Acta Societatis Botanicorum Poloniae
Journal homepage: pbsociety.org.pl/journals/index.php/asbp
ORIGINAL RESEARCH PAPER Received: 2012.01.04 Accepted: 2012.12.06 Published electronically: 2013.03.29 Acta Soc Bot Pol 82(1):13–24 DOI: 10.5586/asbp.2013.002

The wind and fire disturbance in Central European mountain spruce forests: the regeneration after four years

Monika Budzáková[1]*, Dobromil Galvánek[1], Pavol Littera[2], Jozef Šibík[1,3]
[1] Institute of Botany, Slovak Academy of Science, Dúbravská cesta 9, 845 23 Bratislava, Slovakia
[2] Department of Ecosozology and Physiotactics, Comenius University, Mlynska dolina Ch-2, 842 15 Bratislava, Slovakia
[3] Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colorado 80523, USA

Abstract

A strong windstorm in November 2004 resulted in a huge blown-down spruce forest area in the southern part of the Tatra National Park in the Western Carpathians in Slovakia, Central Europe. The aim of this work is to study the vegetation composition of spruce forest at differently managed sites four years after this disturbance. Four study areas were selected for this purpose: (***i***) an area where the fallen trees were extracted and new seedlings were planted; (***ii***) an area, which was hit by a forest fire after the extraction; (***iii***) an area where no active management was applied; (***iv***) a reference forest unaffected by such disturbance. A total of 100 plots were selected, 25 of each area type. The result of DCA and CCA analyses consistently indicated that after this short period the non-extracted and extracted areas are currently most similar to the reference forest area, while the fire affected area differed. A one-way ANOVA comparing species cover for the different plot sizes indicated some significant differences between the extracted and non-extracted plots. The abundance of certain species commonly occurring in spruce forests, such as *Dyopteris carthusiana* agg., *Vaccinium myrtillus* and *Avenella flexuosa*, correlated well with the non-extracted plots, compared to the extracted plots. Coverage of these species was lowest on burned plots. The lowest Shannon-Wiener's diversity values were recorded in burned plots. This was most likely a consequence of mono-dominant competitive species spread, (mainly *Chamerion angustifolium*) which profited from the altered ecological conditions following the fire. Although some differences were also registered in the Shannon-Wiener diversity index between the remaining research plots, however these were not statistically significant. The most important results of our investigations include the extensive influence of fire disturbance on vegetation. Study revealed that the wind-disturbed area is able to regenerate sufficiently without human intervention.

Keywords: disturbance, diversity, ordination, regeneration, spruce forest

Introduction

Disturbances are a common phenomenon in European temperate and boreal natural forests [1], and they are generally a natural and integral part of forest ecosystems [2]. Natural disturbance factors such as windbreak play a major role in the successional cycle of natural forests [3] and in plant community dynamics [4,5]. In addition, emulation of natural disturbances forms part of management practices in many Canadian and European forests to ensure a healthy level of biodiversity [6,7], since these disturbances can create heterogeneity in plant communities [1,8]. Fires can be especially crucial in nutrient cycling. Here, large amounts of organically bound nutrients are mineralized and enter the soil column [9]. Disturbances also deeply influence plant community diversity [10], and according to the Intermediate Disturbance Hypothesis, the highest diversity can be expected at sites which are neither too rarely nor too frequently disturbed [11,12]. This hypothesis relies on the assumption that one or a few species will dominate the community in the absence of disturbance [13]. Natural disturbances contribute to the selective pressure between organisms [14], and a mosaic of microhabitats with open stands and areas with standing and felled trees can result from small dimensional disturbances. Consequently, there is a more resistant forest and age structure [15].

The wind disturbance in November 2004 triggered a significant change in ecological conditions in a large area of mountain spruce forests in the High Tatras. The aim of this work is to compare the vegetation four years after the calamity in four areas affected by windbreak. It focuses firstly on the influence of fire and wind disturbance on vegetation composition and secondly on the effects of different management techniques on tree regeneration and on the subsequent resurgence of typical spruce forest species. Species diversity in the early successional stage following creation is also discussed herein.

* Corresponding author. Email: monika.budzakova@savba.sk
Handling Editor: Aleksandra Samecka-Cymerman

Material and methods

Study sites

The mountain spruce forest affected by wind destruction is situated in the High Tatras (Fig. 1), in the protected Tatra National Park in northern Slovakia. Strong winds, described as "bora" winds, affected the southern slopes of the mountains below 1300 m a.s.l. [16]. The gusts reached 170 km/h, and affected an area of 12600 ha from villages Podbanské to Tatranská Lomnica [17]. Soils on this land are classified as rocky podzolic cambisols formed from glacial and fluvoglacial sediments, with a soil texture ranging from loam to sandy loam [18]. The mean annual precipitation in this area fluctuates from 800 to 1000 mm dependent on altitude [19] and the mean annual air temperature is 2°C, with highest values registered in July with minima in January [20]. According to the geo-botanical map of Slovakia [21], the potential natural vegetation in this area consists of fir forests, fir-spruce forests (*Abietion albae*, *Vaccinio-Abietenion* p.p.), and spruce forests with *Vaccinium myrtillus* (*Piceion excelsae* p.p.) mainly in the association *Vaccinio myrtilli-Piceetum* Šoltés 1976. The actual vegetation on the study area before the windstorm consisted of planted spruce stands 40–110 years old [17] resulting from human intervention in previous centuries. The main devastation problem emanated from excessive exploitation of previously existing trees and the subsequent planting of a spruce monoculture. This human intervention lasted from the 16th century to the establishment of the national park in 1949. The situation then improved, but the main objective of the Tatra National Park trust was to raise a green forest without dead wood. This was in accordance with knowledge of the best way of managing forests at that time [22].

Sampling variants

Following the wind disturbance in the Tatra National Park in November 2004, part of the windblown area was left for natural development and the predominant part was cleared. In July 2005, a vast portion of this cleared area was affected by large fire which was most likely due to human negligence in attending an open fire. Based on these combined circumstance four sampling variants of approximately 100 hectares were located at altitudes of 950–1100 m a.s.l. All sites were located in areas of equal wind disturbance intensity, with the similar ecological conditions of southern and south-eastern slopes inclined up to 15 degrees. This provided the following four habitat types after the windstorm and fire:

(***i***) A disturbed site near Tatranská Lomnica was left to natural succession without intervention (NEXT – non-extracted area). This uncleared area was very rich in many types of microhabitats where many plant species with different demands could thrive. These included a wind-blown bare-soil area, a shaded and an open area and an area with decaying logs.

(***ii***) A site near the village Tatranské Zruby, where the fallen trees were entirely extracted and new trees were planted. This area was hit by a forest fire in July 2005, which affected approximately 225 ha of its area (FIR – fired area). This was a surface fire, as the root system was not destroyed [23]. Following the fire, this area was subjected to the following treatment; planted samples of *Picea abies*, *Larix decidua*, *Pinus sylvestris* and *Acer pseudoplatanus*, mowing and subsequent biomass removal.

