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Vegetation state and extreme drought as factors determining differentiation and succession of Carabidae communities in forests damaged by a windstorm in the High Tatra Mts

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Abstract: Succession of Carabidae communities in spruce forests in the High Tatra Mts damaged by the windstorm of November 2004 exhibited two trends. The first trend includes the communities differentiation according to the state and management of damaged sites into three groups: (1) the site with fallen timber *in situ* shows only quantitative and reversible changes in rapport to the intact stand, (2) the sites with extracted timber, where less tolerant forest species disappeared, more tolerant forest species were favored and non-forest mountain species appeared, (3) the sites with extracted timber, additionally burned in July/August 2005, where number of the forest species and their abundance declined and temporal invasions of xenocoenous open-landscape species occurred. This differentiation is explained by autecology of individual species and state of vegetation. In 2010, the communities in burned and unburned sites started to converge due to partial restoration of the vegetation cover, but they continued to strongly differ from the site with timber *in situ*. The second trend includes a striking decline of the number of species and individuals and cumulative biomass in all sites in 2008 and a slow increase of these parameters up to 2011. The extreme dry summer of 2012 caused a decline of these parameters about to the levels from 2009. This trend represents a long lasting consequence of the extremely dry year 2007 and an immediate response to the drought in 2012. The Standardized Precipitation Index (SPI24) and Standardized Evapotranspiration Index (SPEI24) fitted best these changes.

Key words: Carabidae; succession; restoration; ecosystem; forests; vegetation; extreme drought; High Tatra Mts

Introduction

The increased incidence of extreme climatic situations is the most manifest effect of the obvious warming of the climate in recent decades. Such situations, like the windstorm Kyrill on 15 January 2007, cause extensive destructions or damaging of ecosystems on large territories and evoke sharp discussions about approaches to their restoration (Kindelmann et al. 2011) or influence of drought on animal communities (Marshall 2000). A similar situation, on a smaller territory, arose after the destruction of Norway spruce forests on the southern slopes of the High Tatra Mts by the windstorm of 19 November 2004 (Fleischer & Homolová 2011). The caused damages were enhanced by fire on an extensive part of the damaged area by the turn of July and August 2005. In this case, a small part of the damaged area has been kept without any human intervention, while on the major part the timber was exploited. In this way, a unique opportunity arose there to study impacts of these factors on different biota groups and restoration of the damaged ecosystem and influence of various collateral damages and human activities, which already were in focus of many scientists (Fleischer & Homolová 2011). Carabids in particular were studied in this area

by Šustek (2007, 2008) and Šustek & Vido (2012). Similar studies abroad were undertaken by Boháč & Matejíček (2010, 2011). Influence of climatic changes and drought on beetle fauna in lowland broadleaved a forest in South Slovakia was studied by Cunev & Šiška (2006) and Šiška & Cunev (2012), while in the field ecosystems by Šiška & Takáč (2009). Changes of abundance of some insects groups in Great Britain, inclusively of carabids, due to increasing drought were compared by Morecroft et al. (2002).

The aim of this contribution is to show how the annual climatic changes interact with momentary state of vegetation and undertaken management measures and how these factors together influence differentiation and the succession of the carabid communities in this area.

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 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

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Table 1. Survey of study sites in the area affected by the wind disaster in the High Tatra Mts on 19 November 2004 and on 30 July – 1 August 2005 by fire on 250 ha.

| Site	Vyšné Hágy	Tatranská Lomnica Jamy	Danielov dom	Tatranské Zruby lower site	Tatranské Zruby upper site	Nový Smokovec Vodný les
Site abbreviation	REF	NEXT	EXT	FIRd	FIRh	V
Latitude N	49°07′17.5″	49°09′33.7″	49°07′15.3″	49°07′49.3″	49°08′02.7″	4°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 a.s.l.)	1233	1062	1060	1015	1095	1022
Trophic series	AB	AB	AB	AB	AB	AB
Group of geobiocoens	*Sorbi Piceeta*	*Sorbi Piceeta*	*Sorbi Piceeta*	*Sorbi Piceeta*	*Sorbi Piceeta*	*Sorbi Piceeta*
Damaging degree	Intact mature forest	Timber *in situ*	Timber extracted	Timber extracted, burned, herbs cut	Timber extracted, burned, herbs cut	Timber extracted
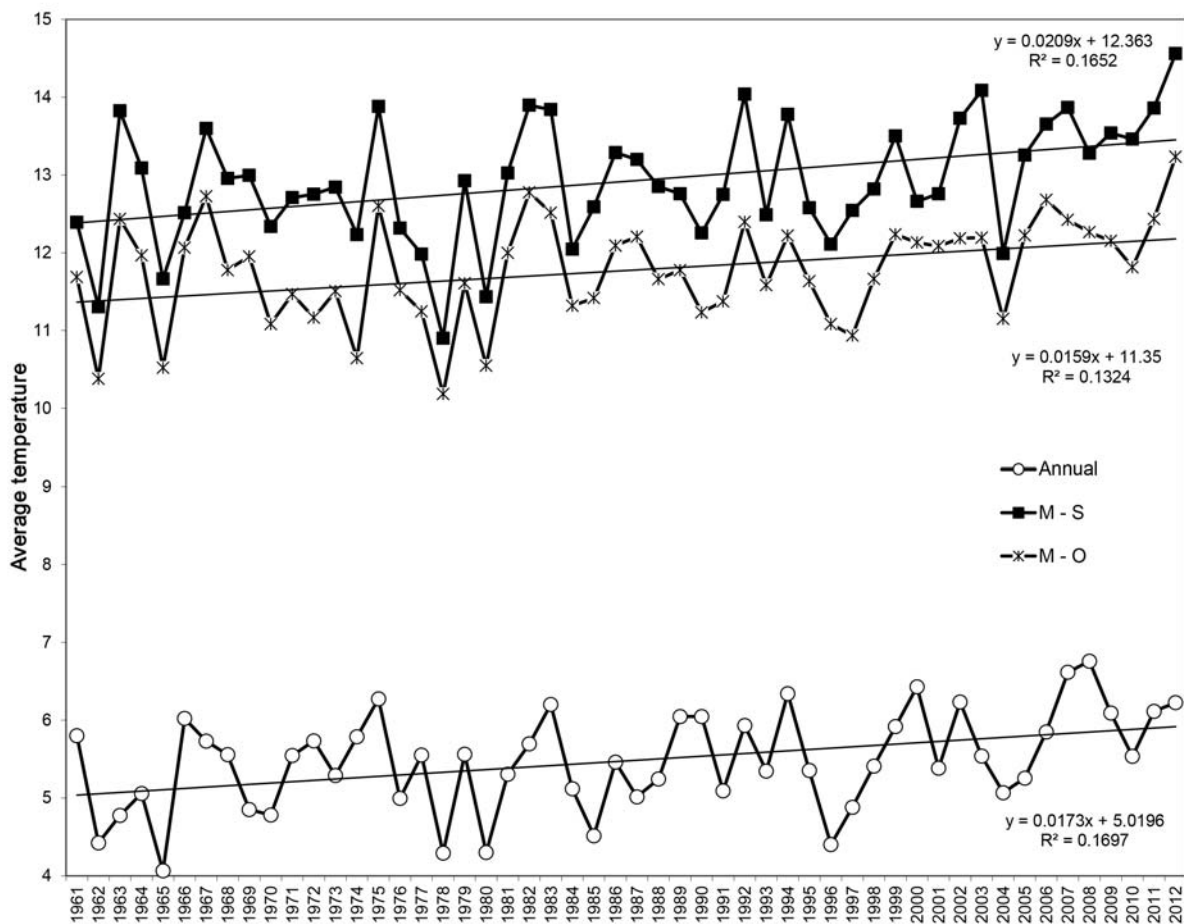
Fig. 1. Average annual temperatures in ℃ in Tatranská Lomnica in the years 1961–2012 and average temperatures in the periods May – September (M – S) and May – October (M – O).

