CARABID COMMUNITIES (COLEOPTERA: CARABIDAE) IN SPRUCE FORESTS IN CENTRAL EUROPE

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Abstract. The paper synthetises the results of the investigation of Carabid communities in Central European spruce forests carried out from 1960 until 2012. The communities in more or less natural spruce forests consist of about 30 species with optimum of vertical distribution in fir-beech to fir-beech-spruce vegetation tier (altitudes of ca. 700 – 1,500 m). Unlike the Hercynian mountain ranges, the communities in the Carpathian mountain ranges also consist of the endemic and abundant *Pterostichus foveolatus* and *P. pillosus*. The abundance of individual species indirectly depends on trophicity of geologic substrate. The communities on basic substrates are richer than those on acid or neutral substrates. The continuous and thick layer of mosses eliminates medium- and large sized species. The communities in spruce monocultures, especially in those cultivated at altitudes bellow the natural vertical distribution of spruce represent impoverished derivates of the Carabid fauna of natural forests, in whose place the monocultures are cultivated. The destruction of the spruce forests by windstorms reduces abundance of all species, but the species composition and proportion of species remain almost intact. The harvesting of the fallen timber causes the disappearance of more stenotopic forest species, the increase of abundance of more tolerant forests species (*Carabus violaceus, C. glabratus*) and the invasion of species mountain meadows. The extensive fire on the harvested areas results in a still stronger reduction of the stenotopic forests species and temporary invasion of the species of arable land. The occurrence of extreme drought causes, with about one year delay, decreases of the number of recorded species and caught individuals, irrespectively of the naturalness of the habitat. In contrast, the humid years support gradual regeneration of the communities and the dry years inhibit it. Standardized precipitation index (SPI 24) and standardized precipitation and evaporation index (SPEI 24) calculated for 24 months characterize the best the reactions of Carabid communities to climate changes.

Keywords: spruce forests, Carabidae, monocultures, climatic factors, Central Europe.

Rezumat. Cenozele carabidelor (Coleoptera: Carabidae) din pădurile de molid din Europa Centrală. Lucrarea reprezintă o sinteză a cercetărilor asupra cenozelor de carabide din molidişurile central europene, efectuate în perioada 1960-2012. Cenozele din molidişurile naturale sau seminaturale constau din aproximativ 30 de specii cu optimul de răspândire verticală în zonele de vegetaţie de brad, fag şi brad, fag şi molid (altitudine de cca. 700 - 1500 m). Spre deosebire de munţii lanţului hercinic, cenozele din lanţul carpatic constau din specii endemice şi abundente (*Pterostichus foveolatus* şi *Pterostichus pillosus*). Abundenţa speciilor depinde indirect de troficitatea substratului geologic. Cenozele de pe substraturile bazice sunt mai bogate decât cele de pe substraturile acide sau neutre. Stratul gros şi continuu al muşchilor elimină speciile de talie medie sau mare. Cenozele din monuculturile de molid, mai ales cele cultivate la altitudinile de sub nivelul de răspândire verticală naturală a molidului, reprezintă derivatele degradate ale faunei de carabide din pădurile naturale, pe locul cărora se cultivă monoculturi. Distrugerea molidişurilor de vânt se reflectă în scăderea abundenţei tuturor speciilor, dar compoziţia speciilor şi reprezentarea lor relativă este păstrată. Exploatarea trunchiurilor căzute determină dispariţia speciilor stenotopice de pădure şi creşterea abundenţei speciilor de pădure mai tolerante (*Carabus violaceus, Carabus glabratus*) şi invazia speciilor din pajiştele montane seminaturale. Incendiile pe suprafeţe mari în zonele cu lemnul exploatat, pricinuiesc o reducere mai puternică a reprezentării speciilor stenotopice de pădure şi invazii scurte ale speciilor de teren arabil. Secetele extreme cauzează, cu o întârziere de un an, scăderea numărului speciilor înregistrate şi a abundenţei lor, indiferent de starea habitatului. Invers, anii mai umezi suportă regenerarea graduală a cenozelor. În schimb, secetele împiedică regenerarea lor. Indicele standartizat al precipităţilor (SPI 24) şi indicele standartizat al evaporării şi al precipităţilor (SPEI 24) calculate pentru 24 luni caracterizează cel mai bine reacţia cenozelor de carabide la schimbările climatice.

Cuvinte cheie: molidişuri, carabide, monocultură, factori climatici, Europa Centrală.

INTRODUCTION

The composition of Carabid communities in Norway spruce in Central Europe is strongly influenced by the fact that the major part of the existing stands is not original and replaces other types of stands, which would be natural in the respective localities and correspond to the permanent ecotope conditions. The deviation of the natural state of forests increases in the case of spruce forests toward lower altitudes, where the spruce is cultivated out of its natural vertical distribution. Therefore, only in the zone of spruce, spruce-fire-beech and to certain degree also of the fire-beech vegetation tier (RAUŠER & ZLATNÍK, 1966) the forest stands can be considered as natural or to show a considerable degree of naturalness. However, in these vegetation tiers the species composition and spatial structure of spruce are often influenced by the human interventions.

The Carabid communities in the spruce stands correspond to it. In higher altitudes (vegetation tiers) they can be natural or almost natural. However, their naturalness can be rather independent on the species structure of the forests itself. More important it is the presence of a tree stand and the microclimatic conditions offered by it than the species composition of trees forming the stand. At lower altitudes the carabid communities are secondary, being derived from the communities natural in such conditions.

As spruce tends to acidify the soil upper layers in comparison with the natural pH of the geological substratum, the soil pH in spruce stands growing on neutral (trophic series B in the Zlatník´s geobiocoenological classification) and eutrophic basic or nitrophilous substrata (trophic series BC, BD, C and D) shifts toward the acid oligotrophic substrates (series A). Thus, out of cultivation mode, it worsens the existence condition for many plants and animals on which the Carabids depend. Beside it, the artificial spruce monocultures tend to accumulate the undecayed needles and row humus, which also worsen life conditions for soil animals. Therefore, the Carabid communities in unnatural spruce forests are poorer than in more or less natural forests in analogical ecotopes.

The aim of this paper is to synthetize the data published earlier and to emphasize the variability of Carabid communities in the spruce stands and how they react to the deforestation and subsequent human interventions, mid-termed climatic changes.

MATERIAL AND METHODS

The material used in this study was obtained during the years 1970 and 2012 in 25 localities in three mountain ranges of the Hercynic system (Jizerské hory, Český masiv, Českomoravská vrchovina, Jeseníky) and in the West Carpathians (Malá Fatra, Belanské Tatry and Tysoké Tatry), (ŠUSTEK, 1972, 1976, 1982, 1986, 2006, 2007a, 2007b, 2007c, 2009). The beetles were pitfall-trapped. The jars used as traps varied during the time, according to jars available at the moment on the market and according to possibility to transport them in difficult alpine conditions. Up to the early 80's 1-litre glass jars with opening diameter of 95 mm were used, while in the mid 80's, 0.75 l glass jars with opening diameter 75 mm and since the mid 90's, the 0.5 l plastic jars with opening diameter 80 mm. The traps were always filled up to about ¼ by formol. The number of traps per site differed according to purposes on individual studies. Thus, in Juzerské hory (ŠUSTEK, 1982) and Malá Fatra (ŠUSTEK & ŽUFFA, 1986, 1988), the traps were installed in transects of 10-40 traps in length of about 2 km and crossing different types of forests ecosystems or different treatment by insecticides. In the sizes in the Český masiv (ŠUSTEK, 1984), Českomoravská vrchovina and Jeseníky (ŠUSTEK, 1972, 1976) 10 traps were used, while in all sites in Belanské Tatry and Vysoké Tatry 6 traps were used. Out of it, the species lists obtained by pitfall trapping published by other authors were taken into account (KULA & PURCHART, 2004; MARTINEK, 1960; ROHÁČOVÁ, 2001, STANOVSKÝ et al., 2005).

As methodical basis for the data evaluation, Zlatník´s classification of forest geobiocen (RAUŠER & ZLATNÍK, 1966; ZLATNÍK, 1963, 1976) was used. In this system the basic classification units is the type of geobiocoen groups representing the potential natural vegetation bound to the permanent abiotic condition of the locality (ecotope). The types of geobiocoen groups are divided into several minor units – the geobiocen types differing mostly by herbage stratum. The types of geobiocoen groups are classified into a three-dimensional system of upper units expressing vertical zonation and expositional climate (nine vegetation tiers – 1. oak, 2. beech-oak, 3. oak-beech, 4. beech in the Carpathians or oak-pine in the Hercynic system, 5. beech-fir, 6. beech-fir-spruce, 7. spruce, 8. dwarf-pine, 9. alpine grasslands), trophicity of the geological substrate (four trophic series A – acid, B – neutral, C – nitrophilous, D – basic with three transition AB. BC and BD) and level of soil humidity (a – dry, b – mesohygrophilous, c – polyhygrophilous with ground water reaching to the root layer or regularly overflooded). The type of geobiocoens includes the natural vegetation as well as he seminatural or anthropogenically changed ecosystems (gebiocoenoids) existing on its places and spontaneously renaturing under suitable conditions.

