

Drought impact on ground beetle assemblages (Coleoptera, Carabidae) in Norway spruce forests with different management after windstorm damage – a case study from Tatra Mts. (Slovakia)

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Abstract: After the windstorm of November 2004, the ground beetle assemblages (*Coleoptera, Carabidae*) differentiated after the windstorm into four groups reflecting degree of damaging and forestry management (intact stand, fallen timber *in situ*, extracted timber, fire). The stand with fallen timber reduced abundances of original species. Removal of timber eliminated sensitive forest species and favored tolerant species, whereas the fire allowed invasions of field species. Later, the assemblages on burned sites converged to those in the unburned sites. Their restoration has a sigmoid-like course.

Independently on the above differentiation and course assemblage succession, episodes of severe drought resulted with a 1–2-years delay in sudden decline of number of individuals and species. Their numbers were restoring after longer humid periods. Because these extremes occur with a considerable regularity, the observed extremes of fluctuations of number of species and individuals represent the variability limits of the Carabid assemblages in such conditions. The Standardized Precipitation Evapotranspiration Index was shown, using the cross-correlation of SPEI and number of individuals and species of Carabids, as a suitable means to explain and predict such changes for the period of 1–2 years.

Keywords: Drought; Ground beetle; Windstorm; Forest management; Norway spruce.

INTRODUCTION

The Tatra Mountains – the highest mountain range of the West Carpathians have a specific climatic, orographic and ecological character. Because of this, unique fauna and flora have been formed there. However, because of the mountain orography, damaging downslope wind called as Bora occurs periodically (Fleischer et al., 2009). This winds cause severe damages on forest ecosystems repeatedly on the same places and influence structure of the biocoenoses. For the first time they were described and mapped by Mrkos (in Gregor, 1929). The last Bora downslope wind occurred in November 2004. This was a huge devastating catastrophe that damaged almost 25% of the Norway spruce forests on southern slopes of High Tatra. In addition, in 2005 a considerable part of this area was affected by a wide-spread forest fire. It had a profound impact on the biota (Mezei et al., 2014a, 2014b; Renčo et al., 2015; Šustek and Vido, 2013; Urbanovičová et al., 2013). The ecosystems disturbed in this way are more prone to hydro-meteorological hazards, in particular to drought (Ježík et al., 2015; Kurjak et al., 2012). Because of the wide concept of ecosystem, it is necessary to study impacts of drought using proper bioindicators. The Carabids (ground beetles) are especially suitable for this purpose because of their enormous ecological differentiation, high sensitivity to humidity changes and limited mobility (Lövei, 2008).

The Carabid assemblages in mountain forests ecosystems of High Tatra damaged in November 2004 by the wind catastrophe showed two types of changes. The first type of changes was connected with destruction of the stands, the subsequent human activities in the damaged area and with the spontaneous or

artificial restoration of the ecosystem (Šustek, 2009, 2013; Šustek and Čejka, 2009; Šustek and Vido, 2013). The second type of changes was common as for the assemblages in intact stands as for those in differently damaged and restoring stands. They included simultaneous declines or increases in number of individuals, species and biomass in one-year samples. The eight-year investigation indicated that they have periodical character correlated with the occurrence of short termed drought episodes (Šustek and Vido, 2013). In addition there was observed a slight trend of spreading species with occurrence optimum in lower altitudes and increase of representation of species having the lower limit of altitudinal distribution in lowlands (Lövei, 2008).

The aims of this paper are: (1) to describe the periodic and non-periodic changes in mountain Carabid assemblages linked to different forestry management and, first of all, occurrence of short-term drought episodes and; (2) to compare the suitability of the Standardized Precipitation Evapotranspiration Index for 6 and 12 months, using the cross-correlation, to explain or even predict changes in Carabid assemblages for about 1–2 years.

MATERIAL AND METHODS

Study area

The investigations were carried out in six study plots representing an intact Norway spruce stand and a habitat with fallen timber *in situ*, two habitats with extracted timber and two habitats with extracted timber additionally damaged by large scale fire in July and August 2005. The plots were selected by the staff of the Investigation Station of the High Tatra National Park (Fleischer, 2008) to coordinate the international investigations

Table 1. Survey of study plots in the area affected by the windstorm in High Tatra on 19 November 2004.

| Locality | Vyšné Hágy reference plot | Tatranská Lomnica, Jamy, | Tatranská Polianka, Danielov dom | Nový Smokovec, Vodný les | Tatranské Zruby lower plot | Tatranské Zruby upper plot |
|-----------------------------|-----------------------------------|--------------------------------|--|----------------------------------|----------------------------------|----------------------------------|
| Locality abbreviations | REF | NEXT | EXTd | EXTI | FIRI | FIRh |
| Geographical coordinates | 49°07'17.5"N 20°06'15.0"E | 49°09'33.7"N, 20°15'07.9" E | 49°07'15.3"N 20°09'46.0"E | 49°08'07.6"N, 20°12'24.8" E | 49°07'49.3"N 20°11'49.1"E | 49°08'02.7"N 20°11'30.1"E |
| Altitude [m] | 1233 | 1062 | 1060 | 1022 | 1015 | 1095 |
| Vegetation zone | Spruce | Spruce | Spruce | Spruce | Spruce | Spruce |
| Tropical series | Acidophilou mesophilous | Acidophilou mesophilous | Acidophilou mesophilous | Acidophilou mesophilous | Acidophilou mesophilous | Acidophilou mesophilous |
| Forest type | <i>Sorbi</i> <i>Piceeta</i> | <i>Sorbi</i> <i>Piceeta</i> | <i>Sorbi</i> <i>Piceeta</i> | <i>Sorbi</i> <i>Piceeta</i> | <i>Sorbi</i> <i>Piceeta</i> | <i>Sorbi</i> <i>Piceeta</i> |
| Degree of damaging | Intact mature spruce forest | Timber <i>in situ</i> | Timber extracted, unburned | Timber extracted, unburned | Timber extracted, burned | Timber extracted, burned |

started after the windstorm. In this study, the sites (Table 1) are described according to the Zlatník's phytocoenological system of forests ecosystems (Raušer and Zlatník, 1966; Zlatník, 1976).

Mountain climate of spruce vegetation zone is characterized by a short growing season (from 70 to 100 days) and excess precipitation (Hlavatá et al., 2011). According to the measurements at the stations of the Slovak Hydro–Meteorological Institute (SHMI), mean annual precipitation total fluctuates between 870 and 965 mm, and from 550 to 575 mm in the growing season (April to September). Mean annual totals of potential evapotranspiration are in the range from 420 to 445 mm. Mean annual air temperature is from 3.6 to 4.6°C, and from 9.0 to 10.4°C in the growing season. January is the coldest month (−5.3°C), and July is the warmest month (13.8°C). The amplitude of air temperature (19.1°C) indicates the interior, montane continentality. Snow cover lasts for about 110 to 155 days, and its average height is between 88 and 180 cm. Climatically, the studied region is classified as a humid cool climatic region, and a cool mountainous subregion (Hlavatá et al., 2011; Lapin et al., 2002).