ecosystems and their components. The densely laying fallen timber in 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 site Vodný les made possible a moderate penetration of some hydrophilous species.

The studied period lies at the end of a continuous series of increasing temperatures (Fig. 1), in which the average annual temperatures have increased approximately by 1 ℃. Similar increase was also observed in the average temperature of the growing period calculated for May – September and for May to October. The studied period started by a local temperature maximum in 2007 that followed after a strong local minimum in 2004. Then a moderate decrease of temperatures followed. A new increasing period started in 2011 and 2012 (Fig. 1). The highest average monthly temperatures in the period 2006–2012 were recorded in 2007 and especially in the second part of growing season 2012 (Fig. 2). These temperature culminations were accompa-
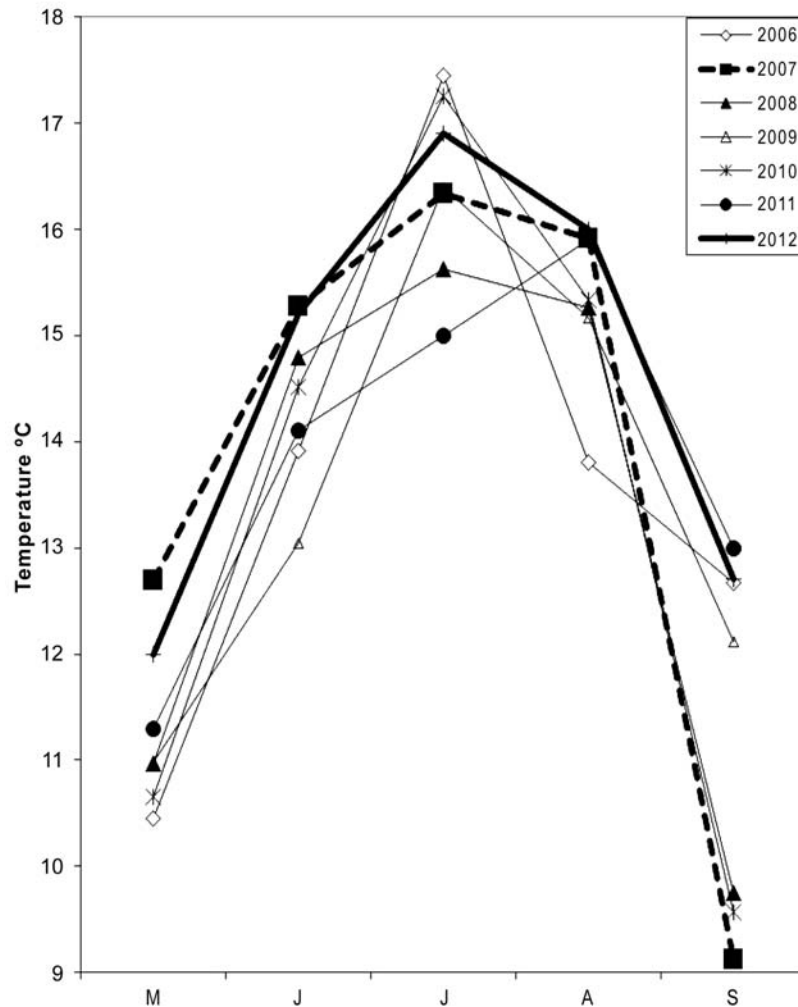
Fig. 2. Average monthly temperatures in growing seasons of 2006–2012.

nied by the lowest monthly sums of precipitation in 2007 and 2012 (Fig. 3).

The beetles were pitfall trapped. Six traps (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 from May to late October. They were emptied approximately once a month. The investigations started in May 2007, when extraction of timber in the damaged sites 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 $100\,^{\circ}$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 4-degree semiquantitative scale of the preference for shadowing (1 – open landscape species, 4 – stenotopic forest species) and an 8-degree scale of humidity preference (1 – strongly xerophilous, 8 – strongly hydrophilous) was constructed (Šustek 2004) and used for the direct ordination (Poole 1974) of one-year samples from individual localities. 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 Horn's index expressing the proportional similarity of the samples and compensating size of the samples. For ordination of samples the non-parametric mustidimensional scaling was used. 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 1961–2012. 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 potential overlap of two subsequent generations. The advantage of SPEI is integration of the elementary climatologic parameters like temperature, precipitation and humidity.

