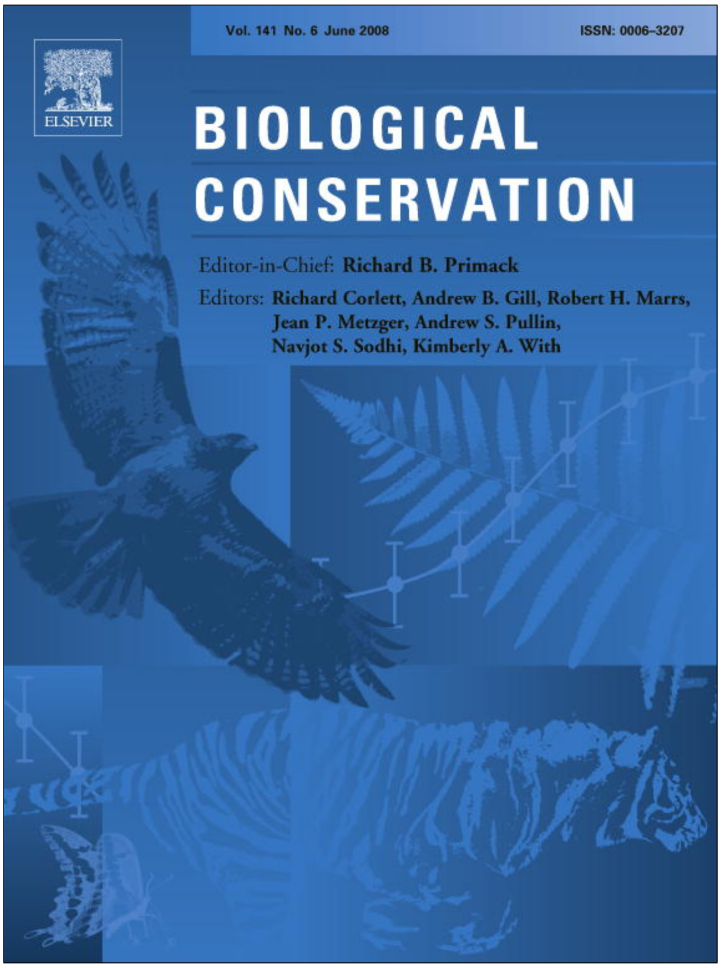
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The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests

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ABSTRACT

Changes in the herb and moss layers of mountain spruce (*Picea abies* (L.) Karst.) forests after bark beetle (*Ips typographus* (L.)) outbreak were compared with and without forestry intervention. The study area is situated in the Šumava National Park (Czech Republic, Central Europe), where an extensive bark beetle outbreak occurred in the 1990s. Parts of forests were left without interventions, while salvage logging was applied in other areas. Altogether, 18 permanent research plots were established in: (1) climax stands with completely dead canopy, (2) climax stands where salvage logging was applied (clearcuts), and (3) waterlogged stands with only partly dead canopy. Vegetation composition of the ground layer and species numbers were evaluated in 1997 and 2002.

The effect of salvage logging on vegetation was greater than that of the bark beetle outbreak itself. Forest herb species and partly also bryophytes survived relatively well under untouched dead canopy. The fewest changes occurred under the partly dead canopy in waterlogged forests. The herb layer expanded in clearcuts originated due to salvage logging, being dominated by grasses. Bryophytes were more susceptible to logging than herbs; their cover in clearcuts was markedly lower and composition changed towards pioneer species. The results show that a natural succession of mountain spruce forests after a bark beetle outbreak, if left without interventions, will probably avoid a pioneer stage and direct recovery of the forests will be possible. Salvage logging had negative effects on species composition of the spruce forests, delayed the forest recovery, and should not be permitted in the national park.