Natural montane Norway spruce (*Picea abies*) vegetation zone is a typical example of the extrazonal occurrence of the boreal taiga biome in the nemoral zone of the European mountains (Plesník, 2004; Škvarenina et al., 2004). A forest type of *Sorbi Piceeta* represents communities where spruce is a dominant tree species. Admixed tree species are European larch (*Larix decidua*), and Swiss stone pine (*Pinus cembra*). Both larch and Swiss pine are more abundant on rocky soils, where spruce cannot compete with them. Larch as a relatively short-living (successional) tree species occurs also on deeper, loamy soils, in particular at sites with frequent wind-throws. From coniferous tree species, the Scotch pine (*Pinus sylvestris*) occurs individually in the forests. Broadleaved tree species naturally occur only sparsely, in particular at sites with open stand canopy of spruce forests (after the disturbance by wind, insects, but also due to ageing). From broadleaved tree species, rowan (*Sorbus aucuparia*), and Carpathian hairy birch (*Betula pubescens* ssp. *carpatica*) are frequent, and at moister, nutrient-rich sites we can also find the sycamore maple (*Acer pseudo-platanus*). In this part of the Tatras, the spruce vegetation zone forms the upper timberline. Above the continuous spruce stands there is a zone of open stands, tree groups and individual trees, often mixed with dwarf mountain pine (*Pinus mugo*) (Škvarenina et al., 2004; Zlatník, 1976).

Methods

Occurrence of drought episodes are characterized by The Standardized Precipitation Evapotranspiration Index (SPEI) (Hayes et al., 1999; Vicente-Serrano, 2010) calculated for the period 1960–2014 based on the data from the meteorological station Tatranská Lomnica. SPEI is logically based on calculation principle of the Standardized Precipitation Index (McKee et al., 1993). However the main advantage comparing to the SPI is that the SPEI calculates balance between precipitation and potential evapotranspiration. In 99%, the SPEI values move within the limits −3 and +3 and basing on the cumulative probability distribution the concrete values can be interpreted by means of the Table 2. Thus this interpretation indicates significance of the drought episode that means a period with continuous occurrence of negative values of SPEI.

Table 2. Cumulative probability distribution of the SPEI.

| Values of SPEI | Character of deviation | Number of occurrence of situations within 100 years |
|-------------------|---------------------------|--|
| ≥ 2.0 | Extremely humid | 2.5 |
| 1.5 to 1.99 | Very humid | 5 |
| 1.0 to 1.49 | Medium humid | 10 |
| −0.99 to 0.99 | Close to normal | 66 |
| −1.0 to −1.49 | Medium dry | 10 |
| −1.5 to −1.99 | Very dry | 5 |
| ≤ −2.0 | Extremely dry | 2.5 |

For purposes of our study we calculated continuous SPEI for 12 months (further SPEI-12). The SPEI-12 has been also used to uncover the influence of winter precipitation regime on spring ecological response of the spruce ecosystem in the High Tatra Mountains. SPEI-12 has been cross-correlated (using the PAST program, Hammer, 2012) with number of individuals and of species of ground beetle assemblages on the localities described above.

The beetles were pitfall trapped. Six formalin traps (0.75 l plastic jars with 90 mm opening) were exposed in a line in 10 m distances in each plot from end of May until early November 2007–2014 and emptied approximately in on month intervals. The beetles from each set of traps were summed to obtain one-season samples (see Supplementary material) that were used at further analyses. Scientific names of species are adopted according to Hůrka (1996). The habitat and humidity preference of each species (Table 3) was characterized by semi-quantitative scales elaborated by Šustek (2004) basing on literature (Burmeister, 1939; Desender, 1986a, b, c, d; Freude et al.,

1976; Lindroth, 1949; Lövei, 2008; Sharova, 1981; Šustek, 1992, 1994a, 1994b; Šustek, 2000; Thiele, 1977) and on the author's field experience in many ecosystems types in Central Europe. The humidity scale is represented by eight degrees ranging from 1 to 8 (1 = extremely xerophilous species of steppe-like habitats, 4 = mesohydrophilous, 8 = extremely hydrophilous species of riverbank or swampy habitats), while the habitat preference by four degrees (1 = heliophilous species of open habitats, with discontinuous cover, 4 = stenotopic forest species preferring shadowing by completely closed canopy). These values were used to calculate the humidity preference and vegetation cover preference indices of Carabid assemblage. They were calculated as the average preference of all species in one-year samples weighted by number of individuals of each species as it is used in methods of direct ordination (Poole, 1974). The structural changes of assemblages are quantified by number of species and cumulative number of individuals in one-year catches (see Supplementary material). The ordination of the assemblages was carried out by non-parametric multidimensional scaling (NMS) using the program PAST (Hammer, 2012) and Horn's index as a measure of proportional similarity.

RESULTS AND DISCUSSION

In the whole investigation period altogether 50 species were recorded in all study plots (Table 3 and Supplementary material). They include two sharply differing ecological groups – stenotopic forest species unable to fly and requiring permanent shadowing by closed tree canopy and heliophilous mostly well flying species bound to non-forests, natural and artificial ecosystems and several species showing obvious preference for forest, but tolerating substitution of closed forest vegetation with the high grassy stands, like *Carabus violaceus* and *Carabus glabratus* (Magura, 2002). Among them, 7–21 species were recorded in individual plots and years. Their number was moderately positively correlated ($r = 0.3148$) with number of trapped individuals that fluctuated from 22 to 376. The higher cumulative numbers of individuals have been obtained especially from abundant occurrence of small (2.4–7.0 mm, genera *Microlestes*, *Bembidion*) and medium sized species (7.0–18.0 mm, especially genera *Amara*, *Poecilus*, *Harpalus*) (for body sizes of individual species see Freude et al. (1976) or Hůrka (1996)) predominating in the damaged plots with extracted timber. In contrast of these patterns big species (16–40 mm, almost exclusively genus *Carabus*) represented a major part of the assemblages in the intact plot and in the plot with timber *in situ*.

The between-year changes of number of species and cumulative number of individuals (Figs. 1–2) show a similar trend independently on the momentary degree of damaging the assemblage.

In 2008, they suddenly dropped deeply under the level of the precedent year, but since 2009 they gradually increased. Number of species and individuals culminated in 2010 or 2011. The extremely high values in 2011 in both burned plots are due to invasion of the well flying *Amara nitida* (see Supplementary material). In 2012 numbers of individuals and species deeply dropped again and approximated their minimum values of 2008.

In the next two years the numbers of species and individuals stabilized at the approximately same level. However, in individual plots they show moderately different directions. In the intact reference plot number of individuals continued to decrease, but in one of the burned plots FIRE-1 it increased. Number of species also moderately decreased on most plots, but it slightly increased in the burned plot FIRE-h (see Supplementary material).