The hierarchical classification of the communities was carried out by unweighted pair method using the Horn´s index of proportional similarity, while the ordination of the communities was carried out by non-parametric multidimensional scaling. All calculations were made by the program PAST version 2,16 (HARMLER, 2012).

The medium-termed climatical changes were characterized by the Standardized Precipitation Index (SPI24) and Standardized Precipitation and Evapotranspiration Index (SPEI24), which were calculated on the basis of monthly average temperatures and monthly precipitation sums obtained from the meteorological station Tatranská Lomnica for the years 1961-2012. In order to make possible between-year comparisons of the state of communities with the climatic characteristic of the years, average values of SPI and SPEI were calculated for each year (ŠUSTEK & VIDO, 2012). This calculation is a modification of the original method by MCKEE (1993). Both indices were calculated for 24 months in order to obtain more smooth data series and to characterize a sufficiently long period covering the length ontogenesis of individual Carabid species, which can last in mountain condition 1-2 years, and to cover the potential overlap of two subsequent generations.

Species diversity of Carabid communities in spruce forests

Potentially, the natural Carabid communities in Central European spruce forests in the fire-beech-spruce to spruce vegetation tier are formed approximately by 30 species (Fig. 1) (ŠUSTEK, 2000), which represent only 5% of species occurring in Central Europe (HŮRKA, 1996). Among them, the most characteristic species have the optimum of vertical distribution in the fire-beech to dwarf pine vegetation tier, hence at altitudes of about 800 – 1700 m a.s.l. Zoogeographically, they are represented first of all by 16 stenotopic forests species viz. *Carabus linnei* PANZER, 1810, *Cychrus caraboides* (LINNAEUS, 1758), *Cychrus attenuatus* (FABRICIUS, 1792), *Leistus piceus* FRÖLICH, 1799, *Trechus latus* PUTZEYS, 1847, *Trechus pulchellus* PUTZEYS, 1846, *Trechus pilisensis* CSIKI, 1918, *Trechus striatulus* PUTZEYS, 1847, *Pterostichus burmeisteri* HEER, 1841, *Pterostichus unctulatus* (DUFTSCHMIDT, 1812), *Pterostichus pumilio* (DEJEAN, 1838), *Pterostichus rufitarsis* (DEJEAN, 1828), *Pterostichus quadrifoveolatus* LETZNER, 1852, *Calathus* *micropterus* (DUFTSCHMIDT, 1812), *Calathus ambiguus* (PAYKULL, 1790) and *Trichoticnus laevicollis* (DUFTSCHMIDT, 1812). These species are relatively widely distributed in all Central European mountain ranges. While most of them take subdominant to eudominant position, *Pterostichus rufitarsis* and *Pterostichus quadrifoveolatus* are usually a recedent, but characteristic component of the community. In the Carpathians, the species spectrum is enriched by *P. foveolatus* (DUFTSCHMIDT, 1812), and *Pterostichus pillosus* (HOST, 1789), also with the optimum in the fire-beech to dwarf-pine vegetation tier. Locally, the species spectrum is also enriched by the Carpatho-Balkan species *Calathus metalicus* DEJEAN, 1828 with the optimum in the dwarf pine vegetation tier, which sometimes descends to the spruce stands in the lower vegetation tiers. It prefers open stands. In the closed stand, it takes only recedent or subdominant position.

In addition, the communities in spruce forests consist of further four species, viz. *Carabus auronitens* FABRICIUS 1792*, Carabus glabratus* PAYKULL, 1790*, Carabus violaceus* LINNAEUS, 1758 and *Molops piceus* (PANZER, 1793). *Carabus auronitens, Carabus glabratus* and *Molops piceus* are stenotopic forests species distributed from the oak-beech to the dwarf-pine vegetation tier. *M. piceus* never exceeds subdominant representation, but its presence indicates a high degree of the community naturalness. *Carabus violaceus* has, in Central Europe, the natural optimum of vertical distribution in the fire-beech to spruce vegetation tier, but at the same time, it has enormously wide amplitude of vertical distribution reaching from the lowlands (oak vegetation tier) to the margin between the dwarf-pine and alpine vegetation tier. Its occurrence in the concrete habits is strongly influenced by moderately increased demands to humidity and, at the same time, by increased tolerance to the reduced shadowing. It allows it to successfully colonize differently disturbed habitats (in lowlands drying of floodplain forests, in mountains temporal deforestation). Thanks to the elimination of competition of similar species, it is able to reach in such habitats very abundant representation.

In spruce forests of spruce-fire-beech and spruce vegetation tiers, the occurrence of the Eurosiberian *Pterostichus oblongopunctatus* (FABRICIUS, 1787) and *Pterostichus melanarius* (ILLIGER, 1798) afterglows. Their occurrence optimum is in lowlands and uplands and both have moderately increased demands to humidity. *Pterostichus oblongopunctatus* is a relatively stenotopic forest species. On the contrary, *Pterostichus melanarius* is extraordinarily eurytopic owing to the good ability to fly also very expansive. Similarly localized in spruce stands or in places of their disintegration, *Carabus arvensis* has a very wide amplitude of vertical distribution, from lowlands up to dwarf-pine vegetation tier and prefers light sandy substrates and is highly tolerant to the absence of shadowing. In the West Carpathians (Malá Fatra Mts., Belianske Tatry Mts.), it often co-occurs in spruce forests with *Calathus metallicus*. On the contrary, only in the Hercynic mountains, the high alpine species *Carabus sylvestris* (PANZER, 1796) descend as a subrecedent or recedent species to the spruce forests in the spruce and spruce-fire-beech vegetation tier, whereas in the Carpathians it descends only the boundary between the alpine and dwarf-pine vegetation tier.

Besides the species mentioned above, the communities in the spruce stands also include several species with a wide ecological valence. Their most frequent representative is *Notiophilus biguttatus* (FABRICIUS, 1799) occurring in light places with nude layer of needles. The further three species *Poecilus virens* (O. F. MÜLLER, 1776) (= *P. lepidus* LESKE, 1785), *Agonum gracilipes* (DUFTSCHMIDT, 1812) and *Demetrias atricapilus* (LINNAEUS, 1758) occur in spruce forests sporadically and do not belong to the characteristic component of Carabid communities in them. *Poecilus virens* is an open landscape species living on coarse sandy soils and alternates on them *P. cupreus* at lower altitudes and *P. versicolor* at higher altitudes. *Agonum gracilipes* is predominantly a rare species with a wide ecological valence in different non-forest ecosystems. *Demetrias atricapilus* is also a rare species hunting prey on grassy vegetation in non-forests ecosystems.

In Slovakia and in the adjacent parts of Poland, a striking difference exists in the representation of the species of the genus *Trechus* between High Tatra and other mountains. In other mountains, in one locality 2-4 species co-occur (*T. pilisensis, T. latus, T. pulchellus, T. striatulus*), among which at least one reaches a subdominant or dominant position, in High Tatra only *Trechus striatulus* occurs and has a high abundance up to the alpine tier. The coexistence of several species of the genus *Trechus* or even their coexistence with further similarly sized species (*Pterostichus pumilio, Pterostichus unctulatus*) in other localities excludes that this difference would result from their mutual competition. As an explication, it can be taken the glaciation of High Tatra and the worser condition for their later colonization by other species of the genus *Trechus*. Only *T. amplicollis* FAIRMAIR, 1859 sporadically occurs along the creek at the High Tatra foothills.

Variability of the structure of Carabid communities in spruce forests

The number of species in Carabid communities in mountain spruce forests in concrete sites is always lower than the potential number of species that can occur in them (Figs. 1-4). In individual sites, it is mostly around 10 species. In less favourable conditions, it declines to 5-6 species, whereas in the most favourable conditions it exceeds 20 species. As a rule, 2-5 species are dominant or eudominant, other species are much less represented. Out of the geographic position of the locality, the species composition and structure of the community are managed by the substrate trophicity and litter character, extent of coverage by mosses and character of herbage stratum. Especially, at the boundary of mosaic of two trophically strongly different substrata an almost discontinuous transition between two Carabid communities appears. Such situation occurs in the Malá Fatra, Velká Fatra and Belanské Tatry Mts., where the crystalline and basic substrata alternate within short distances.