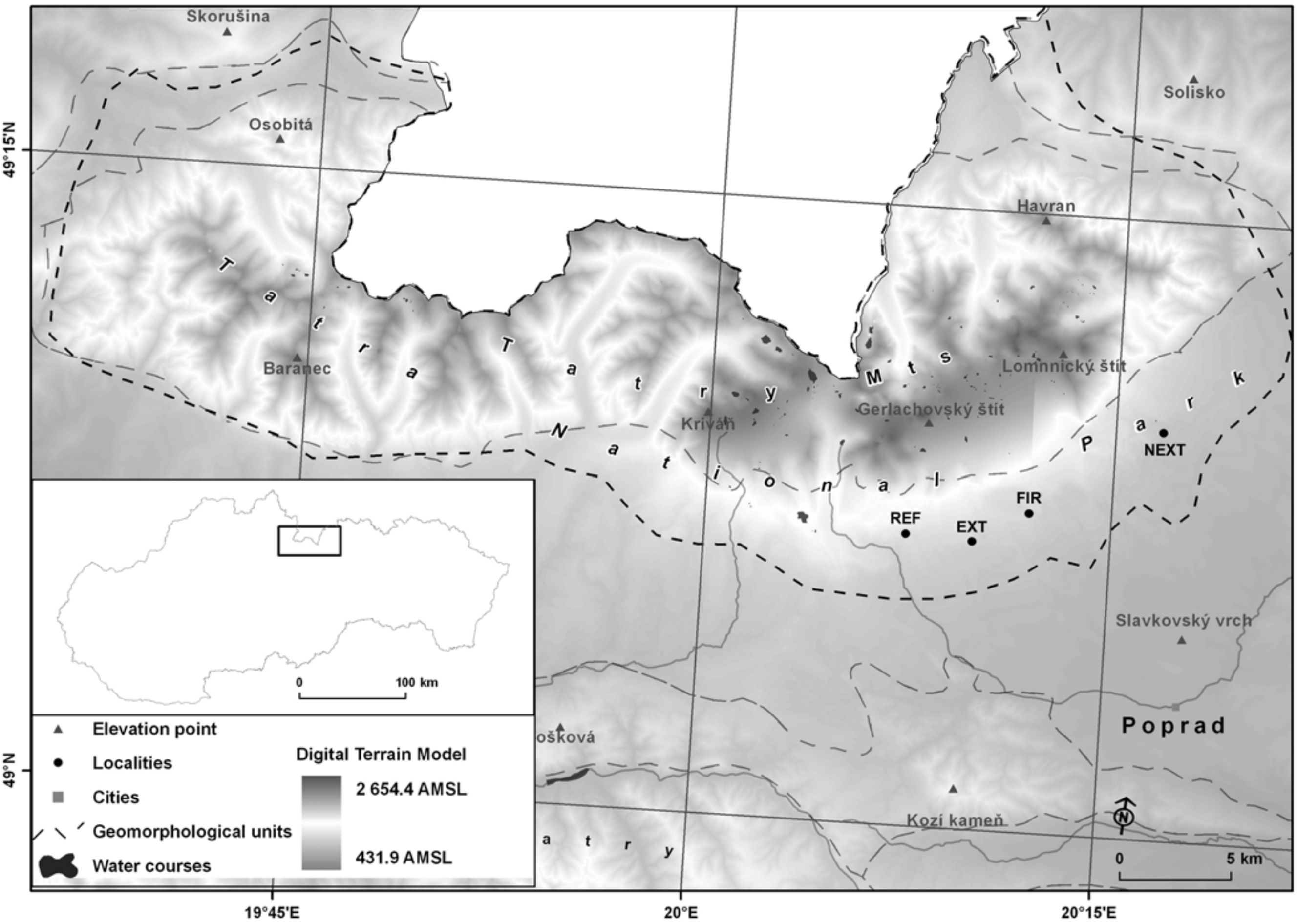

Fig. 1 Location of study area within the Slovak Republic.

(***iii***) A reference site near Vyšné Hágy in an adjacent undisturbed area (REF – reference forest). This area was unaffected by both wind and fire disturbance, and it served for comparative purposes.

(***iv***) A site near Danielov dom, where the fallen trees were entirely extracted and new trees were planted (EXT – extracted area). We have recorded seedlings of *Picea abies*, *Pinus sylvestris* and *Larix decidua* originated from plantation. This area was also cleared by mowing and removal of the biomass.

Vegetation sampling

During the vegetation season in July, August, and September 2008, twenty-five plots with 200 m^2 surface area were chosen at random on each of these four areas, and data was collected. All plots were then sampled according to the 7-degree Braun-Blanquet Cover Abundance Scale [24,25]. The presence of seedlings was recorded as well. The syntaxa nomenclature was as in Jarolímek and Šibík [26], and plant nomenclature generally following the checklist in Marhold and Hindák [27].

Data analysis

The main gradients in species composition were analyzed by detrended correspondence analysis (DCA) in the CANOCO 4.5 program package [28]. Canonical correspondence analysis (CCA) was used to elucidate the relationships between biological assemblages of species and their environment. Two plots were determined by DCA analysis as outliers according to the first analysis and these were subsequently excluded from the data set. The remaining 98-sample dataset was analyzed by unimodal methods (DCA and CCA) because the length of the gradient exceeded 3 SD units [29]. Data on species coverage was transformed from the scale used for sampling into percentage values using the median values of the scale intervals. The percentage values were then logarithmically transformed [$y' = \log(A \times y + C)$; $A = 1.0$, $C = 1.0$] to emphasize the role of less frequent taxon in the dataset and to weaken the role of the dominant species. Ellenberg indicator values were used in DCA as supplementary data for the interpretation of ecological differences between the variants [30]. Ellenberg indicator values and Shannon-Wiener's index of diversity [31,32] were calculated in the JUICE 6 program [33]. CCA was conducted to analyze relationships of the plant communities with environmental variables. These environmental variables included: moss layer cover, deadwood cover, type of management (NEXT, FIR, REF, EXT), information on mowing in the area and the occurrence of native and planted seedlings. Supplementary data included in this analysis comprised total cover and also the cover of tree, shrub and herb layers. Since ecological factors such as slope, altitude and aspect were similar in all plots, these factors exerted no direct influence on the distribution of the samples in the ordination diagram, and they were therefore eliminated from analysis. Statistica 8.0 (http://www.statsoft.com) was used for correlation analyses and Box and Whisker plot construction. The Box and Whisker Plots were used for comparison of interesting variables in each management type (NEXT, FIR, REF, EXT). Box and Whisker plots were constructed for environmental variables such as Shannon-Wiener's index of diversity, species' number, average cover of particular vegetation layers and the cover values for the most abundant and important species. Tukey's HSD post-hoc test was used to determine the differences between study sites at the significance level of $\alpha = 0.05$. The Spearman rank correlation test (non-parametric measure of correlation) was used to determine the correlation between environmental variables. Finally, the synoptic table was generated in the JUICE 6 program [33], and each taxon was characterized by the percentage frequency and index of median cover. Species exhibiting greater than 20% frequency are marked in bold type.

Results

DCA ordination

The results of DCA analysis of the study plots and species are shown in Fig. 2. The plots on the NEXT and EXT management

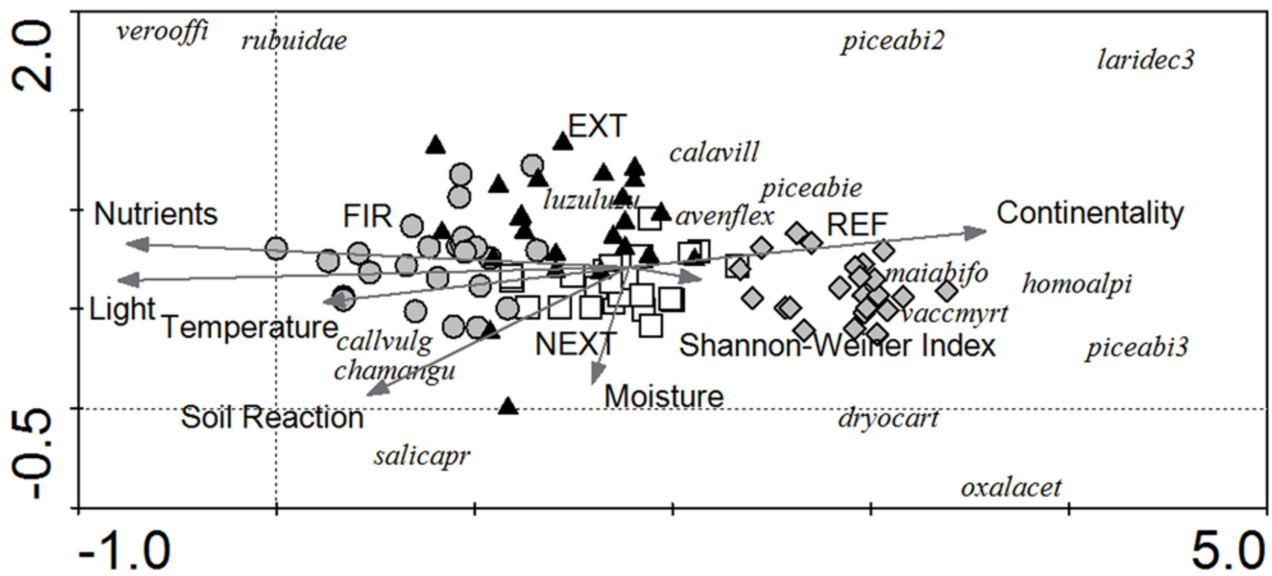

Fig. 2 Detrended correspondence analysis (DCA), ordination diagram of the species, supplementary variables and study plots (Species Weight Range from 5%). EXT – extracted plots; FIR – fired plots; NEXT – non-extracted plots; REF – reference plots.