Table 3. Scientific names of species and characteristics of their demands to vegetation cover (scale 1 – 4 discontinuous herbage stratum, without wooden plants to complete shadowing by trees) and humidity (scale 1 – 8 = strongly xerophilous to strongly hydrophilous). The species are aggregated in major ecologic groups.

| Species | Vegetation cover | Humidity |
|--|------------------|----------|
| 1. Stenotopic forests species | | |
| <i>Pterostichus nigrita</i> (Fabricius, 1792) | 4 | 8 |
| <i>Pterostichus strenuus</i> (Panzer, 1797) | 4 | 7 |
| <i>Pterostichus niger</i> (Schaller, 1783) | 4 | 6 |
| <i>Carabus coriaceus</i> (Linnaeus 1758) | 4 | 5 |
| <i>Carabus glabratus</i> (Paykull, 1790) | 4 | 5 |
| <i>Carabus linnei</i> (Dejean, 1826) | 4 | 5 |
| <i>Carabus violaceus</i> (Linnaeus, 1758) | 4 | 5 |
| <i>Cychrus caraboides</i> (Linnaeus, 1758) | 4 | 5 |
| <i>Leistus piceus</i> (Frölich, 1799) | 4 | 5 |
| <i>Leistus terminatus</i> (Hellwig in Panzer, 1793) | 4 | 5 |
| <i>Pterostichus angustatus</i> (Duftschmidt, 1812) | 4 | 5 |
| <i>Pterostichus burmeisteri</i> (Heer, 1801) | 4 | 5 |
| <i>Pterostichus aethiops</i> (Panzer, 1797) | 4 | 5 |
| <i>Pterostichus foveolatus</i> (Duftschmidt, 1812) | 4 | 5 |
| <i>Pterostichus oblongopunctatus</i> (Fabricius, 1787) | 4 | 5 |
| <i>Pterostichus unctulatus</i> (Duftschmidt, 1812) | 4 | 5 |
| <i>Trechus latus</i> (Puzey, 1847) | 4 | 5 |
| <i>Trechus striatulus</i> (Putzeys, 1847) | 4 | 5 |
| <i>Trichotichnus laevicollis</i> (Duftschmidt, 1812) | 4 | 5 |
| <i>Carabus auronitens</i> (Fabricius, 1792) | 4 | 4 |
| <i>Carabus hortensis</i> (Linnaeus, 1758) | 4 | 4 |
| <i>Carabus nemoralis</i> (O. F. Müller, 1764) | 4 | 4 |
| <i>Loricera caerulea</i> (Linnaeus, 1758) | 4 | 4 |
| <i>Molops piceus</i> (Panzer, 1793) | 4 | 4 |
| 2a. Eurytopic species preferring open landscape | | |
| <i>Calathus metallicus</i> (Dejean, 1828) | 3 | 5 |
| <i>Calathus micropterus</i> (Duftschmidt, 1812) | 3 | 3 |
| <i>Carabus arvensis</i> (Herbst, 1784) | 2 | 5 |
| <i>Agonum micans</i> (Nicolai, 1822) | 2 | 7 |
| <i>Anisodactylus binotatus</i> (Fabricius, 1792) | 2 | 6 |
| <i>Agonum sexpunctatum</i> (Linnaeus, 1758) | 2 | 5 |
| <i>Europhilus gracilipes</i> (Duftschmidt, 1812) | 2 | 5 |
| <i>Notiophilus biguttatus</i> (Fabricius, 1779) | 2 | 4 |
| <i>Notiophilus palustris</i> (Duftschmidt, 1812) | 2 | 4 |
| 2b. Strictly open landscape species | | |
| <i>Trechus amplicollis</i> (Fairmair, 1859) | 2 | 5 |
| <i>Harpalus quadripunctatus</i> (Dejean, 1829) | 2 | 4 |
| <i>Poecilus cupreus</i> (Linnaeus, 1758) | 2 | 4 |
| <i>Poecilus versicolor</i> (Sturm, 1824) | 2 | 4 |
| <i>Harpalus distinguendus</i> (Duftschmidt, 1812) | 1 | 4 |
| <i>Harpalus latus</i> (Linnaeus, 1758) | 1 | 4 |
| <i>Pseudoophonus rufipes</i> (De Geer, 1774) | 1 | 4 |
| <i>Harpalus affinis</i> (Schrank, 1784) | 1 | 3 |
| <i>Amara aenea</i> (De Geer, 1774) | 1 | 3 |
| <i>Amara erratica</i> (Duftschmidt, 1812) | 1 | 3 |
| <i>Amara eurynota</i> (Panzer, 1797) | 1 | 3 |
| <i>Amara familiaris</i> (Duftschmidt, 1812) | 1 | 3 |
| <i>Amara lunicollis</i> (Schiodte, 1837) | 1 | 3 |
| <i>Amara nitida</i> (Sturm, 1825) | 1 | 3 |
| <i>Amara ovata</i> (Fabricius, 1792) | 1 | 3 |
| <i>Bembidion lampros</i> (Herbst, 1784) | 1 | 3 |
| <i>Microlestes maurus</i> (Sturm, 1827) | 1 | 2 |

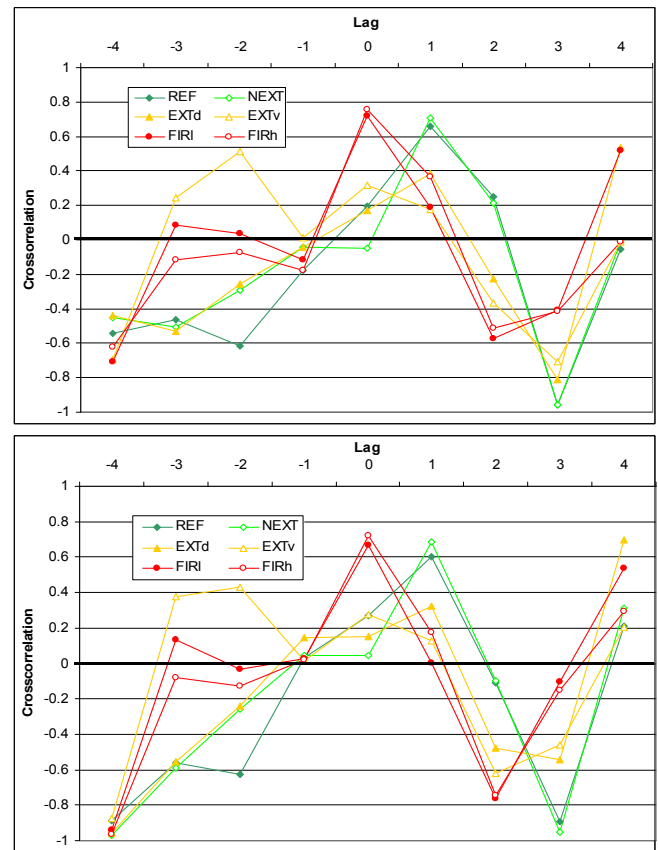


Figs. 1–3. Changes in number of species (1), cumulative number of individuals (2) and changes SPEI-12 (3) in six sites in High Tatra in 2007–2014 (abbreviations as in Table 1).

The changes described above coincided with course of changes of SPEI-12 (Figs. 1–3). In late 2006 and in 2007, there occurred a drought indicated by a sudden drop of this index. SPEI-12 was low in whole 2007 and rarely also 2008. In 2010, when number of species and individuals started to increase, SPEI-12 also showed high values ranging from 1.0 and 2.0. Occurrence of high values of this index is the more continuous; the longer periods are represented by it (Fig. 3). SPEI-12 in 2012 declined to the interval 0.0 to –1.0. This drop anticipated the strong decline of number of species and individuals in 2012–2014 (Figs. 1–2).

