

## **DROUGHT AS ONE OF MAJOR FACTORS INFLUENCING SUCCESSION OF CARABID COMMUNITIES IN THE FORESTS DAMAGED BY THE WIND CATASTROPHE IN HIGH TATRA IN 2004**

**Zbyšek Šustek<sup>1</sup>, Jaroslav Vido<sup>2</sup>**

<sup>1</sup>**Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, 845 06 Bratislava,  
Slovak Republic; e-mail: [zbysek.sustek@savba.sk](mailto:zbysek.sustek@savba.sk)**

<sup>2</sup>**Slovak Technical University, T. G. Masaryka 8024/24, 960 01 Zvolen,  
Slovak Republic; e-mail: [jaroslav.vido@gmail.com](mailto:jaroslav.vido@gmail.com)**

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### **Abstract**

Succession of the Carabid Communities in the spruce forests in High Tatra damaged by the wind catastrophe of 2004 exhibited two main trends. The first trend includes the communities differentiation according to state of the damaged sites into three groups: (1) the site with the timber remaining *in situ* shows only quantitative and easily reversible changes in comparison with the intact stand, (2) the sites with extracted timber, where a part of original species disappeared, while other part was favored by freed ecological niches, and number of non-forests mountain of species and their abundance and biomass increased, (3) the sites with extracted timber and additionally damaged by the fire in July/August 2005, where number of the original species and their abundance were reduced and temporal invasions of several open-landscapes species occurred. This differentiation is explained by autecology of individual species, the state of habitats and undertaken forest management measures. By the end of the studied period, the communities in both, the burned and unburned sites converged due to restoration of vegetation cover, but continuously strongly differed from the site with timber *in situ*.

The second trend includes a striking decline of number of species and individuals and cumulative biomass in all sites in 2008 and a gradual increase of these parameters in the next years. This trend was very similar in all sites and can be explained as a retarded and long lasting consequence of the extremely dry growing season of 2007 and winter 2006/2007. The Standardized Precipitation index (SPI) and the Standardized Evapotranspiration index (SPEI) calculated for 24 months fitted best these changes. The results show that the next succession will depend not only on the restoration of vegetation, but will be essentially influenced by climatic changes.

### **Introduction**

The damaging of Norway spruce forests on the southern slopes of High Tatra in November 2004, an extensive fire in a part of the area in July/August 2005 and the subsequent management of the damaged area led to differentiation of the earlier almost identical communities into three groups with characteristic shifts in the community structure and its ecologic parameters. In the study site with timber laying *in situ*, only abundance of individual species declined, but the species composition and proportion of individual species have not changed. In the sites with extracted timber, essential quantitative and qualitative changes occurred. These changes were still more profound in the sites additionally affected by the fire (ŠUSTEK 2007, 2008). The differences between these three groups of localities can be explained by ecological requirements of individual species and by the changes in vegetation in each locality and short-term impacts of cutting the herbage vegetation to protect the newly planted trees. But there were also observed general trends, especially in number of species and individuals, which were common for all localities in this area. Because the most important factor regulating the occurrence and distribution of Carabids is the humidity (THIELE 1977), we tried to

explain them using the Standardized Precipitation Index (SPI) (MCKEE 1993, HAYES et al. 1999) and the Standardized Precipitation and Evapotranspiration index (SPEI) (VINCENTE-SERRANO et al. 2010) to characterize the annual climatic changes, which could influence the course of the community succession. The aim of this contribution is to show how the annual climatic changes influence the succession of the communities and the restoration of their more or less natural state.

### Material and methods

The study sites were selected by the Research Branch of the State Forests Management of the High Tatra National Park and well represent all types of habitats arisen after the wind catastrophe and the subsequent fire. Their principal characteristics are surveyed in the Table 1. The sites belong to the same trophical series according to the Zlatník's geobiocoenological classification (RAUŠER & ZLATNÍK, 1966), what means very similar conditions for productivity of the ecosystems and their components. The densely laying fallen timber in the site Jamy shadows the soil surface and protects it against the direct insolation. The position of the upper site in Tatranské Zruby on a northeastern and relatively steep slope above the deeply cut creek may cause a lateral discharge and increase the soil drying. The presence of an unnamed creek and a narrow waterlogged alluvium in the site Vodný les made possible a moderate penetration of some hydrophilous species.

Tab. 1. Survey of study sites in the area affected by the wind disaster in High Tatra on 19 November 2004 and on 30 July - 1 August 2005 by an extensive fire on 250 ha.

Locality	Vyšné Hágy	Tatranská Lomnica Jamy	Danielov dom	Tatranské Zruby lower site	Tatranské Zruby upper site	Nový Smokovec Vodný les
Locality abbreviation	REF	NEXT	EXT	FIRd	FIRh	VL
Latitude N	49°07'17.5"	49°09'33.7"	49°07'15.3"	49°07'49.3"	49°08'02.7"	49°08'07.6"
Longitude E	20°06'15.0"	20°15'07.9"	20°09'46.0"	20°11'49.1"	20°11'30.1"	20°12'24.8"
Exposition	S	E	S	SE	NE	SW
Slope	10°	20°	10°	0-2°	15	5°
Altitude [m]	1,233	1,062	1,060	1,015	1,095	1,022
Trophic series	AB	AB	AB	AB	AB	AB
Group of geobiocoens	<i>Sorbi Piceeta</i>	<i>Sorbi Piceeta</i>	<i>Sorbi Piceeta</i>	<i>Sorbi Piceeta</i>	<i>Sorbi Piceeta</i>	<i>Sorbi Piceeta</i>
Damaging degree	Intact mature forest	Timber <i>in situ</i>	Timber extracted	Timber extracted, burned, herbs cut	Timber extracted, burned, herbs cut	Timber extracted

The beetles were pitfall trapped. Six traps consisting of plastic jars of 0.5 liter and a mouth of 90 mm filled with formalin were exposed in each locality in distances of about 5 m since May to late October. They were emptied approximately once a month. The investigations started in May 2007, when extraction of timber was finished and the area was open to public.

The biomass of the beetles was established by multiplying number of individuals of each species by the average weight of at least six individuals dried at 100°C for 24 hours (ŠUSTEK 1984). The ecological data on Carabids were taken from BURMEISTER (1939), HŮRKA (1996), LINDROTH (1949), (ŠUSTEK (2000) and THIELE (1977). On their base a four-degree semiquantitative scale of the preference for vegetation cover (1 – open landscape species, 4 – stenotopic forests species) and an eight-degree scale of humidity preference (1 – strongly xerophilous, 8 – strongly hydrophilous) was constructed (ŠUSTEK 2004) and used for the direct ordination (POOLE 1974) of the communities from individual localities and years. These characteristics are given in Table 2. The ordination scores were calculated as arithmetical means of preferences of each species weighted by their abundance. The hierarchical classification was carried out by the unweighted average linkage methods using the chord distance expressing the proportional similarity of the samples and compensating size of the samples.

The Shannon-Wiener index was used as diversity index. All calculations were made by the program Past version 2,16 (HARMLER 2012).

The SPI24 and SPEI24 were calculated on the base of monthly average temperatures and monthly precipitation sums obtained from the meteorological station Tatranská Lomnica for the years 1961-2010. 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. 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 onthogenesis of individual Carabid species, which can last in mountain condition 1-2 years, and to cover possible overlap of two subsequent generations. The advantage of SPEI is integration of the elementary climatologic parameters like temperature, precipitation and humidity.

## Results

In 2007-2011 altogether 45 Carabid species were recorded in all localities (Tab. 2 and 3). In individual sites and years their number fluctuated form 7 to 21 (mean 13.7, s.d. 4.2). They belonged to two principle ecological groups. The first group represents the stenotopic forest species, requiring shadowing by closed tree vegetation. like *Pterostichus foveolatus*, *Pretostichus burmeisteri*, *Pterostichus unctulatus*, *Molops piceus*, *Calathus micropterus*, *Carabus linnei*, *Carabus auronitens* and *Cychrus caraboides* and also includes some more tolerant forest species like *Carabus violaceus* and *Carabus glabratus*. Their amplitude of vertical distribution mostly reaches from 300 to 1400 m a.s.l. and optimum of their distribution lays in the middle of this range or in the fire-beech-spruce to the spruce vegetation tier (RAUŠER & ZLATNÍK, 1966), where they form characteristic communities.