1. Introduction

Coniferous forests are sensitive to both natural and human-made disturbances, but they usually easily regenerate after natural ones, which are even often needed for persistence of the forests (Pickett and White, 1985; Lässig and Močalov, 2000; Ulanova, 2000). In Central European mountain spruce forests, bark beetle (*Ips typographus* (L.)) outbreaks together with storm events are the most important natural disturbances determining the dynamics of the forests (Korpel,

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1995; Schelhaas et al., 2003). It has been supposed that the frequency of bark beetle outbreaks is recently increasing due to decreased resistance of the forests affected by air pollution and perhaps due to climate change (Ayres and Lombardero, 1999; Schelhaas et al., 2003). Vegetation composition and species diversity of the herb and moss layers closely interact with tree layer composition and structure (Ewald, 2000; Holeksa, 2003). For this reason, the extensive mortality of the dominant tree Norway spruce (*Picea abies*) in mountain spruce forests by bark beetle, which occurred in some Central European mountains in the 1990s, could potentially lead to large-scale vegetation changes in the ground layer vegetation. Most information about the influence of disturbances on the ground layer vegetation originates from boreal coniferous forests of Europe (Segerstrom, 1997; Uotila and Kouki, 2005; Zobel et al., 2007) or North America (Matsuoka et al., 2001; Allen et al., 2006). Observations of natural succession of Central European mountain spruce forests after natural disturbances are rare, because salvage logging has been the main traditional management technique in Europe to deal with the results of natural disturbances like wind and bark beetle outbreaks. Salvage logging is considered ecologically to be an additional, unnatural disturbance. The first data about the natural development of spruce forests after large-scale natural disturbances were gathered from the Bayerischer Wald National Park, where large areas of near-natural spruce forests were affected by a windstorm in 1983. The forests in the strictly protected zone of the park were left without any interventions, and natural regeneration and vegetation succession of blown-over forests were monitored in permanent plots (Fischer et al., 1990; Jehl, 2001). Studies of the natural development of mountain spruce forests after bark beetle outbreak were also conducted in Bayerischer Wald and indicated only few changes in understory vegetation composition over a few years after the outbreak (Heurich, 2001; Bauer, 2002), but without direct comparison with sites where salvage logging was applied.

Salvage logging consists of felling infested trees, which usually results in complete clearcutting. Lindenmayer and Noss (2006) reviewed the literature on impacts of salvage logging worldwide and concluded that forest ecosystems may be more strongly affected by salvage logging than by the initial natural disturbance. Similar conclusions were drawn by Foster and Orwig (2006), who contrasted ecological effects of windstorms, invasive pests and pathogens with the impacts of salvage logging in the forests of New England. Felling and removing all trees in infested stands results in extreme changes in light conditions (Wermelinger, 2004). Compared to that, the changes in infested stands left without interventions are relatively slower and of a lower magnitude, because attacked trees remain standing and the dead canopy is then reduced gradually. The importance of even a reduced canopy for maintaining favourable microclimatic conditions (Heithecker and Halpern, 2006) and survival of forest species and tree regeneration is known (Hannerz and Hånell, 1997). Another usually reported effect of salvage logging is direct mechanical disturbance of vegetation, tree regeneration and soil surface by logging operations (e.g. Fischer, 1992; Fernandes et al., 2008). Early successional plant species usually increase and late successional species decrease after clearcutting (Hannerz and Hånell, 1997; Roberts and Zhu, 2002); significant vegetation changes have been reported even with partial cutting (Deal, 2001) and thinning (Brunet et al., 1996).

