

PERIODIC AND NON-PERIODIC CHANGES IN CARABID COMMUNITIES FROM THE NORWAY SPRUCE FORESTS OF THE HIGH TATRA IN THE ZONE DAMAGED BY WINDSTORMS

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Abstract. The interrelationships between the succession of Carabid assemblages in the spruce forests of the High Tatra affected by windstorms and the intensity of the damages were studied for the period 2007-2014. The assemblages were differentiated into four groups, according to the degree of forest damaging and subsequent silvicultural intervention, into the assemblage (1) in the intact stand, (2) in the site with fallen timber *in situ*, (3) in the sites with extracted timber and (4) in the additionally burned sites. The stand damaging as such did not affect the proportion of all forest species, just the number of individuals declined here. On the contrary, timber extracting led to the disappearance of two sensitive stenotopic forest species, favoured two tolerant species and, especially in the burned sites, made possible invasions of expansive open landscape species. Later, the assemblages in the burned sites converged to those in the unburned ones. In all of them a sigmoid-like course of restoration is observed. Independently on the restoration stage of the assemblages and their present composition, the changes in the number of individuals and species were clearly correlated with climatic fluctuations. In particular, they were sensitive to episodes of extreme drought that were followed by sudden the decline of the number of species, individuals and biomass. On the contrary, after longer humid periods, they restored. These changes occurred usually with a 1-2 -year lag after the respective climatic extreme. As these extremes occur with a considerable regularity, the observed extremes of fluctuations of the coenotic parameters represent the variability limits of the Carabid assemblages in such conditions. The Standardized Precipitation and Evapotranspiration Index was shown as a suitable means to explain and to predict such changes for the period of 1-2 years. There was also observed spreading of three thermophilous forest species in some sites suggesting the influence of warming. However, this interpretation is uncertain.

Keyword: Carabidae, succession, mountain fauna, spruce forests, climate, windstorms.

Rezumat. Schimbări periodice și neperiodice în cenozele Carabidelor din molidișurile din Tatra Înalta în zona de doborâturi de vânt. Relațiile între succesiunea cenozelor de Carabidele din molidișurile din zona de doborâturi de vânt episoade de secetă și intensitatea distrugerilor, au fost studiate în Tatra Înalță în anii 2007-2014. Cenozele s-au diferențiat în patru grupe: (1) din molidișul intact, (2) din molidișul cu lemn lăsat pe loc, (3), din site-uri cu lemn extras și (4) din site-uri cu lemn extras și afectate ulterior de foc. Doborârea ca atare n-a afectat proporția reprezentării a tuturor speciilor de pădure, ci a redus numai numărul de indivizii. Spre deosebire, în site-ul cu exploatarea lemnului doborât a exclus specii stenotope de pădure, a favorizat două specii mai tolerante și a făcut posibilă invazia de specii expansive ale peisajului deschis. Mai târziu, cenozele din site-uri afectate de foc convergeau la ceacu lemn extras. Cursul restituirii are un caracter sigmoid. Independent de stagiul restituirii cenozelor și de compoziția lor actuală, schimbarea numărului de specii și indivizii este strâns corelat cu fluctuațiile climatice. În mod deosebit, cenozele erau sensibile la episoadele de secetă extremă, care au fost urmate de scăderea bruscă a numărului speciilor și indivizilor. Aceste schimbări au fost observate cu o întârziere de 1-2 ani după extremul climatic respectiv. Deoarece aceste extreme se întâlnesc cu regularitate certă, extremele observate a fluctuațiilor numărului de specii și indivizii reprezintă limitele variabilității cenozelor de Carabidae în condiții montane. S-a arătat că Indicele standardizat al precipitațiilor și evapotranspirației este un instrument potrivit pentru explicarea acestor schimbări cenotice, precum și pentru predicția lor pentru o perioadă de 1-2 ani. În afară de asta, s-a observat răspândirea unor specii forestiere mai termofile, care implică influența încălzirii climatului. Dar interpretarea ei este deocamdată incertă.

Cuvintele cheii: carabidele, succesiune, fauna montana, molidișuri, clima.

INTRODUCTION

The catastrophic windstorm in the High Tatra Mountains (West Carpathians) on November 19, 2004 and the timber extraction from the damaged area and an extensive fire on a considerable part of in 2005 profoundly affected the ecosystems on the southern slopes of this mountain range (FLEISCHER & HOMOLOVÁ, 2011). The impact on fauna was studied on several groups, for example Collembola (URBANOVIČOVÁ et al., 2013). The Carabid assemblages in this area showed two types of changes. The first type of changes was connected with the destruction of the stands, the subsequent human activities in the damaged area and with the beginning of the restoration of the ecosystem (ŠUSTEK, 2007, 2008, 2013; ŠUSTEK & ČEJKA, 2009; ŠUSTEK & VIDO, 2012, 2013). The second type of changes was common as for assemblages in intact stands as for those in differently damaged stands. They included simultaneous declines or increases in the number of individuals, species and biomass in one-year samples. The monitoring undertaken until 2011 suggested that they may have periodical character correlated with the occurrence of short termed drought episodes (ŠUSTEK & VIDO, 2013).

The first aim of this paper is to describe all periodic and non-periodic changes observed in mountain Carabid assemblages in 2007-20014 and linked to the occurrence of short-term drought episodes (WILWHITE, 2002). The second aim is to test the suitability of two different length of the Standardized Precipitation Evapotranspiration Index to explain or even predict changes 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 a large scale fire by turn of July and August 2005. The plots were selected by the staff of the Investigation Station of the High Tatra National Park (FLEISCHER & HOMOLOVÁ, 2011) to coordinate the international investigations started after the windstorm. The sites (Table 1) are described according to the Zlatník's geobiocoenological system of classification of forests (RAUŠER & ZLATNÍK, 1966). It classifies similar forest phytocoenoses into a group of geobiocoens and the groups of geobiocoens into a tridimensional system defined by nine vegetation zones according to altitude and exposition climate (1 – oak forests, 2 – beech-oak, 3 – oak-beech, 4– beech, 5 – beech-fire, 6 – beech-fire-spruce, 7 – spruce, 8 – dwarf pine, 9 – grasslands), four trophic series (A – oligotrophic, B – mesophilous, C – nitrophilous, D – calciphilous) and four hydric series (a xerophilous to periodically flooded).

Table 1. Survey of study plots in the area affected by the windstorm in the High Tatra on November 19, 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	EXTl	FIRl	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	060	1022	1015	1095
Vegetation tier	Spruce	Spruce	Spruce	Spruce	Spruce	Spruce
Trophic series	Acidophilous - mesophilous	Acidophilous-mesophilous	Acidophilous - mesophilous	Acidophilous - mesophilous	Acidophilous - mesophilous	Acidophilous - mesophilous
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 Piceetum</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

Data and methods

The occurrence of drought episodes is characterized by the Standardized Precipitation Evapotranspiration Index SPEI (VICENTE-SERRANO et al., 2010) calculated for the period 1960 – 2014 based on the data from the meteorological station Tatranská Lomnica. SPEI is logically based on the calculation principle of the Standardized Precipitation Index (MCKEE et al., 1993; HAYES, 1999). However the main advantage comparing to SPI is that SPEI calculates the balance between precipitation and potential evapotranspiration. In 99%, SPEI values move within the limits – 3 and + 3 and based on the cumulative probability distribution the concrete values can be interpreted by means of table 2. The data are taken from ŠUSTEK et al. ,(in press).

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 do 1.99	Very humid	5
1.0 do 1.49	Medium humid	10
-0.99 do 0.99	Close to normal	66
-1.0 do -1.49	Medium dry	10
-1.5 do 1.99	Very dry	5
≤ -2.0	Extremely dry	2.5

Thus, this interpretation indicates the significance of the drought episode that means a period with continuous occurrence of negative values of SPEI.

For the purposes of our study, SPEI was calculated for 6- and 12-month for September. The reason to use the 6-month SPEI for September is that the growing season overlapping with the activity and reproduction period of Carabids starts in mountain conditions of the High Tatra in mid-April and lasts to late September. Thus, the drought episodes influence ground beetle assemblages just in this period. In addition, the previous paper of ŠUSTEK & VIDO (2013) also implied this period as relevant in such a research. The 12-month SPEI has been also used because of the missing knowledge regarding the influence of winter precipitation regime on spring ecological response of the spruce ecosystem in the High Tatra Mountains.

These indices were cross-correlated (using the PAST program by HAMMER (2012)) with the zoocenotic parameters (number of individuals and number of species) of ground beetle assemblages on the localities described above.

The beetles were pitfall trapped. Six formalin traps, protected against rain, were exposed in each plot from the end of May until early November 2007 – 2014 and emptied approximately monthly. The position of the traps did not change during the whole study period. Only in the reference plot in Vyšné Hágy the trap line was to be shifted about 150 m eastwards, because of the damaging of the stand by the windstorm in April 2014 and following extraction of the fallen timber. The character of the new plot in the mature spruce stand is identical and the shift of the trap line has not influenced the results.