In 2012 and 2013, SPEI-12 declined to –2.0. In 2014 this index started to increase again. This moderate increase coincides with increase of number of individuals of Carabids in some plots in 2014 (Figs. 1–2). Comparison of course of changes in number of individuals and species with occurrence of drought periods indicated by SPEI index show that changes in both number of species and individuals mostly occur with an approximate delay of 1–2 years after incidence of extreme drought or rainy years.

Figures 1–2 show that a sudden decline of number of species and individuals of Carabids follows after a longer occurrence of values of SPEI close to –1.0 or lower. On contrary, a longer occurrence of values around 0 already anticipate a moderate increasing of number of species and cumulative number of



Figs. 4–5. Cross-correlations of fluctuations of number of Carabid species (above) and individuals (below) with SPEI-12 months.

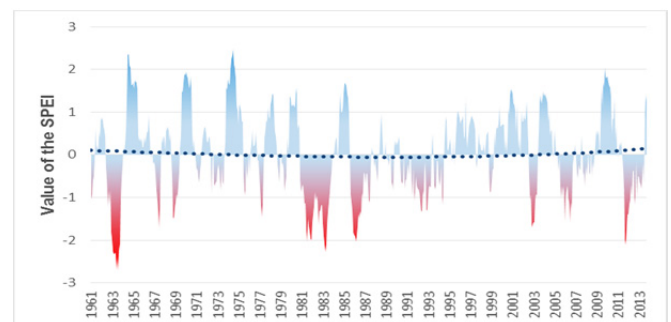


Fig. 6. Long-termed fluctuations of SPEI 12 months in High Tatra in 1960–2013.

individuals. After a prolonged increase of SPEI-12 to the level 1.0 to 2.0, a strong increase of number of individuals and species followed.

The fluctuations in number of species and individuals are cross-correlated with fluctuations in SPEI-12 months. The maximums of the cross-correlation coefficients occur mostly with a 0–2-year lag (Figs. 4–5).

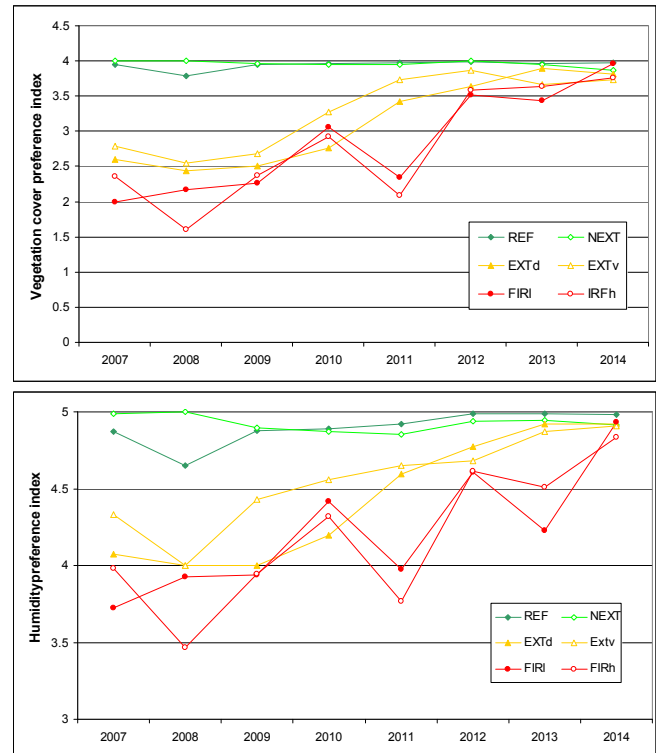
For prognosis of development of the cumulative number of individuals of Carabid assemblages basing on climatic fluctuations it seems that the SPEI-12 has a considerable indicative value. The similar, but slightly moderately phase shifted course of fluctuation of the climatic factors and of number of individuals and species in 2007–2012 puts question of periodicity of climatic fluctuation and their influence on animal communities. Changes of SPEI-12 (Fig. 6) calculated for meteorological station Tatranská Lomnica for 1961–2014

show that fluctuations of SPEI-12 in range of -1.5 to $+1.5$, or rarely even in the range of -2.0 to $+2.0$ occur regularly within 3–6 years, similarly as they did in the studied period 2007–2014. The long-termed fluctuations of SPEI and short-termed reactions of Carabids allow to make a hypothesis concerning long-termed fluctuations of Carabid populations and assemblages.

At the same time the observed maximum and minimal values of number of individuals and species probably represent limits of variability of the Carabid assemblages in similar mountain ecosystems (Figs. 1–2). However, from the viewpoint of zoocenological classification the Carabid assemblages, the observed values can be indicative just for the assemblages in forests on oligotrophic acid crystalline substrates, while in the ecosystems on the polytrophic nitrogenous or basic substrates, the extremes will be situated at a higher level (Šustek, 2009) and their establishing needs an extensive field research in future.

The phase shift (lag) of fluctuations in Carabid assemblages after the climatic fluctuations has two different, but closely connected reasons. The shortage of humidity reduces activity of all edaphic organisms. Thus it simultaneously reduces the momentary activity of adult Carabids and their chance to mate and lay eggs, as well as chance of adults and larvae to find enough prey, to complete the development and to survive. Therefore the effect of drought is combined and occurs at several levels. The Carabids are monovoltine, with two principal reproduction types in the holarctic region – the spring breeders mating and laying eggs in spring, where the new generation hibernates as pupae or adults, and the summer breeders mating and laying eggs in late summer or early autumn, where new generation hibernates as larvae (den Boer and den Boer-Daanje, 1990; Lövei, 2008; Thiele, 1977). There also exist a plastic reproduction type, but it is represented just by very few species, like *Pterostichus melanarius* (de Boer and de Boer-Daanje, 1990). In lowlands, with long growing season, species of both reproduction types are represented in assemblages in an approximately balanced proportion. Different timing of their reproduction reduces competition pressures of species and forms clear seasonal aspects of Carabid assemblages in some ecosystems. In mountain conditions, the spring breeders predominate to effectively use the short growing season that can be even insufficient for the complete development of one generation. Thus development of some species can be prolonged on two growing seasons and generation can overlap. Under such circumstances, the extreme drought in a growing season or even in a short period can essentially inhibit development of next generation, but with an impact visible as late as in following growing season, if the beetles are monitored using pitfall traps. On contrary, the restoration of the decimated population will need a longer period of normal or increased humidity, as it was observed in the years 2009 and 2010.