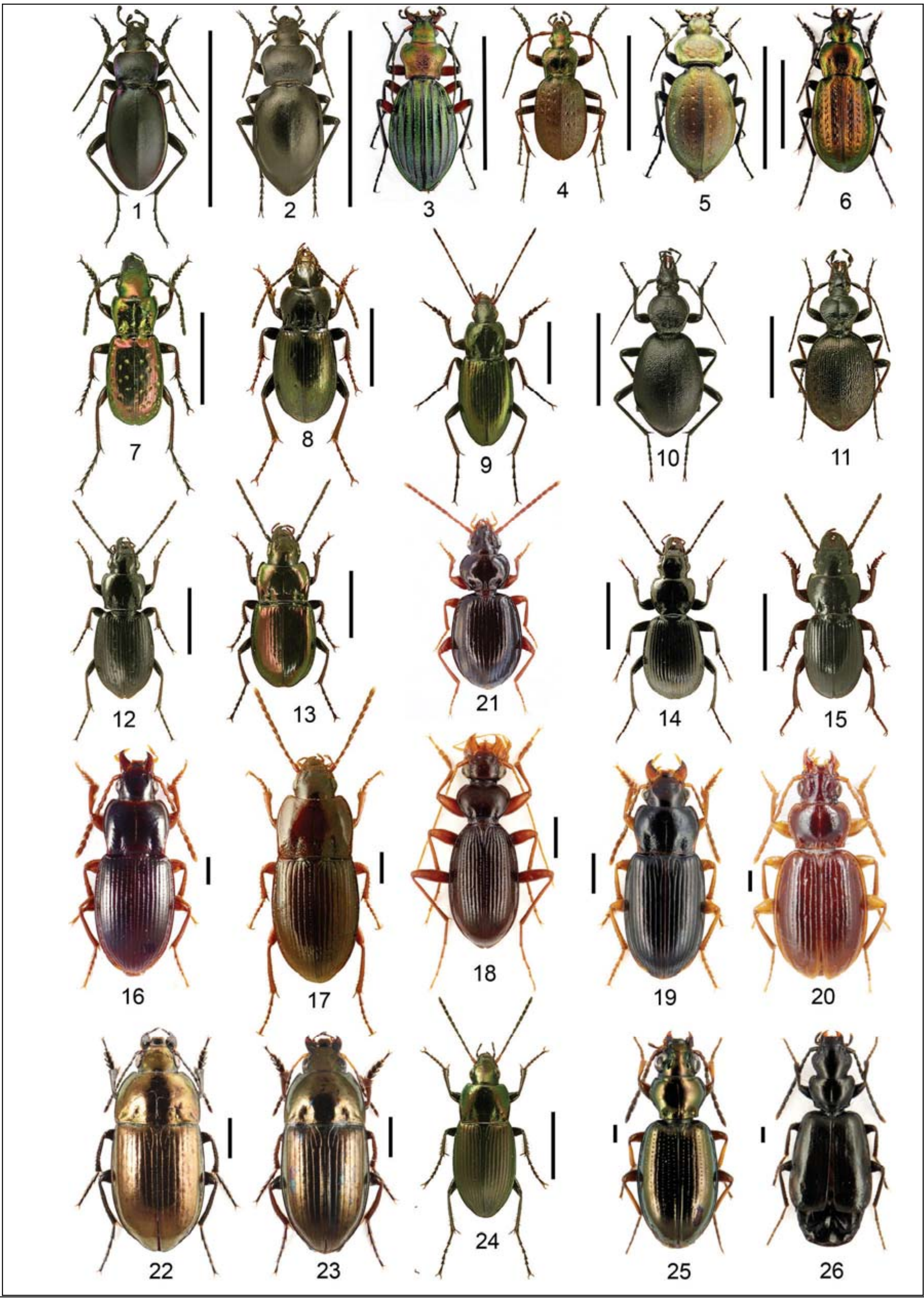

Figure 1. Main representatives of carabid communities in the Central European mountain spruce forests (1 – 21) and in wind-affected forests in the High Tatra Mountains (22 – 26) and their body size. (original).
1. *Carabus violaceus*, 2. *C. glabratus*, 3. *C. auronitens escheri*, 4. *C. linnei*, 5. *C. sylvestris*, 6. *C. arvensis*, 7. *Pterostischus pilosus*, 8. *P. foveolatus*, 9. *Calathus metallicus*, 10. *Cychrus caraboides*, 11. *C. attenuatus*, 12. *Pterostichus oblongopunctatus*, 13. *P. burmeisteri*, 14. *P. rufitarsis*, 15. *Molops piceus*, 16. *Pterostichus pumilio*, 17. *P. unctulatus*, 18. *Leistus piceus*, 19. *Trichotichnus laevicollis*, 20. *Trechus pillisensis*, 21. *T. latus*, 22. *Amara erratica*, 23. *A. aenea*, 24. *Poecilus cupreus*, 25. *Bembidion lampros*, 26. *Microlestes minutulus.*

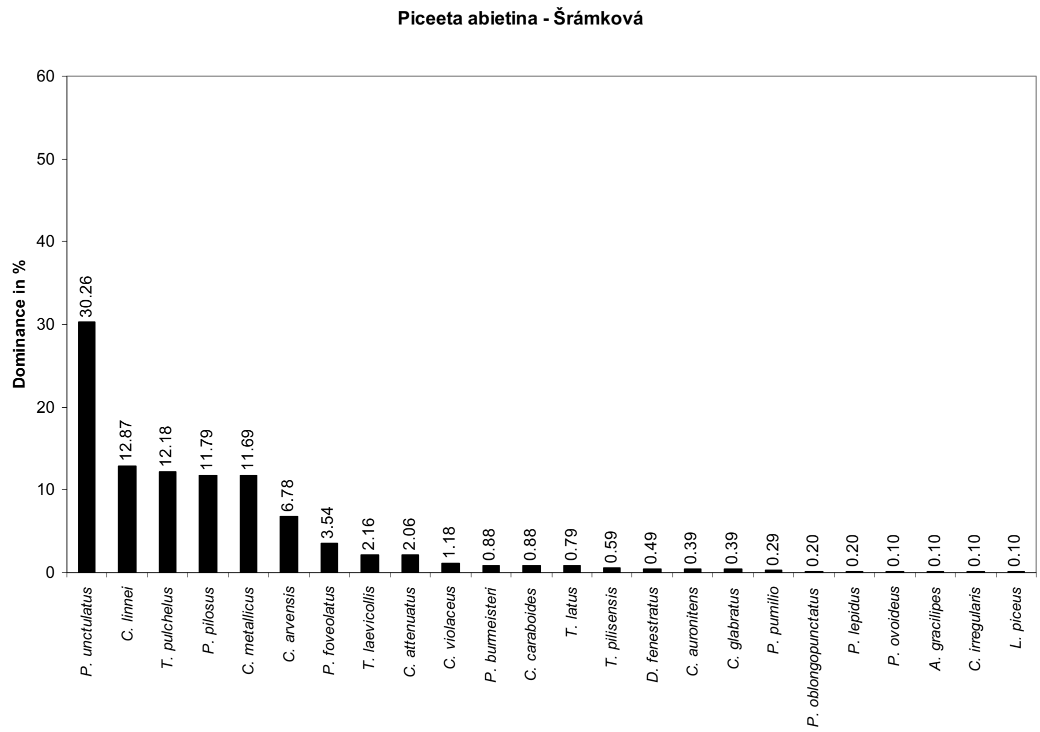

Figure 2. Structure of a community of 1,018 individuals and 24 species of Carabids in the fire-spruce stand (*Piceeta abietina*) in the State Nature Reserve Šrámková in the Malá Fatra Mts. (ŠUSTEK & ŽUFFA, 1986).

In the area of occurrence of the endemic Carpathian species *Prerostichus pillosus* and *Pterostichus foveolatus* ecological vicarization occurs in the forests (not only in the spruce forests) with similarly sized species of larger areas of distribution. As a rule, it occurs more frequently in the interior of the Carpathian zone and towards higher altitudes the elsewhere frequent *Pterostichus oblongopunctatus* and *Pterostichus burmeisteri* recede before both Carpathians endemits or are even absent in some sites in the Carpathian interior. On the contrary, in spruce forests on southern slopes of High Tatra the endemic *Pterostichus pillosus* is absent. It can be connected not only with the southern exposition, warmer and drier microclimate, trophically poorer substrate, but also with long termed deforestation of this area and its transformation into pastures (about up to the mid 19th century) and thus from the secondary character of these spruce forests.