Forests of the Šumava Mountains (Bohemian Forest, Czech Republic) and Bayerischer Wald (Bavarian Forest, Germany) form the most extensive forest complex in Central Europe. The area is protected by two national parks: the Šumava National Park in the Czech part and the Bayerischer Wald National Park in the German part of the mountains. A large complex of mountain spruce forests situated in the central part of the mountains was affected by a bark beetle outbreak in the 1990s (Zemek and Heřman, 2001). Moreover, in the national park where this study was conducted, a conflict exists between the interests of nature conservancy and those who favour using the traditional forestry approach to combat bark beetle because of economic interests (Furlong, 2006). This study was performed as part of a long-term observation of permanent research plots located in spruce forests affected by bark beetle outbreak with and without forestry interventions. The results about natural regeneration of tree species have already been published (Jonášová and Prach, 2004). This study deals with ground layer vegetation and aims to answer the following questions: (1) What are the differences and changes over time in the species composition of the ground layer. (2) How does plant species richness differ in forests with or without interventions? (3) Are changes in herb and moss layers similar or not? Special attention was paid to typical spruce forest, i.e. target, species. Some implications of the results are outlined in regards to conservation of mountain spruce forests.

2. Methods

2.1. *Study area*

The study area was located in the central part of the Šumava Mts. (48° 56′–48° 59′ N, 13° 25′–13° 29′ E). The altitude ranged from 1175 to 1280 m a. s. l. and the investigated area of 5 km^2 encompassed homogenous climax mountain spruce forests accompanied by waterlogged spruce forests in wet sites (Neuhäuslová, 2001). The area represents a relatively cold climatic region with a short, cold and humid summer and a long, cold and humid winter with abundant and long-lasting snow cover (Quitt, 1971). Mean annual precipitation is about 1500 mm and mean annual temperature about 4 °C. The bedrock is predominantly gneiss, partly combined with granodiorites. Podzols are the prevailing soil type under the mountain spruce forests; histosols and gleysols occur under the waterlogged spruce forests (Novák, 1989–1993).

Based on historical evidence, large bark beetle outbreaks occurred several times in the past in this area (Svoboda and Wild, 2007). The current spruce forests originated partly after a wind disturbance, which was connected with a bark beetle outbreak. These were followed by some salvage logging activity at the end of the 19th century, but these forests exhibit a natural character (Jelínek, 1988).

The tree layer of climax mountain spruce forests is dominated almost exclusively by spruce (*P. abies*). Rowan (*Sorbus* *aucuparia*) grows often on edges and in open sites. Acidophilous grasses and herbs, such as *Calamagrostis villosa, Avenella flexuosa,* and *Vaccinium myrtillus*, dominate in the herb layer. *Homogyne alpina*, *Trientalis europea*, *Luzula sylvatica*, and *Dryopteris dilatata* are also frequently present. The dominant bryophyte species are *Polytrichastrum formosum*, *Dicranum scoparium*, and *Sphagnum girgensohnii*.

The tree layer of waterlogged spruce forests consists only of spruce owing to the permanently waterlogged soil. *V. myrtillus* is dominant in the herb layer, while *A. flexuosa*, *Vaccinium vitis-idaea* and *C. villosa* can also be found with higher constancy. *T. europea*, *H. alpina*, *Lycopodium annotinum*, *Soldanella montana*, and *Listera cordata* are present with low constancy and dominance. The moss layer is well developed typically with *Bazzania trilobata* and *Sphagnum* sp. div. Additional species of bog communities, such as *Eriophorum vaginatum* and *Carex nigra*, and *Polytrichum commune* in the moss layer, may be present (Moravec et al., 2002). Nomenclature of vascular plants is according to Kubát et al. (2002), bryophytes according to Kučera and Váňa (2003).

2.2. *Research plots*

Altogether, 18 permanent research plots, 400 m^2 each, were selected in representative parts of available stands of spruce forests both with and without interventions. The selection reflected the real situation in the field, i.e. the advance of the bark beetle attack and the contemporary creation of clearings by foresters, both of which were out of the control of the authors. All the research plots, both untouched and those in clearcuts, were fixed in the same year when the bark beetle attack was recognized, thus no changes in the ground layer vegetation were expected between the attack and the onset of our study, except those directly caused by the forestry interventions.