areas have the same floristic variability as the reference plot. According to the first axis, their distance is very similar to the REF. The main differences between EXT and NEXT exist in the distribution of the plots on the ordination diagram. In the EXT area, the plots are more scattered compared to the NEXT and REF. This is most likely due to the similar and more stable plant composition on the NEXT and REF. The first axis of the highest variability refers mainly to the clear differences between the FIR and REF plots, which are most distant from each other. Based on the distributions of the Ellenberg indicator values, the DCA axis 1 shows significant correlations with habitat attributes. Species typical for the association *Vaccinio myrtilli-Piceetum*, such as *Picea abies*, *Vaccinium myrtillus*, *Maianthemum bifolium*, *Dryopteris carthusiana* agg. and *Oxalis acetosella* are concentrated close to the right side of the ordination diagram, while species connected with burning, such as *Calluna vulgaris* and the forest clearing vegetation with *Chamerion angustifolium*, such as *Salix caprea* and *Rubus idaeus* occur on the left side. This assertion is supported by Ellenberg indicator values of light and temperature, which negatively correlate with this axis. The afore-mentioned heliophilous species recorded the highest abundance on FIR plots. The amount of nutrients and the soil reaction were also significant factors, with both having a negative correlation with the first axis. Species with higher demands for nutrients and soil reaction are placed on the left side of the ordination diagram. Axis 2 explains only a small proportion of variability compared to axis 1. The eigenvalues of axes 1 and 2 are 0.432 and 0.098, respectively. The cumulative percentage variance of species data for axis 1 is 20.4%, and for 2 is 25%.

CCA ordination

The results of CCA for species and environmental and supplementary variables are presented in Fig. 3. Discrimination here can be shown in a similar manner to that utilized in the DCA diagram. The first axis is positively correlated with samples of REF, and also with the presence of species

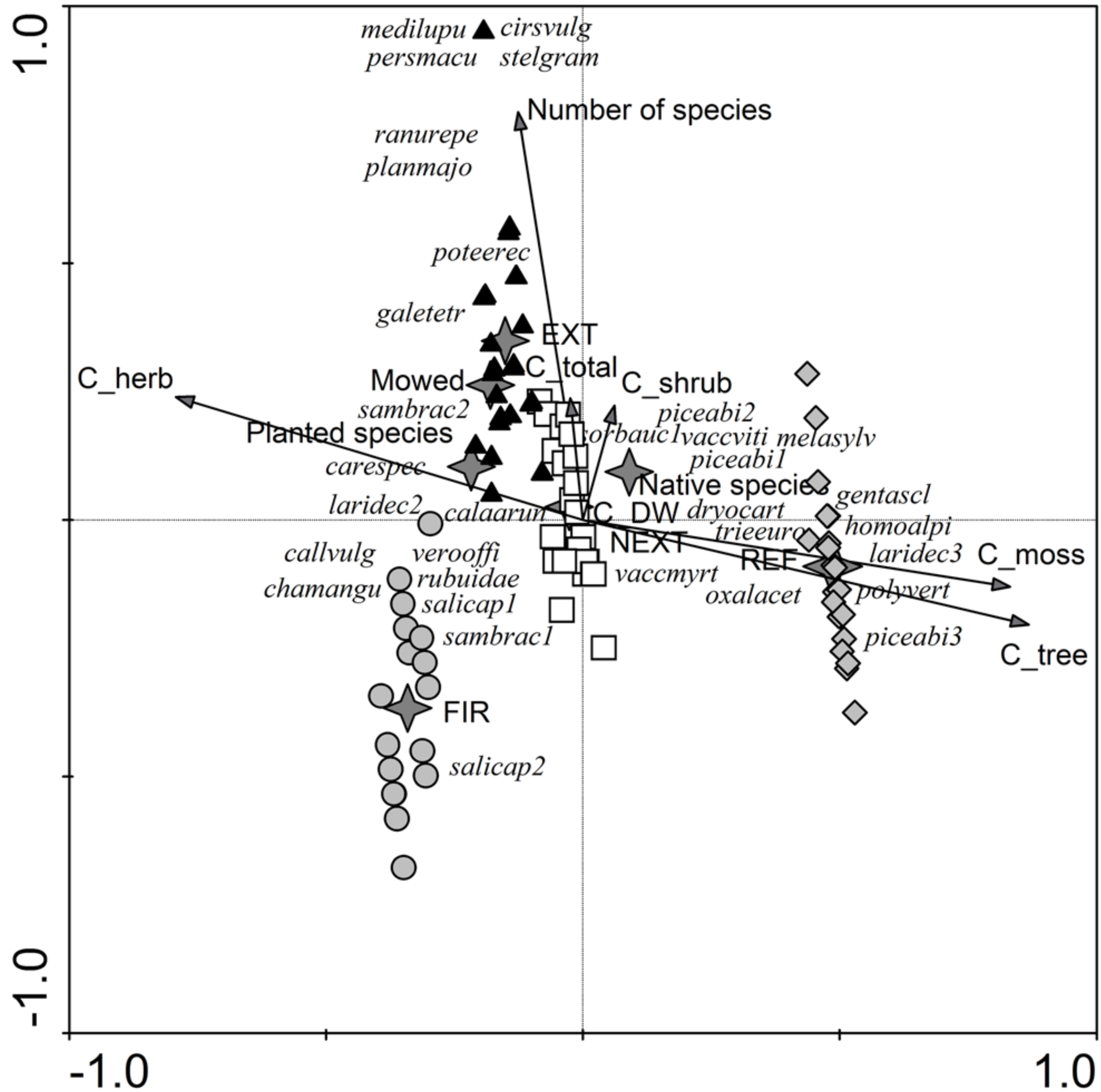

Fig. 3 Canonical correspondence analysis (CCA), ordination diagram of the species, supplementary variables, environmental variables and study plots (species fit range from 10%). C DW – cover of dead wood; C herb – cover of herb layer; C moss – cover of moss layer; C shrub – cover of shrub layer; C total – total cover; C tree – cover of tree layer; EXT – extracted plots; FIR – fired plots; Mowed – mowed plots; Native – occurrence of native seedlings; NEXT – non-extracted plots; Planted – occurrence of planted seedlings; REF – reference plots.

typical in Central-European mountain spruce forests, such as *Dryopteris carthusiana* agg., *Gentiana asclepiadea*, *Oxalis acetosella*, *Picea abies* and *Vaccinium myrtillus*. Open areas (FIR, EXT and NEXT) containing the dominant species *Chamerion angustifolium*, *Calamagrostis arundinacea* and other species of forest clearings, including *Rubus idaeus* and *Salix caprea*, appear on the left side of the CCA diagram. The FIR plots are most distant from the reference forest, as occurred in the DCA, while the logged plots (NEXT and EXT) are quite close to each other. The main difference between these plots is in the management treatment. EXT plots correlate with seedling planting and biomass mowing. The NEXT plots underwent no intervention management so the species regenerated naturally, with deadwood cover dominating this site. According to the CCA ordination diagram, axis 2 is related to species richness. The number of species positively correlating with this axis is at the top of the diagram, and here the most extracted and non-extracted samples occur. This suggests that the highest diversity occurred in these plots. The eigenvalues of axis 1 and 2 were 0.339 and 0.098, respectively. The cumulative percentage variance of species data of axes 1 and 2 is 48.4 % and 62.3 %, respectively.

The results of one-way ANOVA

The number of species and the values of Shannon-Wiener's index are highest for the NEXT plots, followed by EXT, REF and FIR (Fig. 4a–b). According to the results of Tukey's HSD post-hoc test, the differences in the number of species and