The scientific names of the species are adopted according to HŮRKA (1996). The habitat and humidity preference of each species (Table 3) were characterized by semi-quantitative scales elaborated by ŠUSTEK (2004) based on an extensive literature (BURMEISTER, 1939; DESENDER, 1986 a, b, c, d; FREUDE et al., 1976; LINDROTH, 1949; SHAROVA, 1981; ŠUSTEK, 1984; THIELE, 1977) and on the author's field experience. The humidity scale is represented by eight degrees ranging from 1 to 8 (1 = extremely xerophilous species of steppe-like habitats, 4 = mesohygrophilous, 8 = extremely hygrophilous 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 the number of individuals of each species as it is used in the methods of direct ordination (POOLE, 1974). In the same way, the average lower and upper limit of vertical distribution, its optimum and amplitude and difference between the upper limit and optimum were calculated. The vertical distribution was characterized by the vegetation tiers according to ŠUSTEK (2000), who graphically characterized the amplitude of the vertical distribution of species and optimum of their occurrence within this amplitude. The optimum was characterized according to usual dominance position of a species taken in communities in different natural or semi-natural ecosystems in Central Europe. In this study, the lower and upper limits of distribution were expressed by the number of the respective vegetation tier (see above). Structural changes of assemblages are quantified by two zoocenotic parameters – number of species and cumulative number of individuals in one-year catches. 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 DISCUSSIONS

In the investigation period, a material of 5,329 individuals belonging to 50 species was obtained in all study plots (Table 4). They represent 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. Among them, 7-21 species were recorded in individual plots and years. Their number was positively correlated ($r = 0.3148$) with the number of trapped individuals that fluctuated from 22 to 376. The higher cumulative numbers of individuals resulted especially from the abundant occurrence of little species.

The periodic changes in the assemblages

The between-year changes of all three zoocenotic parameters (Figs. 1-3) show a similar trend, independently on the present degree of damaging of the assemblage. In 2008, they suddenly dropped deeply under the level of the precedent year, but since 2009 they have gradually increased. The number of species and individuals culminated in 2010 or 2011. The extremely high values in 2011 in both burned plots are due to the invasion of the well flying *Amara nitida* Sturm, 1825 (Table 4). In 2012, the values of both parameters deeply dropped again. The numbers of species and individuals approximated their minimum of 2008.

In the next two years the numbers of species and individuals stabilized at the approximately the same level. However, in individual plots they show moderately different directions. In the intact reference plot the number of individuals continued to decrease, but in one of the burned plots FIREI it increased. The number of species also moderately decreased on most plots, but it slightly increased in the burned plot FIREh (Table 4).

The figures 1 - 3 show that a sudden decline of the number of species and individuals and of the biomass of Carabids follows after a longer occurrence of values of SPEI close to -1.0 or lower (Figs. 4-5). On the contrary, a longer occurrence of values around 0 already anticipated a moderate increase of both zoocenotic parameters. After a prolonged increase of SPEI to the level 1.0 to 2.0, a strong increase of both zoocenotic parameters followed.

The fluctuations in the number of species and individuals are cross-correlated with the fluctuations in SPEI 6 and 12 in a very similar way and the maximums of the cross-correlation coefficients occur mostly with a 0-2-year lag (Figs. 6 - 9).

From the viewpoint of prognosis of development of the production parameters of Carabid assemblages based on climatic fluctuations it seems that, unlike the conclusion of ŠUSTEK & VIDO (2013), SPEI 12 followed by SPEI 6 display the highest indicative values. SLPEI 12 better characterizes long-termed tendencies, whereas fluctuations of SPEI 6 (for example the sudden drop in mid-2011) can represent warning signals of later decline of the number of individuals and species.

Table 3. Scientific names of the species and their ecologic characteristics (vertical distribution in vegetation tiers: L – lower limit, OP – optimum, U – upper limit, A – average, D – difference between upper and optimum; humidity requirements: scale 1-8 = strongly xerophilous to strongly hygrophilous; vegetation cover: scale 1-4 = discontinuous herbage stratum, without wooden plants to complete shadowing by trees; flying ability: F – flying species, N – non-flying species; B – biomass in grams).

Species	Ecological property								
	L	OP	U	A	D	HU	VC	FL	B
<i>Agonum micans</i> (Nicolai, 1822)	1	2	6	5	4	7	2	F	0.0313
<i>Agonum sexpunctatum</i> (Linnaeus, 1758)	1	3	7	6	4	5	2	F	0.0350
<i>Amara aenea</i> (De Geer, 1774)	1	2	6	5	4	3	1	F	0.0413
<i>Amara erratica</i> (Duftschmidt, 1812)	5	7	9	4	2	3	1	F	0.0457
<i>Amara eurynota</i> (Panzer, 1797)	2	4	6	4	2	3	1	F	0.0444
<i>Amara familiaris</i> (Duftschmidt, 1812)	1	2	6	5	4	3	1	F	0.0413
<i>Amara lunicollis</i> Schiodte, 1837	2	4	6	4	2	3	1	F	0.0398
<i>Amara nitida</i> Sturm, 1825	1	2	5	4	3	3	1	F	0.1561
<i>Amara ovata</i> (Fabricius, 1792)	1	2	6	5	4	3	1	F	0.213
<i>Anisodactylus binotatus</i> (Fabricius, 1792)	1	2	6	5	4	6	2	F	0.0457
<i>Bembidion lampros</i> (Herbst, 1784)	1	1.5	6	5	4.5	3	1	F	0.0172
<i>Calathus metallicus</i> Dejean, 1828	5	7	9	4	2	5	3	N	0.1411
<i>Calathus micropterus</i> Duftschmidt, 1812	3	5	7	4	2	3	3	N	0.0196
<i>Carabus arvensis</i> Herbst, 1784	3	5	7	4	2	5	2	N	1.1332
<i>Carabus auronitens</i> Fabricius, 1792	3	5.5	8	5	2.5	4	4	N	1.3251
<i>Carabus coriaceus</i> Linnaeus 1758	1	2	6	5	4	5	4	N	6.5950
<i>Carabus glabratus</i> Paykull, 1790	1	5.5	7	6	1.5	5	4	N	1.7415
<i>Carabus hortensis</i> Linnaeus, 1758	1	2	6	5	4	4	4	N	1.7800
<i>Carabus linnei</i> Dejean, 1826	3	5.5	8	5	2.5	5	4	N	1.0568
<i>Carabus nemoralis</i> O. F. Müller, 1764	1	2.5	6	5	3.5	4	4	N	1.7370
<i>Carabus violaceus</i> Linnaeus, 1758	1	5.5	8	7	2.5	5	4	N	1.7457
<i>Cychrus caraboides</i> (Linnaeus, 1758)	1	5.5	8	7	2.5	5	4	N	0.9256
<i>Europhilus gracilipes</i> Duftschmidt, 1812	1	3	7	6	4	5	2	F	0.0612
<i>Harpalus affinis</i> (Schrank, 1784)	1	1.5	6	5	4.5	3	4	F	0.1873
<i>Harpalus distinguendus</i> Duftschmidt, 1812	1	2	7	6	5	4	1	F	0.1761
<i>Harpalus latus</i> (Linnaeus, 1758)	1	1.5	6	5	4.5	4	1	F	0.1561
<i>Harpalus quadripunctatus</i> (Dejean, 1829)	4	6	7	3	1	4	1	F	0.0956
<i>Leistus piceus</i> Frölich, 1799	4	6	8	4	2	5	4	N	0.0610
<i>Leistus terminatus</i> (Hellwig in Panzer, 1793)	3	6.5	8	5	1.5	5	4	N	0.0520
<i>Loricera caerulea</i> (Linnaeus, 1758)	1	3	8	7	5	4	4	F	0.0428
<i>Microlestes maurus</i> (Sturm, 1827)	1	1	6	5	5	2	1	F	0.0072
<i>Molops piceus</i> (Panzer, 1793)	2	3	6	4	3	4	4	N	0.0443
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	1	2	7	6	5	4	2	F	0.0240
<i>Notiophilus palustris</i> (Duftschmidt, 1812)	1	3	8	7	5	4	2	F	0.0241
<i>Poecilus cupreus</i> (Linnaeus, 1758)	1	1.5	6	5	4.5	4	2	F	0.2710
<i>Poecilus versicolor</i> (Sturm, 1824)	2	4.5	6	4	1.5	4	2	F	0.2134
<i>Pseudoophonus rufipes</i> (De Geer, 1774)	1	1.5	6	5	4.5	4	1	F	0.4126
<i>Pterostichus aethiops</i> (Panzer, 1797)	5	6	8	3	2	5	1	N	0.0862
<i>Pterostichus angustatus</i> (Duftschmidt, 1812)	5	6	8	3	2	5	4	N	0.1832
<i>Pterostichus burmeisteri</i> (Heer, 1801)	3	4.5	7	4	2.5	5	4	N	0.1546
<i>Pterostichus foveolatus</i> Duftschmidt, 1812	3	5.5	8	5	2.5	5	4	N	0.2152
<i>Pterostichus niger</i> (Schaller, 1783)	1	1.5	6	5	4.5	6	4	F	1.0600
<i>Pterostichus nigrita</i> (Fabricius, 1792)	1	1.5	6	5	4.5	8	4	F	0.0812
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	1	3	6	5	3	5	4	F	0.1941
<i>Pterostichus strenuus</i> (Panzer, 1797)	1	2	6	5	4	7	4	F	0.0511
<i>Pterostichus unctulatus</i> Duftschmidt, 1812	4	6.5	8	4	1.5	5	4	N	0.0530
<i>Trechus amplicollis</i> Fairmair, 1859	4	5	7	3	2	5	2	N	0.0159
<i>Trechus latus</i> Puzey's, 1847	3	6.5	8	5	1.5	5	4	N	0.0248
<i>Trechus striatulus</i> Putzeys, 1847	3	6.5	9	6	2.5	5	4	N	0.0082
<i>Trichotichnus laevicollis</i> Duftschmidt, 1812	3	5.5	7	4	1.5	5	4	F	0.1431