Table 2. List of species found in the studied sites in the area damaged in High Tatra by the wind catastrophe of 2004, their complete scientific names, characteristics of their preference for humidity (H), shadowing by tree vegetation (S) and average dry biomass of on individual (M)

Species	Chracteristics			Species	Chracteristics		
	H	S	M		H	S	M
<i>Agonum sexpunctatum</i> (Linnaeus. 1758)	5	2	0.0350	<i>Leistus terminatus</i> (Hellwig in Panzer. 1793)	5	4	0.0520
<i>Amara aenea</i> (De Geer. 1774)	3	1	0.0413	<i>Loricera caerulea</i> (Linnaeus. 1758)	4	4	0.0428
<i>Amara erratica</i> (Duftschmidt. 1812)	3	1	0.0457	<i>Microlestes maurus</i> (Sturm. 1827)	2	1	0.0072
<i>Amara eurynota</i> (Panzer. 1797)	3	1	0.0444	<i>Molops piceus</i> (Panzer. 1793)	4	4	0.0443
<i>Amara familiaris</i> (Duftschmidt. 1812)	3	1	0.0413	<i>Notiophilus biguttatus</i> (F.. 1779)	4	2	0.0443
<i>Amara nitida</i> Sturm. 1825	3	1	0.1561	<i>Notiophilus palustris</i> (Duftschmidt. 1812)	4	2	0.0241
<i>Amara ovata</i> (F.. 1792)	3	1	0.2130	<i>Poecilus cupreus</i> (Linnaeus. 1758)	4	2	0.2710
<i>Anisodactylus binotatus</i> (F.. 1792)	6	2	0.0457	<i>Poecilus versicolor</i> (Sturm. 1824)	4	2	0.2134
<i>Bembidion lampros</i> (Herbst. 1784)	3	1	0.0172	<i>Pseudoophonus rufipes</i> (De Geer. 1774)	4	1	0.4126
<i>Calathus metalicus</i> Dejean. 1828	5	3	0.1411	<i>Pterostichus aethiops</i> (Panzer. 1797)	5	1	0.0862
<i>Calathus micropterus</i> Duftschmidt. 1812	3	3	0.0196	<i>Pterostichus angustatus</i> (Duftschmidt. 1812)	5	4	0.1832
<i>Carabus arvensis</i> Herbst. 1784	5	2	1.1332	<i>Pterostichus burmeisteri</i> (Heer. 1801)	5	4	0.1546
<i>Carabus auronitens</i> F.. 1792	4	4	1.3251	<i>Pterostichus foveolatus</i> Duftschmidt. 1812	5	4	0.2152
<i>Carabus coriaceus</i> Linnaeus 1758	5	4	6.5950	<i>Pterostichus niger</i> (Schaller. 1783)	6	4	1.0600
<i>Carabus glabratus</i> Paykull. 1790	5	4	1.7415	<i>Pterostichus nigrata</i> (F.. 1792)	8	4	0.0812
<i>Carabus hortensis</i> Linnaeus. 1758	4	4	1.7800	<i>Pterostichus oblongopunctatus</i> (F.. 1787)	5	4	0.1941
<i>Carabus linnei</i> Dejean. 1826	5	4	1.0568	<i>Pterostichus strenuus</i> (Panzer. 1797)	7	4	0.0511
<i>Carabus nemoralis</i> O. F. Müller. 1764	4	4	1.7370	<i>Pterostichus unctulatus</i> Duftschmidt. 1812	5	4	0.0530
<i>Carabus violaceus</i> Linnaeus. 1758	5	4	1.7457	<i>Trechus amplicollis</i> Fairmair. 1859	5	2	0.0159
<i>Cychrus caraboides</i> (Linnaeus. 1758)	5	4	0.9256	<i>Trechus latus</i> Puzey. 1847	5	4	0.0248
<i>Harpalus affinis</i> (Schränk. 1784)	3	4	0.1873	<i>Trechus striatulus</i> Putzeys. 1847	5	4	0.0082
<i>Harpalus quadripunctatus</i> (Dejean. 1829)	4	4	0.0956	<i>Trichotichnus laevicollis</i> Duftschmidt. 1812	5	4	0.1431
<i>Harpalus latus</i> (Linnaeus. 1758)	4	4	0.1561	- - -			

These species formed communities in the intact reference site in Vyšné Hágy (REF) and in Jamy (NEX) with non-extracted fallen timber, where their abundance was lower than in the reference site, but the observed differences had only quantitative and fully reversible character (ŠUSTEK 2008). These species are unable to fly and their spreading is limited.

The second group consists of the species characteristic for the non-forests ecosystems, first of all for arable land. Among them only *Amara erratica* is a mountain species. One species, *Microlestes maurus*, is strongly xerophilous while *Bembidion lampros* is heliophilous. In 2001, this groups was enriched in both burned sites by *Amara ovata* and in a large number of individuals also *Amara nitida* and *Poecilus versicolor*. All these species are able to fly, what allows them to occupy rapidly new habitats and to spread to large distances.

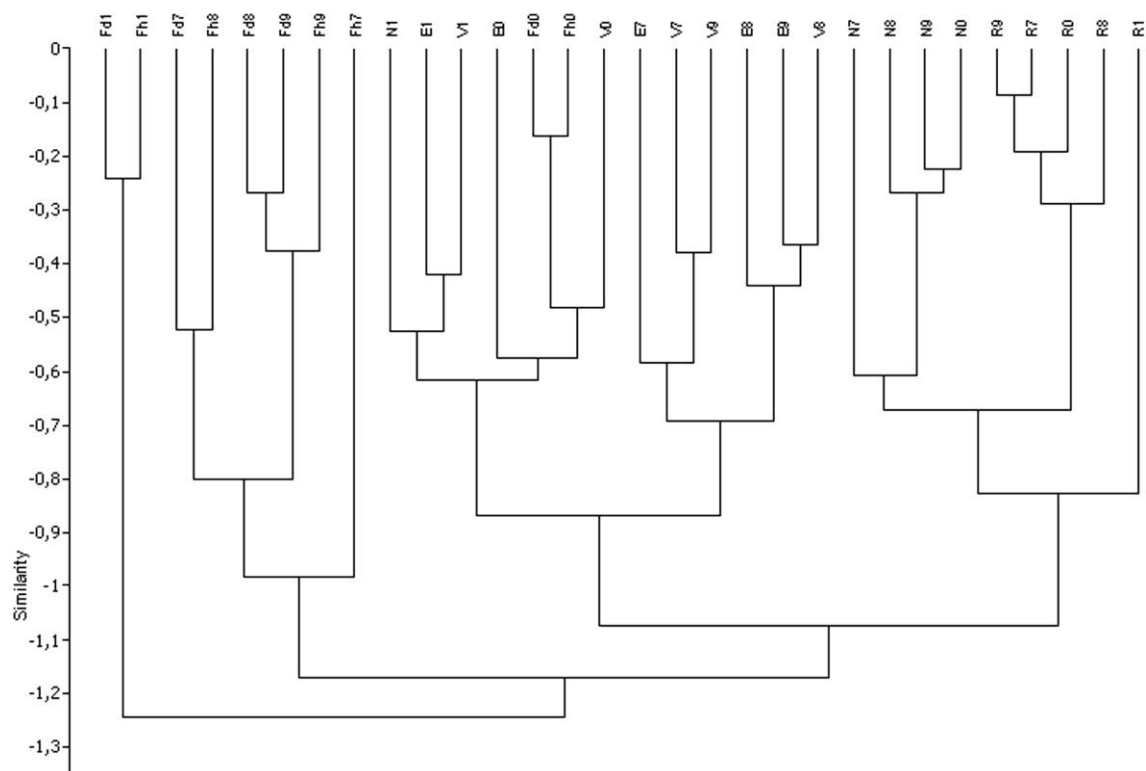


Fig. 1. Hierarchical classification of Carabid communities from study sites in High Tatra (symbols of localities – first letter of locality name abbreviation – see tab. 1, the last digit of sampling year).