The plots were established in three types of stands: (1) Dead canopy, i.e. climax mountain spruce forest, which was attacked by bark beetle in 1997 resulting in nearly complete mortality of trees in the tree layer, left without interventions (eight plots). (2) Clear-cut climax mountain spruce forest, which was attacked by bark beetle and completely cut down in spring 1997. The wood was removed using wheel and crawler pull down machinery, slash was milled into wood chips, which were left on the site (five plots). (3) Waterlogged spruce forest attacked by bark beetle in 1998, partly survived (about 20% of trees in the tree layer), left without interventions (five plots). All three types of plots were more or less equally distributed over the study area.

Only mature, relatively homogenous stands of mountain and waterlogged spruce forests were selected. The crown canopy before the bark beetle outbreak was about 50%. Herb and moss layers in the plots were formed by the typical plant and bryophyte species of these forest communities (see above). Shrubs were not present in the study plots.

2.3. *Data collection*

Percentage cover of each herb and bryophyte species and total cover by tree canopy, herb, and moss layers were visually estimated in each plot (Kent and Coker, 1992). Each plot was divided into four subplots of 100 m^2 and the covers were evaluated in each subplot separately. For further processing, pooled data averaged from the whole plot were used to avoid pseudoreplication (Hurlbert, 1984). All of the data were obtained in 1997 (1998 in the waterlogged forests) and 2002; average cover values of each species in each plot type were calculated (Appendices I and II).

2.4. *Data analyses*

Vegetation composition was evaluated by multivariate methods using Canoco for Windows (ter Braak and Šmilauer, 1998). Square-root transformation of the data was used to obtain normality, and data on herb and bryophyte species covers were evaluated separately. Based on the gradient length from a preliminary detrended correspondence analysis, which was relatively short (2.9), principal component analysis (PCA), a method based on a linear model, was used. Environmental variables (plot type, crown cover, time) were displayed passively in the ordination space. Redundancy Analysis (RDA) was then used to test the relationship between vegetation composition and environmental variables. Plot type, crown cover, and time were used as environmental variables in the first RDA analysis (Analysis I). Altitude was used as a covariate to exclude its influence. Plot type was coded as three dummy variables in all analyses. This was followed by several partial analyses, where the influence of particular environmental variables was eliminated by using them as covariates, and the percent variability in the species cover data explained by particular environmental variables was identified (Analyses II–IV). Then the interaction of plot type with time was tested, which tests the null hypothesis that the temporal trend in species composition is independent of plot type (Analysis V). The tests of within-subject effects (canopy, time) and the interactions were constructed by the use of plot identifiers (coded as dummy variables) as covariables (for further description of the method see Lepš and Šmilauer, 2003). The statistical significance was tested by the Monte Carlo permutation test in all analyses.

The differences in total herb and moss layer covers and total cover of the typical species of mountain spruce forests among plot types and observed time periods were tested by repeated measures ANOVA. In the case of significant effects ($p \leqslant 0.05$), post-hoc comparisons were made using Tukey's honestly significant difference (HSD) test. The data were square-root transformed to meet the assumptions of ANOVA. We considered as typical species of spruce forests those listed as diagnostic, constant, and dominant species in Chytrý and Tichý (2003).

Species richness was expressed as the mean numbers of moss, herb, and typical spruce forest species per plot. Their differences among plot types and time periods were also tested by repeated measures ANOVA.

3. Results

3.1. *Species composition*

PCA ordination separated the plots into distinct groups of samples by plot type (Figs. 1 and 2), with clearcuts and dead