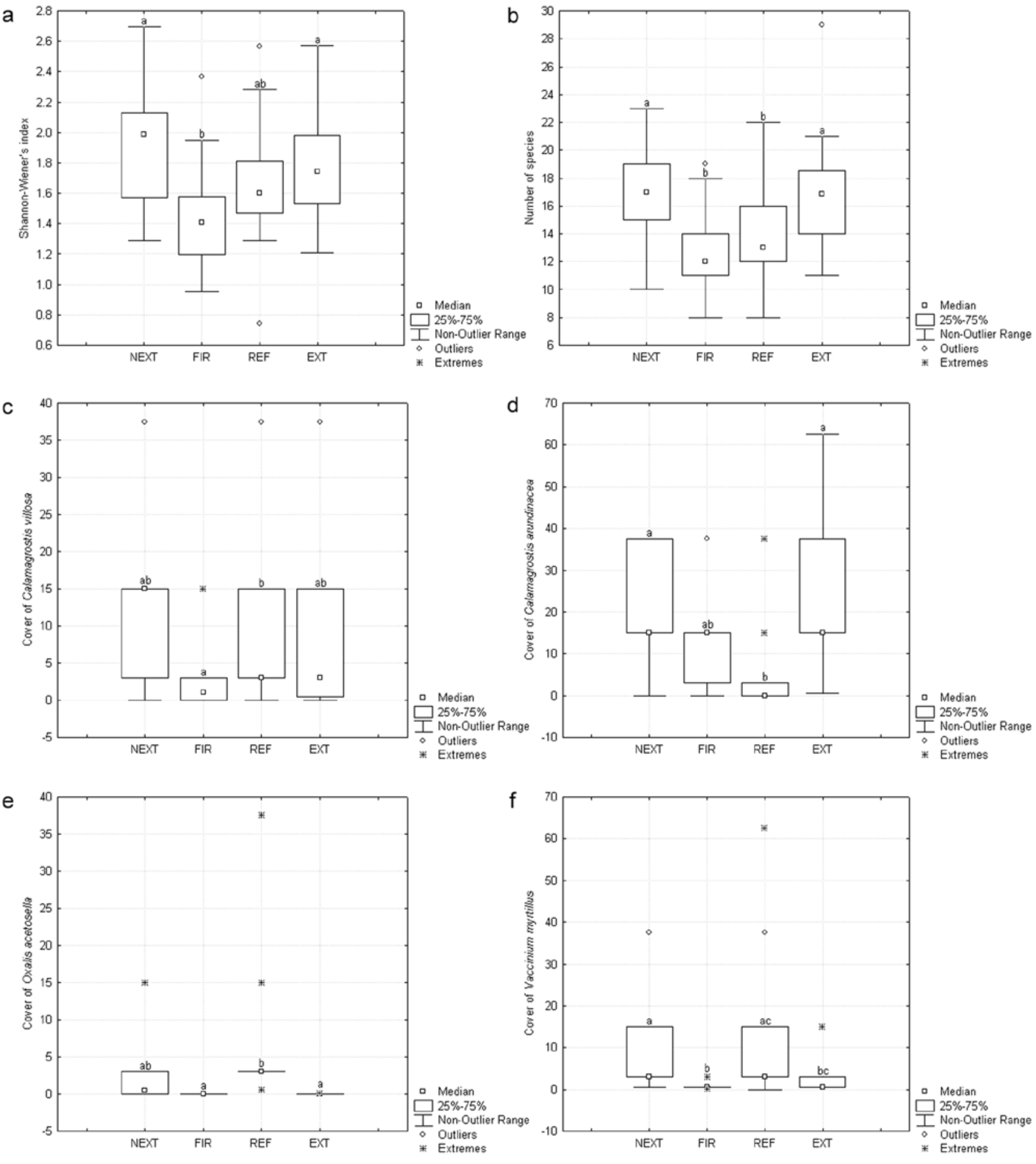

Fig. 4 Box and Whisker plots representing: Shannon-Wiener's index of diversity for clusters (**a**), number of species (**b**), cover of *Calamagrostis villosa* (**c**), cover of *Calamagrostis arundinacea* (**d**), cover of *Oxalis acetosella* (**e**), cover of *Vaccinium myrtillus* (**f**). Labels **a**–**c** indicate homogenous groups according to post-hoc comparisons using ANOVA (Tukey test, $P < 0.05$).

Shannon-Wiener's index values are statistically significant at $\alpha = 0.05$ only between the FIR and NEXT plots and between the FIR and EXT plots. Fig. 3c–f and Fig. 4a–f show the covers of dominant and interesting species in each management type. Based on these results, it can be concluded that species typical for Central-European mountain spruce forests, such as *Oxalis acetosella* (Fig. 4e), *Vaccinium myrtillus* (Fig. 4f) and *Dryopteris carthusiana* agg. (Fig. 5a) mainly dominated in the reference forest (REF) and in the non-extracted plots (NEXT). The coverage of *Calamagrostis villosa* and *Calamagrostis arundinacea* forest grasses increased, particularly after the wind disturbance. The highest abundance of heliophilous and hygrophilous species *Calamagrostis villosa* is recorded on NEXT, followed by REF and EXT, while *Calamagrostis arundinacea* is most abundant on the EXT and NEXT areas. The species most typical for forest clearings, *Rubus idaeus*, *Chamerion angustifolium* and *Salix caprea* (Fig. 5b–d), dominate mostly on the burned areas (FIR). The occurrence of *Calluna vulgaris* is quite interesting, since its abundance significantly increased here after the fire disturbance compared to other areas (Fig. 5f). The coverage of individual layers is shown in Fig. 6a–f. One quite notable result concerns the moss and deadwood layer covers which were significantly

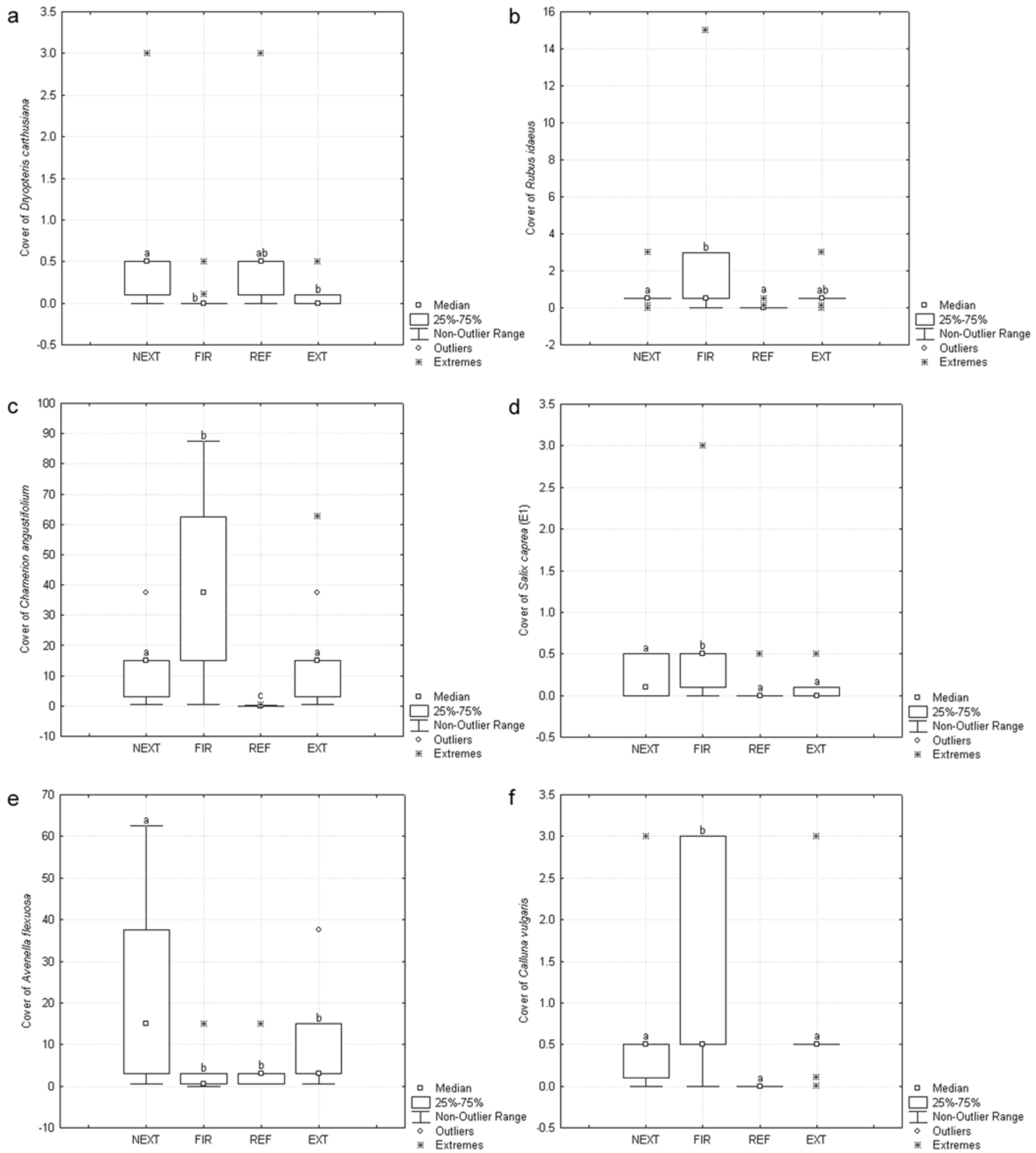

Fig. 5 Box and Whisker plots representing: cover of *Dryopteris carthusiana* agg. (**a**), cover of *Rubus idaeus* (**b**), cover of *Chamerion angustifolium* (**c**), cover of *Salix caprea* (E1; **d**), cover of *Avenella flexuosa* (**e**), cover of *Calluna vulgaris* (**f**). Labels **a**–**c** indicate homogenous groups according to post-hoc comparisons using ANOVA (Tukey test, $P < 0.05$).