The poorest in species are the Carabid communities in the acid spruce stands with undergrowth of *Vaccinium myrtilus* and ferns (Fig. 5 – trophic series A), where almost the whole surface is covered by a thick layer of mosses. This layer does allow the larger species to hide by day in the litter upper layer or to dig deeper in soil in the drier periods. Therefore, only a very small number of individuals of the species smaller than 5 mm (*Trechus* spp., *Leistus piceus*, *Pterostichus pumilio, Pterostichus unctulatus*) are able to move in such substrate. The species of the genus *Carabus* and middle-sized species of the genus *Pterostichus* are absent here. Very sporadically, there appear both species of the genus *Cychrus*. Their extremely low abundance is connected with low trophicity of this type of spruce forests and almost complete absence of molluscs.

The thickness and compactness of the row humus has a similar effect on the Carabid communities in some natural spruce forests. It also results in the absence of large (above 20 mm) and middle sized (about 12 –20 mm) species (*Carabus* spp., *Pterostichus* spp.), but unlike the spruce forests with continuous moss growth the small (2-6 mm) species (*Trechus* spp., *Pterostichus pumilio, Prerostichus unctulatus*) can reach an extremely high abundance (Fig. 4).

The alternation of patches densely covered by mosses and by a thin layer of dry needles allows the large species to hide in soil. Owing to it, middle and large sized species can occur in one place. On the contrary, the abundance of small species uses to be suppressed in such habitats. It is probably a consequence of not only competition pressure, but also of predation of larvae of smaller species. Such community structure is also characteristic for the spruce forests with rich herbage layer.

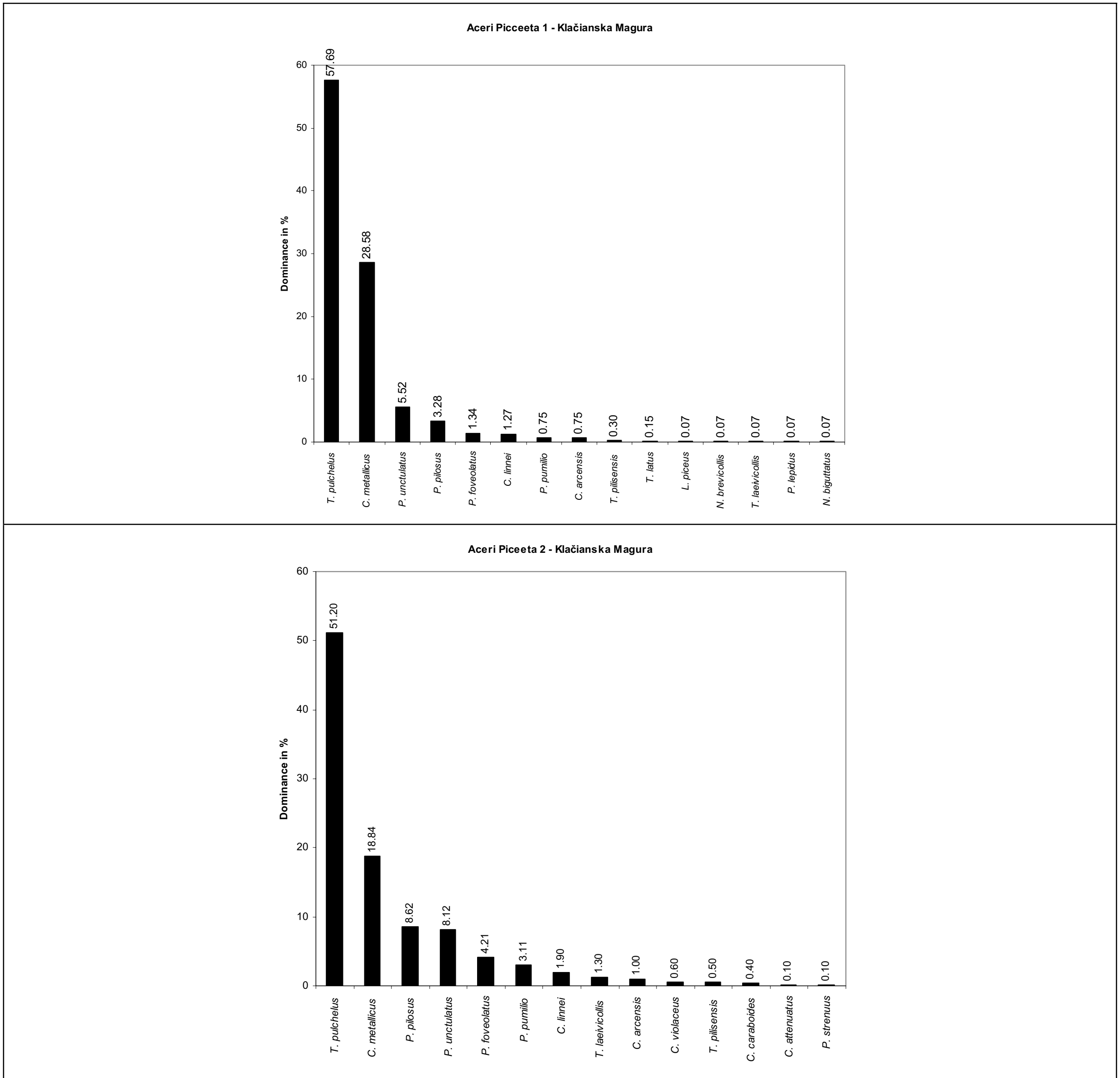

Figure 3. Variability of community structure of Carabids (up 1,340 individuals and 15 species, down 998 individuals and 14 species) in two segments of a maple-pine forest (*Aceri Piceeta*) in the State Nature Reserve Kľačianska Magura in the Malá Fatra Mts. (ŠUSTEK & ŽUFFA, 1988).

Geological substratum trophicity and carabid communities

A very significant factor managing the structure of Carabid communities is the geological substratum trophicity. In most of the territory, the natural and artificial spruce forests growth of crystalline substrata and belong to the poor acid trophic series A, AB or to the neutral series B. In the small part of the territory, in the Carpathians only, in the Belanské Tatry mts., they also occur on the basic substrata or on the places where the crystalline is covered by a thick layer of basic substratum. Thus, these spruce forests belong to the rich transitional trophic series BD. The carabid communities in both groups of spruce strongly differ structurally (Fig. 5). The qualitative differences are not large, but all species, in particular the middle- and large sized ones (Fig. 1) reach multiples of abundance. Evidently, the higher trophicity of the substratum results in richer food offer for small predators, inclusively of the Carabids. A most sensitive response can be observed in the Carpathian or Carpatho-Balkan endemics *Pterostichus foveolatus, Pterostichus pillosus* and *Calathus metalicus*. The higher trophicity also results in a higher representation of both species of the genus *Cychrus*, which are adapted to hunt little molluscs by a narrow pronotum and head allowing them to enter the shells. The favourable influence of higher trophicity of the spruce forests on basic substrata is combined with the effect of rich herbage growth and better litter permeability making easier the digging of the Carabids.

The influence of the trophicity of the geological substratum in mountain ecosystem is combined with terrain slope. The abundance of individual species is larger in the flat parts of the terrain under similar conditions than on steep slopes. It is a common feature of Carabid communities in coniferous stands in geographically very remote areas of eastern Asia (Myongyansan Mts. in North Korea) (ŠUSTEK, 2003).

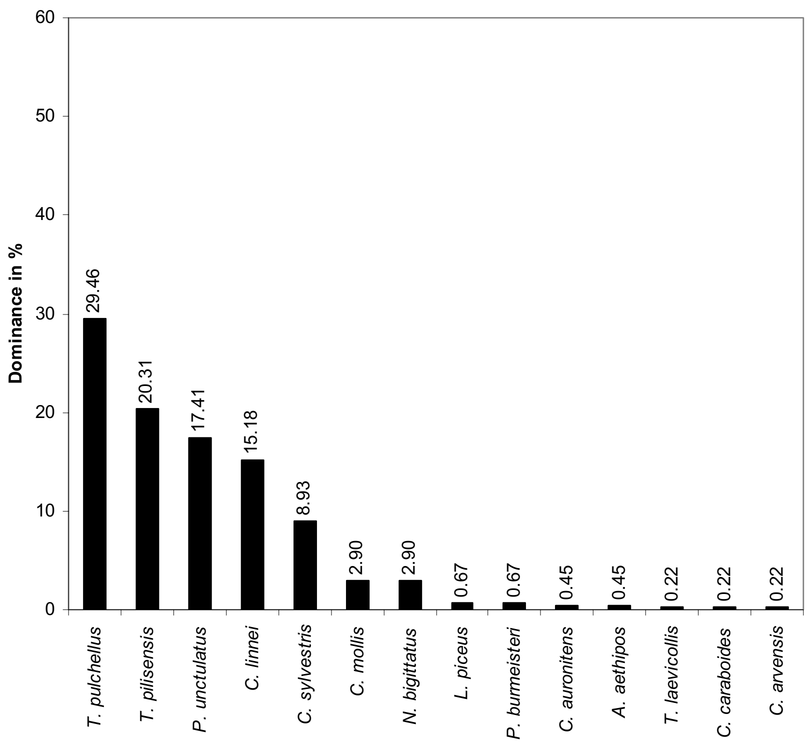

Figure 4. Community structure of Carabids (448 individuals, 14 species) in a humid fire-spruce stands (*Abieti-piceeta paludosa*) in the Hřebínek locality in Jizerské Hory Mts. (ŠUSTEK, 1982).