Table 4 (part 1). Survey of the species and number of individuals caught in six study plots in the High Tatra in 2007-2014: reference plot and plot with timber in situ (years marked just by the last digit).

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>																
<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. oblongopuncatus</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. amplicolis</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 species	13	10	13	15	17	10	10	7	9	7	10	15	13	9	9	8
Number of individuals	372	77	251	376	328	143	93	96	106	24	56	125	80	51	54	46

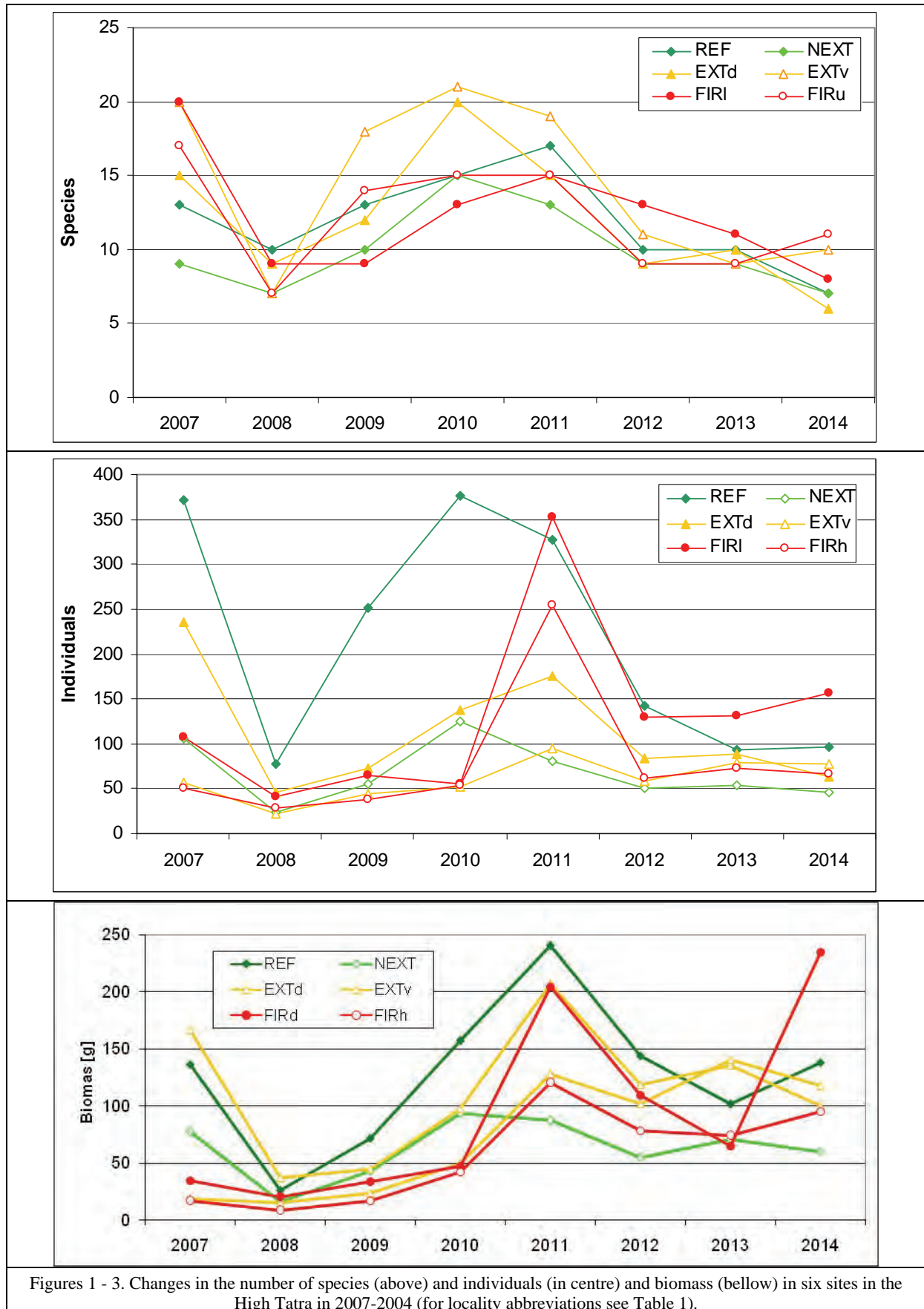
The changes described above coincided with the course of changes of SPEI 6 and 12 (Figs. 4-5). In late 2006 and in 2007, there occurred a drought indicated by a sudden drop of these indices. SPEI 12 was low in 2007 and rarely also in 2008. SPEI 6 continued to indicate short and often interrupted periods of moderate drought (0.0 to 0.5) also in 2009. In 2010, when the number of species and individuals started to increase, both indices (SPEI 6 and 12) also show high values ranging from 1.0 to 2.0. The occurrence of high values of these indices is the more continuous; the longer periods are represented by them (Figs. 4-5). SPEI 12 in 2012 declined to the interval 0.0 to -1.0. Unlike SPEI 12, SPEI 6 in 2011 suddenly dropped in the second third of the year even to -1.0 to -1.5. This drop anticipated the strong decline of the number of species and individuals and cumulative biomass in 2012 - 2014 (Figs. 1 - 3).

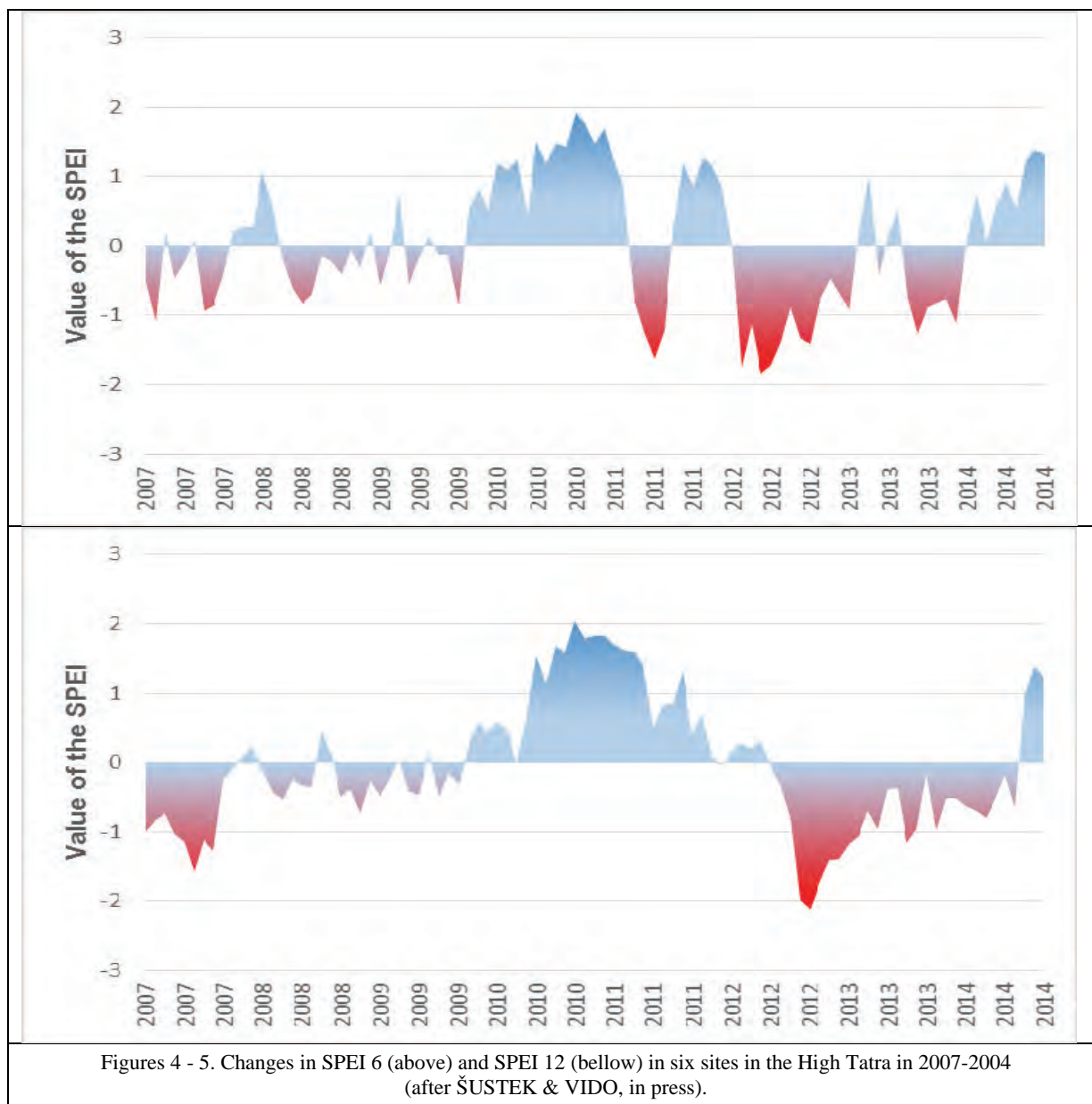
Table 4 (part 2). Survey of the species and number of individuals caught in six study plots in the High Tatra in 2007-2014: unburned plots with extracted timber (years marked by the last digit).