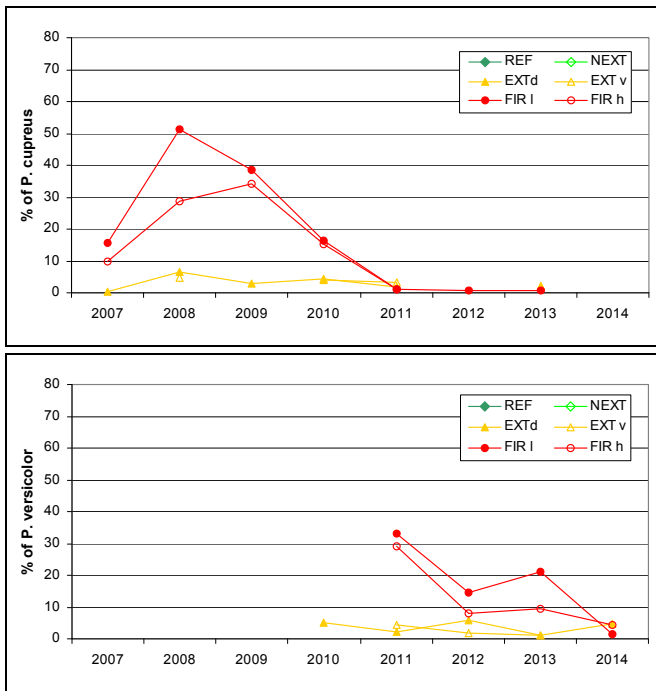
The extreme drought may inhibit, while the increased humidity may speed up restoration process of assemblages in the damaged area. As a result the assemblages will slowly return to their original state. However, the climatic fluctuations little influence the momentary functional structure of Carabid assemblages and direction of their succession (restoration). It is clearly shown by relative representation of species requiring the permanent shadowing (Fig. 7) and higher humidity (Fig. 8). In spite of incidence of the periodic, climatically conditioned changes in number of species and of individuals (Figs. 1–2), representation of these two major groups of species (Table 3) increased in all damaged plots with extracted timber and converged to their stable representation in the intact reference plot (REF Vyšné Hágy) and in the damaged plot with fallen timber



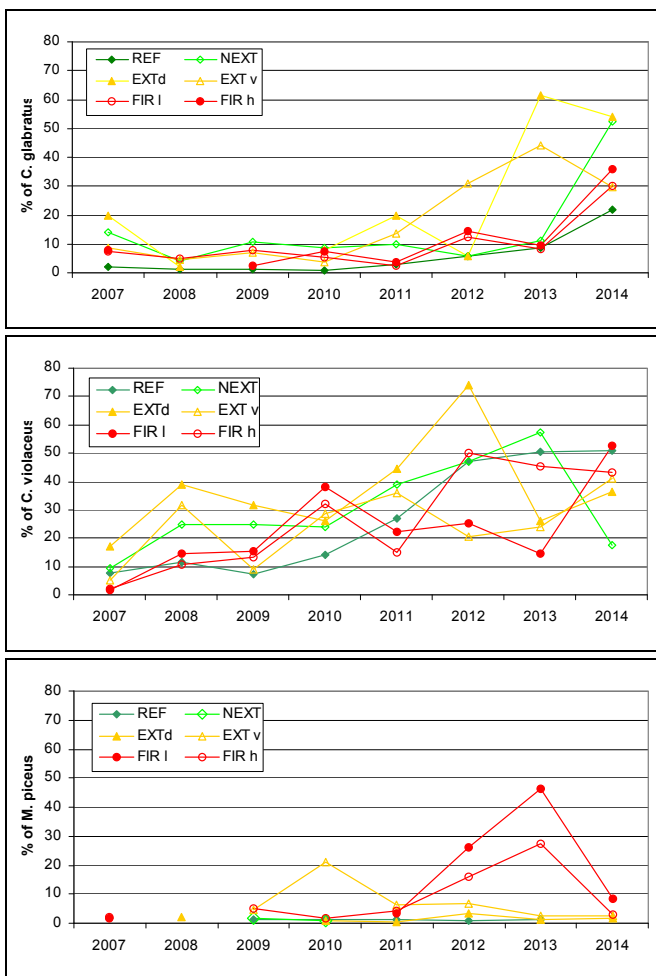
Figs. 7–8. Changes in vegetation cover preference index (above) and humidity preference index (below) of Carabid assemblages in six sites in High Tatra in 2007–2014.

in situ (NEXT Tatranská Lomnica Jamy). In all three cases the growth of their representation has a sigmoid character and the values asymptotically approximate to the level in the intact plot, irrespectively of two periods of extreme drought, which could only temporarily inhibit restoration of the damaged ecosystems by reducing number of individuals and species.

At the same time, succession of Carabid assemblages in all damaged plots had a convergent character and reducing differences between assemblages from the burned plots and other plots with extracted timber. Before all, representation of the open landscape species (*Poecilus cupreus*, *Poecilus versicolor*, *Amara* spp.) declined in the burned plots (Fig. 9–10) while the more tolerant forest species (*Carabus violaceus*, *Carabus glabratus*, *Molops picus*) gradually spread here (Figs. 10–13, see also Supplementary material). It was allowed by emergence of pioneer wooden vegetation (*Populus tremula*, *Sambucus racemosa*, *Salix caprea*, *Betula alba*) providing at least local shadowing, as well as by change of herbage stratum due to mowing the extensive stands of *Chamerion angustifolium* and its replacing by the grassy stands (especially *Calamagrostis epigeios*). The overall course of this process is illustrated by ordination of one-year samples from all studied plots (Fig. 14). The first axis represents gradient of damaging decreasing from left to right. The second axis shows progress of succession of assemblages on damaged plots from 2007 to 2014. In early stages the assemblages on the burned plots differed from unburned plots with extracted timber by pulse-like invasions of species characteristic for arable land, especially by *Poecilus cupres* (later replaced by *Poecilus versicolor*), *Pseudophonus rufipes* and several species of genus *Amara* (see Supplementary material). There also occurred heliophilous species *Microlestes minutus* and *Bembidion lampros* that prefer sites with discontinuous, patchy-like herbage vegetation arising during cutting of herbage vegetation. At the end of the investigation period, all assemblages



Figs. 9–10. Changes in relative abundance of two most abundant open landscape species in six differently damaged and managed sites in High Tatra in 2007–2014 (symbols as in Table 1).



Figs. 11–13. Changes in relative abundance of three tolerant forest species in six differently damaged and managed sites in High Tatra in 2007–2014 (symbols as in Table 1).

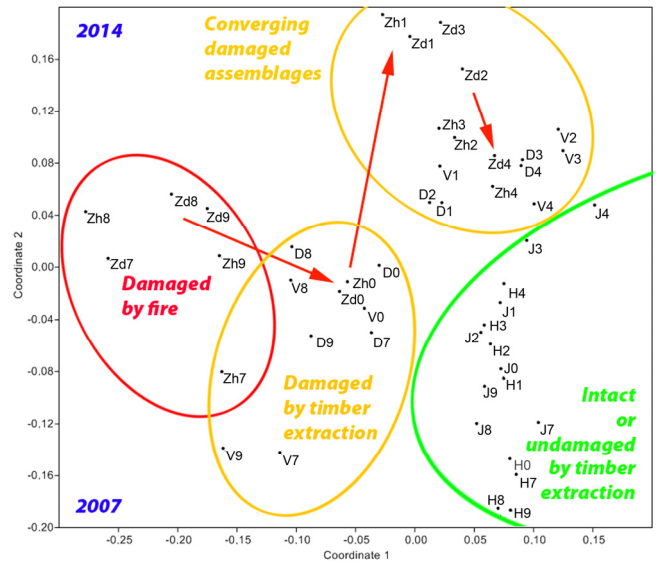


Fig. 14. NMS ordination (Horn’s index) of one-years samples of Carabids in six sites in the windstorm area in High Tatra in 2007–2014 (abbreviations H – reference plot in Vyšné Hágy [= REF], J – plot with fallen timber *in situ* in Jamy [= NEXT], D – unburned plot with extracted timber near Danielov dom [= EXTd], V – unburned plot with extracted timber Vodný les Zd and Zh – lower and upper burned plot with extracted timber in Tatranské Zruby [= FIRI and FIRh]). The arrows show succession direction of assemblages in the burned plots, the second axis shows direction of succession from 2007 towards 2014.

from the plots with extracted timber form a common cluster that shifts to right side of the ordination space, towards to the assemblages from the intact plot and the plot with timber *in situ*. However, the complete restoration of assemblage in the damaged plots will be finished in a relatively remote future. First of all the stenotopic forest *Carabus linnei*, *C. auronitens*, *Cychrus caraboides*, *Leistus piceus*, *Pterostichus unctulatus*, *P. burmeisteri*, *P. foveolatus*, *Calathus micropterus* are missing in them or occur there only exceptionally. Just these species represent the specific component of the assemblages in intact reference plot. To certain degree they also survive in the plot with timber *in situ* (see Supplementary material).