Spatial and temporal spatial trends in changes of communities are visualized by hierarchical classification basing on chord distance (Fig. 1). It shows the processes running in the studied area purely from the viewpoint of Carabids, without taking in consideration of other factors. There is an obvious tendency to formation of two homogenous clusters of communities consisting of one-year catches from the intact reference site and from the site with timber *in situ*. Within the cluster of samples from reference site, a slight tendency of joining of samples in the time sequence from 2007 to 2011 is visible, whereas in the locality with the timber *in situ* is this clustering pattern is absolute. Both clusters form a single major cluster at distance  $-1.05$ . This cluster represents a clear opposite to three relatively heterogeneous clusters. One of them includes exclusively the samples from both localities with extracted timber, but not additionally damaged by fire.

The second includes predominantly the samples from unburned sites and a part of clusters from both burned sites from 2010. This cluster consists of three subclusters formed predominantly according to temporal pattern; joining subsequently samples from the years 2007-2009, 2010 and from 2011.

The third cluster consists exclusively from the samples from both burned sites from 2007-2009, consisting of subclusters joining predominantly of samples from 2007 and 2008 or 2008 and 2009. The difference between the unburned and burned sites laid not only in the destroying vegetation and litter and killing at least the essential part of the soil fauna in the burned sites, but also in a massive invasion of heliophilous *Chamerion angustifolium* (KRIŽOVÁ *et al.* 2011). It formed here a dense stand that structurally strongly differed from the stands of *Calamagrostis* sp. in the unburned sites, but was physiognomically very similar to cultures of cereals. Thus it created favorable conditions for the field Carabids (*Poecilus* spp., *Pseudophonus rufipes*, *Amara* spp., Tab. 2 and 3), which periodically invaded these sites. In addition the stands of *Chamerion angustifolium* were locally cut to protect the planted tree seedlings. In this way, dry strongly insolated and heated patches arose and created conditions for some strongly heliophilous (*Bembidion lampros*) or even strongly xerophilous species (*Microlestes maurus*).

The fourth cluster includes only two samples from the burned sites from 2011, when invasion of *Poecilus versicolor* and *Amara ovata* started. These species replaced the ecologically similar *Poecilus cupreus* predominating in these sites in 2007-2010 and other species of the genus *Amara* (Tab. 3).

The clustering pattern (Fig. 1) shows a clear tendency of transition of all communities from a starting state to a final one.

The processes described by the hierarchical classification can be explained purely on the base of ecological properties of individual species and their interactions with changes in vegetation cover. Although the hierarchical classification also reveals that there exists a general influence of the between-year fluctuations of climatic conditions, it does not allow deciding, what factors are responsible of them.

The weather in 2007 was characterized by an exceptionally hot and dry summer. Several temperature records (for example on 20 July the temperature at Hurbanovo reached 40.2°C), exceeded in Slovakia the highest temperatures having been observed in Slovakia (SHMÚ 2008). The high temperatures and especially a low sum of precipitation were recorded since April to August (KONÔPKA *et* KONÔPKA 2010). Due to it, the growing season of this year was much drier then 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 (SHMÚ 2007). The next years were considered as normal (2008 and 2009) or very humid (2010), (PECHO *et al.* 2010), except of June 2008 and, from a part, also April, May and September 2009, which were dry in High Tatra.

In conformity with the above climatic characteristics, the year 2008 was characterized by a sudden drop of number of species and individuals and of cumulative biomass in all sites (Tab. 3, Fig. 2 and 3). The deepest drop was observed in both burned sites and in the site Vodný les. Number of recorded species in the burned sites and in Vodný les declined to 35% of the state recorded in 2007, while in the unburned extracted site Danielov dom 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, the most moderate drop being in the naturally developing reference site and in the site with timber *in situ*.

The figure 2 shows a one-year delay of this reaction of community to the climatic changes characterized by the decline of SPI24 from 0.27 in 2006 to – 0.40 in 2007.

The above relationship is much better visible in comparison of changes in comparison with the index SPEI24, which integrates the air temperature. Value of this index strongly declined from 0.18 in 2006 to –0.91 in 2007 (Fig. 3). From 2008 both indices show shift of the climato to the more humid conditions. This shift is followed by increase in 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.

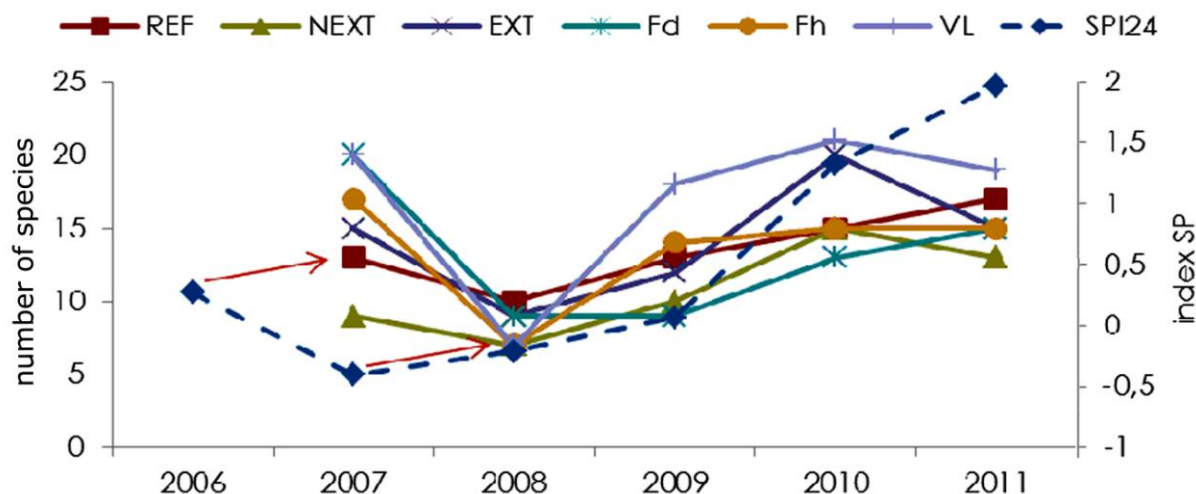


Fig. 2. Changes of number of Carabid species in dependence on dynamics of SPI 24. The arrows show delay of community reaction after the changes in SPI.

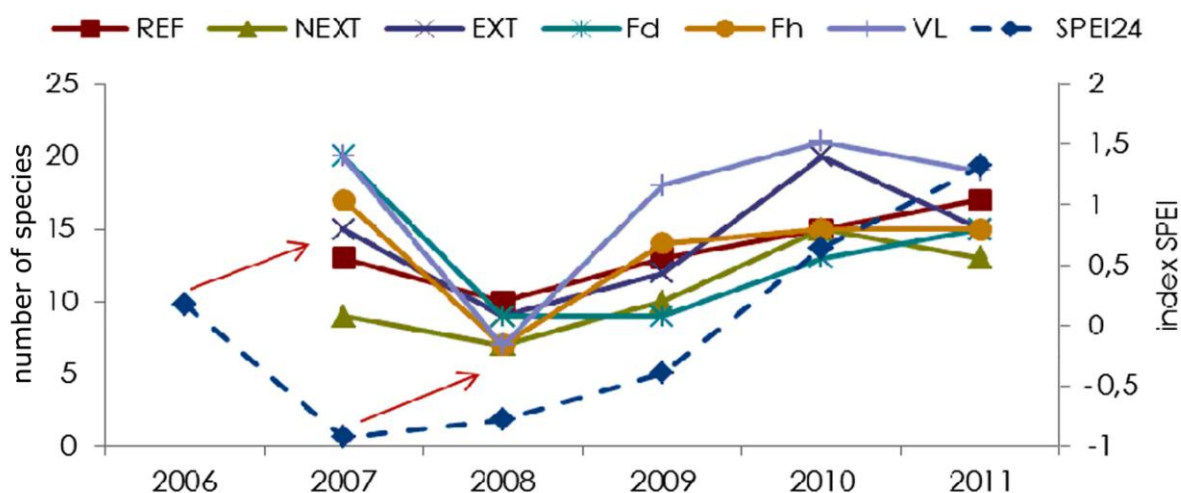


Fig. 3. Changes of number of Carabid species in dependence on dynamics of SPIE 24. The arrows show delay of community reaction after the changes in SPIE.