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. quadripunct.</i>					3		1					1				1
<i>L. piceus</i>																
<i>L. terminatus</i>													1			
<i>L. caeruleus</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	2			
<i>P. strenuus</i>									1		1					
<i>P. unctulatus</i>	28	1	9	15	3		1		2			4				
<i>T. amplicollis</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 species	15	9	12	20	15	9	10	6	20	7	18	21	19	11	9	10
Number of individuals	236	46	73	137	175	84	88	63	57	22	44	52	95	58	79	78

Table 4 (part 3). Survey of the species and number of individuals caught in six study plots in the 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. metalicus</i>																
<i>C. micropterus</i>															1	1
<i>C. arvensis</i>																
<i>C. auronitens</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. caeruleus</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. amplicollis</i>																
<i>T. latus</i>																
<i>T. striatulus</i>																
<i>T. laevicollis</i>					2	1		1					2			1
Number of species	20	9	9	13	15	13	11	8	17	7	14	15	15	9	9	11
Number of individuals	108	41	65	55	352	130	132	156	50	28	38	53	254	62	73	67

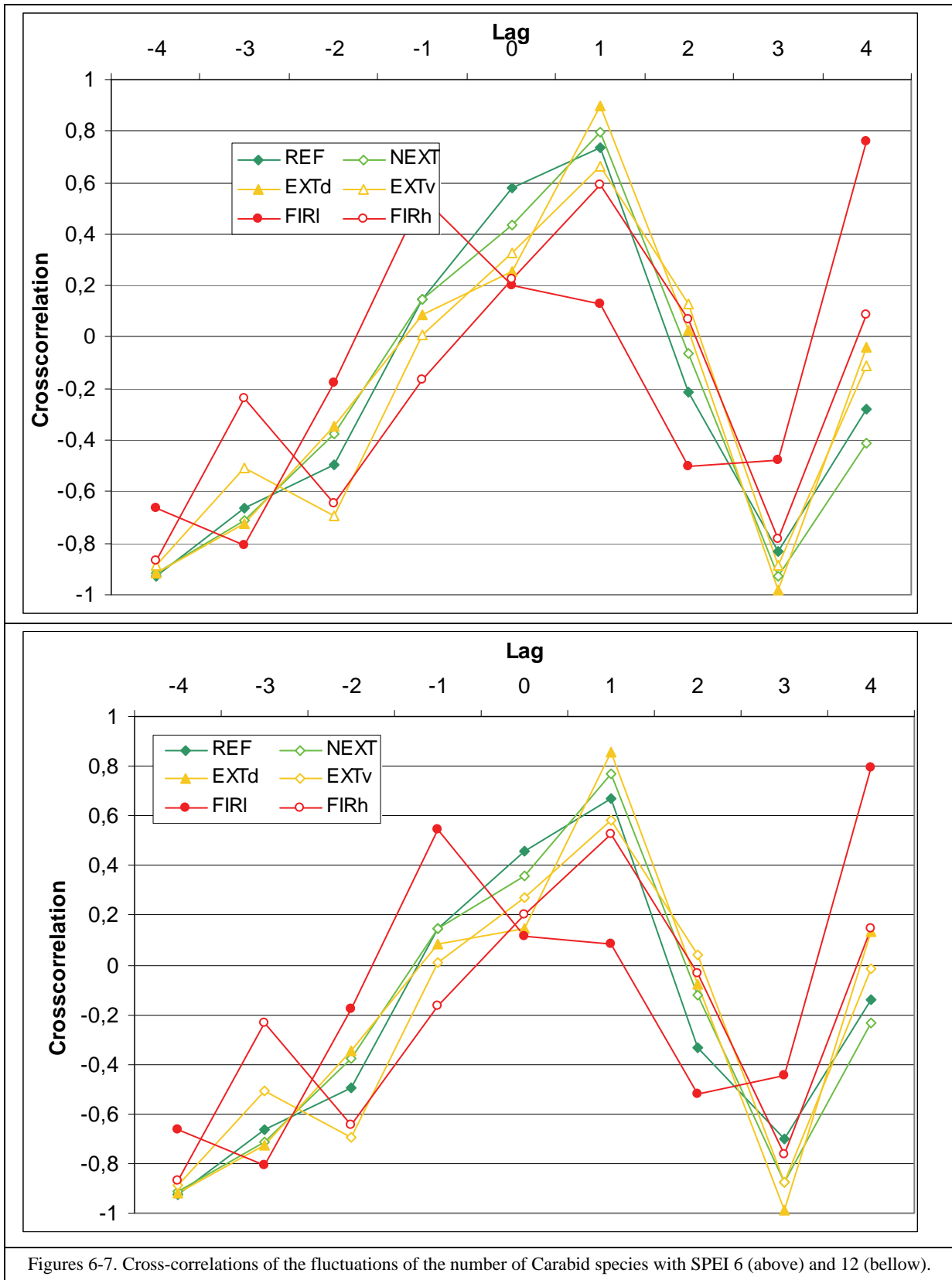




In 2012 and 2013, SPEI 6 and 12 declined approximately below the level of -0.5 , but SPEI 12 decreased to the level of -2.0 . In 2014, these indices started to increase again, but SPEI 6 had increased already in spring, while both other indices increased as late in the last third of 2014. This moderate increase coincides with the increase of the number of individuals and biomass of Carabids in some plots in 2014 (Figs. 1-3). The comparison of the changes in the number of individuals and species as biomass with the occurrence of drought periods indicated by SPEI index shows that the changes in both zoocoenotic parameters mostly occur with an approximate delay of 1-2 years after extremely droughty or rainy years. With this delay, the values of these parameters and SPEI show the highest cross-correlations (Figs. 6-9),