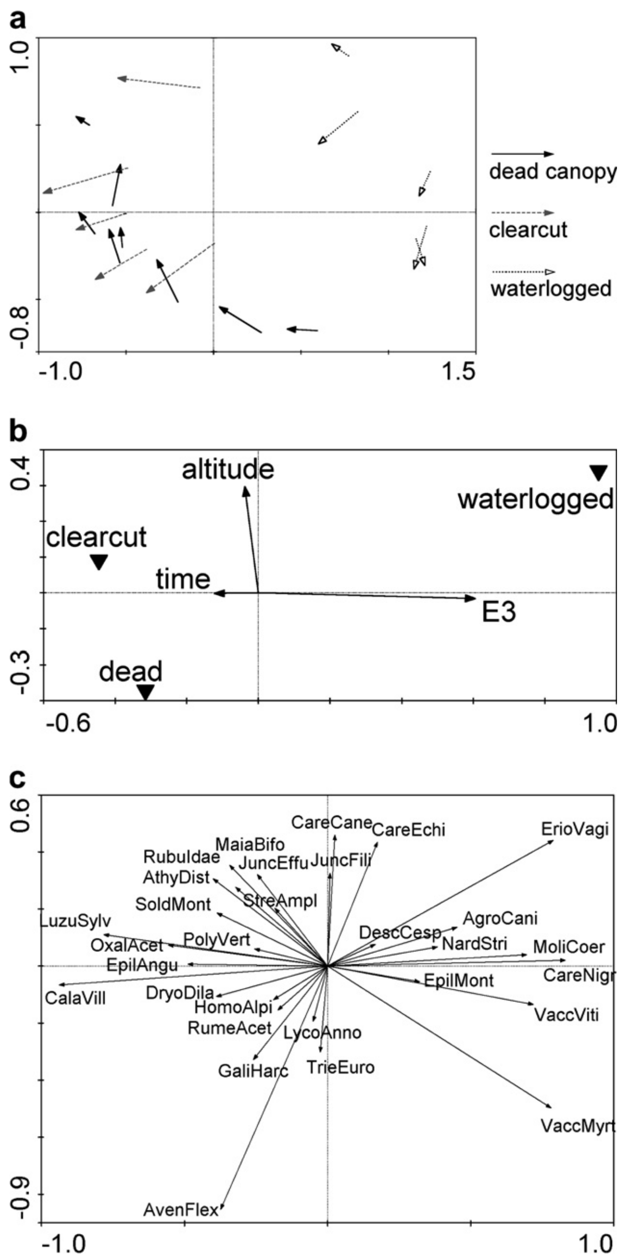

Fig. 1 – (a)–(c) PCA ordination diagrams (herb layer) represent the projections of: (a) 18 research plots at the beginning and end of the observation period (shown as arrows indicating the direction of vegetation change between years for each plot), (b) passively projected environmental variables, and (c) species. The species are labelled by the first four letters of the genus name and the first four letters of the species name (full species names are listed in Appendix I). The quantitative environmental variables are time, altitude, and tree canopy cover (E3). Type of plot is used as dummy variables (triangles).