A very strong decline occurred in number of individuals in all localities in 2008 (Fig. 4), inclusively of the intact forest and in the site with timber *in situ*, where 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 number of individuals (to 19%) in the damaged sites was recorded on Danielov dom (EXT), followed by lower burned site (FIRd, 37%), Vodný les (VL, 38%) and upper burned site (FIRh, 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 number of individuals in both burned sites is partly caused by the invasion of a large number of *Poecilus versicolor* and *Amara anea* characteristic of the arable land and can not be ascribed only to climatic changes. However, irrespectively of it, the SPEI fits better the changes in the cumulative number of individuals then SPI, similarly as in case of number of species (Fig. 3).

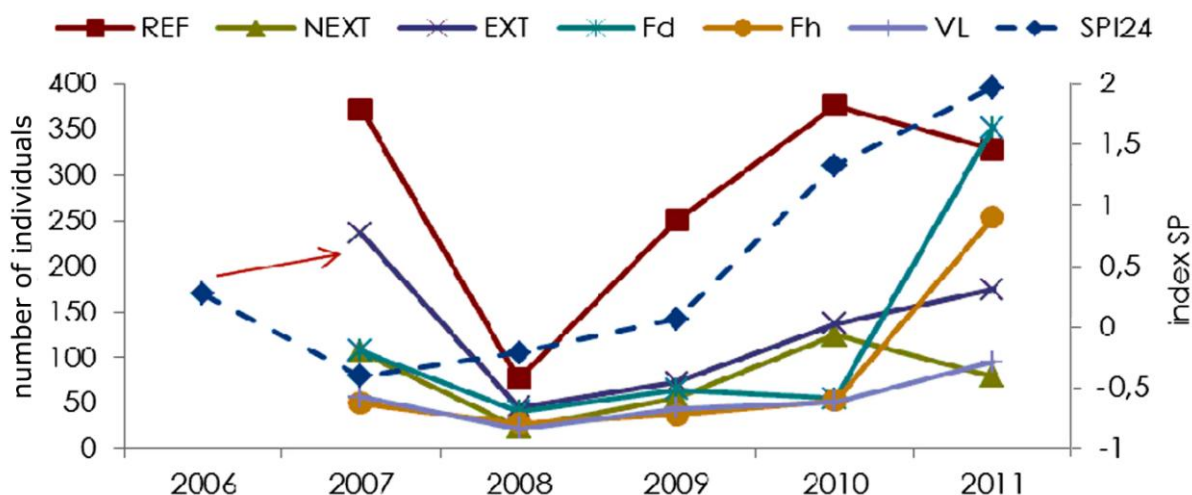


Fig. 4. Change in cumulative number of individuals in Carabid communities and their relationship with the index SPI for 24 months. The arrows show delay of community reaction after the changes in SPI.

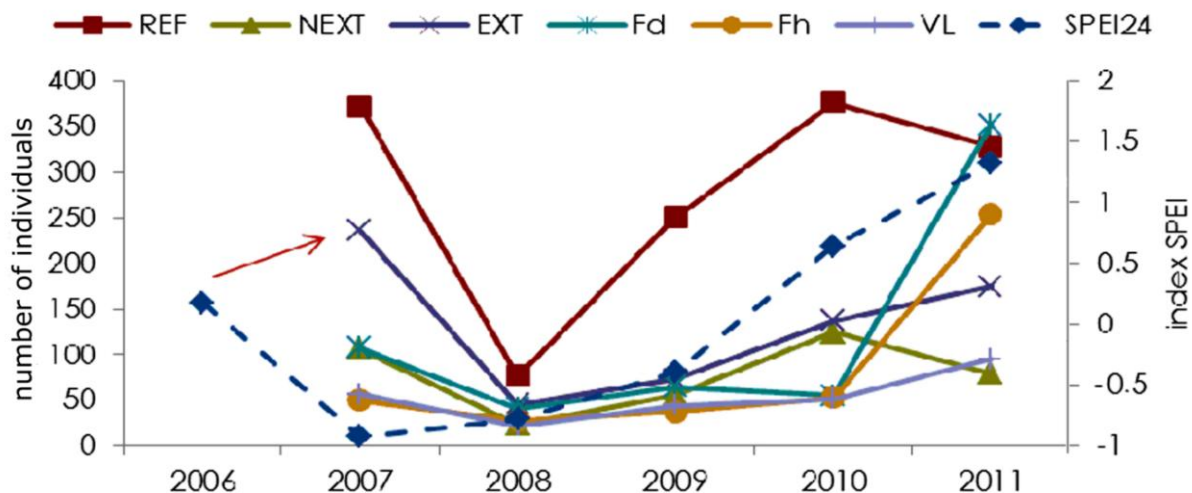


Fig. 5. Change in cumulative number of individuals in Carabid communities and their relationship with the index SPEI for 24 months. The arrows show delay of community reaction after the changes in SPEI.

The strong decline of cumulative biomass of Carabids in the intact forests (Fig. 6-7), which probably resulted from the dry winter 2006/2007 and from the dry growing season 2007 was caused especially by decline of number of individuals of large species like *Carabus glabratus*, *Carabus violaceus* or *Carabus auronitens* binding the essential portion of the community 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 improvement of bioclimatic conditions in 2010. In 2010 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 cumulative number of individuals (Fig. 4-5) was stopped in the intact forest, but the cumulative biomass continued to grow (Fig. 6-7) due to presence of less individuals of large species.



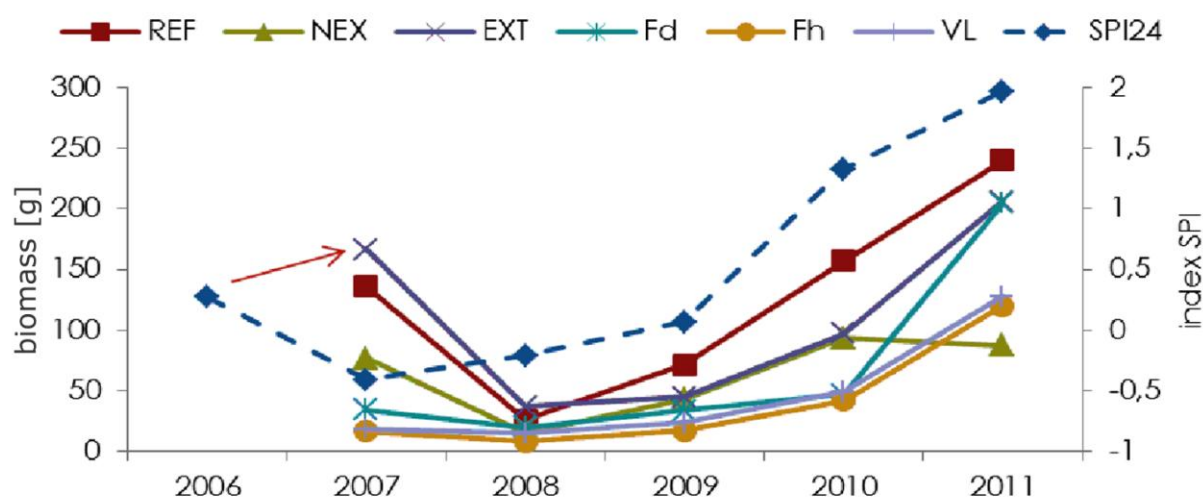


Fig. 6. Change in cumulative biomass of Carabids and their relationship with the index SPEI for 24 months. The arrows show delay of community reaction after the changes in SPI.