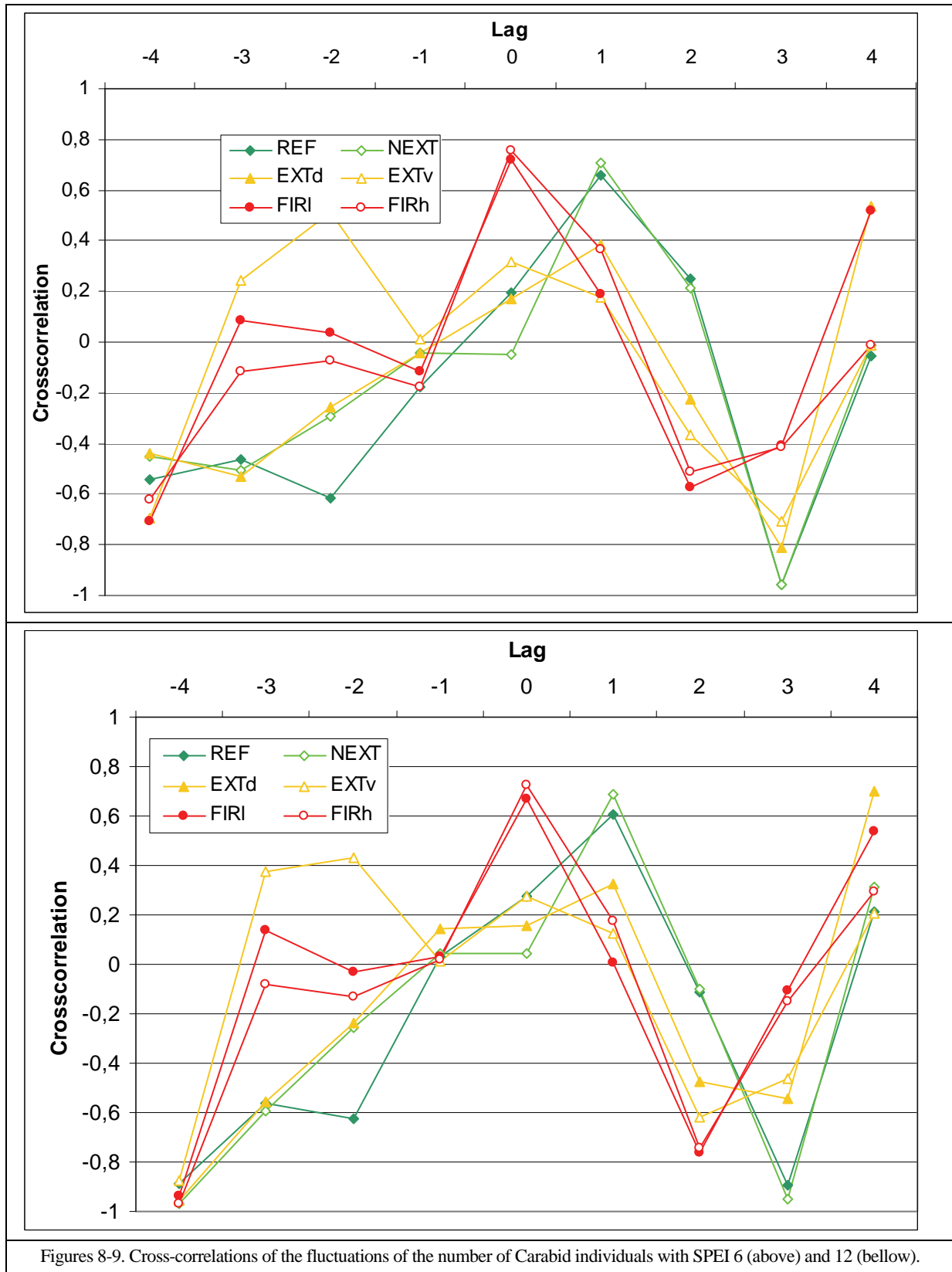
The similar, but slightly moderately phase-shifted course of fluctuation of the climatic factors and of both zoocoenotic parameters in 2007–2012 raises the question of periodicity of climatic fluctuation and their influence on animal communities. The changes of SPEI 6 and 12 (Figs. 10-11) calculated for the meteorological station Tatranská Lomnica for 1961–2014 show that fluctuations of these indices 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. These fluctuations are best explained by SPEI 6, while SPEI 12 covers them up. Therefore it can be concluded that the fluctuations of both zoocoenotic parameters of the Carabid assemblages probably repeat with similar regularity during much longer time.

At the same time the observed maximum and minimal values of these two parameters probably represent limits of variability of the Carabid assemblages in similar mountain ecosystems (Figs. 1-3). However, from the viewpoint of zoocoenological classification the Carabid assemblages the found values can be indicative just for the assemblages in the 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).



Figures 6-7. Cross-correlations of the fluctuations of the number of Carabid species with SPEI 6 (above) and 12 (bellow).

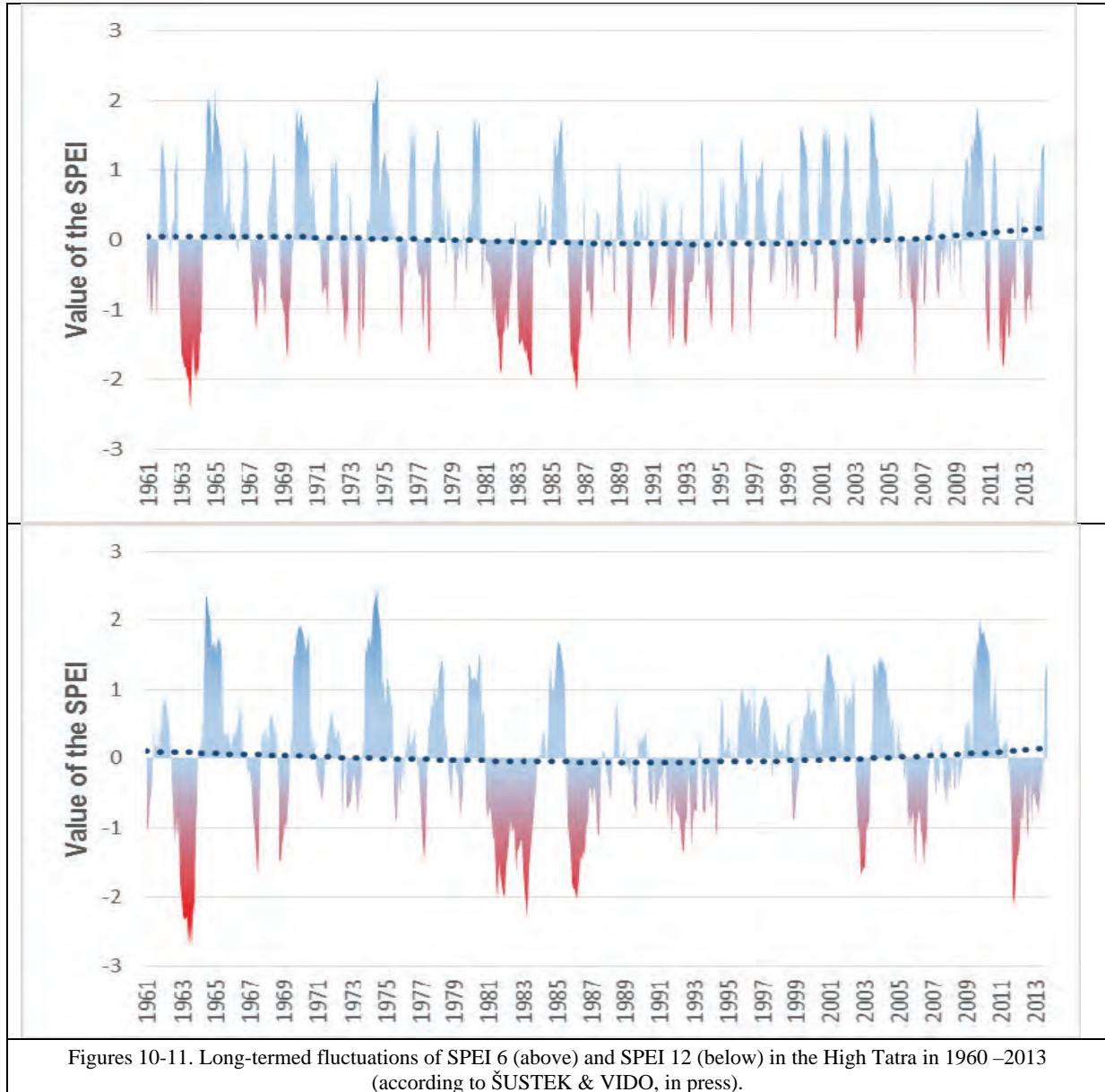
The phase shift (lag) of the fluctuations in Carabid assemblages after the climatic fluctuations has two different, but closely connected reasons. The shortage of humidity reduces the activity of all edaphic organisms. Thus, it simultaneously reduces the momentary activity of adult Carabids and their chance to mate and lay eggs, as well as the 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.



Figures 8-9. Cross-correlations of the fluctuations of the number of Carabid individuals with SPEI 6 (above) and 12 (bellow).