Results

In 2007–2012, altogether 47 carabid species were recorded in all sites (Tables 2 and 3). In individual sites and years the number of species fluctuated from 7 to 21 (mean – 13.7, SD – 4.2). The species belonged to
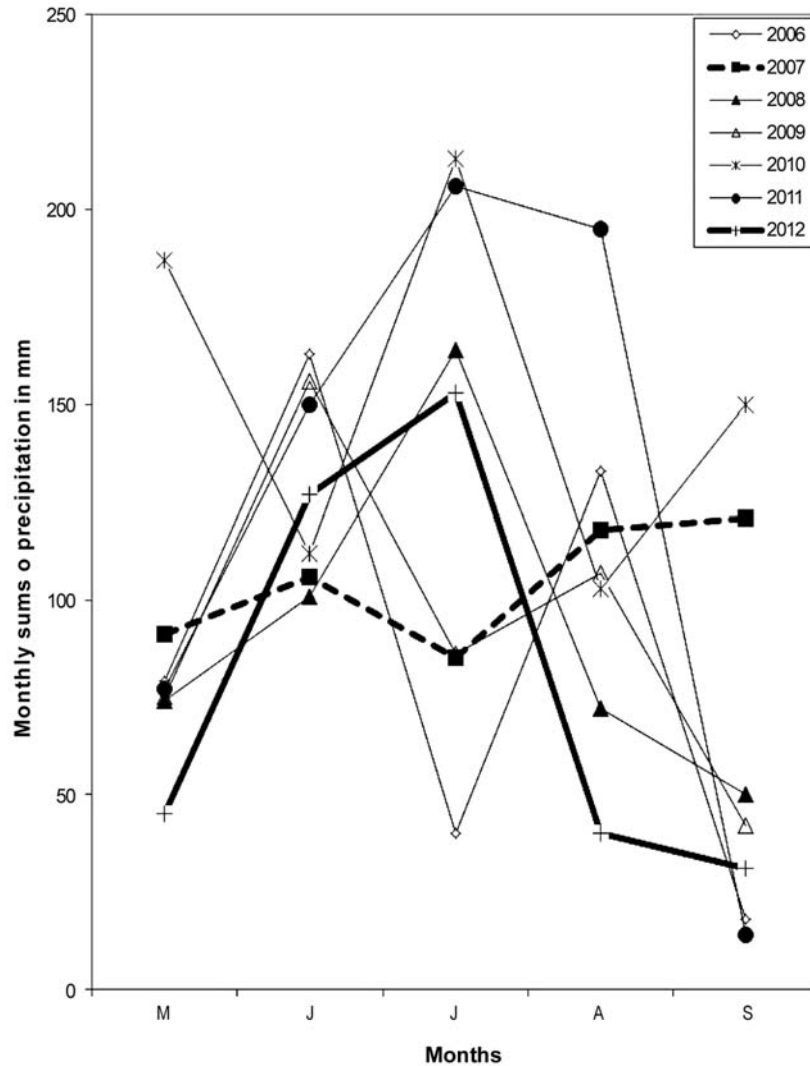
Fig. 3. Monthly sums of precipitations in growing seasons of 2006–2012.

two principal ecological groups. The first group represents the stenotopic forest species, requiring shadowing by closed tree vegetation, like *Pterostichus foveolatus, Pterostichus 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 the optimum of their distribution lays in the middle of this range or in the fir-beech-spruce to the spruce vegetation tier (Raušer & Zlatník 1966), where they form characteristic communities.

These species formed communities in the intact reference site in Vyšné Hágy and in Jamy with the 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 non-forest ecosystems, first of all for arable land. Among them only *Amara erratica* is a mountain

species. The species *Microlestes maurus* is strongly xerophilous, while *Bembidion lampros* is heliophious. In 2001, this groups was enriched in both burned sites by *Amara ovata* and by a large number of *Amara nitida* and *Poecilus versicolor* individuals. All these species are able to fly, what allows them to occupy rapidly new habitats and to spread on large distances.

Spatial and temporal trends in changes of carabid communities are visualized by hierarchical classification using the Horn's index (Fig. 4). 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 the reference site, a slight tendency of joining of samples in the time sequence from 2007 to 2012 is visible, whereas in the site with timber *in situ,* this clustering pattern is still more obvious. Both subclusters form a single major cluster at similarity level of 0.80. This cluster represents a clear opposite to three relatively heterogeneous clusters. The most similar of them includes almost exclusively samples from both sites with extracted timber, but not additionally damaged by fire. The next cluster includes

Table 2. List of carabid species found in study sites in the area damaged by windstorm in the High Tatra Mts in 2004, their complete scientific names, ability to fly (F: F flying species, N – non flying species) characteristics of their preference for humidity (H), shadowing by tree vegetation (S) and average dry biomass of an individual (M).

Species	Characteristics				Species	Characteristics			
	F	H	S	M		F	H	S	M
Agonum sexpunctatum (L., 1758)	F	5	2	0.0350	*Harpalus latus* (L., 1758)	F	4	4	0.1561
Agonum micans (Nicolai, 1822)	F	2	7	0,0313	*Leistus terminatus* (Hellwig in Panzer, 1793)	N	5	4	0.0520
Amara aenea (De Geer, 1774)	F	3	1	0.0413	*Loricera caerulescens* (L., 1758)	N	4	4	0.0428
Amara erratica (Duftschmidt, 1812)	F	3	1	0.0457	*Microlestes maurus* (Sturm, 1827)	F	2	1	0.0072
Amara eurynota (Panzer. 1797)	F	3	1	0.0444	*Molops piceus* (Panzer, 1793)	N	4	4	0.0443
Amara familiaris (Duftschmidt, 1812)	F	3	1	0.0413	*Notiophilus biguttatus* (F., 1779)	F	4	2	0.0443
Amara lunicollis Schiodte, 1837	F	1	3	0,0398	*Notiophilus palustris* (Duftschmidt, 1812)	F	4	2	0.0241
Amara nitida Sturm, 1825	F	3	1	0.1561	*Poecilus cupreus* (L., 1758)	F	4	2	0.2710
Amara ovata (F., 1792)	F	3	1	0.2130	*Poecilus versicolor* (Sturm, 1824)	F	4	2	0.2134
Anisodactylus binotatus (F., 1792)	F	6	2	0.0457	*Pseudoophonus rufipes* (De Geer, 1774)	F	4	1	0.4126
Bembidion lampros (Herbst, 1784)	F	3	1	0.0172	*Pterostichus aethiops* (Panzer, 1797)	N	5	1	0.0862
Calathus metalicus Dejean, 1828	N	5	3	0.1411	*Pterostichus angustatus* (Duftschmidt, 1812)	N	5	4	0.1832
Calathus micropterus Duftschmidt, 1812	N	3	3	0.0196	*Pterostichus burmeisteri* (Heer, 1801)	N	5	4	0.1546
Carabus arvensis Herbst. 1784	N	5	2	1.1332	*Pterostichus foveolatus* Duftschmidt, 1812	N	5	4	0.2152
Carabus auronitens F.,1792	N	4	4	1.3251	*Pterostichus niger* (Schaller, 1783)	N	6	4	1.0600
Carabus coriaceus L., 1758	N	5	4	6.5950	*Pterostichus nigrita* (F., 1792)	N	8	4	0.0812
Carabus glabratus Paykull, 1790	N	5	4	1.7415	*Pterostichus oblongopunctatus* (F., 1787)	N	5	4	0.1941
Carabus hortensis L., 1758	N	4	4	1.7800	*Pterostichus strenuus* (Panzer, 1797)	F	7	4	0.0511
Carabus linnei Dejean,1826	N	5	4	1.0568	*Pterostichus unctulatus* Duftschmidt, 1812	N	5	4	0.0530
Carabus nemoralis O. F. Müller, 1764	N	4	4	1.7370	*Trechus amplicollis* Fairmair. 1859	N	5	2	0.0159
Carabus violaceus L., 1758	N	5	4	1.7457	*Trechus latus* Puzeys, 1847	N	5	4	0.0248
Cychrus caraboides (L., 1758)	N	5	4	0.9256	*Trechus striatulus* Putzeys, 1847	N	5	4	0.0082
Harpalus affinis (Schrank, 1784)	F	3	4	0.1873	*Trichotichnus laevicollis* Duftschmidt, 1812	N	5	4	0.1431
Harpalus quadripunctatus (Dejean, 1829)	F	4	4	0.0956	–				