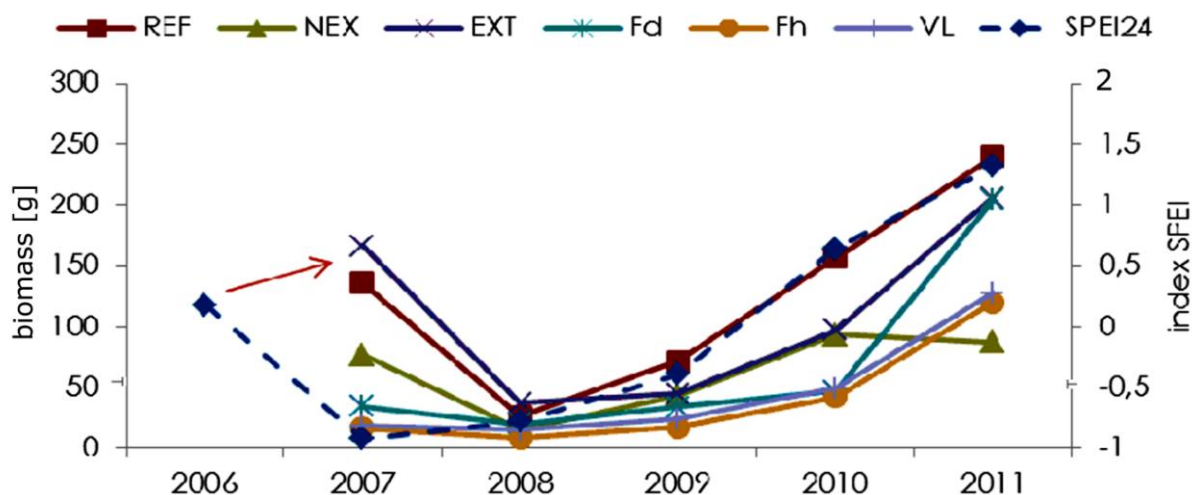


Fig. 7. Change in cumulative biomass of Carabids and their relationship with the index SPEI for 24 months. The arrows show delay of community reaction after the changes in SPEI.

Because of 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 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 the intact forest, less in all damaged localities. In 2010 the starting level 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 (Fig. 4 - 7). The different increase of cumulative biomass in both burned site resulted from a more intensive invasion of *Poecilus versicolor* in the lower site in Tatranské Zruby (FIRd). When comparing the figs. 6 and 7, also in this case the SPEI fits the changes better.



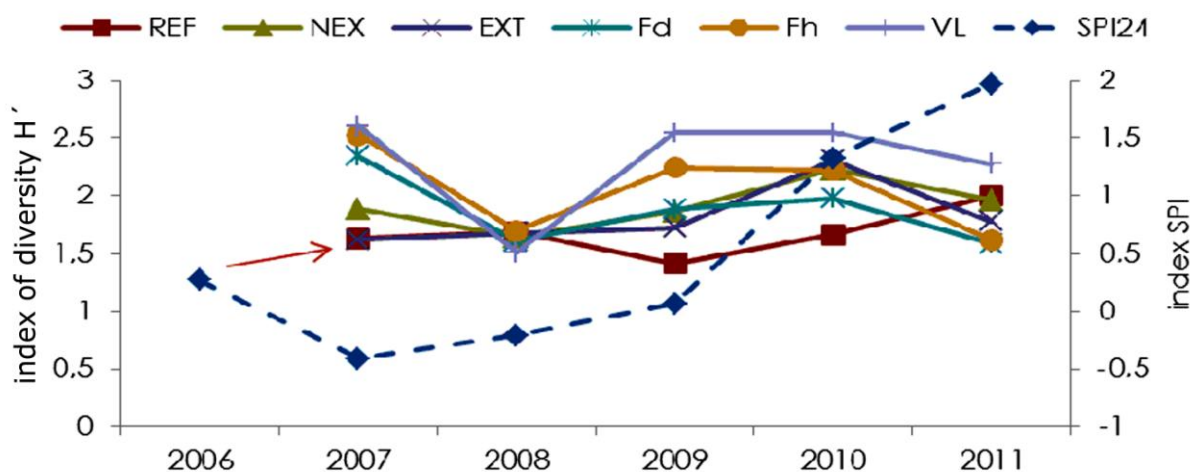


Fig. 7. Changes in Shannon's diversity index  $H'$  of Carabid communities and their relationship with the index SPI for 24 months. The arrows show delay of community reaction after the changes in SPI.

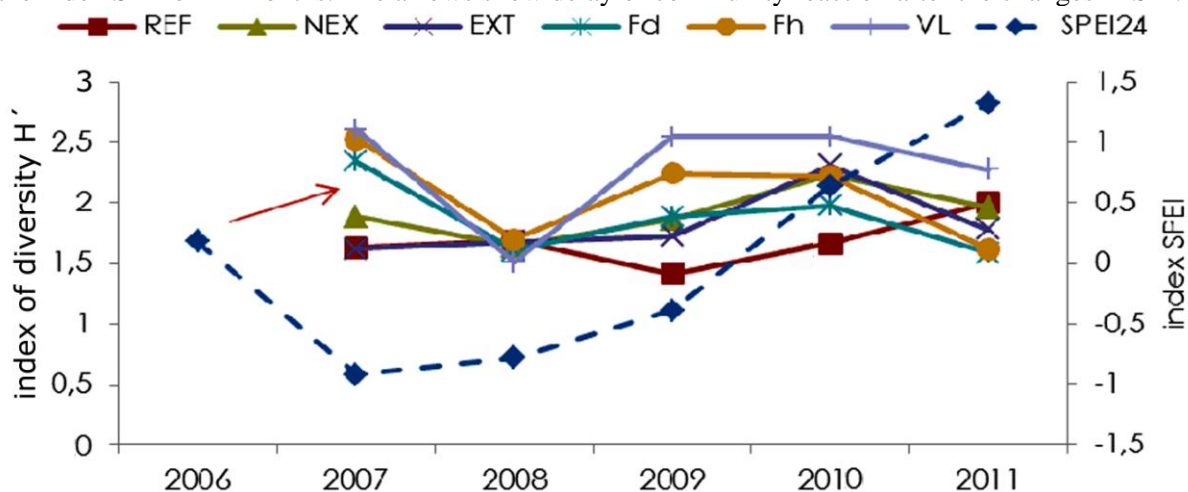


Fig. 8. Changes in Shannon's diversity index  $H'$  of Carabid communities and their relationship with the index SPEI for 24 months. The arrows show delay of community reaction after the changes in SPEI.

Unlike the above purely quantitative parameters, the changes in drought indicated by SPI and SPEI were not reflected so clearly in the values of Shannon-Wiener's index of diversity (Fig. 8-9). The influence of the dry winter 2006 and growing season 2007 also led to decline of this index, which is to be interpreted as a result of simultaneous decline of species number (Tab. 3, Fig. 2-5) and, to a limited degree, as result of slightly increased predominance of few more tolerant or even favored species. In 2009 this decline continued in the intact forests due to strongly increased dominance of stenotopic *Pterostichus unctulatus* (Tab. 3). In other sites the starting values were restored in 2009, but a new decline occurred in 2011 due a new increase of abundance of *Carabus violaceus* and due invasion of *Amara nitida* and *Poecilus versicolor*, especially in both burned sites. The increase of abundance of *Carabus violaceus* can result from the increasing humidity indicated by SPI and SPEI, because this species moderately hydrophilous. On the contrary, invasions of *A. nitida* and *P. versicolor* have only intrinsic reasons and are also connected with character of the herbage vegetation in the burned sites. Thus the changes in indices of diversity of community cannot be so simply interpreted basing on SPI or SPEI.