The spring breeders mate and lay eggs in spring, and the new generation hibernates as pupae or adults, while the summer breeders mate and lay eggs in late summer or early autumn, and the new generation hibernates as larvae (THIELE, 1975). There also exists a plastic reproduction type, but it is represented just by very few species, like *Pterostichus melanarius* Illiger, 1798. 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

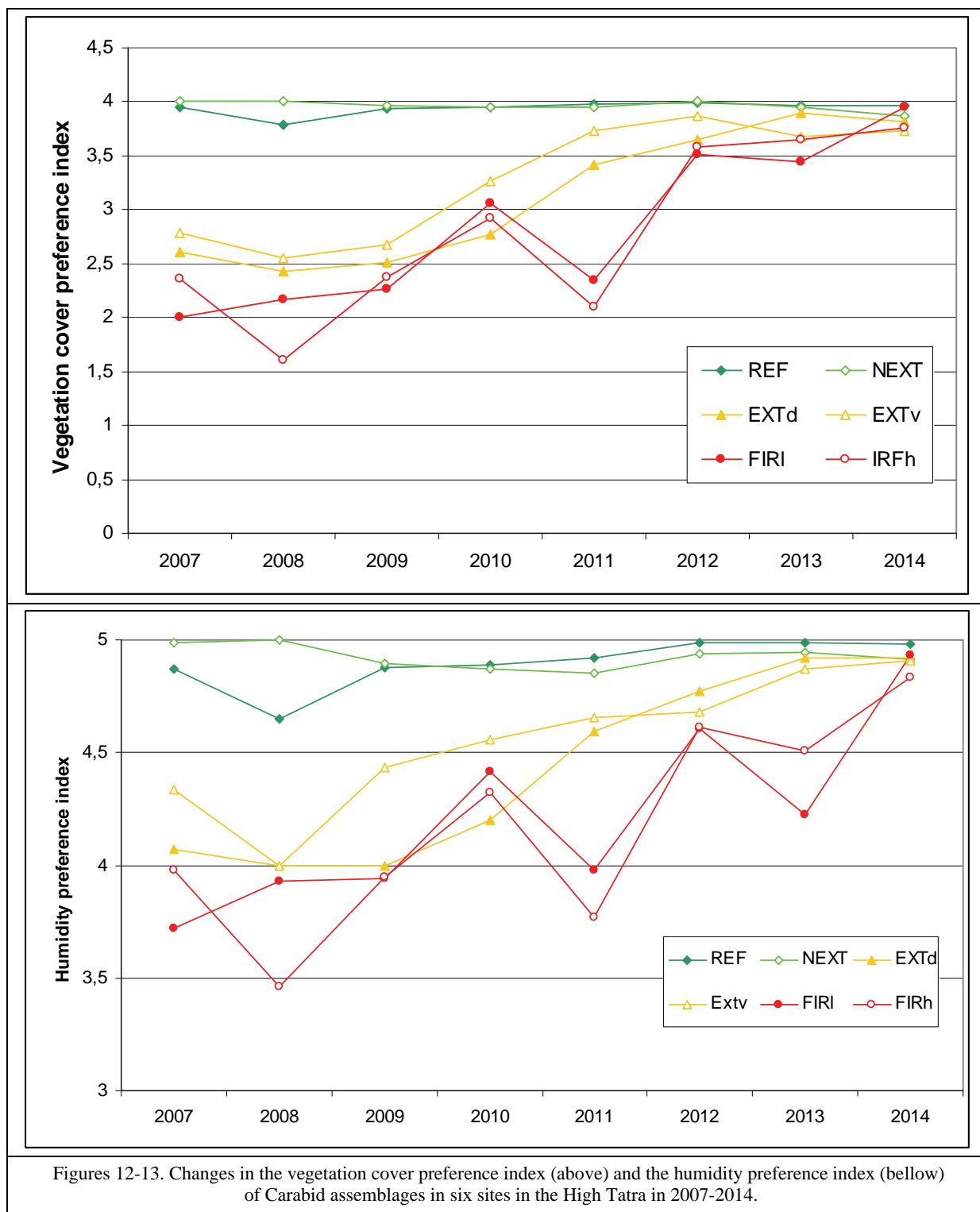
to effectively use the short growing season that can be even insufficient for the complete development of one generation. Thus, the development of some species can be prolonged on two growing seasons and generations can overlap. Under such circumstances, the extreme drought in a growing season or even in a short period can essentially inhibit the development of the next generation, but with an impact visible as late as in the following growing season, if the beetles are monitored using pitfall traps. From this point of view the extreme fluctuations of SPEI 6 like in summer 2012 can have a great predictive value. On the 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.



Figures 10-11. Long-termed fluctuations of SPEI 6 (above) and SPEI 12 (below) in the High Tatra in 1960 –2013 (according to ŠUSTEK & VIDO, in press).

Non periodic changes in the assemblages

The extreme drought or increased humidity doubtlessly influences the course of restoration of the assemblages in the damaged area, but with their momentary composition and their direction of their succession (restoration) it has just a free relationship. This process has a non-periodic character. It is clearly shown by the representation of species requiring permanent shadowing (Fig. 12) and higher humidity (Fig. 13), as well as by the increase of the proportion of non-flying species representing the more tolerant forest species, in particular *Carabus violaceus*, *Carabus glabratus* and, to certain degree also *Molops piceus* (Tab. 5). In spite of the incidence of the periodic, climatically conditioned changes in the number of species and individuals and in the cumulative biomass (Figs. 1-3), the representation of these three groups of species increased as 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 *in situ* (NEXT Jamy). In all three cases the growth has a sigmoid character and the values asymptotically approximate to the level in the intact plot, irrespectively of the two periods of extreme drought, which could only temporarily inhibit the restoration of the damaged ecosystems by reducing the number of individuals and species.



The parameters of the vertical distribution of individual species (Figs. 15-19) changed in the period 2007-2014 as it follows. The average lower limit (Fig. 15) continuously declined in all the study plots from the range of about 1.8-3.2 to values below 2. Hence there increased the representation of species having lower limit of vertical distribution in the oak vegetation tier. The average optimum of the vertical distribution (Fig. 16) was very stable in the intact reference plot (REF in Vyšné Hágy) and in the plot with timber *in situ* (NEXT in Jamy), but in spite of it, it showed a moderate decline from 5.9 in 2007 to 5.6 in 2012-2014. At the same time, the average optimum strongly varied in other damaged plots, with a strong drop in both burned plots in 2007-2009 and a continuous declining trend in EXTv, where it decreased from the initial values of 4.8 in 2007 to 1.6 and 2.7 in 2013 and 2014, respectively. In the case of the communities from the burned plots it was due to the predominance of *Poecilus cupreus*, a typical species of the arable land in lowlands, while in EXTv to spreading and increasing dominance of three species of lowland forests, *Carabus coriaceus*, *Carabus nemoralis* and *Carabus hortensis* (Table 4).

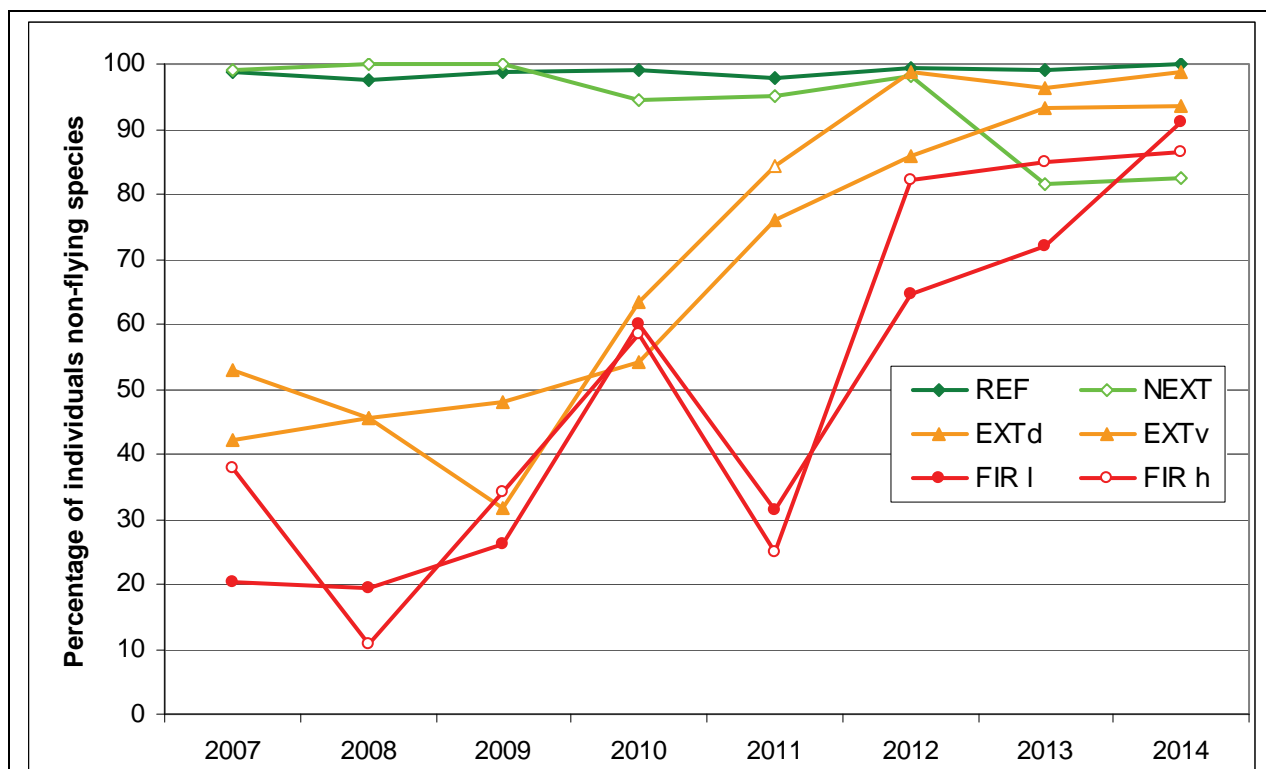


Figure 14. Proportion of non-flying species in Carabid assemblages in six sites in the High Tatra in 2007-2014.