higher on uncleared areas compared to other disturbed areas (Fig. 5e–f). The percentage frequency and median covers of the other species are shown in Tab. 1. The occurrence of Norway spruce (*Picea abies*) in the herb and shrub layer in REF, EXT and NEXT plots is similar. Differences between these types emanate from the origin of the seedlings, where most seedlings in the EXT plots come from planted trees while all trees in the NEXT plots have natural origin. Differences are mainly found in tree layer coverage, which is significantly higher in the REF plots. It is possible to describe the occurrence of *Larix decidua* species in the same manner. This species is the most abundant in the reference forest tree layer. Abundant species in the herb layer occur only in EXT and FIR, and this was achieved only by their planting. Sorbus aucuparia of the *Vaccinio-Piceetea* class is an interesting diagnostic tree. While this species is most abundant on the NEXT, EXT and REF plots, negligible cover is recorded on the fired plots. While planted species including *Pinus sylvestris* and *Acer pseudoplatanus* are noted on the FIR and EXT plots, a special tree composition is found on the burned plots, where species such as *Salix caprea*, *Sambucus racemosa* and *Populus tremula* commonly predominate together with *Larix decidua* and *Pinus sylvestris* conifers.

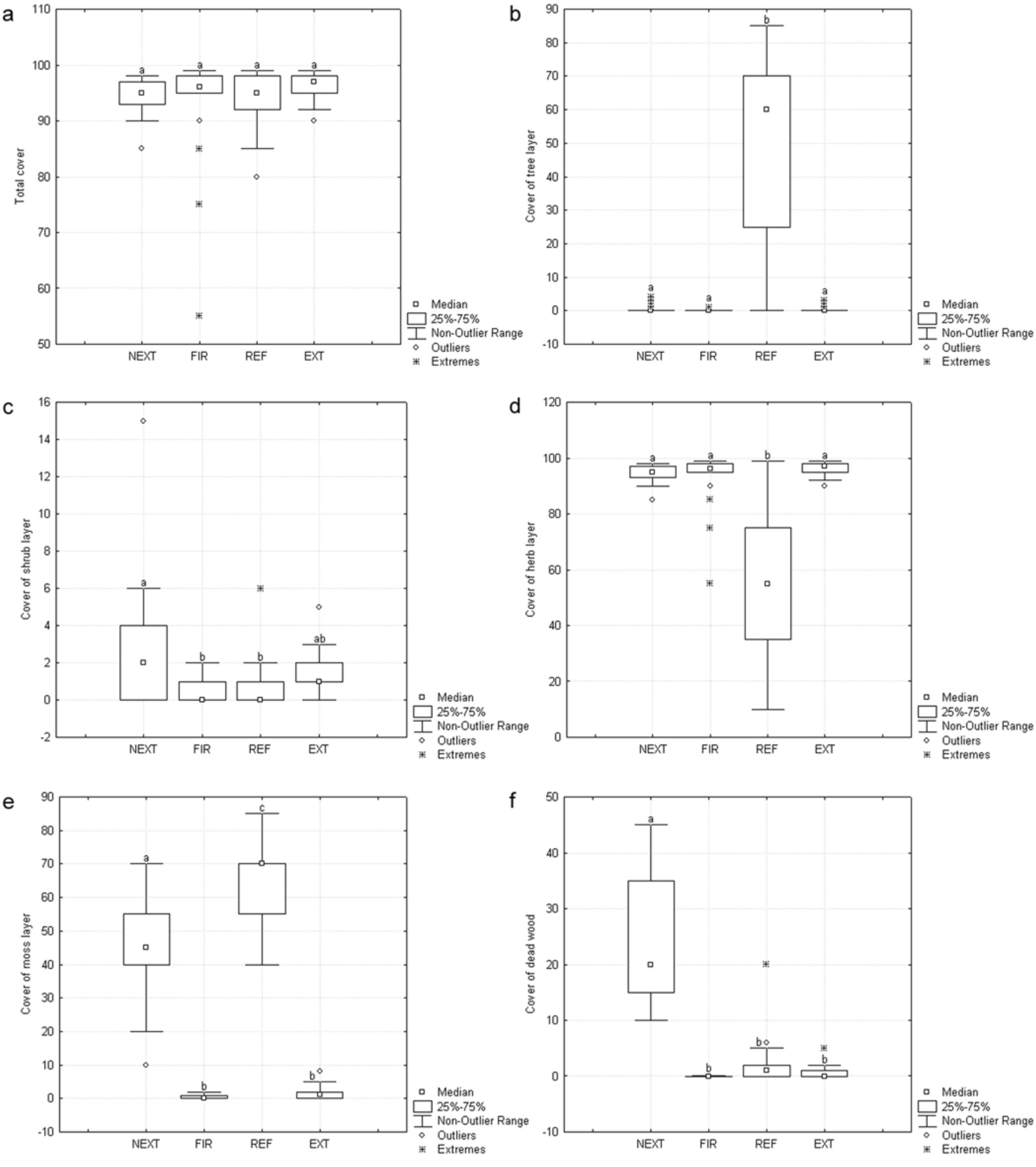

Fig. 6 Box and Whisker plots representing: total cover (**a**), cover of tree layer (**b**), cover of shrub layer (**c**), cover of herb layer (**d**), cover of moss layer (**e**), cover of dead wood (**f**). Labels **a**–**c** indicate homogenous groups according to post-hoc comparisons using ANOVA (Tukey test, $P < 0.05$).

Spearman's correlation coefficient between environmental factors

Correlation statistics, using the same environmental factors as in the ordination analyses, are presented in Tab. 2. Observations concerning these data are summarized here. The correlation matrix allows us to describe non-extracted plots as areas with a large moss layer and deadwood cover. These plots are covered entirely by naturally regenerated trees. The FIR area lacks moss and deadwood and recorded the lowest values of naturally regenerated seedlings and shrub layer cover. The FIR plots negatively correlated with diversity with significantly lower values than the NEXT, EXT and REF. Similar to the non-extracted area, the reference forest negatively correlates with human intervention from tree planting, mowing and biomass removal. The largest coverage of the moss and tree layers occurred on REF plots, while the extracted plots negatively correlated with moss layer cover. A statistically significant positive correlation was recorded between extracted plots, mowing biomass and new seedling plantation.

Discussion

Natural regeneration of the trees

Our study demonstrates the highest abundance of naturally regenerated spruce seedlings on uncleared areas, which may be a result of increased microhabitats, whereas according to Ilisson et al. [34] *Picea abies* do not prefer any particular microsite. One of the key factors responsible for the lower regeneration of spruce in the extracted plots is the absence of dead wood, since it decreases the pressure of competitive species, for which decomposing material is not an optimal substrate [1,35–37]. The importance of dead wood in forest regeneration increases at higher altitudes [38], and it also maintains the necessary microclimate and protects the seedlings from intensive sunlight. According to Rusek and Brůhová [39], the extraction of wood biomass negatively influences the structure of epigeic fauna which is an obligatory function of natural spruce forests. Bače et al, [40] reported that the highest number of spruce seedlings is found on lying dead wood, followed by seedlings at the foot of standing trees and then those on the ground surface. The lowest coverage of spruce was recorded on FIR plots. The reason for this may be tussock-forming grasses such as *Calamagrostis villosa* and *Calamagrostis arundinacea*, which regenerate well after fire, and their dense roots and an abundance of *Chamerion angustifolia* decrease the survival ratio of spruce seedlings [41,42].

Sorbus aucuparia is a diagnostic species in spruce forests [26]. This is mainly found in sites with increased light, and it also thrives after disturbances [21]. Its regeneration is clearly observed on EXT and NEXT plots, but poorly on the FIR areas. The regeneration of *Sorbus aucuparia* could also be affected by competition with herbal vegetation [43], or by the presence of dead wood which, according to Lonsdale et al. [44], positively influences this species.

While species such as *Salix aurita*, *Betula pubescens* and *Populus tremula* were the most abundant on the extracted sites according to Jonášová and Prach [45], our study shows that *Betula pubescens* is most abundant on the non-extracted plots. A possible explanation for this is the affinity of this species to damp microhabitats, such as on bare soil under uprooted trees. According to Ulanova [1], this microhabitat is typical for heliophilous species with small seeds, especially birch,

Tab. 1 Synoptic table of compared vegetation types.