samples from the unburned site Vodný les and from the burned sites from 2011 and 2012, 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* (Table 3). The third cluster consists exclusively of 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 the essential part of the soil fauna in the burned sites, but also in a massive invasion of the 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 cupreus, Poecilus versicolor, Pseudophonus rufipes, Amara* spp.; Tables 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 clustering pattern (Fig. 4) shows a clear tendency of transition of all communities from a starting state to a final one and to the convergence of the communities in the burned and unburned plots, which is allowed by slow elimination of stands of *Chamerion an-* *gustifolium* and their replacement by growths of *Calamagrostis* sp.

Differentiation of the communities according to the momentary state of vegetation cover is clearly shown by the non-parametric scaling (Fig. 5), where the communities from the reference plot and from the plot with timber *in situ* form a compact group in the left side part of the diagram. The communities from two plots with extracted timber form a very free group in the center of the ordination space, where as the communities from the burned plots are situated in the right site and are split into two groups, one from 2007–2010 and the other from 2011 and 2012. In all groups, there is a clear tendency to situating of the communities from 2011 and 2012 in the upper part of the diagram. In addition, the position of the samples from 2010 shows a tendency to convergence of communities within each group. The sparse arrangement of the communities from all sites with extracted timber show an instability of their composition caused especially by invasions of xenocoenous species. The episodic character of their invasions, especially in the burned plots, is reflected by about twice higher coefficient of variance of number of individuals than in other sites (Fig. 6). The variability in the number of species was moderately higher in all affected sites than in the reference plot. Difference between variability in the number of species and individuals can be explained by a generally low number of species that can potentially occur in the studied plots (Table 2).

The processes described by the hierarchical classification and non-parametric scaling can be explained purely on the base of ecological properties of individual

Table 3. Survey of carabid species and numbers of individuals recorded in the study sites in the area damaged by windstorm in the High Tatra Mts in 2004 during 2007–2012 (the years are indicated as the last digit).

Species	Vyšné Hágy						Jamy						Danielov dom						Tatranské Zruby lower						Tatranské Zruby upper						Vodný les					
year	7	8	9	0	1	2	7	8	9	0	1	1	7	8	9	0	1	2	7	8	9	0	1	2	7	8	9	0	1	2	7	8	9	0	1	2
A. sexpunctatum																			1						1				1						1	1
A. micans																								1												
A. aenea													2	2	5	2			1		2				6		2	3	4				1			
A. erratica					1							1	102	12	26	18	7	5	6	4	3	5		1	8	2	2	4		1	1	14	9	12	8	2
A. eurynota													1	6	2	2			21	1	6	1			2	3	1	2			1		1			
A. familiaris													3		1		1		1	1		1							2		1		1			
A. lunicollis																		1						1												
A. nitida															23	22							112	5			1	103	3		1				1	2
A. ovata																												2								
A. binotatus																			2						1										1	1
B. lampros																			26	1	4			1	4	9	3				1	1				
C.metalicus											1																									
C.micropterus	9	12	10	13	1			2	4																											
C.arvensis				1																																
C. auronitens	18	1	6	10	16		1		1	3	9	3	1	1	1		2	1											1	1	3		1	1		3
C. coriaceus																														1			1	2	4	5
C. glabratus	7	1	3	3	9	8	15	1	6	11	8	3	47	1		11	35	5	8	2	5	3	9	16	4		1	4	9	9	5	1	3	2	13	18
C. hortensis																			1															1	3	3
C. linnei	17	2	8	14	15	2	25	2	3	8	2	1	4				1		7																	
C. nemoralis																																			5	5
C. violaceus	29	9	18	53	89	67	10	6	14	30	31	24	40	18	23	36	78	62	2	6	10	21	79	33	1	3	5	17	38	31	3	7	4	15	34	12
C. caraboides	8		2	3	4	4		1	3	3			2			2								1										1	1	1
H. affinis																															1	2				
H. quadripunctatus										3	1							3	2				2	1					1		1					
H. latus																																		1		
L. terminatus																																		1		
L. caerulescens																	1	1	1		1								1		5	1	2	1		
M. maurus																			1	2	4						2	2						1		
M. piceus	7		3	4	4	1				1	1				1		1	1	2				12	34	1		2	1	11	10	1			2	11	6
N. biguttatus	4	2	2	1	1	1					1							1	4	3	6	2			1		1				5	2				
N. palustris				1													1													1						
P. cupreus													1	3	2	6		3	17	21	25	9	4	1	5	8	13	8		3	1				2	3
P. versicolor																7	4	5					117	19					74	5					4	1
P. rufipes													1	2	1	1								1	2	1	2	1						1		
P. aethiops	3	1	1	3	9	4	9	1		4	11	5	1			4	11	2					7						1		2			1	3	5
P. angustatus																	3																			2
P. burmeisteri	17	5	13	25	25	17	16	5	10	14		5	2		1	2	1	2				1		1	1				1	1	5	2	4	3	3	
P. foveolatus	44	9	25	57	94	12	4	1	2	9	2	2					1		1				1						1	1	1		2			
P. niger																											3	16			1		2	1		
P. nigrita																															2	3	1			
P. oblongopunctatus		1	1	1									1						3						1										1	2
P. strenuus																															1		1			
P. unctulatus	208	35	159	186	47	27	25	8	16	29	8	7	28	1	9	15		3	1		2	7			8		2	6	1		2			4		
T. amplicollis																															4	2				
T. latus																															1					
T. striatulus				8					2	1																										
T. laevicollis	1				2	3	1			3	2	1				1	1	2					2	1					2		1		1		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		57	22	44	52	95	59
Number of species	13	10	13	15	17	10	9	7	10	15	13	9	15	9	12	20	15	9	20	9	9	13	15	9	17	7	14	15	15	9	20	7	18	21	19	11

species and their interactions with changes in vegetation cover. Although the hierarchical classification and ordination also reveal that there exists a general influence of the between-year fluctuations of climatic conditions, it does not allow deciding, which factors are responsible for them.

