected in next three years (1995-1997) and some species disappeared in this locality. Even the very tolerant *Trechus quadristriatus*, which was strongly favoured by the changes occurring in Šul'any, finally disappeared in this locality. The role of invaders was, however, played by other three open-landscape species, among which *Lichius depressus* is even expressively xerophilous (c. f. Tab. 1). The community in Dobrohošť can be taken as an example of communities fully destroyed by anthropogenous changes of hydrological regimen of a locality.

The last examples (Tab. 5) represent a series of Carabid communities in three different reed stands in South Slovakia. The first community (Veľké Kosičky) occurs in a pure reed stand on a permanently marshy and often flooded locality. The second (Medved'ov) occurs in a drier reed stand with admixed sedges, periodically flooded by seeping ground water. The third (Veľký Meder) occurs in an artificially drained reed stand with richly admixed nettles. This stand is never flooded. Only occasionally the ground water level rise to a depth of about 10 cm the lowest part of this locality.

In Veľké Kosičky, some extremely hygrophilous and rare species (*Carabus clathratus*, *Oodes gracilis*, *Agonum lugens* and *Platynus livens*) occur which no more find suitable condition on a little drier, but still natural reed stand in Medved'ov. However, both communities have six common, hygrophilous species (*Oodes helopioides*, *Pterostichus niger*, *Pterostichus melanarius*, *Agonum moestum*, *Carabus granulatus*, *Oxytelus obscurus*) having in both stands a high abundance. Most of these species are absent or little represented in the third, artificially drained stand. In contrast to the

first two communities, the community in Veľký Meder is dominated by an extremely large number of the minute (body length 2.8-3.8 mm) and tolerant *Bembidion guttula* and moderately hygrophilous and also minute (body length 5.3-6.8 mm) and very tolerant *Pterostichus strenuus*. In addition, an enormous number of imagines and adult larvae of the carrion-beetle *Silpha obscura* occurs here. This beetle is predominantly a carnivore and scavenger as most Carabids (it does not live of carrions of large vertebrates, like representatives of related genera do) and equally sized as the moderately hygrophilous and very tolerant and expansive species *Pterostichus niger* and *Pterostichus melanarius*. Just the competition pressure of *Silpha obscura* is the cause, why both carabid species could not penetrate in this locality in spite of the fact that humidity condition of this locality lay within their tolerance range. This example shows how the biotical factors may influence structure of a community and, if not taken in consideration, also results of bioindicative studies made, as usual, only on example of one animal group.

Table 5. Comparison of Carabid communities in three different reed stands in South Slovakia (Veľké Kosičky - pure reed stand on a permanently marshy and often flooded locality, Medved'ov, a drier periodically flooded reed stand with admixed sedges, Veľký Meder - an artificially drained reed stand with admixed nettles and sedges, rare species omitted).

Species	Degree of hygrophily	Veľké Kosičky	Medved'ov	Veľký Meder
Polyhygrophilous Carabidae				
<i>Carabus clathratus</i> Linnaeus, 1761	5	7		
<i>Oodes gracilis</i> A. et G. B. Villa, 1833	5	7		
<i>Agonum lugens</i> (Duftschmidt, 1812)	5	21		
<i>Platynus livens</i> (Gyllenhal, 1810)	5	20		
<i>Oodes helopioides</i> (Fabricius, 1782)	5	80	41	
<i>Pterostichus niger</i> (Schaller, 1783)	2	77	62	
<i>Pterostichus melanarius</i> (Illiger, 1798)	2	38	34	1
<i>Agonum moestum</i> (Duftschmidt, 1812)	5	35	8	9
<i>Carabus granulatus</i> Linnaeus, 1758	4	33	20	4
<i>Oxytelus obscurus</i> (Herbst, 1784)	4	32	93	4
<i>Europhilus micans</i> (Nicolai, 1822)	4	1	9	14
<i>Pterostichus vernalis</i> (Panzer, 1796)	4	2	9	26
<i>Stomis pumicatus</i> (Panzer, 1796)	3	1	2	34
<i>Pterostichus strenuus</i> (Panzer, 1797)	3		15	118
<i>Bembidion guttula</i> (Fabricius 1792)	4			345
Mesohygrophilous Silphidae				
<i>Silpha obscura</i> (Linnaeus 1758) imagines and adult larvae		1	2	1,384
Total of individuals		383	322	1962
Total of species		30	21	19

Conclusions

The reliable bioindication has doubtless a great role in the landscape ecology and in assessment of impact of various human activities on the nature and environment. Its place in most decision processes regarding human intervention into the nature is inevitable, because the potential impacts of any human activity can be measured only by the most sensible component of the ecosystem - the living organisms and their communities.

The briefly outlined general characteristics and some simple examples of bioindicative use of Carabids show that the Carabids may represent a very suitable model group for bioindication purposes. However, the reliable interpretation of data needs further theoretical studies based on extensive field observations. It is to be stressed that in spite of seemingly clear and simple (or sometimes intentionally very simplified) characteristics of species, their position in ecological niches is always determined by a very complex set of multidimensional and sometimes hardly identifiable relationships. The same species may behave unexpectedly quite otherwise in an other place even in almost identical or seemingly identical conditions. The complexity of mutual relations of plants, animals and environment shifts the

qualified and responsible bioindication, irrespective of its purely rational nature, in certain sense somewhere between the Science and Art.

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