Relationship of the Carabid communities in spruce forests to the communities in dwarf pine stands

The Carabid communities in natural high mountain spruce forests do not differ qualitatively and mostly also quantitatively from the communities in dwarf-pine stands. It is caused by the direct continuity and gradual transition of both types of ecosystems, in which the patches of dwarf-pines or low spruces with white beams form a mosaic. Unlike lower altitudes, where striking difference in Carabid communities exists between forests and non-forests ecosystems, no essential differences occur between the communities of subalpine meadow and adjacent dwarf-pine stands. The most significant cause of this state is the positive climatic water balance (ŠKVARENINA et al., 2002) in the alpine conditions, which compensates to the stenotopic forests species in the subalpine meadows the increased humidity in forests made possible by shadowing of continuous tree canopy, on which these species are closely dependent at lower altitudes.

Carabid communities in spruce stands in vicinity of springs

In spite of the fact that the Carabid fauna of mountain creek consists of some highly specialized species (*Nebria jockischi hoepferi* DEJEAN 1826, *Nebria rufescens* STROEM, 1768), the communities in the proximity of the water-logged surroundings of springs in the closed spruce stands (but also of the beech or beech-coniferous stands) are very poor in number of species (1-3 species). There occurs, as a rule, occasionally migration of species from a wider surrounding of the spring. The most frequent are the species of the genus *Trechus*, rarely others. The population density and number of species of Carabids in such places is always substantially lower than in the surrounding. Water logging and excessive humidity has a negative impact on the Carabids. Its extent is, however, only local.

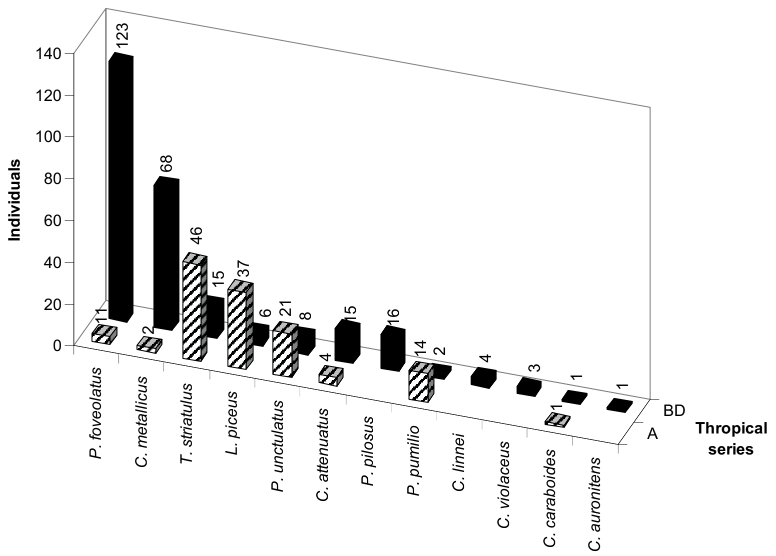

Figure 5. Abundance of Carabid species in mountain-ash-spruce forests (*Sorbi Pieceeta*) in acidophilous (A) and transitional neutral-calciphilous (BD) trophic series in the Zadné Meďodoly valley in the Belianske Tatry Mts. (ŠUSTEK, 2006)

Carabid communities in secondary spruce stands at lower altitudes

Spruce stands in the form of monocultures form extensive forests in the zone of oak-beech to fir-beech vegetation tier. Their cultivation is especially characteristic for the Hercynic part of Central Europe, which was influenced by the s.c. German forestry school and by the requirements of the industry to cultivate quickly growing trees with a strait stem. The composition of Carabid communities in these monocultures is derived from the fauna of the original geobiocoenoses of the oak-beech, oak-coniferous and fire-beech vegetation tiers. In the zone of these three vegetation tier, the occurrence of the species with optimum of vertical distribution lowlands, especially of *Carabus coriaceus* LINNAEUS, 1758, *Carabus nemoralis* O. F. MÜLLER, 1764*, Carabus hortensis* LINNAEUS, 1758*, Carabus problematicus* HERBST, 1768*, Abax paralellopipedus* (PILLER et MITTERPACHER, 1783), *Abax paralellus* (DUFTSCHMIDT, 1812) and *Pterostichus oblongopunctatus* interferes with the species having the optimum of vertical distribution in fore-beech and spruce-fire-beech vegetation tier (*Pterostichus burmeisteri, Carabus auronitens, Carabus violaceus, Carabus glabratus, Cychrus attenuatus, Cychrus caraboides, Trechus pulchelus, Trechus pilisensis, Trechus latus*) and descend to lower altitudes. The lower border of their distribution lies in the oak-beech vegetation tiers. *Cychrus attenuatus* descends on the acid sandy substrates into the oak vegetation tier and owing to the drift by flood waters it also sporadically occurs in the floodplain forest along the Danube. Similarly, *Carabus violaceus* also descends to the oak vegetation tier, but numerously, it occurs exclusively in some dried floodplain forests, where it is also drifted by water. On the contrary, in the mesohygrophilous forests, it mostly does not occur owing to competition pressure of the congeners with the optimum at lower altitudes or occurs there only sporadically. Its occurrence in spruce monocultures follows this pattern.

Thus, the Carabid communities in the oak-beech and beech vegetation tier consists of the species *Abax paralelopipedus, Abax paralellus, Carabus hortensis* and *Carabus nemoralis* (optimum in lowlands) and *Pterostichus burmeisteri, Carabus auronitens, Carabus violaceus, Carabus glabratus* and *Abax ovalis* (DUFTSCHMIDT, 1812) (optimum at middle altitudes) tending to balanced quantitative representation. In the fire-beech, they consist of predominant *Pterostichus burmeisteri, Carabus linei, Carabus auronitens, Carabus violaceus, Carabus glabratus Cychrus attenuatus, Cychrus caraboides* and *Abax ovalis* with admixion of *Abax paralellus, Carabus hortensis* and *Carabus nemoralis*.

A characteristic feature of Carabid communities in the secondary spruce monocultures in lowlands is a low cumulative abundance and poor species spectre. This phenomenon has several causes. The spruce monocultures are mostly cultivated on poor acid or neutral substrata, which offer worse trophic condition for forming the plant biomass and food basis for animals. The low level of calcium in such habitats inhibits development of molluscs representing a important part of food of some carabids, especially of larger species and, in particular of both *Cychrus* species, adapted to eating of molluscs by prolonged and narrow pronotum and head. There are also other synergic factors. The artificial spruce monocultures have a dense canopy that does not allow the development of herbage or shrub strata or these strata begin to form as late as in older stands. It also limits the food offer for small invertebrates representing the food for Carabids. Proportionally to it, the density of the population of Carabids decreases.

In addition, the body shape of some forest Carabids (*Carabus nemoralis, C. ullrichi* GERMAR, 1824*, Abax* spp., *Pterostichus burmeisteri*) is adapted to the movement in the litter formed from leaves (s.c. abacetoid morphotype with wide pronotum and body resembling the species of the genus *Abax*, for which this body shape is especially characteristic). Due to this reason, their movement in a compact layer of needles is more difficult than for the species with narrower body (*Carabus hortensis, C. auronitens, C. violaceus, Pterostichus* spp.). It is the response, why the narrower species easier survive in the spruce monocultures at lower altitudes.

Windstorms and Carabid communities in spruce stands

The factor significantly influencing the Carabid communities in spruce stands are windstorms causing wide scale destruction of homogeneous stands. One of such windstorm occurred in November 2004 in the southern slopes of the High Tatra in Slovakia (FLEISCHER & HOMOLOVÁ, 2011) or in 2007 in the Šumava Mts. in Bohemia (BOHÁČ & MATĚJKA, 2010; 2011), as well as in other places. From a part, it is a phenomenon that repeats periodically in the High Tatra in the same places (GREGOR, 1929; ŠUSTEK, 2007a, 2007b, 2007c, 2009) and it results from the unsuitable mode of afforestation in the 19th centure and in the first decades of the 20th century.