Within this differentiation of communities another change was observed in two plots laying at the lowest altitudes (1015 and 1022 m a.s.l.; Table 1), hence the lower burned plot in Tatranské Zruby and especially in the extracted plot Vodný les at the western margin of Nový Smokovec. Out of the species constituting the major part of the communities (see above), one individual of *Carabus hortensis* was also recorded in Tatranské Zruby in 2007 as a representative of forest species having optimum of its vertical distribution in lowlands (Table 2). However, in 2009 another similar species, *Carabus coriaceus*, appeared in Vodný les being followed in 2008 by *C. hortensis* and in 2011 even by *C. nemoralis*. Expansion of these thermophilous low-
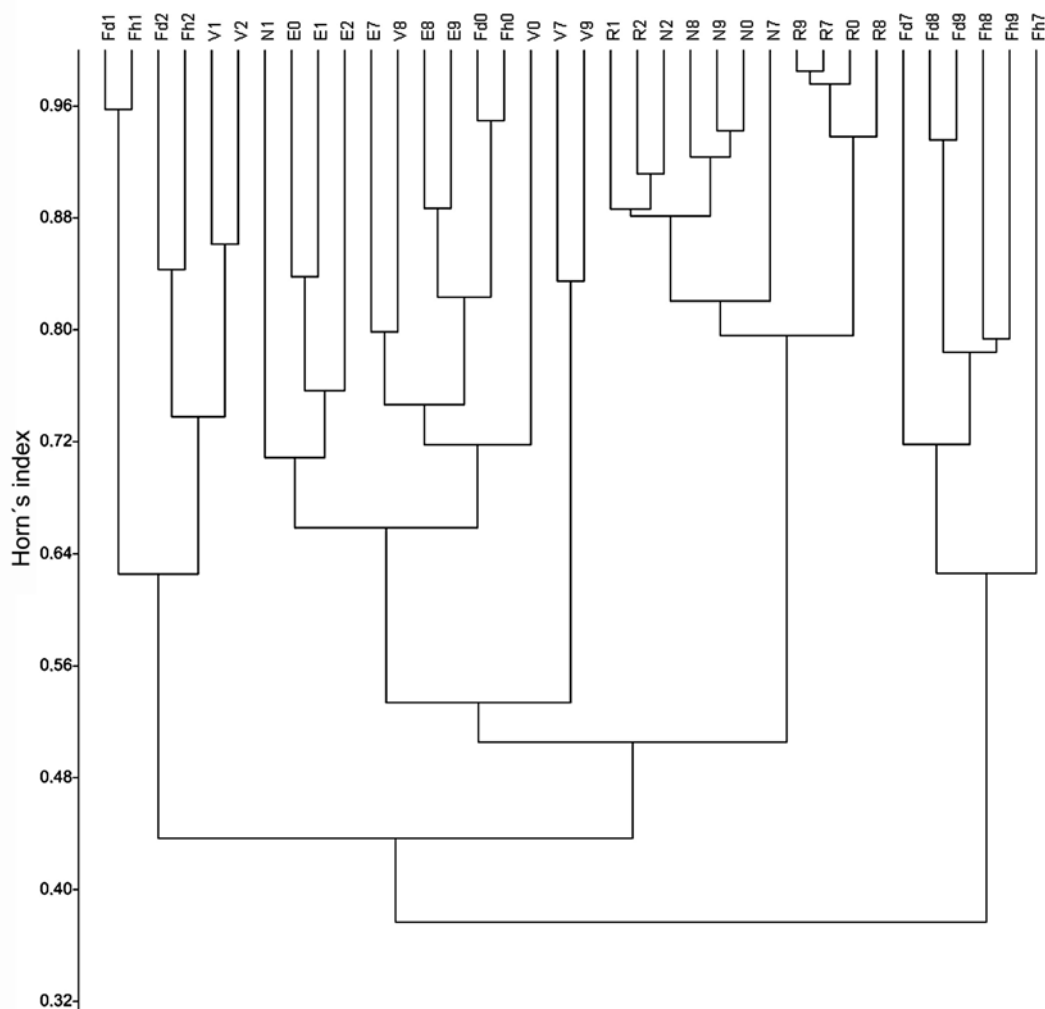
Fig. 4. Hierarchical classification of carabid communities from study sites in the High Tatra Mts (symbols of sites – first letter of site name abbreviation – see Table 1, the last digit of sampling year).

land species had a progressive tendency and in 2011 and 2012 they became even subdominant species in this site. Their cumulative abundance reached almost 12% in 2011 and even 22% in 2012 (Fig. 7). This phenomenon might be interpreted on the background of the increasing temperatures in the area studied (Fig. 1), making possible shifting of the upper border of their distribution to higher altitudes. However, it will be more realistic to interpret it as pure result of dynamics of occurrence foci of these species in the adjacent areas. For example, *Carabus coriaceus* was observed in the interior of Nový Smokovec already one year prior to its appearance in Vodný les. Irrespectively of its real cause it evidently represents at least the beginning of a medium-termed tendency. This process is also confirmed by individual finds of *C. coriaceus* in the upper burned plot (Table 2), and there appears also a slight indication of spreading of two forest species, *Molops piceus* and *Pterostichus angustatus* in all plots (Table 2).

The very striking difference in structure of the studied communities was due to qualitative and quantitative proportion of the wingless species unable to fly and representing the major part of the forest fauna, and of the fully winged and well flying species (Fig. 8).

In the intact plot and in the plot with timber *in situ* the communities consisted exclusively or almost exclusively of the wingless, non-flying species. The only flying species are two eurytopic species of the genus *Notiophilus* (Table 2), which also represent the regular fauna of forests in insolated patches without herbage stratum. In the damaged plots the proportion of wingless species declined suddenly. Their proportion decreased still more in both burned plots. In these plots their representation was also more variable than in the unburned plots. The variability reflects the short time invasions of the field species and the cutting of stands of *Chamerion angustifolium*. The gradual restoration of herbage and wooden vegetation of the damaged plots, however, made the damaged plots less attractive for invasion of the xenocoenous species in the second part of the studied period. Thus in spite of the strong decline of number of species, individuals and of the biomass in 2012, the portion of wingless species of the communities in the plots with exploited timber continued to increase.