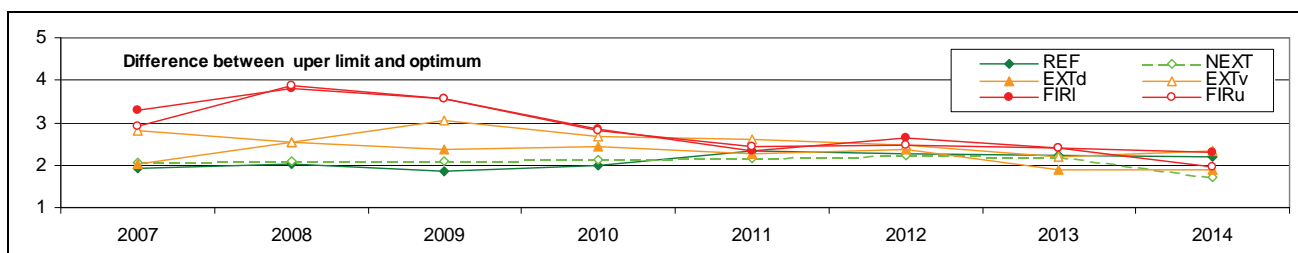
The average upper limit of the upper distribution (Fig. 17) was very stable in all plots. In the intact reference plot (REF in Vyšné Hágy) and in the plot with timber *in situ* (NEXT in Jamy) it moderately fluctuated around the level 7.8, while around 6.5 in the burned lots and moderately increased in these plots in 2014. A visible decline from 7.5 to 6.3 occurred in EXTv (Vodný les) especially due to *Carabus coriaceus*, *Carabus nemoralis* and *Carabus hortensis*. The stability of the values of the average upper limit results from the fact that all recorded species occurred here at their upper limit of distribution amplitude or close to it (Table 2).

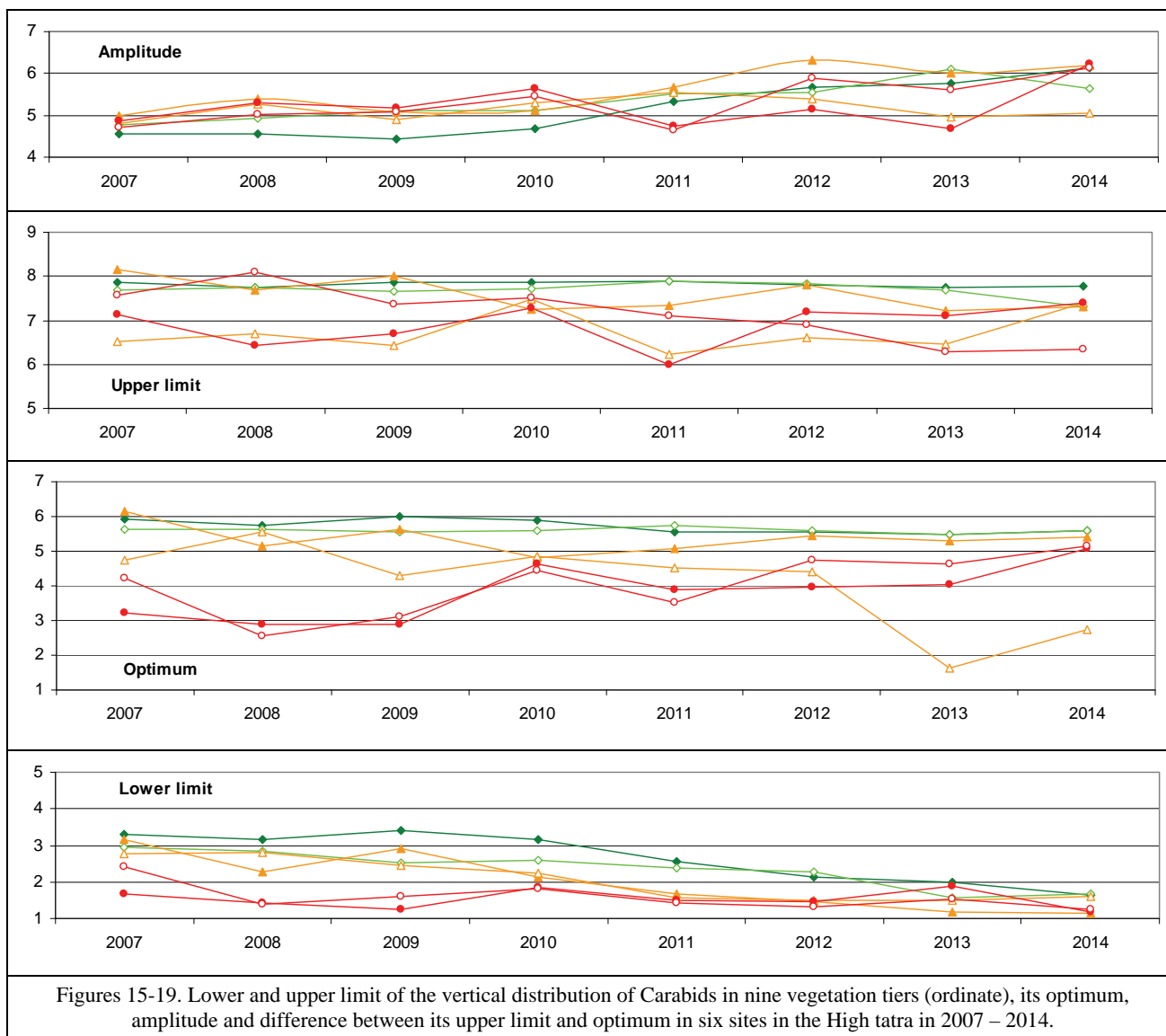
The average amplitude of the vertical distribution (Fig. 18) showed a stable level around the values 4.5 in all plots in the period 2007 – 2009, but later on, there started a slight increasing trend to the values ranging from 5.1 to 6.2 in 2014. This increase represents other expression of the increasing representation of the species having their lower limit of vertical distribution in the oak vegetation tier (Table 2).

The average difference between the upper limit of the vertical distribution and its optimum also shows stability in all plots, but in the burned plots, the difference decreased from the initial values ranging from 3.8 to 4.0 to the values close to 2.0. This is also just another expression of the strong changes in the representation of *Poecilus cupreus*, as shown above in the case of average optimum.

In general, the shift in the representation of species with different amplitude of vertical distribution is best shown by the lower limit (Fig. 15) and width of the distribution amplitude (Fig. 18).

The described changes might indicate a trend to warming in all, intact and damaged plots. However, in the studied period, it is in contradiction to the average annual temperatures, which culminated in 2007, then declined to 2010 and again culminated in 2012 and then slightly decreased. At the same time, there was a culmination of humidity in 2010, which was followed by a decline that reached even lower values than in 2007, which caused dramatic changes in the Carabid communities in 2008-2009 (ŠUSTEK & VIDO, 2013). Thus, it seems that the humidity or drought have a stronger effect on the structure of Carabid communities than the temperature. Of course, the species having its optimum in lower vegetation tiers live in drier conditions as shown by ŠKVARENINA et al. (2002).





At the same time, the succession of Carabid assemblages in all damaged plots had a convergent character and reducing differences between the assemblages from the burned plots and other plots with extracted timber. It was allowed by the development of pioneer wooden vegetation and at least local shadowing, as well as by the change of herbage stratum due to mowing the extensive stands of *Chamerion angustifolium* and its gradual replacing by the grassy stands (mostly *Calamagrostis* spp.), as well as the gradual spreading of more tolerant forest Carabid species. This process is illustrated by the ordination of one-year samples from all studied plots (Fig. 21). The first axis represents the gradient of shadowing and damaging degree, respectively. The second axis shows the progress of succession from 2007 to 2014. At the beginning, the communities on the burned plots differed from unburned plots with extracted timber by pulse-like invasions of the species characteristic for arable land, especially by *Poecilus cupres* (later replaced by *Poecilus versicolor* (Sturm 1824), *Pseudophonus rufipes* (De Geer, 1774) and several species of the genus *Amara* (Table 4). At the beginning, there also occurred heliophilous species *Microlestes minutus* (Sturm, 1827) and *Bembidion lampros* (Herbst, 1784) that prefer sites with discontinuous, patchy-like herbage vegetation. At the end of the investigation period, all assemblages from the plot with extracted timber form a common cluster that shifts to the 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 the assemblage in the damaged plots is still a question of remote future. First of all, the stenotopic forest species *Carabus linnei* Dejean, 1826, *C. auronitens* Fabricius, 1792, *Cychrus caraboides* (Linnaeus, 1758), *Leistus piceus* Frölich, 1799, *Pterostichus unctulatus*, *P. burmeisteri*, *P. foveolatus* and *Calathus micropterus* miss or occur there only exceptionally. These species represent the specific component of the assemblages in the intact reference plot. To certain degree, they also survive in the plot with timber *in situ* (Table 4).