In the last years, there also appeared other trend in all assemblages – increasing portion of two species having optimum of distribution in highlands or lower limit of (*Carabus violaceus*, *Carabus glabratus*) and showing a considerable tolerance to deforestation also in other regions (Magura, 2002). In the plot EXTl *Carabus coriaceus*, *C. hortensis* and *C. nemoralis* having optimum of vertical distribution in lowlands started to occur in 2009–2011 (Fig. 15 and Supplementary material). Thus the assemblage structure slowly shifts toward the assemblages that are characteristic of lower altitudes (Šustek, 2014). However, interpretation of spreading of these three species is not simple, because it started and furthermore is concentrated in the plot at western margin of the Nový Smokovec town, where a temperature island may occur and where *Carabus coriaceus* was observed one year before its recording in this plot.

The obtained data indicate that three processes run simultaneously in Carabid assemblages in the windstorm area in High Tatra: (1) overall periodic changes connected with the short-termed, more or less regularly occurring climatic fluctuations,

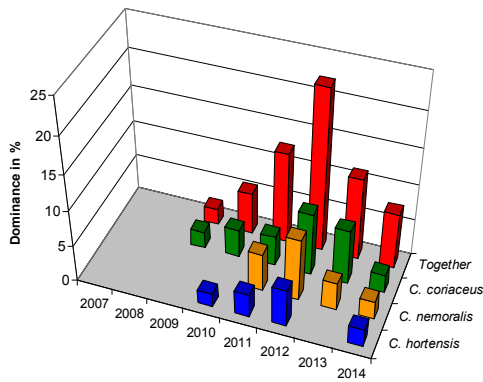


Fig. 15. Spreading of three thermophilous species of the genus *Carabus* with optimum of vertical distribution in lowlands in the plot EXT 1.

(2) non-periodic changes connected with spontaneous or artificial restoration of plant cover and Carabid assemblages in the damaged plot and (3), at present relatively slight, but probably also long-termed changes resulting from the moderate warming of the climate and spreading of species with distribution optimum at lower altitudes.

Although the studied localities are situated in a 12 km long strip and difference of altitude of the lowest and highest plot is approximately 250 m, values SPEI-12 calculated on the base of data from a single meteorological station (NEXT Tatranská Lomnica Jamy), situated at the eastern part of the study area, are sufficiently representative for characterizing climatic condition for existence of Carabid assemblages in the whole studied area.

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SUPPLEMENTARY MATERIAL

Table S1. Survey of species and number of individuals caught in six study plots High Tatra in 2007–2014: reference plot and plot with timber in situ (years marked just by the last digit), considerable part of the data match to that published by Šustek and Vido (2013).

| Species | Vyšné Hágy - REF | | | | | | | | Jamy - NEXT | | | | | | | |
|------------------------|------------------|---|---|---|---|---|---|---|-------------|---|---|---|---|---|---|---|
| | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 |
| <i>A. micans</i> | | | | | | | | | | | | | | | | |
| <i>A. sexpunctatum</i> | | | | | | | | | | | | | | | | |
| <i>A. aenea</i> | | | | | | | | | | | | | | | | |
| <i>A. erratica</i> | | | | | 1 | | | | | | | | 1 | | | |
| <i>A. eurynota</i> | | | | | | | | | | | | | | | | |
| <i>A. familiaris</i> | | | | | | | | | | | | | | | | |
| <i>A. lunicollis</i> | | | | | | | | | | | | | | | | |
| <i>A. nitida</i> | | | | | | | | | | | | | | | | |
| <i>A. ovata</i> | | | | | | | | | | | | | | | | |
| <i>A. binotatus</i> | | | | | | | | | | | | | | | | |
| <i>B. lampros</i> | | | | | | | | | | | | | | | | |
| <i>C. metallicus</i> | | | | | | | | | | | | | 1 | | | |

| | | | | | | | | | | | | | | | | |
|----------------------------|-----|----|-----|-----|-----|-----|----|----|-----|----|----|-----|----|----|----|----|
| <i>C. micropterus</i> | 9 | 12 | 10 | 13 | 1 | | | | | | 2 | 4 | | | | |
| <i>C. arvensis</i> | | | | 1 | | | | | | | | | | | | |
| <i>C. auronitens</i> | 18 | 1 | 6 | 10 | 16 | | | 2 | 1 | | 1 | 3 | 9 | 3 | | |
| <i>C. coriaceus</i> | | | | | | | | | | | | | | | | |
| <i>C. glabratus</i> | 7 | 1 | 3 | 3 | 9 | 8 | 8 | 21 | 15 | 1 | 6 | 11 | 8 | 3 | 6 | 24 |
| <i>C. hortensis</i> | | | | | | | | | | | | | | | | |
| <i>C. linnei</i> | 17 | 2 | 8 | 14 | 15 | 2 | 1 | 11 | 25 | 2 | 3 | 8 | 2 | 1 | 1 | |
| <i>C. nemoralis</i> | | | | | | | | | | | | | | | | |
| <i>C. violaceus</i> | 29 | 9 | 18 | 53 | 89 | 67 | 47 | 49 | 10 | 6 | 14 | 30 | 31 | 24 | 31 | 8 |
| <i>C. caraboides</i> | 8 | | 2 | 3 | 4 | 4 | | | | | 1 | 3 | 3 | | 3 | 3 |
| <i>E. gracilipes</i> | | | | | | | | | | | | | | | | |
| <i>H. affinis</i> | | | | | | | | | | | | | | | | |
| <i>H. distinguendus</i> | | | | | | | | | | | | | | | | |
| <i>H. latus</i> | | | | | | | | | | | | | | | | |
| <i>H. quadripunctatus</i> | | | | | | | | | | | | 3 | 1 | | 3 | 4 |
| <i>L. piceus</i> | | | | | | | 1 | | | | | | | | | |
| <i>L. terminatus</i> | | | | | | | | | | | | | | | | |
| <i>L. caerulescens</i> | | | | | | | | | | | | | | | | |
| <i>M. maurus</i> | | | | | | | | | | | | | | | | |
| <i>M. piceus</i> | 7 | | 3 | 4 | 4 | 1 | 1 | | | | 1 | 1 | | | | |
| <i>N. biguttatus</i> | 4 | 2 | 2 | 1 | 1 | 1 | | | | | | 1 | | | | |
| <i>N. palustris</i> | | | | | 1 | | | | | | | | | | | |
| <i>P. cupreus</i> | | | | | | | | | | | | | | | | |
| <i>P. versicolor</i> | | | | | | | | | | | | | | | | |
| <i>P. rufipes</i> | | | | | | | | | | | | | | | | |
| <i>P. aethiops</i> | 3 | 1 | 1 | 3 | 9 | 4 | 1 | 1 | 9 | 1 | | 4 | 11 | 5 | 1 | 2 |
| <i>P. angustatus</i> | | | | | | | | | | | | | | | | |
| <i>P. burmeisteri</i> | 17 | 5 | 13 | 25 | 25 | 17 | 14 | | 16 | 5 | 10 | 14 | | 5 | | |
| <i>P. foveolatus</i> | 44 | 9 | 25 | 57 | 94 | 12 | 6 | 4 | 4 | 1 | 2 | 9 | 2 | 2 | 2 | |
| <i>P. niger</i> | | | | | | | | | | | | | | | | |
| <i>P. nigrita</i> | | | | | | | | | | | | | | | | |
| <i>P. oblongopunctatus</i> | | | 1 | 1 | 1 | | | | | | | | | | 1 | |
| <i>P. strenuus</i> | | | | | | | | | | | | | | | | |
| <i>P. unctulatus</i> | 208 | 35 | 159 | 186 | 47 | 27 | 13 | 8 | 25 | 8 | 16 | 29 | 8 | 7 | | 1 |
| <i>T. amplicollis</i> | | | | | | | | | | | | | | | | |
| <i>T. latus</i> | | | | | | | | | | | | | | | | |
| <i>T. striatulus</i> | | | | | 8 | | | | | | | 2 | 1 | | | |
| <i>T. laevicollis</i> | 1 | | | 2 | 3 | | 1 | | 1 | | | 3 | 2 | 1 | 6 | 4 |
| Number of individ. | 372 | 77 | 251 | 376 | 328 | 143 | 93 | 96 | 106 | 24 | 56 | 125 | 80 | 51 | 54 | 46 |
| Number of species | 13 | 10 | 13 | 15 | 17 | 10 | 10 | 7 | 9 | 7 | 10 | 15 | 13 | 9 | 9 | 7 |