	Type of management	NEXT	FIR	REF	EXT
	Number of relevés	25	25	25	25
EA	*Chamerion angustifolium* (E1)	100^{2}	100^{3}	32^{r}	100^{2}
	Avenella flexuosa (E1)	100^{2}	76^{+}	100^{1}	100^{1}
VP	*Vaccinium myrtillus* (E1)	100^{1}	88^{+}	92^{1}	100^{+}
	Luzula luzuloides (E1)	100^{+}	64^{+}	72^{+}	96^{+}
VP	*Maianthemum bifolium* (E1)	100^{+}	72^{+}	92^{+}	88^{+}
VP	*Calamagrostis arundinacea* (E1)	96^{2}	88^{2}	36^{2}	100^{2}
VP	*Calamagrostis villosa* (E1)	92^{2}	64^{1}	96^{1}	88^{1}
EA,VP	*Rubus idaeus* (E1)	88^{+}	92^{1}	24^{r}	88^{+}
VP	*Picea abies* (E1)	100^{+}	4^{r}	88^{+}	88^{+}
VP	*Dryopteris carthusiana* (E1)	84^{+}	12^{r}	76^{+}	36^{r}
	Betula pendula (E1)	60^{r}	.	.	8^{r}
VP	*Picea abies* (E2)	44^{1}	.	44^{1}	32^{+}
	Senecio sylvaticus (E1)	40^{r}	32^{r}	8^{r}	20^{r}
VP	*Sorbus aucuparia* (E2)	36^{+}	12^{+}	4^{1}	24^{+}
	Urtica dioica (E1)	20^{+}	.	4^{r}	4^{r}
	Calluna vulgaris (E1)	88^{+}	96^{+}	.	88^{+}
EA	*Salix caprea* (E1)	68^{+}	88^{+}	12^{+}	44^{r}
	Sambucus racemosa (E1)	28^{r}	76^{+}	.	40^{+}
	Veronica officinalis (E1)	32^{r}	56^{+}	16^{r}	44^{r}
	Larix decidua (E1)	.	44^{+}	4^{+}	24^{r}
	Salix caprea (E2)	4^{+}	32^{+}	.	.
VP	*Oxalis acetosella* (E1)	64^{+}	.	100^{1}	8^{r}
VP	*Picea abies* (E3)	20^{1}	.	88^{3}	4^{+}
	Homogyne alpina (E1)	28^{+}	.	88^{+}	4^{+}
	Larix decidua (E3)	.	.	64^{1}	8^{1}
VP	*Sorbus aucuparia* (E1)	52^{r}	16^{r}	64^{r}	64^{r}
	Melampyrum sylvaticum (E1)	24^{+}	.	52^{+}	40^{+}
	Trientalis europaea (E1)	20^{+}	4^{r}	48^{+}	.
VP	*Gentiana asclepiadea* (E1)	4^{r}	.	48^{r}	4^{+}
VP	*Polygonatum verticillatum* (E1)	.	.	28^{r}	.
	Vaccinium vitis-idaea (E1)	44^{+}	.	48^{+}	52^{+}
	Carex species (E1)	28^{r}	32^{+}	.	48^{+}
	Sambucus racemosa (E2)	12^{+}	20^{+}	.	48^{+}
	Solidago virgaurea (E1)	4^{r}	20^{r}	8^{r}	36^{+}
VP	*Luzula sylvatica* (E1)	20^{r}	28^{r}	16^{r}	36^{r}
	Galeopsis tetrahit (E1)	.	.	.	28^{r}
	Potentilla erecta (E1)	4^{r}	.	.	24^{r}
	Pinus sylvestris (E1)	4^{+}	20^{r}	.	20^{r}
EA,VP	*Senecio ovatus* (E1)	4^{r}	12^{r}	4^{r}	20^{r}
	Betula pendula (E2)	8^{+}	.	.	8^{+}
	Populus tremula (E2)	8^{+}	4^{+}	.	.
EA	*Galium odoratum* (E1)	8^{r}	.	.	.
	Senecio vulgaris (E1)	4^{+}	.	.	.
	Huperzia selago (E1)	4^{+}	.	.	.
EA,VP	*Dryopteris filix-mas* (E1)	4^{+}	.	4^{r}	.
	Corylus avellana (E1)	4^{r}	.	.	4^{r}
	Hieracium murorum (E1)	4^{r}	4^{r}	.	.
EA	*Scrophularia nodosa(E1)*	4^{r}	.	.	4^{r}
	Juncus conglomeratus (E1)	4^{r}	.	.	.
	Epilobium collinum (E1)	4^{r}	.	.	.
	Populus tremula (E1)	.	16^{r}	.	.
	Taraxacum species (E1)	.	8^{r}	4^{r}	8^{r}
	Hieracium lachenalii (E1)	.	8^{r}	.	.
	Mycelis muralis (E1)	4^{r}	8^{r}	.	.
	Hypochaeris radicata (E1)	.	8^{r}	.	.
	Hieracium murorum (E1)	.	8^{r}	4^{r}	.
	Linaria vulgaris (E1)	.	4^{+}	.	.
	Acer pseudoplatanus (E1)	.	4^{+}	.	.

Tab. 1 *(continued)*

	Type of management	NEXT	FIR	REF	EXT
	Number of relevés	25	25	25	25
	Trifolium montanum (E1)	.	4^{r}	.	.
	Tanacetum vulgare (E1)	.	4^{r}	.	.
	Trifolium pratense (E1)	.	4^{r}	.	4^{r}
	Leontodon autumnalis (E1)	.	4^{r}	.	.
VP	*Prenanthes purpurea* (E1)	.	.	8^{r}	.
	Petasites albus (E1)	.	4^{r}	4^{+}	4^{r}
	Dryopteris dilatata (E1)	.	.	4^{r}	.
VP	*Gymnocarpium dryopteris* (E1)	.	.	4^{r}	.
	Asplenium viride (E1)	.	.	4^{r}	.
	Ranunculus repens (E1)	.	.	.	8^{+}
	Epilobium alsinifolium (E1)	4^{+}	4^{r}	.	8^{r}
	Crepis paludosa (E1)	.	4^{r}	.	8^{r}
	Plantago major (E1)	.	.	.	8^{r}
	Campanula patula (E1)	.	.	.	8^{r}
	Hypericum maculatum (E1)	.	.	.	8^{r}
	Pinus sylvestris (E2)	.	.	.	4^{1}
	Cirsium vulgare (E1)	.	.	.	4^{+}
	Acetosa pratensis (E1)	.	.	.	4^{+}
	Cerastium cerastioides (E1)	.	.	.	4^{r}
	Medicago lupulina (E1)	.	.	.	4^{r}
	Persicaria maculosa (E1)	.	.	.	4^{r}
	Stellaria graminea (E1)	.	.	.	4^{r}

Species are sorted according to their percentage values of frequency in the plots with individual management (upper index means median of species cover). The species with frequency higher then 20% are shaded. EA – diagnostic species for class *Epilobitea angustifolii*; VP – diagnostic species for class *Vaccinio-Piceetea*.

willow and alder. Lässig and Močalov [46] recorded species diagnostic of the class *Epilobitea angustifolii Salix caprea*, only on non-extracted sites. Our results are similar, since it was present mainly on NEXT plots and to a much less extent on EXT plots. However, the greatest abundance of *Salix caprea* was found on FIR plots, most likely due to this species' affinity with nitrophilous habitats. Similarly, the nitrophilous *Sambucus racemosa* has the highest coverage here since it most likely profited from nutrients released by the fire. Since the FIR plots were returned to earlier succession stages by the fire, this could be the reason for the lowest coverage of some typical spruce forest species such as *Picea abies* and *Sorbus aucuparia*. The most abundant seedlings in FIR were the non-demanding pioneer tree species of *Populus tremula*, the resistant *Salix caprea* and the nitrophilous *Sambucus racemosa* species.