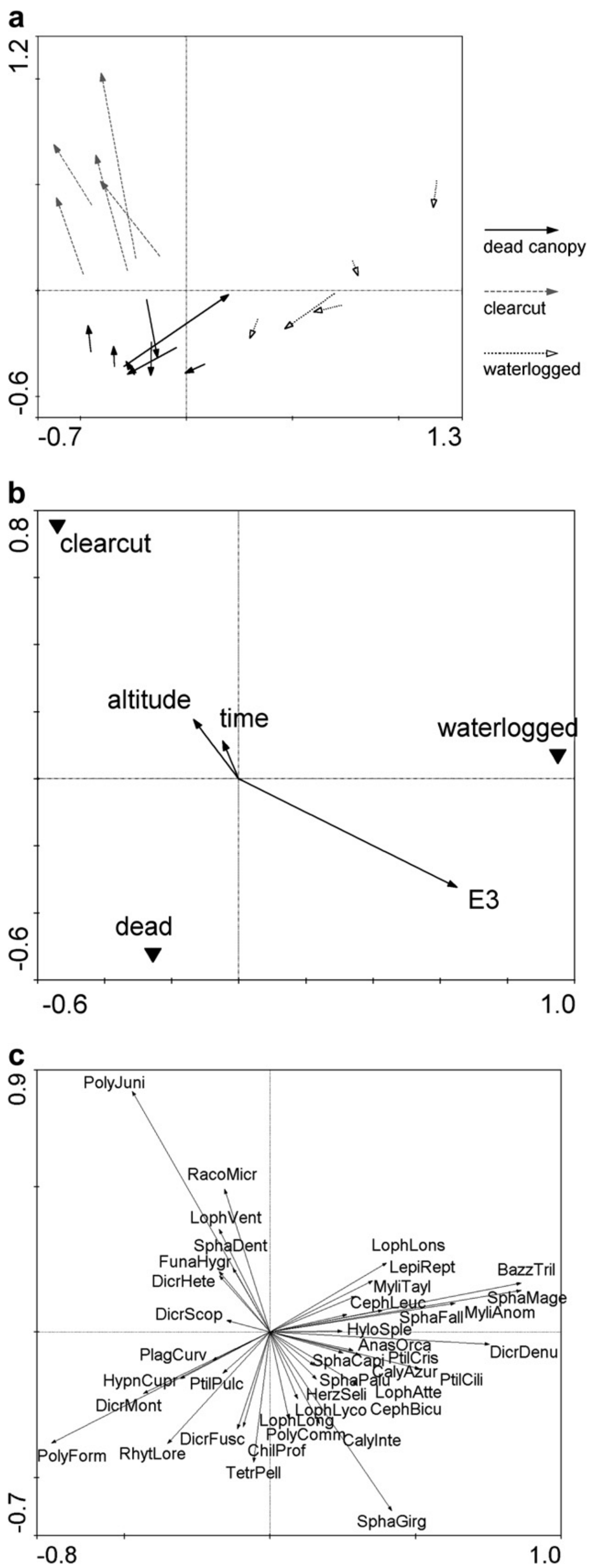

Fig. 2 – (a)–(c) PCA ordination diagrams of moss layer composition. Full species names are listed in Appendix II. For other explanation see Fig. 1.

canopy being to the left and waterlogged spruce forests to the right on axis 1. The results are somewhat different for ordinations of herbs and of bryophytes. The composition of the herb layer under dead canopy and in clearcuts did not differ very much at the beginning of the study. Nevertheless, further development of the vegetation was rather different, as can be seen from the direction of the arrows in Fig. 1a. In clearcuts the cover of the grasses *C. villosa* and *A. flexuosa* increased and pioneer species (*Juncus effusus*, *Rumex acetosella*, *Rubus idaeus*) appeared in between the two sampling times (Appendix I). Almost no pioneer species appeared under dead canopy and typical spruce forest species, such as *Oxalis acetosella*, *H. alpina*, and *Trientalis europaea*, even slightly increased. Waterlogged spruce forests exhibited somewhat different species composition of both herb and moss layers from the beginning. *V. myrtillus* dominated these forests and even slightly increased in cover during the study. Partial death of the tree layer resulted in only a few changes in cover of other species. Species such as *Nardus stricta*, *L. sylvatica*, *A. flexuosa* and *C. villosa* slightly increased their cover at the expense of moisture demanding *Carex* species. This partly increased the similarity of waterlogged plots with other plot types (see the arrows in Fig. 1a).

Moss layer composition was rather different under dead canopy and in clearcuts from the beginning of the study (Fig. 2, Appendix II). Especially liverworts of the genera *Calypogeia* and *Cephalozia* were missing in clearcuts. *Lophozia attenuata*, *L. floerkei*, and *L. longiflora* disappeared between the two sample times whereas pioneer species such as *Ceratodon purpureus*, *Funaria hygrometrica*, and *Polytrichum juniperinum* appeared instead. Most bryophyte species present under dead canopy at the start of the study survived and no new pioneer species appeared. In waterlogged spruce forests the typical bryophyte species of spruce forests were present in similar cover both at the beginning and end of the observation period.

The results of RDA analyses (Table 1) confirmed that the greatest amount of variability in species composition (both herbs and bryophytes) was explained by the type of plot (about 50%). Nevertheless, the effects of time, crown canopy, and the interaction between the plot type and time were also significant.