Table S2. Survey of species and number of individuals caught in six study plots High Tatra in 2007–2014: unburned plots with extracted timber (years marked just by the last digit).

| Species | Danielov dom EXTd | | | | | | | | Vodný les EXTv | | | | | | | |
|---------------------------|-------------------|----|----|----|----|----|----|----|----------------|---|----|----|----|----|----|----|
| | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 |
| <i>A. micans</i> | | | | | | | | | | | | | | | | |
| <i>A. sexpunctatum</i> | | | | | | | | | | | | 1 | 1 | | | |
| <i>A. aenea</i> | 2 | 2 | 5 | 2 | | | | | | | 1 | | | | | |
| <i>A. erratica</i> | 102 | 12 | 26 | 18 | 7 | 5 | | | 14 | 9 | 12 | 8 | 2 | | | |
| <i>A. eurynota</i> | 1 | 6 | 2 | 2 | | | | | 1 | | | 1 | | | | |
| <i>A. familiaris</i> | 3 | | 1 | 1 | | | | | 1 | | 1 | | | | | |
| <i>A. lunicollis</i> | | | | | | 1 | | | | | | | | | | |
| <i>A. nitida</i> | | | | 23 | 22 | | | | 1 | | | | 1 | 2 | | |
| <i>A. ovata</i> | | | | | | | | | | | | | | | | |
| <i>A. binotatus</i> | | | | | | | | | | | 1 | 1 | | | | |
| <i>B. lampros</i> | | | | | | | | | | 1 | 1 | | | | | |
| <i>C. metallicus</i> | | | | | | | | | | | | | | | | |
| <i>C. micropterus</i> | | | | | | | | | | | | | | | | |
| <i>C. arvensis</i> | | | | | | | | | | | | | | | | |
| <i>C. auronitens</i> | 1 | 1 | 1 | 2 | 1 | | | | | | | | | | | |
| <i>C. coriaceus</i> | | | | | | | | | | | 1 | 2 | 4 | 5 | 6 | 2 |
| <i>C. glabratus</i> | 47 | 1 | | 11 | 35 | 5 | 54 | 34 | 5 | 1 | 3 | 2 | 13 | 18 | 35 | 23 |
| <i>C. hortensis</i> | | | | | | | | | | | 1 | 3 | 3 | | | 2 |
| <i>C. linnei</i> | 4 | | | 1 | | | | | | | | | | | | |
| <i>C. nemoralis</i> | | | | | | | | | | | | | 5 | 5 | 3 | 2 |
| <i>C. violaceus</i> | 40 | 18 | 23 | 36 | 78 | 62 | 23 | 23 | 3 | 7 | 4 | 15 | 34 | 12 | 19 | 32 |
| <i>C. caraboides</i> | 2 | | | 2 | | | | | | | | 1 | 1 | 1 | | |
| <i>E. gracilipes</i> | | | | | | | | | | | | | | | | |
| <i>H. affinis</i> | | | | | | | | | 1 | | 2 | | | | | |
| <i>H. distinguendus</i> | | | | | | | | 1 | | | | | | | | |
| <i>H. latus</i> | | | | | | | | | | | | | 1 | | 2 | |
| <i>H. quadripunctatus</i> | | | | | 3 | | 1 | | | | | 1 | | | | 1 |
| <i>L. piceus</i> | | | | | | | | | | | | | | | | |
| <i>L. terminatus</i> | | | | | | | | | | | | | 1 | | | |
| <i>L. caerulescens</i> | | | | 1 | 1 | | | | 5 | 1 | 2 | 1 | | | | |
| <i>M. maurus</i> | | | | | | | | | | | | 1 | | | | |
| <i>M. piceus</i> | | | 1 | | 1 | 1 | 3 | 1 | 1 | | | 2 | 11 | 6 | 4 | 2 |
| <i>N. biguttatus</i> | | | | | | 1 | | | 5 | | 2 | | | | | |
| <i>N. palustris</i> | | | | 1 | | | | | | | | | | | | |
| <i>P. cupreus</i> | 1 | 3 | 2 | 6 | 3 | | 2 | | | 1 | | 2 | 3 | | | |