Changes in herb vegetation

Rubus idaeus and *Chamerion angustifolium* were very frequent on all disturbed plots, and according to reports by Mayer et al. [47], *Rubus idaeus* was the most abundant species following soil disturbance. Disturbed soil provides ideal conditions for germination of its seeds and also for the vegetative spread of this shade-intolerant species. The growth of *Rubus idaeus* is stimulated by nitrates [48], and this is most likely why this species has the highest coverage on FIR plots. *Chamerion angustifolium* mainly occupies humus and moisture patches with lower nitrogen content. It colonizes new sites due to the production of a very high amount of seeds with good spreading capability [42]. This nitrophilous species has the highest abundance on sites affected by fire [49]. There are also other species such as *Calluna vulgaris* and *Veronica officinalis* which penetrate calamity sites, and these are particularly noted on the FIR site here. The presence of *Veronica officinalis* on sites disturbed by fire was also noted by Marozas et al. [49], who recorded this species occurrence only on burned areas rather than on control plots. However, some forest species including *Gentiana asclepiadea*, *Oxalis acetosella*, *Dryopteris filix-mas* and *Polygonatum verticillatum* were completely absent here. The highest abundance of some forest species and species typical in nutrient-poor sites such as *Oxalis acetosella*, *Homogyne alpina*, and *Trientalis europaea* was registered on the control plots (REF), with their next highest abundance on non-extracted plots. According to studies by Hannerz and Hånell [50], species such as *Oxalis acetosella*, *Maianthemum bifolium* and *Vaccinium myrtillus* decrease dramatically in coverage in clear-cut areas. In our study, although the *Maianthemum bifolium* and *Vaccinium myrtillus* species diagnostic of the *Vaccinio-Piceetea* class mainly dominated on the non-extracted areas, they also occurred on all management types including the burned plots. The dominant grasses *Calamagrostis villosa* and *Calamagrostis arundinacea* are constant species in spruce forest where they spread when the canopy becomes thinner following disturbance. The abundance of these grasses increases in proportion to the extent of the disturbance.

Species diversity

The lowest Shannon-Wiener's values were recorded on the burned plots where the forest fire caused significant damage to the vegetation on this area. Significant differences in Shannon-Wiener's diversity values were recorded only in this site, and not on the EXT and NEXT plots which were also disturbed. Moreover, forest fires alter ecological conditions of affected areas [51], and this favors the regeneration of a relatively small number of competitive nitrophilous species. In our work, this was mainly evident in *Chamerion angustifolium*. Investigations by Ilisson et al. [34] showed that the Shannon-Wiener's diversity is highest in areas with moderate damage then followed by heavily damaged areas. The diversity of intermediately disturbed forests is higher than in the final succession stages. According to Widenfalk and Weslien [52], species diversity is significantly higher in the early successional stages than in mature forests. In this study, the highest species diversity is in the affected areas (NEXT and EXT), followed by the control plots (REF). The highest diversity in disturbed areas is most likely caused by the richness of microhabitats arising after the disturbance and forming beneficial conditions for heliophilous, thermophilous and sciophilous species [1].

Conclusions

The most important results of our investigations include the extensive influence of fire disturbance on vegetation. The burned plots registered the greatest differences compared to all other research areas, thus indicating that the fire caused a significant alteration in soil and ecological attributes including nutrient content and pH. In addition, the fire pushed succession to its very initial stages. The burned plots were quite different to the other research plots in many respects including plant composition and species abundance and diversity.

Tab. 2 Spearman's rank correlation coefficient.

C tree	C shrub	C herb	C moss	C DW	NEXT	FIR	REF	EXT	Mowed	Native	Planted	Diversity	
n.s.	n.s.	0.697461	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	C tot
	n.s.	−0.577298	0.576203	n.s.	n.s.	n.s.	0.787301	n.s.	n.s.	n.s.	n.s.	n.s.	C tree
		n.s.	n.s.	n.s.	n.s.	−0.333012	n.s.	n.s.	n.s.	0.351111	n.s.	0.363007	C shrub
			−0.57689	n.s.	n.s.	n.s.	−0.629001	n.s.	0.362999	n.s.	n.s.	n.s.	C herb
				0.447973	0.340291	−0.585316	0.668875	−0.42385	−0.48781	0.599333	−0.567591	n.s.	C moss
					0.798187	−0.518304	n.s.	n.s.	n.s.	0.493753	−0.4432	0.348901	C DW
						−0.333333	−0.333333	−0.333333	−0.351123	0.342224	−0.360041	n.s.	NEXT
							−0.333333	−0.333333	n.s.	−0.921372	0.360041	−0.371696	FIR
								−0.333333	−0.351123	0.342224	−0.360041	n.s.	REF
									0.741261	n.s.	0.360041	n.s.	EXT
										n.s.	0.523735	n.s.	Mowed
											−0.34121	0.421833	Native
												n.s.	Planted

Marked correlations are significant at $P < 0.001$. C DW – cover of dead wood; C herb – cover of herb layer; C moss – cover of moss layer; C shrub – cover of shrub layer; C total – total cover; C tree – cover of tree layer; EXT – extracted plots; FIR – fired plots; Mowed – mowed plots; n.s. – non significant; Native – occurrence of native seedlings; NEXT – non-extracted plots; Planted – occurrence of planted seedlings; REF – reference plots.

Regarding forest management, results from this study didn't provide strong evidence concerning the completely negative effect of forest practices on vegetation regeneration after the wind disturbance, or better said perhaps those effects were not sufficiently highlighted. Despite this deficit, this study unambiguously revealed that the wind-disturbed areas here were able to regenerate perfectly and sufficiently without human intervention, what was evident from of all our analyses. The essential difference between extracted and non-extracted sites was that intensive forest management, such as the extraction of the fallen trees and the planting of new seedlings, requires large investment in both financial expense and working capital, while the uncleared areas obviously do not. On the base of this results, we can conclude, that the natural regeneration is the best management practice in the national parks as the quality of growing forest is natural and healthy. The economic aspect of these results is not negligible, as well.

Acknowledgments

This work was supported by VEGA, grant No. 2/ 0121/ 09 and 2/ 0090/ 12. We are indebted to anonymous reviewers for valuable suggestions for previous version of manuscript. We are also indebted to Dušan Senko for creating the map.

Authors' contributions

The following declarations about authors' contributions to the research have been made: designing the experiments: MB, DG; field research: MB, PL; data analyses: MB, DG, JS; comments on the manuscript: DG, JS, PL; writing the manuscript: MB.