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
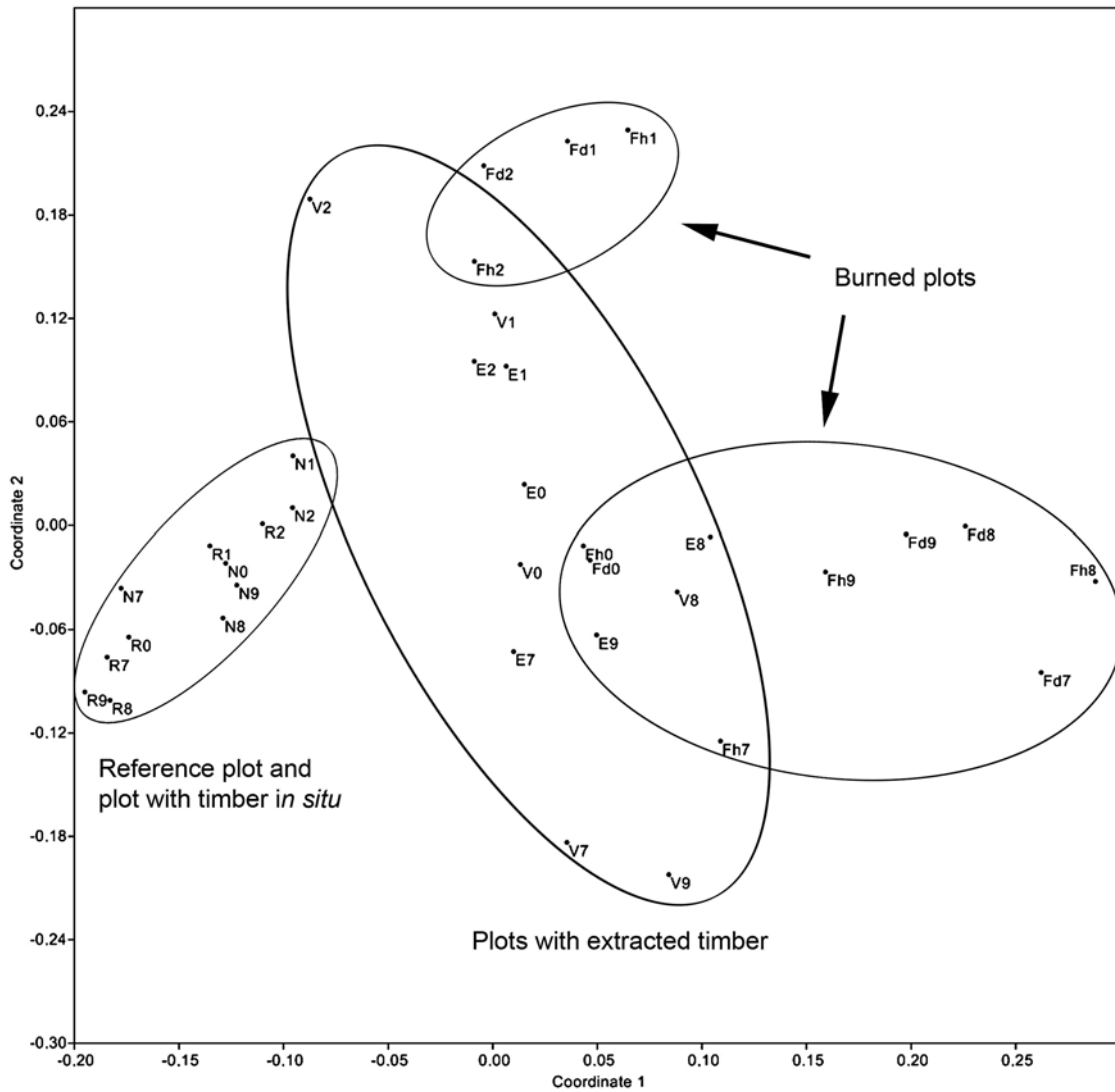
Fig. 5. Non-parametric scaling of one-year samples of carabids from study sites in the High Tatra Mts (symbols of sites – first letter of site name abbreviation – see Table 1, the last digit of sampling year).
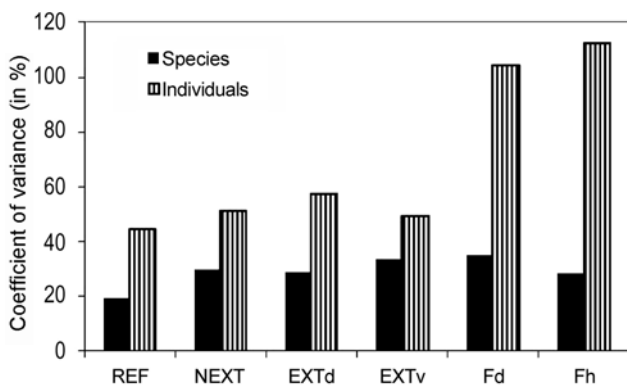
Fig. 6. Coefficients of variance of number of species and number of individuals of carabids in the period 2007–2012 in six sites in the High Tatra Mts in the area affected by the windstorm.

highest temperatures having been observed in Slovakia (SHMÚ 2008). The high temperatures and especially a low sum of precipitation were recorded from April to August (Konôpka & 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, partly April, May and September 2009, which were dry in the High Tatra Mts.