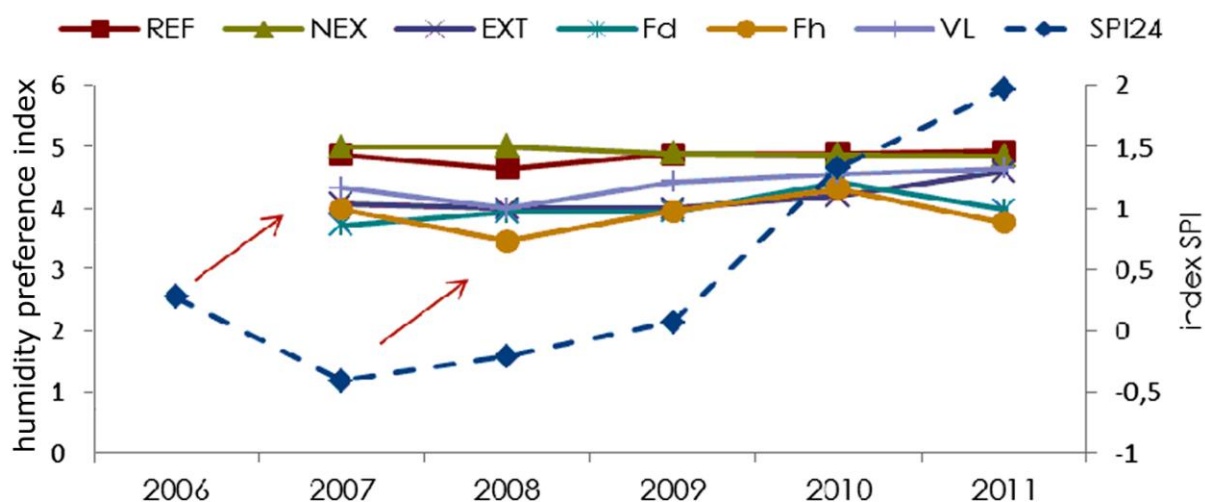


Fig. 10. Changes in humidity preference index of Carabid communities and their relationship with the index SPI for 24 months. The arrows show delay of community reaction after the changes in SPI.

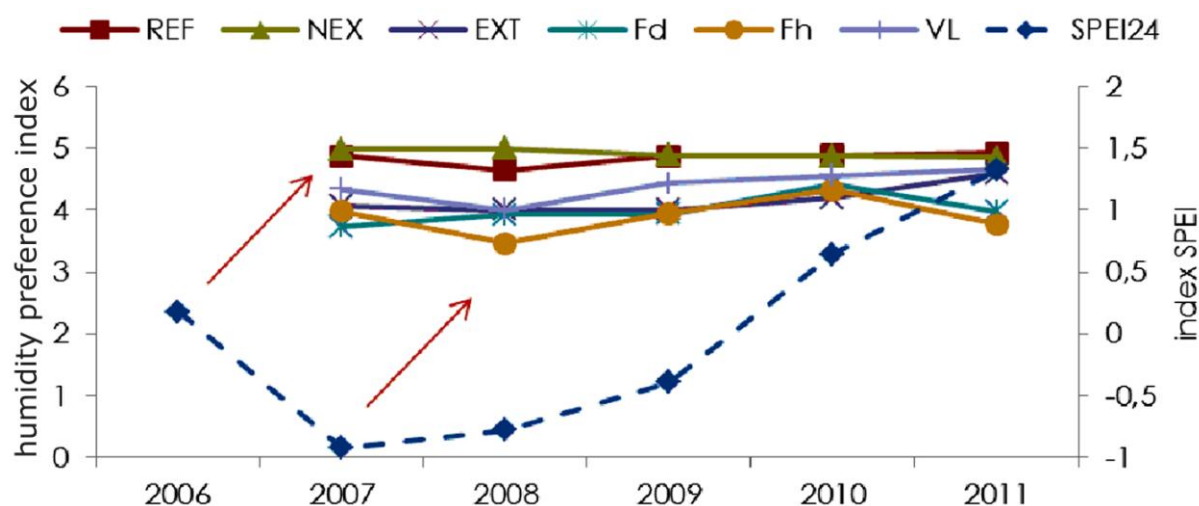


Fig. 11. Changes in humidity preference index of Carabid communities and their relationship with the index SPI for 24 months. The arrows show delay of community reaction after the changes in SPI.

According to changes of index of humidity preference, the communities differentiated into two seemingly indistinct groups (Fig. 10-11). The first group includes the communities from the intact reference site (REF) and from the site with timber *in situ* (NEXT). Their position is very stable during the whole period of investigation, except for a light decline in the reference site in 2008. Index of humidity preference in both these communities was always at least by 0.5 higher than the values from other four sites. This resulted from the homogeneous composition of species (Tab. 3), as also illustrated by the clustering pattern of hierarchical classification (Fig. 1).

The second group includes communities from the sites with extracted timber. Within these communities, two different trends can be detected: (1) a slight decline of humidity preference index in 2008 in the unburned sites (EXT, VL) and in the upper burned site (FIRh), which is followed by a moderate increase up 2011, especially on the unburned site VL; (2) a decline in the burned sites in 2008 followed by an increase in both burned sites in 2009 and 2010 that was followed by a decline in 2011. This decline resulted from momentary intensity of invasions of the open landscape species

*Poecilus cupreus*, *Poecilus versicolor* and *Amara* spp. and from their proportion with *Carabus violaceus* (Tab. 3). But in general these changes follow the trend of both indices SPI and SPEI.

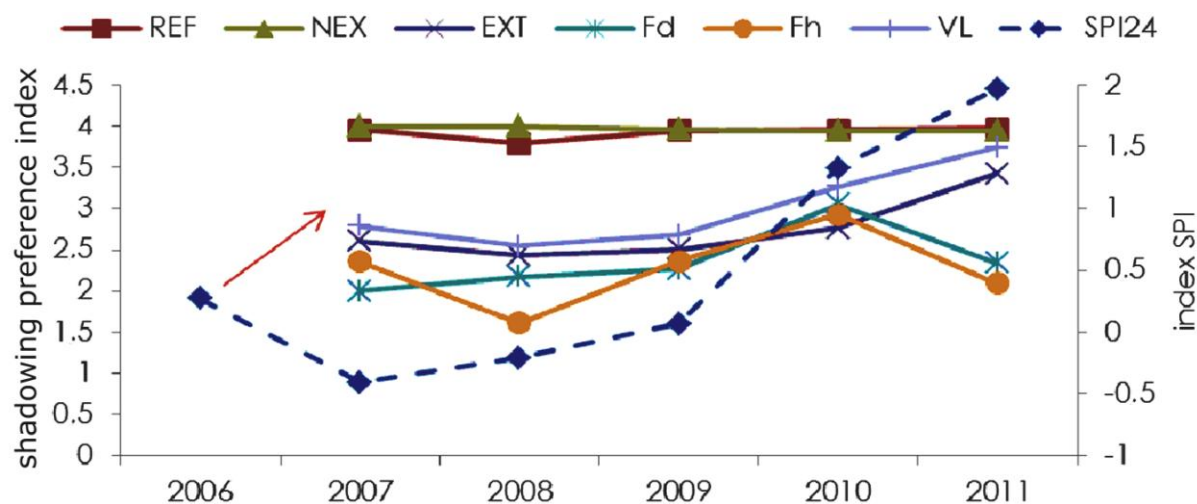


Fig. 12. Changes in shadowing preference index of Carabid communities and their relationship with the index SPI for 24 months. The arrows show delay of community reaction after the changes in SPI.