| | | | | | | | | | | | | | | | | | |
|----------------------------|--|-----|----|----|-----|-----|----|----|----|----|----|----|----|----|----|----|----|
| <i>P. versicolor</i> | | | | | 7 | 4 | 5 | 1 | 3 | | | | | 4 | 1 | 1 | |
| <i>P. rufipes</i> | | 1 | 2 | 1 | 1 | | | | | | | 1 | | | | | |
| <i>P. aethiops</i> | | 1 | | | 4 | 11 | 2 | 1 | 1 | 2 | | | 1 | 3 | 5 | 8 | 7 |
| <i>P. angustatus</i> | | | | | | 3 | | | | | | | | 2 | | | |
| <i>P. burmeisteri</i> | | 2 | | 1 | 2 | 1 | 2 | | | | 5 | 2 | 4 | 3 | 3 | | |
| <i>P. foveolatus</i> | | | | | 1 | | | | | | 1 | | | 2 | | | 4 |
| <i>P. niger</i> | | | | | | | | | | | 1 | | 2 | 1 | | | |
| <i>P. nigrita</i> | | | | | | | | | | | 2 | | 3 | 1 | | | |
| <i>P. oblongopunctatus</i> | | 1 | | | | | | 1 | | | | | 1 | 1 | 2 | | |
| <i>P. strenuus</i> | | | | | | | | | | 1 | | 1 | | | | | |
| <i>P. unctulatus</i> | | 28 | 1 | 9 | 15 | 3 | | 1 | | 2 | | | 4 | | | | |
| <i>T. amplicolis</i> | | | | | | | | | | 4 | | 2 | | | | | |
| <i>T. latus</i> | | | | | | | | | | 1 | | | | | | | |
| <i>T. striatulus</i> | | | | | | | | | | | | | | | | 1 | 3 |
| <i>T. laevicollis</i> | | | | 1 | 1 | 2 | | 1 | | 1 | | 1 | | 1 | 1 | | |
| Number of individ. | | 236 | 46 | 73 | 137 | 175 | 84 | 88 | 63 | 57 | 22 | 44 | 52 | 95 | 58 | 79 | 78 |
| Number of species | | 15 | 9 | 12 | 20 | 15 | 9 | 10 | 6 | 20 | 7 | 18 | 21 | 19 | 11 | 9 | 10 |

Table S3. Survey of species and number of individuals caught in six study plots High Tatra in 2007–2014: burned plots with extracted timber (years marked just by the last digit).

| Species | Tatranské Zruby lower FIRI | | | | | | | | Tatranské Zruby upper FIRh | | | | | | | |
|--------------------------|----------------------------|----|----|----|-----|-----|-----|-----|----------------------------|----|----|----|-----|----|----|----|
| | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 |
| <i>A. micans</i> | | | | | | 1 | | | | | | | | | | |
| <i>A. sexpunctatum</i> | 1 | | | | | | | | 1 | | | | | 1 | | |
| <i>A. aenea</i> | 1 | | | 2 | | | | | 6 | | 2 | 3 | 4 | | 1 | 1 |
| <i>A. erratica</i> | 6 | 4 | 3 | 5 | 1 | | 4 | 1 | 8 | 2 | 2 | 4 | 1 | 1 | 2 | |
| <i>A. eurynota</i> | 21 | 1 | 6 | 1 | | | | | 2 | 3 | 1 | 2 | | | | |
| <i>A. familiaris</i> | 1 | 1 | | 1 | | | | | | | | 2 | | | | |
| <i>A. lunicollis</i> | | | | | | 1 | | | | | | | | | | |
| <i>A. nitida</i> | | | | | 112 | 5 | | | | | | 1 | 103 | 3 | | |
| <i>A. ovata</i> | | | | | | | | | | | | | 2 | | | |
| <i>A. binotatus</i> | 2 | | | | | | | | 1 | | | | | | | |
| <i>B. lampros</i> | 26 | 1 | 4 | | | 1 | | | 4 | 9 | 3 | | | | | |
| <i>C. metallicus</i> | | | | | | | | | | | | | | | | |
| <i>C. micropterus</i> | | | | | | | | | | | | | | | 1 | 1 |
| <i>C. arvensis</i> | | | | | | | | | | | | | | | | |
| <i>C. aurontens</i> | | | | 1 | 1 | | 2 | | 3 | | 1 | 1 | 3 | | 1 | 1 |
| <i>C. coriaceus</i> | | | | | | | | | | | | | | 1 | | |
| <i>C. glabratus</i> | 8 | 2 | 5 | 3 | 9 | 16 | 11 | 47 | 4 | | 1 | 4 | 9 | 9 | 7 | 24 |
| <i>C. hortensis</i> | 1 | | | | | | | | | | | | | | | |
| <i>C. linnei</i> | 7 | | | | | | | | | | | | | | | |
| <i>C. nemoralis</i> | | | | | | | | | | | | | | | | |
| <i>C. violaceus</i> | 2 | 6 | 10 | 21 | 79 | 33 | 19 | 82 | 1 | 3 | 5 | 17 | 38 | 31 | 33 | 29 |
| <i>C. caraboides</i> | | | | | 1 | | | | | | | | | | | |
| <i>E. gracilipes</i> | | | | | | | 2 | | | | | | | | 1 | 3 |
| <i>H. affinis</i> | | | | | | | | | | | | | | | | |
| <i>H. distinguendus</i> | | | | | | | | | | | | | | | | |
| <i>H. latus</i> | | | | | | | 1 | | | | | | | | | |
| <i>H. quadripunctus</i> | 2 | | | | 2 | 1 | 1 | 2 | | | | | 1 | | | 1 |
| <i>L. piceus</i> | | | | | | | | | | | | | | | | |
| <i>L. terminatus</i> | | | | | | | | | | | | | | | | |
| <i>L. caerulescens</i> | 1 | | | 1 | | | | | | | | | 1 | | | |
| <i>M. maurus</i> | 1 | 2 | 4 | | | | | | | 2 | 2 | | | | | |
| <i>M. piceus</i> | 2 | | | | 12 | 34 | 61 | 13 | 1 | | 2 | 1 | 11 | 10 | 20 | 2 |
| <i>N. biguttatus</i> | 4 | 3 | 6 | 2 | | | | | 1 | | | 1 | | | | |
| <i>N. palustris</i> | | | | | 1 | | | | | | | | | 1 | | |
| <i>P. cupreus</i> | 17 | 21 | 25 | 9 | 4 | 1 | 1 | | 5 | 8 | 13 | 8 | 3 | | | |
| <i>P. versicolor</i> | | | | | 117 | 19 | 28 | 2 | | | | | 74 | 5 | 7 | 3 |
| <i>P. rufipes</i> | | | | 1 | | | | | 2 | 1 | 2 | 1 | | | | |
| <i>P. aethiops</i> | | | | | 7 | | | | 1 | | | | 1 | | | |
| <i>P. angustatus</i> | | | | | | | | | | | | | | | | |
| <i>P. burmeisteri</i> | | | | 1 | | 1 | | | 1 | | 1 | 1 | | | | |
| <i>P. foveolatus</i> | 1 | | | | 1 | | 2 | | | | 1 | 1 | | | | |
| <i>P. niger</i> | | | | | 3 | 16 | | 8 | | | | | | | | |
| <i>P. nigrita</i> | | | | | | | | | | | | | | | | |
| <i>P. oblongopunctus</i> | 3 | | | | | | | | 1 | | | | | | | |
| <i>P. strenuus</i> | | | | | | | | | | | | | | | | |
| <i>P. unctulatus</i> | 1 | | 2 | 7 | | | | | 8 | | 2 | 6 | 1 | | | 1 |
| <i>T. amplicolis</i> | | | | | | | | | | | | | | | | |
| <i>T. latus</i> | | | | | | | | | | | | | | | | |
| <i>T. striatulus</i> | | | | | | | | | | | | | | | | |
| <i>T. laevicollis</i> | | | | | 2 | 1 | | 1 | | | | | 2 | | | 1 |
| Number of individ. | 108 | 41 | 65 | 55 | 352 | 130 | 132 | 156 | 50 | 28 | 38 | 53 | 254 | 62 | 73 | 67 |
| Number of species | 20 | 9 | 9 | 13 | 15 | 13 | 11 | 8 | 17 | 7 | 14 | 15 | 15 | 9 | 9 | 11 |