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 (Table 3, Figs 9–11). 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
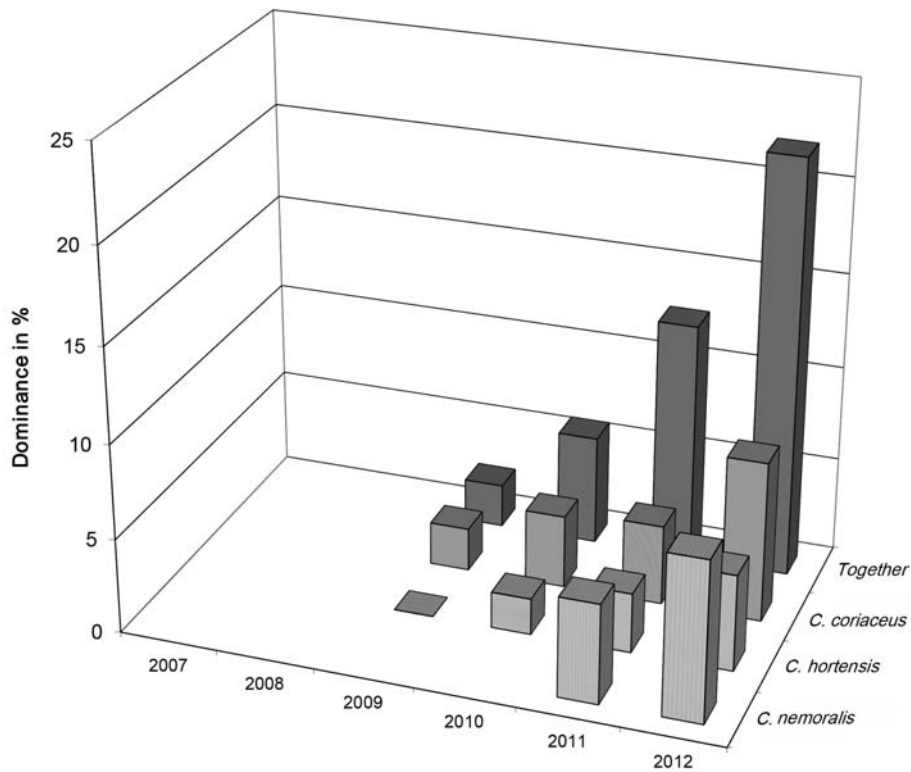
Fig. 7. Dynamics of penetration of three carabid species with occurrence optimum in lowlands into the site Vodný les at the western margin of Nový Smokovec.
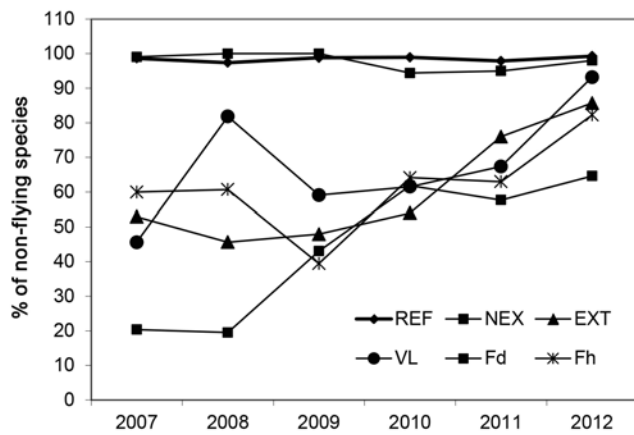
Fig. 8. Changes in representation of the fully winged carabid species able to fly and of the wingless or micropterous species unable to fly in six study sites in the damaged area of the High Tatra Mts.
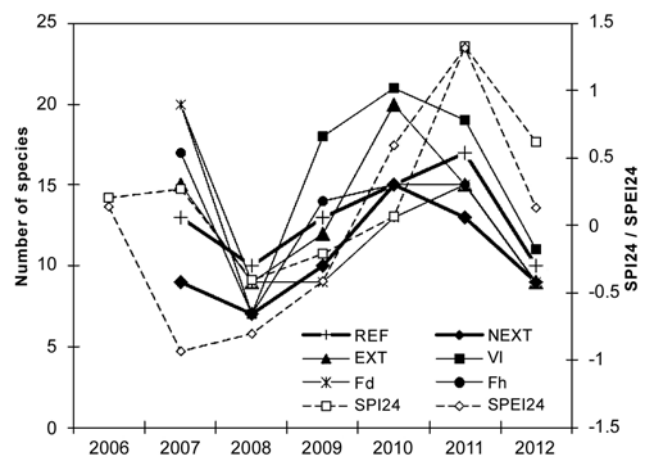
Fig. 9. Changes of the number of carabid species in dependence on dynamics of the indices SPI 24 and SPEI 24 in 2007–2012.

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 same relationship is still 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. From 2008 both indices showed a shift of

the climatop to more humid conditions. This shift is followed by increase in number of recorded species in all sites. The reaction was more balanced in both sites (REF and NEXT) without additional anthropogenic interventions, whereas they were 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 2, 3, 9–11).

Figures 9–11 show a one-year delay of this reaction of the carabid community to climatic changes, characterized by the decline of SPI24 from 0.27 in 2006 to −0.40 in 2007, but also a unmediated re-
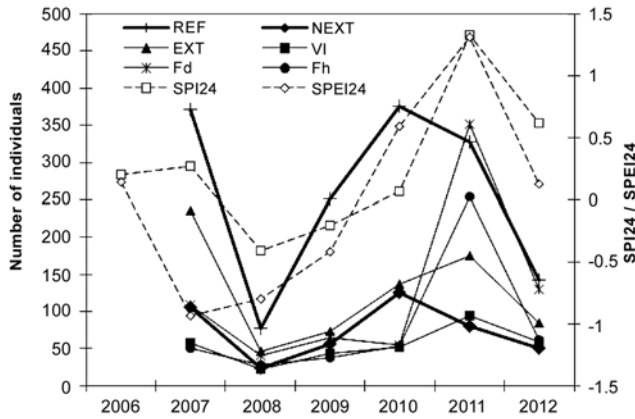
Fig. 10. Change in cumulative number of individuals in carabid communities and their relationship with the indices SPI 24 and SPEI 24 in 2007–2012.
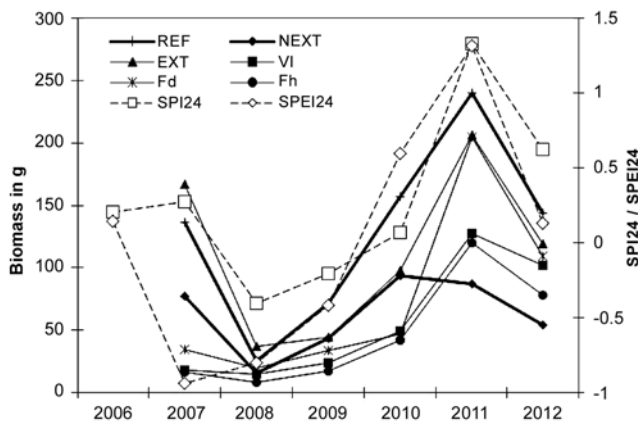
Fig. 11. Change in cumulative biomass of carabids and their relationship with the index SPI 24 and SPEI in 2007–2012.

action of the community in summer and autumn 2012.

A very strong decline occurred in the number of species and individuals in all sites in 2008 (Figs 9 and 10), inclusively of the intact forest and 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 Danielov dom (EXT), followed by the 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. 2). The decline

of SPI24 and SPEI 24 in 2012 caused by the extremely warm and dry second part of summer was not as strong as in 2007 and correspondingly, it did not provoke such strong reaction as in 2008.

The strong decline of cumulative biomass of carabids in the intact forests (Fig. 11), 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, C. violaceus* or *C. auronitens* binding the essential portion of the community biomass. The freed ecological niche was quickly occupied by small species like *Calathus micropterus* or *Pterostichus unctulatus.* But these species were later probably subjected to predation pressure of the large carabid species (or relatively abundant insectivorous soricids), which could restore their earlier position in the community after improvement of climatic conditions in 2010. In 2010, the number of individuals of the small species declined again (180 individuals of *P. unctulatus* in 2010, but 47 in 2011). Due to it, the increasing trend in cumulative number of individuals (Fig. 10) was stopped in the intact forest, but the cumulative biomass continued to grow (Fig. 11) due to presence of less individuals of large species.

Because of remarkable differences in body size of carabids (body length ca. 20×, but body weight even ca. 1000×), 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 in the intact forest, less in all damaged sites. In 2010 the starting level was restored and in 2011 it was even exceeded, except the site with timber *in situ.* This trend corresponded, with certain delay, with the increase of SPI and SPEI (Figs 9–11). The different increase of cumulative biomass in both burned sites resulted from a more intensive invasion of *Poecilus versicolor* in the lower site in Tatranské Zruby (FIRd). When comparing Figs 9–11, also in this case the SPEI fits the changes better. The warm dry summer of 2012 indicated by decline of SPE and SPEI was followed by a sudden drop of biomass to a level of about 2010 (Fig. 11).