The Carabid communities react on consequence of windstorms in different ways that depend first of all on the synergism of humidity and conditions created by windfall and modes of liquidation of it consequences, direction and speed of succession secondary, spontaneously or artificially formed wooden vegetation. The windfall itself results only in the decline of the abundance of all present species (Fig. 8), but it does not affect essentially the species composition and their proportional representation. The lying timber and surviving herbage and lower wooden vegetation protect the soil surface against heating and drying. They maintain, to a certain degree, the microclimatic conditions similar to the intact stand. The abundance of individual species declines in individuals yearly approximately to the level of a third of the momentary abundance in the close intact stands (Fig. 8). Owing to it, none of the original species disappears from the affected localities; only the less abundant species start to occur with lower frequency. At the same time, the xenocoenous species being characteristic for other types of ecosystems do not invade.

In the destroyed stands, where the fallen timber was harvested, the herbage stratum is damaged during harvesting, patches of *Vaccinium myrtilus* disappeared, but there are formed continuous grassy growths resembling the mountain meadows. In such places, there appear the majority of more sensitive forest species (*Carabus linnei, Carabus auronitens, Cychrus caraboides, Cychrus attenuatus, Pterostichus foveolatus, Pterostichus unctulatus, Calathus ambiguus* (PAYKULL, 1790)). They are replaced by two more tolerant forest or moderately eurytopic species *Carabus glabratus* and *Carabus violaceus*, which reach there even a higher abundance in comparison with the intact spruce stands. It results from the reduced competition pressure of similarly sized species and from the remarkable adaptability of *Carabus violaceus*. This species is able to use even in extremely different types of ecosystems (floodplain forests with disturbed hydrological regimen) coincidence of eliminated competition pressure of congeners with its moderately increased demands for humidity to enormous increase of its abundance. Moreover, the destruction of the tree stratum favours the species typical to mountain non-forest ecosystem, like *Amara erratica* (DUFTSCHMIDT, 1812). In spite of the substantial changes there do not occur the invasion of species of the arable lands. As a consequence, the artificially provoked state of the carabid communities approximates to the communities in other types of relatively natural ecosystems.

A completely different situation arises in the damaged forests affected additionally by extensive fire, which completely destroyed the surviving herbage stratum and litter. Such places were rapidly overgrown by the heliophilous *Chamerion angustifolium*, which formed a dense growth resembling with spatial structure and microclimatic conditions stand of some agricultural crops, particularly of the cereals in the stage immediately before their ripening. It formed suitable conditions for the invasion of the field species. As a result, the original forests species disappeared in the burned localities almost completely or they occur at the beginning only occasionally. Among the original species only *Carabus violaceus* and *Carabus glabratus* survive most successfully on the burned places, or just these two species are able to re-colonize them quickest. Their migration ability can be also observed on meadows in highlands, at altitudes of about 700-800 m, where they spread in maturing grassy growth and disappear after mowing (ŠUSTEK, 1995). At the same time, the burned areas are colonized by the arable land species, even if the burned areas are isolated from the potential sources of immigration of such species. Their presence in the concrete places depends on the momentary state of the secondary herbage vegetation, which is cut in a part of the burned areas in order to protect the planted seedlings of trees.

Out of *Amara erratica* the burned places are mostly colonized by *Poecilus cupreus* (LINNAEUS, 1758) (with optimum in lowlands, primarily in floodplain terraces covered by high herbage vegetation, secondarily with a high abundance in meadows and fields) or *Poecilus versicolor* (STURM, 1824) (optimum in arable land in highlands). In the mown places, the heliophilous species *Bembidion lampros* (HERBST, 1784) and strongly xerophilous and thermophilous *Microlestes minutus* (GOEZE, 1777), which inhabits the strongly isolated patches without continuous vegetation cover arisen after mowing the stands of *Chamerion angustifolium*. Individually, there also occur other species typical of field ecosystems, like *Pseudoophonus rufipes* (DE GEER, 1774) and *Amara aenea* (DE GEER, 1774), but their abundance is low. In addition, the occurrence of the field species on the burned places is instable in time. It is caused by the shortness of the periods when these species fly over long distances, as a rule during farm spring days or during warm nights before passing of frontal systems. These periods represent the only occasion, when they can effectively pass the large distances separating the colonized areas of the damaged spruce forests from the arable land and to colonize them in a significant degree. This is a strategy of the species propagation, which is characteristic for species inhabiting the catastrophic climax ecosystems. It enables the species to escape the temporary damaged habitats and quickly search for new suitable sites.

The described differentiation of the Carabid communities in the areas damaged by windstorms with harvested timber is characteristic for the first years after the windstorm. In the subsequent years, these differences disappear and the communities in the burned areas start to converge to the communities in the non-burned areas as shown in figures 7 and 8. This convergence is connected with two factors. The first one is the development of quickly growing wooden plants (*Salix* sp., *Populus tremula, Betula pendula, Sambucus racemosa*), which reach a height of 2-4 m within 6-8 years after the windstorm and form groups and partly shadow their vicinity. The second factor is mowing of *Chamerion angustifolium,* what enables the development of grassy vegetation and convergence of the conditions to those in unburned areas.

The described changes and the course of succession are illustrated by the hierarchical classification of the communities (Fig. 6) and by their ordination (Fig. 7), which show a strong differentiation of the communities shortly after the windstorm after the momentary state of damaging of vegetation into three groups described above and a tendency to convergence of the communities from all plots with harvested timber in the last years of investigation. However, the differentiation between the intact forest and plot with timber *in situ* on one hand and all the plots with extracted timber on other hand persit. At the same time, especially the ordination shows a common trend of shift of all one year samples from 2010-2012 in the left upper part of the ordination space. It reveals common trends in the composition of all communities, irrespectively on their actual state.

Generally, it can be stated that the invasion of the non forest species into spruce stands destroyed by windstorm is much more reduced in mountain condition at altitudes of 1000-1200 m than at lower altitudes (ŠUSTEK, 1984), where the forests species use to be completely replaced by the open-landscape species within a very short period. The laying fallen timber in situ seems to be optimal from the viewpoint of Carabids. Similarly, BOHÁČ & MATĚJKA (2010, 2011) have shown in the Šumava Mts in Bohemia that laying the staying dry spruce damaged by bark beetles is beneficent for the soil fauna, while any (of the) mode of human management of the damaged stands has destructive effects on the soil fauna.

Medium-termed climatic changes and Carabid communities in the spruce forests

The medium-termed changes of climate characterized by the standardized precipitation and evaporation index (ŠUSTEK & VIDO, 2012, in press) show that the carabid communities in spruce forests, irrespectively of their state or succession stage after a large scale destruction, very sensitively react, with about one year delay, on the incidence of the climatic drought by a strong decline of the number of recorded species and number of species. In the studied area of the High Tatra, the weather in 2007, when the study started, was characterized by an exceptionally hot and dry summer. Several temperature records (for example on July 20, the temperature at Hurbanovo reached 40.2ºC) exceeded the highest temperatures ever recorded in Slovakia (ŠUSTEK & VIDO, 2012, in press). The high temperatures and especially a low sum of precipitation were recorded since April to August 2007. Due to it, the growing season of this year was much drier than in the climatically normal year 2006. However, indications of a starting dry period were observed already by the end of 2006, when a hot air streamed to Slovakia from an area of high pressure above the Mediterranean Sea. It started the warmest winter recorded since the beginning of the meteorological observations in Slovakia. At the same time, December 2006 was evaluated as very dry. The next years were considered as normal (2008 and 2009) or very humid (2010), except of June 2008 and, from a part, also April, May and September 2009, which were dry in the High Tatra.

In conformity with the above climatic characteristics, the year 2008 was characterized by a sudden drop of the number of species and individuals and of cumulative biomass in all sites (Figs. 8-10). The deepest drop was observed in both burned sites and in the site VL. The number of recorded species in the burned sites and in VL declined to 35% of the state recorded in 2007, while in the unburned harvested site EXT to 60%, whereas in the reference site and in the site with timber *in situ* only to 77%. Thus, this decline was proportional to the anthropogenic pressure, to which individual sites were exposed. On the contrary, the most moderate drop was observed in the naturally developing reference site and in the site with timber *in situ*. The same relationship is still better visible in comparison with the index SPEI24, which integrates the air temperature. The value of this index strongly declined from 0.18 in 2006 to –0.91 in 2007. From 2008, both indices show shifting of the climatop to the more humid conditions. This shifting is followed by the increase in the number of recorded species in all localities. The reaction is more balanced on both sites (REF and NEXT) without additional anthropogenic interventions, whereas they are less obvious in both burned sites. A very strong decline of these three parameters was also observed in the second half of the growing season of 2012 (Figs. 8-10).