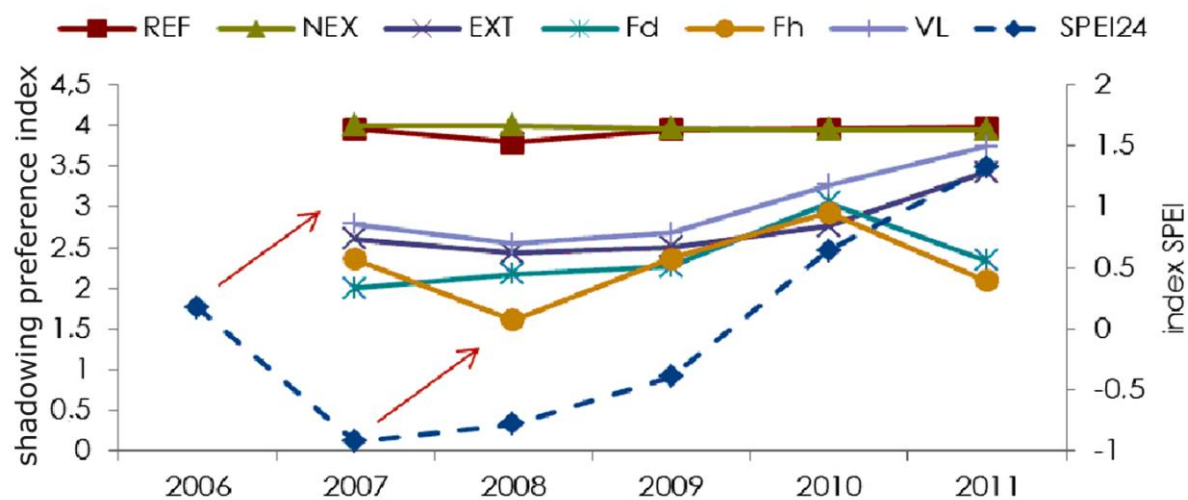


Fig. 13. Changes in shadowing preference index of Carabid communities and their relationship with the index SPEI for 24 months. The arrows show delay of community reaction after the changes in SPEI.

According to shadowing preference index the communities form two groups (Fig. 12 - 13). In the first group consisting of the communities from the intact forests (REF) and from the site with timber *in situ* (NEXT) with almost exclusive presence of the forests species, only a negligible decline of this index was observed in 2008 due to an increase of relative abundance of the eurytopic and heliophilos *Notiophilus biguttatus* (Tab. 3). In the second group including the communities from all sites with extracted timber, a decline of shadowing preference index was observed in three communities in 2008. Only in the community from the unburned site Danielov dom (EXT) this index increased in 2008 due to a deep drop in representation of the open landscape species *Amara erratica* (Tab. 3). Then this

index increased in all these communities and indicated a slow process of the community restoration. Only in both burned communities the index suddenly declined in 2011 due to the massive invasion of the open landscape species *Poecilus versicolor* and *Amara ovata*. This decline was independent on the course of values of SPI and SPEI, but it was more expressive than the decline in the humidity preference index (Fig. 12-13).

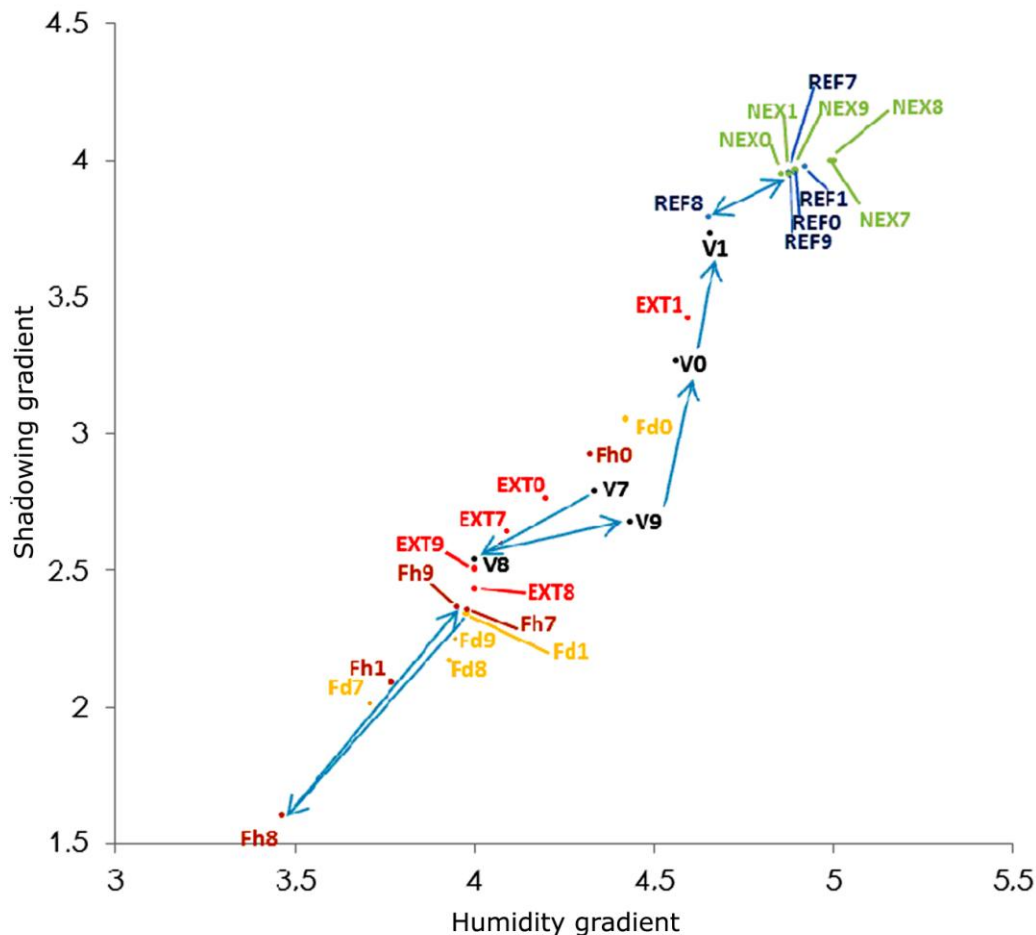


Fig. 14 Direct ordination of the one-year samples basing on preference for shadowing and humidity in 2007-2011.

The variations in mutual relationship of individual one-year samples are clearly shown by the direct ordination (Fig. 14) basing on indices of species preference for humidity and for shadowing. Both indices are derived purely empirically, basing on habitat preference of individual species and comparison of their position in different types of ecosystem. The direct ordination shows separation of the samples into two clusters. The first one is compact and consists of the samples from the intact forests (REF) and from the site with timber *in situ* (NEXT). The second one is heterogeneous and includes all samples from the sites with extracted timber. The samples in the first cluster show a much higher preference for shadowing and humidity than the samples in the second one. Within each clusters, the samples from 2007 and from the second half of the investigation period (2009-2011) show a higher preference for shadowing and humidity than the samples from 2008. An especially remarkable shift to preference for shadowing and humidity in the period 2007-2011 is visible in the samples from the locality Vodný les, where the general climatic shift to more humid conditions indicated by SPI and SPEI is enhanced by the small creek crossing this site and existence of a narrow waterlogged alluvium on the center of this site, where some hydrophilous or even strongly hydrophilous species (*Pterostichus niger*, *Pterostichus nigrita*, *Pterostichus strenuus*, *Trechus amplicollis*) sporadically occurred (Tab. 2 and 3).

## Discussion

The about one-year delay in response of the community structure on bioclimatic conditions indicated by the SPI and even more expressively by SPEI is connected with the reproductive cycle of the Carabids. Most species have one-year cycle of two types (LARSON 1939). In the first one, the adults hibernate, mate and lay eggs in spring and adults of the next generation hatch in late spring. In the second type, the adults mate and lay eggs in late summer or autumn, the larvae hibernate and adults of next generation hatch in late spring. There exists, of course, certain overlap of generations, but most individuals do not survive longer than one year. A longer life span (even 3-4 years) is known only in large species (genera *Carabus* and *Calosoma*) and mostly was observed only in captivity. In unfavorable high mountain condition a prolongation of reproduction cycle to two years is also known (THIELE 1977). Thus the unfavorable climatic conditions in a year can affect the Carabid populations in several, direct or indirect ways. They doubtless reduce the activity of adults, inclusively of the mating and feeding activity, and also affect the larvae that inhabit the litter. In these ways, they reduce the reproduction success. At the same time they also reduce activity of other small arthropods serving as food for carnivorous (almost all forests species) or omnivorous (a considerable part of the open landscape species) Carabids. In this way, they also reduce the survival chance of them. Obviously, this combined effect was clearly reflected by an approximately one-year delay in the purely quantitative parameters of populations (number of individuals or biomass), and to a limited degree also in the structural parameter represented by the Shannon-Wiener's diversity index. It was also clearly reflected by the qualitative parameters of the community indicating preference of individual species for habitat properties (humidity, shadowing). Within the studied material, the effect of drought indicated by SPI and SPEI was better reflected by the shadowing preference index than by the humidity preference index. This seeming paradox results from two facts. These parameters are to certain degree positively correlated because the species preferring forests automatically prefer an environment with more balanced temperature and increased humidity than those living the open habitats, without tree vegetation. The species occurring in the studied localities are much more sharply differentiated according relationship to the presence of tree vegetation than according to humidity. There were few species indifferent to shadowing (taking the position 2 or 3 in the 4-degrees scale (Tab. 2) and at the same time most open landscape species and forest were, in a wider sense, mesohygrophilous, taking an intermediary positions (4-5) in the 8-degree semiquantitative scale (Tab. 2), whereas there almost did not occur expressively hygrophilous species (taking position 6-8, like *Pterostichus niger* and *Pterostichus nigrata* in Vodný les), while a single xerophilous species, *Microlestes maurus* (Tab. 2), was found only in the burned sites. Therefore, the values of indices of humidity preference could move only within relatively narrow limits, irrespectively of the running climatic fluctuations.