References

1. Ulanova NG. The effects of windthrow on forests at different spatial scales: a review. For Ecol Manage. 2000;135(1–3):155–167. http://dx.doi.org/10.1016/S0378-1127(00)00307-8
2. Dale VH, Joyce LA, McNulty S, Neilson RP. The interplay between climate change, forests, and disturbances. Sci Total Environ. 2000;262(3):201–204. http://dx.doi.org/10.1016/S0048-9697(00)00522-2
3. Bouget C, Duelli P. The effects of windthrow on forest insect communities: a literature review. Biol Conserv. 2004;118(3):281–299. http://dx.doi.org/10.1016/j.biocon.2003.09.009
4. White PS, Jentsch A. The search for generality in studies of disturbance and ecosystems dynamics. Prog Bot. 2001;62:399–449.
5. Frelich LE. Forest dynamics and disturbance regimes. Cambridge: Cambridge University Press; 2002.
6. Chao L. Simulating forest fire regimes in the foothills of the Canadian Rocky Mountains. In: Perera AH, Buse LJ, Weber MG, editors. Emulating natural forest landscape disturbances: concepts and aplications. New York NY: Columbia University Press; 2004. p. 98–111.
7. Wohlgemuth T, Bürgi M, Scheidegger C, Schütz M. Dominance reduction of species through disturbance – a proposed management principle for central European forests. For Ecol Manage. 2002;166(1–3):1–15. http://dx.doi.org/10.1016/S0378-1127(01)00662-4
8. Jonsson BG. Treefall disturbance – a factor structuring vegetation in boreal spruce forests. In: Krahulec F, Agnew ADQ, Agnew S, Willems JH, editors. Spatial processes in plant communities – proceedings of the workshop held in Liblice, 18–22 September 1989. Prague: Academia; 1989. p. 89–98.
9. McClain ME, Bilby RE, Triska FJ. Nutrient cycles and responses to disturbance. In: Naiman RJ, Bilby RE, editors. River ecology and management: lessons from the Pacific Coastal ecoregion. New York NY: Springer; 1998. p. 347–372.
10. Fox JF. Intermediate levels of soil disturbance maximize alpine plant diversity. Nature. 1981;293(5833):564–565. http://dx.doi.org/10.1038/293564a0
11. Grime JP. Competitive exclusion in herbaceous vegetation. Nature. 1973;242(5396):344–347. http://dx.doi.org/10.1038/242344a0
12. Huston MA. A general hypothesis of species diversity. Am Nat. 1979;113(1):81. http://dx.doi.org/10.1086/283366
13. Svensson JR, Lindegarth M, Jonsson PR, Pavia H. Disturbance-diversity models: what do they really predict and how are they tested? Proc Biol Sci B. 2012;279(1736):2163–2170. http://dx.doi.org/10.1098/rspb.2011.2620
14. Begon M, Harper JR, Townsend CR. Ecology: individuals, populations and communities. 3rd ed. Oxford: Blackwell; 1996.
15. Fischer A. Long term vegetation development in Bavarian Mountain Forest ecosystems following natural destruction. Plant Ecol. 1992;103:93–104.
16. Zielonka T, Holeksa J, Fleischer P, Kapusta P. A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. J Veg Sci. 2010;21(1):31–42. http://dx.doi.org/10.1111/j.1654-1103.2009.01121.x
17. Motyčka V. Vítr v Tatrách. Fakty a rozhovory o Vysokých Tatrách. Jaké byly, jsou a budou. Ružomberok: EPOS, s.r.o.; 2005.
18. Mičuda R, Šimonovičová A, Ďuriš M, Šimkovic I, Lancuch P, Hanajík P, et al. Soil-ecological characteristics of localities and evaluation of some soil properties in the High Tatra mountains after the windthrow. Phytopedon. 2005;4:12–18.
19. Faško P, Šťastný P. Priemerné ročné úhrny zrážok. Mapa 1 : 2000000. Atlas krajiny Slovenskej republiky. Bratislava: MŽP SR, SAŽP; 2002.
20. Šťastný P, Nieplová E, Melo M. Priemerná ročná teplota vzduchu. Mapa 1 : 2000000. Atlas krajiny Slovenskej republiky. Bratislava: MŽP SR, SAŽP; 2002.
21. Michalko J, editor. Geobotanická mapa ČSSR. Bratislava: Veda; 1986.
22. Houdek I, Bohuš I. Osudy Tatier. Bratislava: Šport; 1976.
23. Mičuda R, Blahút L. Vplyv požiaru na biomasu bylinnej vrstvy na území Vysokých Tatier. Phytopedon. 2007;6:6–10.
24. Braun-Blanquet J. Pflanzensoziologie, Gründzüge der Vegetationskunde. 3rd ed. Wien: Springer; 1964.
25. Westhoff V, van der Maarel E. The Braun-Blanquet approach. In: Whittaker RH, editor. Classification of plant communities. Hague: Junk; 1978. p. 287–399.
26. Jarolímek I, Šibík J, editors. Diagnostic, constant and dominant species of the higher vegetation units of Slovakia. Bratislava: Veda; 2008.
27. Marhold K, Hindák F, editors. Zoznam nižších a vyšších rastlín Slovenska. Bratislava: Veda; 1998.
28. Ter Braak CJF, Šmilauer P. CANOCO reference manual and CanoDraw for Windows user's guide: software for Canonical Community Ordination (version 4.5). Wageningen: Biometris; 2002.
29. Lepš J, Šmilauer P. Multivariate analysis of ecological data using CANOCO. Cambridge: Cambridge University Press; 2003.
30. Ellenberg H. Zeigerwerte von Pflanzen in Mitteleuropa. Scr Geobot. 1992;18:9–166.
31. Hill MO. Diversity and evenness: a unifying notation and its consequences. Ecology. 1973;54(2):427. http://dx.doi.org/10.2307/1934352
32. Tichý L, Holt J. JUICE, program for management, analysis and classification of ecological data. First part of the program manual. Brno: Vegetation Science Group, Masaryk University; 2006.
33. Tichý L. JUICE, software for vegetation classification. J Veg Sci. 2002;13(3):451–453. http://dx.doi.org/10.1111/j.1654-1103.2002.tb02069.x
34. Ilisson T, Köster K, Vodde F, Jõgiste K. Regeneration development 4–5 years after a storm in Norway spruce dominated forests, Estonia. For Ecol Manage. 2007;250(1–2):17–24. http://dx.doi.org/10.1016/j.foreco.2007.03.022
35. Mori A, Mizumachi E, Osono T, Doi Y. Substrate-associated seedling recruitment and establishment of major conifer species in an old-growth

subalpine forest in central Japan. For Ecol Manage. 2004;196(2–3):287–297. http://dx.doi.org/10.1016/j.foreco.2004.03.027

36. Jonášová M, Matějková I. Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances. Can J For Res. 2007;37(10):1907–1914. http://dx.doi.org/10.1139/X07-062
37. Svoboda M, Pouska V. Structure of a Central-European mountain spruce old-growth forest with respect to historical development. For Ecol Manage. 2008;255(7):2177–2188. http://dx.doi.org/10.1016/j.foreco.2007.12.031
38. Holeksa J, Saniga M, Szwagrzyk J, Dziedzic T, Ferenc S, Wodka M. Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Pol'ana biosphere reserve, Central Slovakia. Eur J For Res. 2006;126(2):303–313. http://dx.doi.org/10.1007/s10342-006-0149-z
39. Rusek J, Brůhová J. Impact of bark beetle outbreak on epigeic communities of Collembola (Insecta: Entognatha) in climax spruce forests in the Šumava National Park, Czech Republic. In: Contributions to soil zoology in Central Europe II: proceedings of the 8th Central European workshop on soil zoology, České Budějovice, Czech Republic, April 20–22, 2005. České Budějovice: Institute of Soil Biology, Biology Centre, Academy of Sciences of the Czech Republic; 2007. p. 121–126.
40. Bače R, Janda P, Svoboda M. Vliv mikrostanoviště a horního stromového patra na stav přirozené obnovy v horském smrkovém lese na Trojmezní. Silva Gabreta. 2009;15:67–84.
41. Gömöry D, Dovčiak M, Gömöryová E, Hrivnák R, Janišová M, Ujházy K. Demekologické, synekologické a genetické aspekty kolonizácie nelesných plôch lesnými drevinami. Zvolen: Lesnícka fakulta Technickej Univerzity; 2006.
42. Šoltés R, Školek J, Homolová Z, Kyselová Z. Sekundárna sukcesia na kalamitných plochách vo Vysokých Tatrách v rokoch 2005–2007. In: Fleischer P, Matejka F, editors. Windfall research in the High Tatras Mts. Proceedings of the conference. Tatranská Lomnica: Geophysical Institute of the Slovak Academy of Sciences; 2007.
43. Holeksa J, Zywiec M. Spatial pattern of a pioneer tree seedling bank in old-growth European subalpine spruce forest. Ekológia. 2005;24:263–276.
44. Lonsdale D, Pautasso M, Holdenrieder O. Wood-decaying fungi in the forest: conservation needs and management options. Eur J For Res. 2008;127(1):1–22. http://dx.doi.org/10.1007/s10342-007-0182-6
45. Jonášová M, Prach K. Central-European mountain spruce [*Picea abies* (L.) Karst.] forests: regeneration of tree species after a bark beetle outbreak. Ecol Eng. 2004;23(1):15–27. http://dx.doi.org/10.1016/j.ecoleng.2004.06.010
46. Lässig R, Močalov SA. Frequency and characteristics of severe storms in the Urals and their influence on the development, structure and management of the boreal forests. For Ecol Manage. 2000;135(1–3):179–194. http://dx.doi.org/10.1016/S0378-1127(00)00309-1
47. Mayer P, Abs C, Fischer A. Colonisation by vascular plants after soil disturbance in the Bavarian Forest – key factors and relevance for forest dynamics. For Ecol Manage. 2004;188(1–3):279–289. http://dx.doi.org/10.1016/j.foreco.2003.07.027
48. Ricard JP, Messier C. Abundance, growth and allometry of red raspberry (*Rubus idaeus* L.) along a natural light gradient in a northern hardwood forest. For Ecol Manage. 1996;81(1–3):153–160. http://dx.doi.org/10.1016/0378-1127(95)03643-1
49. Marozas V, Racinskas J, Bartkevicius E. Dynamics of ground vegetation after surface fires in hemiboreal *Pinus sylvestris* forests. For Ecol Manage. 2007;250(1–2):47–55. http://dx.doi.org/10.1016/j.foreco.2007.03.008
50. Hannerz M, Hånell B. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. For Ecol Manage. 1997;90(1):29–49. http://dx.doi.org/10.1016/S0378-1127(96)03858-3
51. Driscoll K., Arocena J., Massicotte H. Post-fire soil nitrogen content and vegetation composition in Sub-Boreal spruce forests of British Columbia's central interior, Canada. For Ecol Manage. 1999;121(3):227–237. http://dx.doi.org/10.1016/S0378-1127(99)00003-1
52. Widenfalk O, Weslien J. Plant species richness in managed boreal forests – effects of stand succession and thinning. For Ecol Manage. 2009;257(5):1386–1394. http://dx.doi.org/10.1016/j.foreco.2008.12.010