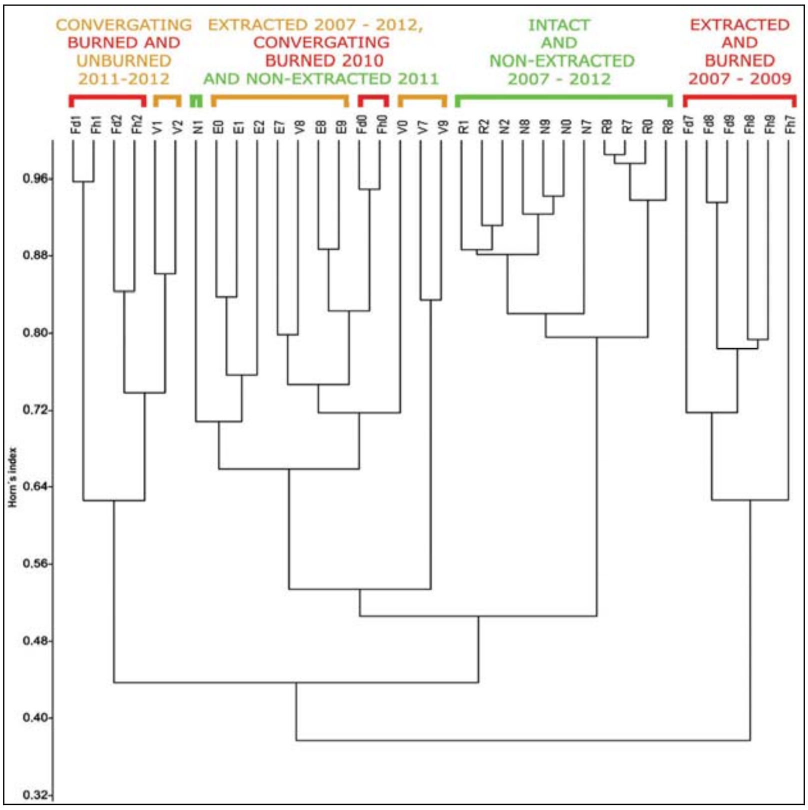

Figure 6. Hierarchical classification of Carabid communities from the study sites in the High Tatra (symbols of localities – first letter of locality name abbreviation and the last digit of sampling year [REF – intact reference stand, NEXT – stand with fallen timber in situ, EXT and Vl – stands with extracted timber, Fd and Fh stands with extracted timber additionally affected by an extensive fire), (ŠUSTEK & VIDO, in press).

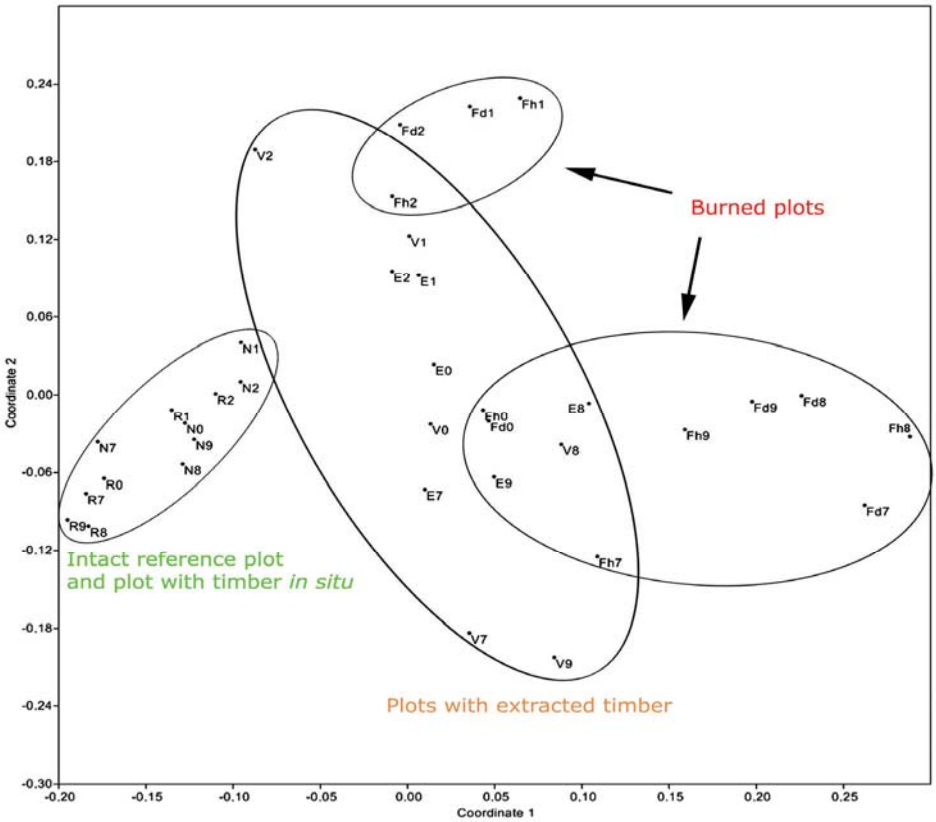

Figure 7. Non-parametric scaling of one-years samples of Carabids from study sites in the High Tatra (symbols of localities as in Fig. 6), (ŠUSTEK & VIDO, in press).

The figures 8-10 show a one-year delay of this reaction of the community to the climatic changes characterized by the decline of SPI24 from 0.27 in 2006 to-0.40 in 2007, but also an unmediated reaction of the community in the summer and autumn of 2012.

A very strong decline occurred in the number of species and individuals in all localities in 2008 (Figs. 8 and 9), inclusively of the intact forest and in the site with timber *in situ,* where the number of individuals decreased to 20%. But even in this case, the reaction was most moderate in the intact forests, where an increase to almost 60% of the starting value appeared already in 2009. The largest decline of the number of individuals (to 19%) in the damaged sites was recorded in the harvested site EXT, followed by the burned site Fd (37%), unburned harvested VL (38%) and burned site Fh (56%). In the years 2010 and 2011, the number of individuals from 2007 was restored in the site with timber *in situ.* In other sites, even larger numbers of individuals were recorded. A strong increase in the number of individuals in both burned sites is partly caused by the invasion of a large number of *Poecilus versicolor* and *Amara aenea* characteristic of the arable land and cannot be ascribed only to climatic changes. However, irrespectively of it, the SPEI fits better the changes in the cumulative number of individuals than SPI, similarly as in the case of the number of species (Fig. 8). The decline of SPI24 and SPEI 24 in 2012 caused by the extremely warm and dry second part of summer 2012 was not so strong as in 2007 and correspondingly it did not provoke such a strong reaction as in 2008.

The strong decline of the cumulative biomass of Carabids in the intact forests (Fig. 10), which probably resulted from the dry winter 2006/2007 and from the dry growing season 2007, was caused especially by the decline of the number of individuals of large species like *Carabus glabratus*, *Carabus violaceus* or *Carabus auronitens* binding the essential portion of the community cumulative biomass. The freed ecological niche was quickly occupied by little species like *Calathus micropterus* or *Pterostichus unctulatus.* But these species were later probably subjected to predation pressure of the large species of Carabids or relatively abundant insectivorous Soricids, which could restore their earlier position in the community after the improvement of the climatic conditions in 2010. In 2010, the number of individuals of the small species declined again (180 individuals of *Pterostichus unctulatus* in 2010, but 47 in 2011). Due to it, the increasing trend in the cumulative number of individuals (Fig. 9) was stopped in the intact forest, but the cumulative biomass continued to grow (Fig. 10) due to the presence of fewer individuals of large species.

Because of the remarkable differences in body size of Carabids (body length ca. 20x, but body weight even ca. 1000x), the cumulative biomass of their communities represents an important parameter. Similarly as in the number of individuals, the cumulative biomass dropped in all localities in 2008 to about 20 % of the level observed in 2007. In the next years, the cumulative biomass increased, more visibly in the intact forest, less in all damaged localities. In 2010, the starting level on 2007 was restored and in 2011, it was even exceeded, except the locality with timber *in situ*. This trend corresponded, with certain delay, with the increase of SPI and SPEI (Figs. 8-10). The different increase of the cumulative biomass in both burned site resulted from a more intensive invasion of *Poecilus versicolor* in the burned site Fd. When comparing the figures. 8-10, also in this case the SPEI fits the changes better. The warm dry summer of 2012 indicated by decline of SPE and SPEI and was followed by a sudden drop of the biomass to level of 2010 (Fig. 10).