A relationship was much less visible between SPI and SPEI and Shannon diversity index. It was due to the fact, that the diversity index measures just equality of distribution of individuals among the species, without any respect to their role in a community. This equality was not essentially changed during the investigated period (Tab. 3), in spite of the observed species composition turnover (Tab. 3, Fig. ).

However significance of the characteristics of humidity and shadowing preference derived empirically basing on literary data and comparison of a large material from other localities and geographical regions (ŠUSTEK 2004) perfectly fitted the results explained more accurately by means of SPI and SPEI. However, unlike the empirical semiquantitative characteristics, the indices SPI and SPEI also have a predictive value for development of Carabid communities in at least one or two next growing seasons. In any case they represent a valuable methodical mean for evaluation of results of long-termed monitoring of Carabid communities. Their application showed that the succession course and processes observed in the area affected by the wind disaster of 2004, by the subsequent fire of 2005 and forest management measures are a result of vegetation changes in local scale and of the climatic changes in the regional scale.

## Conclusions

1. Succession of the Carabid communities in the spruce forests in High Tatra damaged by the wind catastrophe of 2004 exhibited two main trends. The first trend includes differentiation of the communities according to the momentary state of the damaged sites into three groups. This differentiation can be explained by autecology of individual species, the state of habitats and undertaken forest management measures like cutting the stands of *Chamerion angustifolium*.
2. The second trend includes a striking decline of number of species and individuals and of cumulative biomass in all sites in 2008 and a gradual increase of these parameters in the next years. This trend was very similar in all sites and can be explained as a retarded and long lasting consequence of the extremely dry growing season of 2007 and winter 2006/2007. The Standardized Precipitation index (SPI) and the Standardized Evapotranspiration index (SPEI) calculated for 24 months fitted best these changes.
3. The results show that the next succession will depend not only on the restoration of vegetation, but will be essentially influenced by climatic changes.
4. The Standardized Precipitation index (SPI) and the Standardized Evapotranspiration index (SPEI) were show as very suitable means to characterize the climatic changes for needs of interpretation of long-termed zoocoenological data and for a short-termed prognoses of changes in the community succession.

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Table 3. Survey of species and numbers of individuals in the study sites in the area damaged by wind catastrophe in High Tatra in 2004 in the years 2007-2011 (the years are indicated as the last digit).

Species	Study site and year																													
	Vyšné Hágy - R					Jamy - NT					Danielov dom - T					Tatranské Zruby - d					Tatranské Zruby - Fh					Vodný les - V				
	7	8	9	0	1	7	8	9	0	1	7	8	9	0	1	7	8	9	0	1	7	8	9	0	1	7	8	9	0	1
<i>Agonum sexpunctatum</i>																1					1								1	1
<i>Amara aenea</i>											2	2	5	2		1			2		6		2	3	4			1		
<i>Amara erratica</i>					1					1	102	12	26	18	7	6	4	3	5	1	8	2	2	4	1	14	9	12	8	2
<i>Amara eurynota</i>											1	6	2	2		21	1	6	1		2	3	1	2		1		1		
<i>Amara familiaris</i>											3		1	1		1	1		1				2		1		1			
<i>Amara nitida</i>														23	22					112				1	103	1				1
<i>Amara ovata</i>																								2						
<i>Anisodactylus binotatus</i>																2					1						1	1		
<i>Bembidion lampros</i>																26	1	4			4	9	3				1	1		
<i>Calathus metallicus</i>										1																				
<i>Calathus micropterus</i>	9	12	10	13	1				2	4																				
<i>Carabus arvensis</i>					1																									
<i>Carabus auronitens</i>	18	1	6	10	16	1		1	3	9	1	1	1	2	1				1	1	3		1	1	3					
<i>Carabus coriaceus</i>																												1	2	4
<i>Carabus glabratus</i>	7	1	3	3	9	15	1	6	11	8	47	1		11	35	8	2	5	3	9	4		1	4	9	5	1	3	2	13
<i>Carabus hortensis</i>																1												1	3	
<i>Carabus linnei</i>	17	2	8	14	15	25	2	3	8	2	4			1		7														
<i>Carabus nemoralis</i>																														5
<i>Carabus violaceus</i>	29	9	18	53	89	10	6	14	30	31	40	18	23	36	78	2	6	10	21	79	1	3	5	17	38	3	7	4	15	34
<i>Cychrus caraboides</i>	8		2	3	4			1	3	3	2			2						1								1	1	
<i>Harpalus affinis</i>																										1		2		
<i>Harpalus quadripunctatus</i>									3	1					3	2			2					1				1		
<i>Harpalus latus</i>																														1
<i>Leistus terminatus</i>																														1
<i>Loricera caerulescens</i>														1	1	1			1					1		5	1	2	1	
<i>Microlestes maurus</i>																1	2	4				2	2					1		
<i>Molops piceus</i>	7		3	4	4			1	1				1		1	2			12		1		2	1	11	1		2	11	
<i>Notiophilus biguttatus</i>	4	2	2	1	1				1							4	3	6	2		1		1			5		2		
<i>Notiophilus palustris</i>					1								1						1											

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Bratislava, 15.11.2012

Species	Study site and year																								
	Vyšné Hágy - R					Jamy - NT					Danielov dom - T					Tatranské Zruby - d					Tatranské Zruby - Fh				
	7	8	9	0	1	7	8	9	0	1	7	8	9	0	1	7	8	9	0	1	7	8	9	0	1
<i>Poecilus cupreus</i>											1	3	2	6	3	17	21	25	9	4	5	8	13	8	3
<i>Poecilus versicolor</i>													7	4					117				74		
<i>Pseudoophonus rufipes</i>											1	2	1	1					1		2	1	2	1	
<i>Pterostichus aethiops</i>	3	1	1	3	9	9	1		4	11	1			4	11				7	1				1	
<i>Pterostichus angustatus</i>															3										
<i>Pterostichus burmeisteri</i>	17	5	13	25	25	16	5	10	14		2		1	2	1				1	1	1	1	1	5	2
<i>Pterostichus foveolatus</i>	44	9	25	57	94	4	1	2	9	2				1		1				1	1	1	1	1	2
<i>Pterostichus niger</i>																			3					1	2
<i>Pterostichus nigrata</i>																								2	3
<i>Pterostichus oblongopunctatus</i>			1	1	1						1					3				1					1
<i>Pterostichus strenuus</i>																								1	1
<i>Pterostichus unctulatus</i>	208	35	159	186	47	25	8	16	29	8	28	1	9	15	3	1		2	7		8		2	6	1
<i>Trechus amplicollis</i>																								4	2
<i>Trechus latus</i>																								1	
<i>Trechus striatulus</i>					8					2	1														
<i>Trichotichnus laevicollis</i>	1		2	3		1			3	2			1	1	2				2			2		1	1
Number of individuals	372	77	251	376	328	106	24	56	125	80	236	46	73	137	175	108	41	65	55	352	50	28	38	53	254
Number of species	13	10	13	15	17	9	7	10	15	13	15	9	12	20	15	20	9	9	13	15	17	7	14	15	15