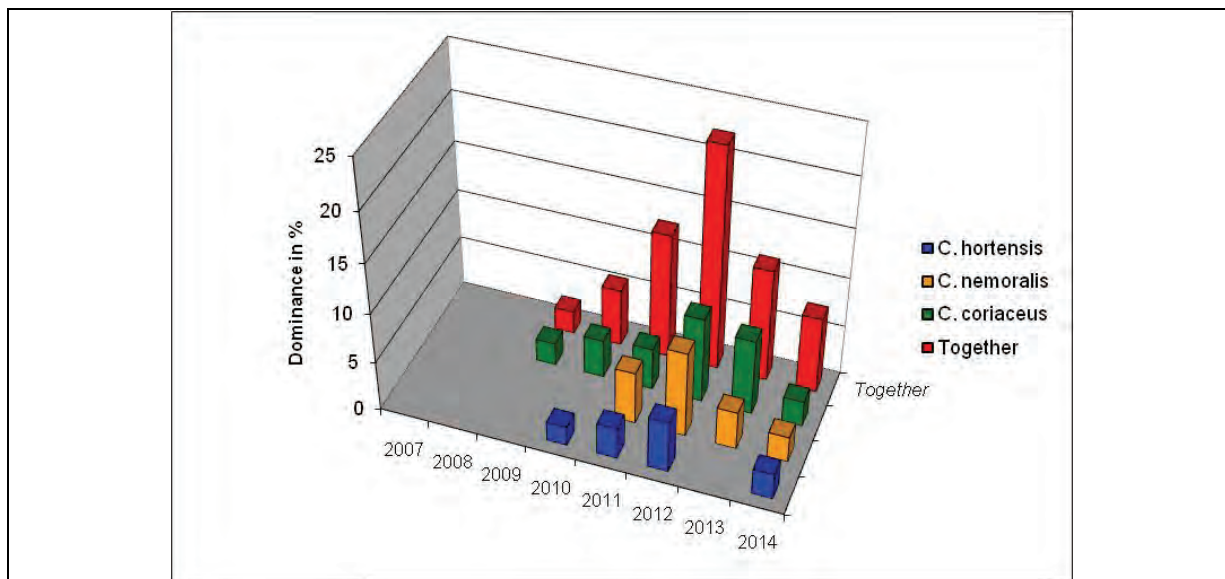


Figure 20. Spreading of the three species of the genus *Carabus* having occurrence optimum in lowlands in the damaged plot EXTv at margin of Nový Smokovec in 2007-2014.

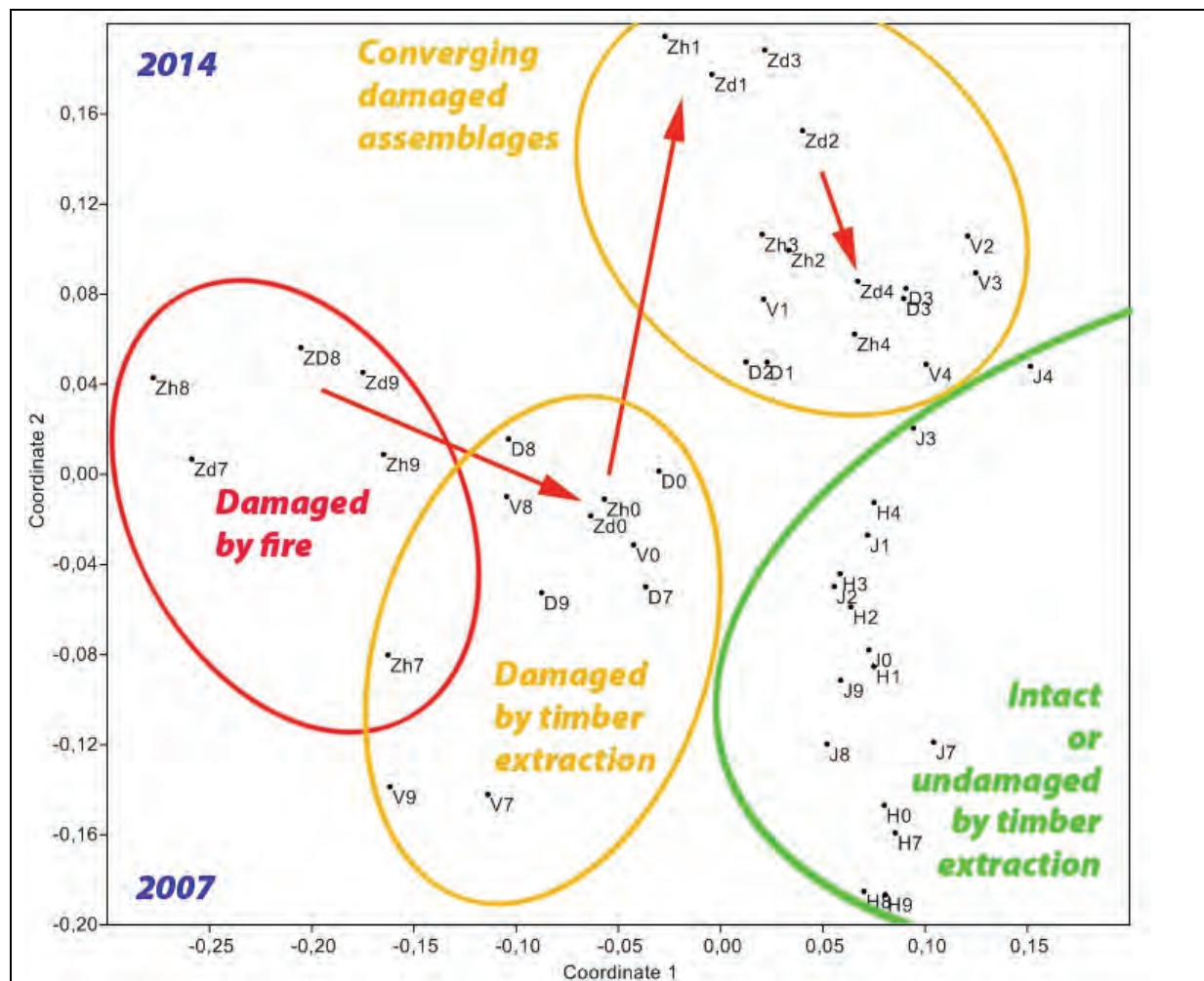


Figure 21. NMS ordination (Horn's index) of one-years samples of Carabids in six sites in the windstorm area in the High Tatra in 2007-2014 (abbreviations H – reference plot in Vyšné Hágy [= REF]. J – plot with fallen timber *in situ* in Jamy [= NEXT]. D – unburned plot with extracted timber near Danielov dom (=EXTd). V – unburned plot with extracted timber Vodný les Zd and Zh – lower and upper burned plot with extracted timber in Tatranské zruby [= FIRl and FIRh). The arrows show the succession direction of the assemblages in the burned plots. The first axis shows the damage degree, the second axis shows the direction of succession from 2007 towards 2014.

In the last years, there also appeared other trends in all assemblages – the penetrating (*Carabus coriaceus*, *Carabus hortensis*, *Carabus nemoralis*) and increasing portion of species having the optimum of distribution in highlands or lower limit of vertical distribution in lowlands (*Carabus violaceus*, *Carabus glabratus*). Thus, the assemblage structure slowly shifts toward the assemblages that are characteristic to lower altitudes. However, the interpretation of the spreading of *Carabus coriaceus*, *Carabus hortensis* and *Carabus nemoralis* is not simple, because it started and furthermore is concentrated in the plot at the western margin of the Nový Smokovec town, where a temperature island can occur and where *Carabus coriaceus* was observed one year before its recording in this plot.

Thus it is obvious, that three processes run simultaneously in the studied communities: (1) periodic changes connected with the short-termed, more or less regularly occurring climatic fluctuations, (2) strong long-termed non-periodic changes connected with the restoration of the more or less original state of the damaged communities and (3) a relatively slight, but probably also long-termed changes resulting from the moderate warming of the climate.

Although the studied localities are situated in a 12 km long strip and the difference of altitude of the lowest and highest plot is of approximately 250 m, the values of SPEI 6 and 12 calculated on the base of the data from a single meteorological station (Tatranská Lomnica), situated at the eastern part of the study area, are sufficiently representative for characterizing the climatic conditions for the existence of Carabid assemblages in the whole studied area.

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