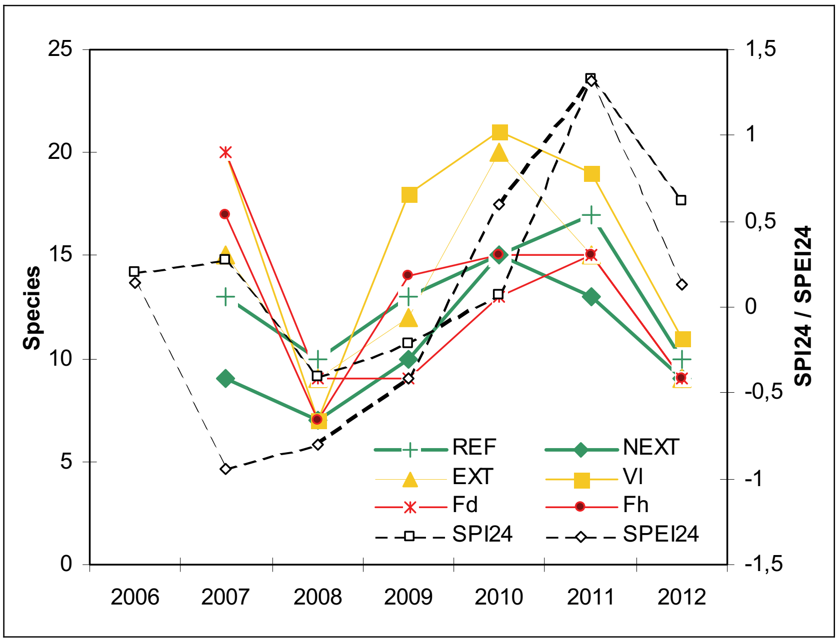

Figure 8. Changes of the number of Carabid species in spruce forests depending on the stand damaging and dynamics of the indices SPI 24 and SPEI 24 in 2007-2012 (REF – intact reference stand, NEXT – stand with fallen timber in situ, EXT and Vl – stands with extracted timber, Fd and Fh stands with extracted timber additionally affected by an extensive fire), (ŠUSTEK & VIDO in press).

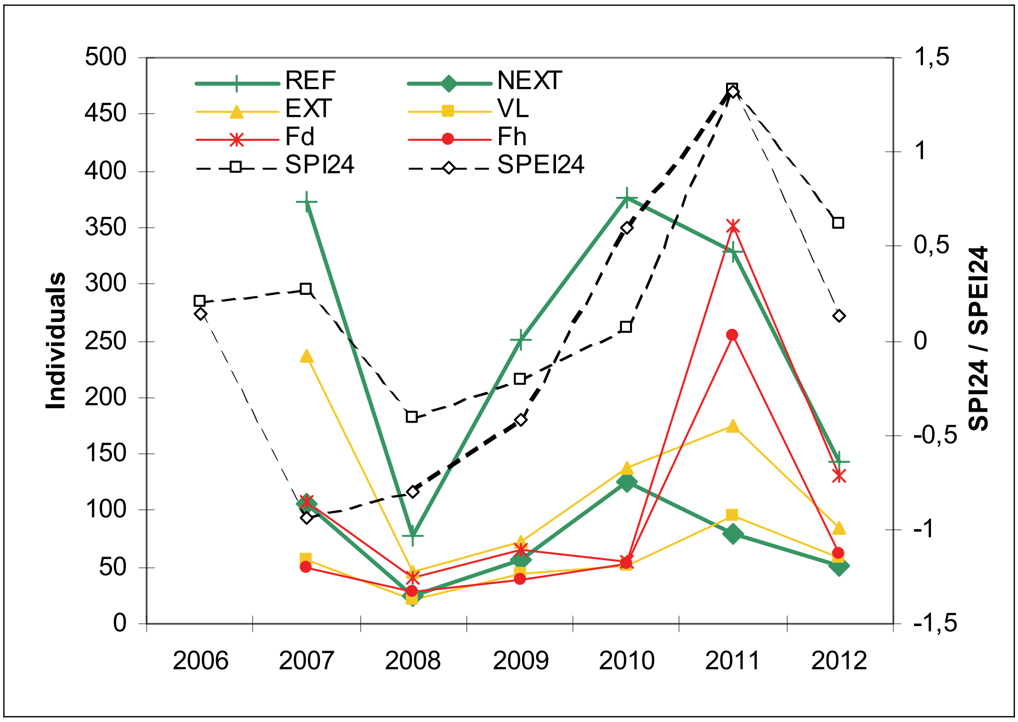

Figure 9. Changes of the number of individuals of Carabid in spruce forests depending on stand damaging and dynamics of the indices SPI 24 and SPEI 24 in 2007-2012 (symbols as in Fig. 6), (ŠUSTEK & VIDO, in press).

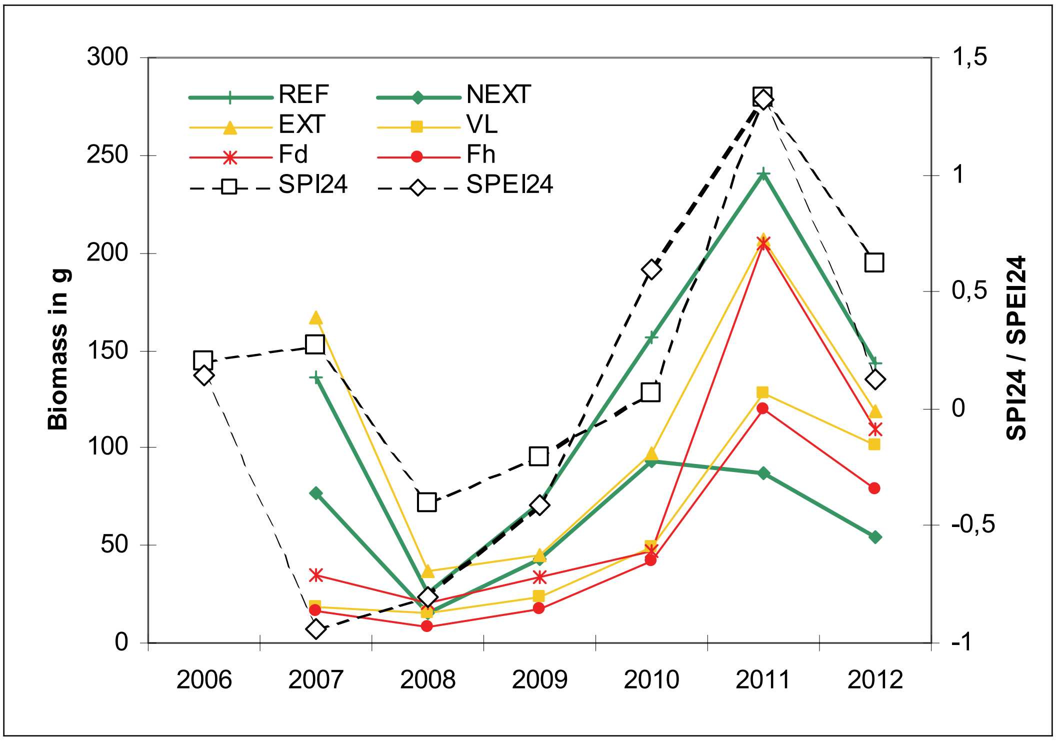

Figure 10. Changes of biomass of Carabids in spruce forests depending on the stand damaging and dynamics of the indices SPI 24 and SPEI 24 in 2007-2012 (symbols as in Fig. 6.), (ŠUSTEK & VIDO, in press).

CONCLUSIONS

The carabid communities in spruce stands in Central Europe represent a very variable complex of communities and their successional stages. They reflect the zoogeographical position of the locality, vertical zonality of distribution of Carabids, as well as the soils reaction. Their differentiation in the stands damaged by windstorm depends on the mode of the management of the damaged sites. The absence of human interventions seems to be optimal from the viewpoint of Carabid communities, while the human interventions cause, according to their intensity, substantial structural and long-termed changes, which can inhibit the restoration of the stands. Coenologic parameters of both natural and secondary Carabid communities sensitively react on the weather fluctuations with about one year delay. The incidence of a strong drought combined with increased temperature can effectively inhibit the succession for a considerable period. On the contrary, the pluvial and colder periods accelerate the restoration of the communities and contribute to the convergence of Carabid communities from differently managed localities. The Standardized precipitation index and Standardized precipitation and evaporation index seem to be adequate parameters to characterize the changes in the Carabid communities.

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