The variations in mutual relationship of individual one-year samples are clearly shown by the direct ordination (Fig. 12) based on indices of species preference for humidity and for shadowing. Both indices are derived purely empirically, based 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
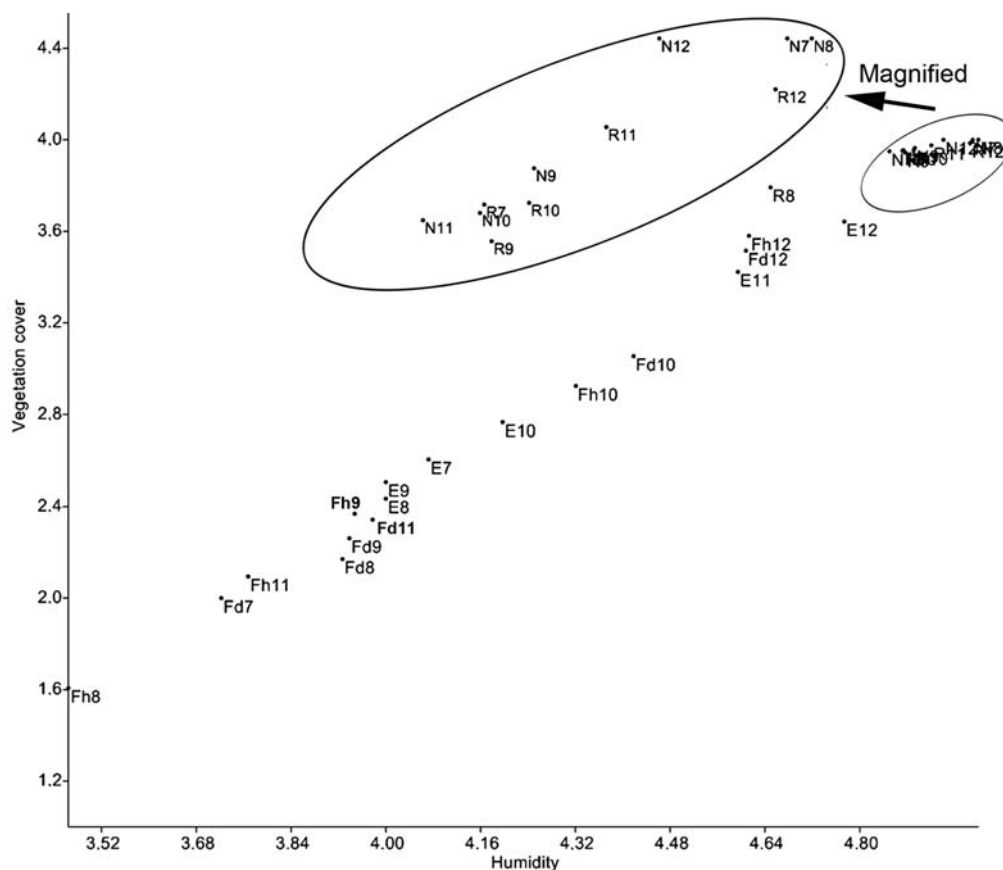
Fig. 12. Direct ordination of the one-year samples based on preference of carabid species for shadowing and humidity in 2007–2012.

from 2007 and from the second half of the investigation period (2009–2012) 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 2007–2012 is visible in samples from the site Vodný les, where the general climatic shift to more humid conditions indicated by SPI and SPEI was enhanced by a small creek crossing this site and the existence of a narrow waterlogged alluvium in the center of this site, where some hydrophilous or even strongly hydrophilous species (*Pterostichus niger, P. nigrita, P. strenuus, Trechus amplicollis*) sporadically occurred (Tables 2, 3).

Discussion and conclusions

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, adults mate and lay eggs in late summer or autumn, the larvae hibernate and adults of next generation hatch in late spring. Certain overlap of generations exists, of course, but most individuals do not survive longer then 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 mating and feeding, and also affect larvae that inhabit the litter. These ways, they reduce the reproduction success. At the same time they also reduce the 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. This way, they also reduce their survival chance. Obviously, the combined effect was reflected by an approximately one-year delay in purely quantitative parameters of carabid populations (number of individuals or biomass). It was also clearly reflected in 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 then those living in open habitats, without tree vegetation. The species

occurring in the studied sites are more sharply differentiated according the 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-degres scale (Table 2) and at the same time, most open landscape species and forest were, in a wider sense, mesohygrophilous, taking an intermediary position (4–5) in the 8-degree semiquantitative scale (Table 2), whereas almost no expressively hygrophilous species occurred (taking position 6–8, like *Pterostichus niger* and *P. nigrita* in Vodný les), while a single xerophilous species, *Microlestes maurus* (Table 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. In essentially different conditions of a lowland oak-hornbeam forest, a sensitive reaction of beetles, inclusive carabids, and a decline or disappearance of hydrophilous species due to warming and drying of the climate was observed by Cunev & Šiška (2006) and Šiška & Cunev (2012). Also Marshal (2000) showed that the variability in community structure of carabids in a Canadian forest caused by drought exceeded those caused by different human interventions including different modes of harvesting. In Great Britain, Morecroft et al. (2002) observed different reactions of individual carabid species in the 1990s – abundance of more hydrophilous species like *Nebria salina* Fairmaire & Laboulbene, 1854 declined while that of the less hydrophilous *Carabus glabratus* increased, but response of most species to changing climate was not unambiguous.

However, the significance of the characteristics of humidity and shadowing preference derived empirically based on literary data and comparison of a large material from other sites and geographical regions (Šustek 2004) perfectly fitted the results explained more accurately by means of SPI and SPEI. But, 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 methodological mean for evaluation of results of long-term monitoring of carabid communities. Their application showed that the succession course and processes observed in the area affected by the windstorm of 2004, by the subsequent fire of 2005 and forest management measures are a result of vegetation changes on a local scale and of the climatic changes on the regional scale.

In spite of two major factors responsible of the differentiation and succession of the carabid communities in the affected area, the obtained results support the opinion that letting the timber *in situ* is more favorable for restoration of the damaged forests in nature reserves than extracting of the timber and all subsequent forests management measures. This conclusion is also in conformity with the observations by Boháč & Matějka (2010, 2011), who showed a similar positive effect of staying dry spruces killed by bark beetles in the forests in the National park Šumava in Bohemia damaged by the Kyrill windstorm in 2007.

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