3.2. Total cover and numbers of species

Total cover of the herb layer was the highest under dead canopy at the beginning of the study and in that plot type it did not change significantly during the observation period (Tables 2 and 3). It was lower in waterlogged forests and increased slightly during the observation period. The greatest change in herb layer cover occurred in clearcuts, where it doubled over the five years. Cover of the moss layer was the highest in waterlogged forests and the lowest in clearcuts. In waterlogged forests it decreased slightly (not significant), while under dead canopy it decreased by about half. It was very low in clearcuts just after the operation and there was no significant increase. The total cover of typical forest species differed significantly among plot types and also changed differently in plot types (Tables 2 and 3). At the beginning, it was the highest under dead canopy and the lowest in clearcuts. It decreased a bit over time under dead canopy and increased in clearcuts so that it was rather similar at the end of the study. The small increase in the waterlogged forest was not significant. The increase in clearcuts was almost exclusively caused by increased cover of the grasses *C. villosa* and *A. flexuosa* (Appendix I).

A total of 36 herb and 57 bryophyte species were found (Appendices I and II). Among them were three endangered species of herbs (*L. annotinum*, *Soldanella montana*, *Streptopus amplexifolius*) (Procházka and Štech, 2002) and 2 endangered species of bryophytes (*Bazzania tricrenata*, *Cephalozia leucantha*) (Kučera and Váňa, 2003). Two species are indicated as rare and requiring more attention (*Athyrium distentifolium*, *Lophozia longidens*).

The total number of herb species did not differ significantly among plot types and only dead canopy showed an increase over time (Tables 2 and 3). The increase in clearcuts and waterlogged forests was not significant. The number of bryophytes differed among plot types with changes over time also differing. The highest number was recorded in waterlogged plots and the lowest in clearcuts in all years. The number significantly decreased under dead canopy and in clearcuts, while the increase in waterlogged forests was not significant. The number of typical species of mountain spruce forests (herbs and bryophytes together) did not differ at the start of the study and was significantly lower in clearcuts compared to dead canopy and waterlogged plots at the end of the study. Changes over time were not significant in any plot type.

4. Discussion

Generally, changes in vegetation composition over time were minor as compared to the differences among plot types. The significant effect of time indicates a partly similar temporal change in species composition in all plot types. This change is caused by a decrease of wet- and shade-demanding species and increase of light-demanding species in all the plots. The significant interaction between plot type and time implies also a temporal change in vegetation composition dependent on plot type (Lepš and Šmilauer, 2003).

Table 1 – Results of RDA analyses

Analysis	Explanatory variables	Covariables	Explained variability (%)	
			Herb layer	Moss layer
I	Plot type, time, tree canopy	Altitude	52.4	53.5
II	Plot type	Time, altitude	50.6	50.4
III	Tree canopy	Plot	0.8	1.4
IV	Time	Plot	1.1	1.5
V	Plot type × time	Plot, time	1.3	2.2

Explained variability represents percentage of the total variation in the dependent data, i.e. species composition of the herb and moss layers, explained by particular explanatory variables. × = interaction between the variables, plot = plot identifier.

Table 2 – Total covers of particular layers and numbers of species per 400 m^2 plot in the types of plots at the beginning and end of the observation period

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Total cover						
Herb layer	75.2 ± 8.2^{c}	73.6 ± 7.7^{bc}	43.8 ± 14.1^{a}	88.9 ± 2.7^{c}	46.6 ± 16.2^{a}	57.6 ± 21.3^{ab}
Moss layer	19.5 ± 8.1^{b}	11.5 ± 3.9^{a}	6.5 ± 1.1^{a}	7.1 ± 1.9^{a}	46.5 ± 5.1^{c}	39.0 ± 5.6^{c}
Typical species	98.9 ± 5.8^{c}	87.7 ± 11.7^{b}	56.4 ± 18.8^{a}	85.8 ± 13.3^{bc}	66.1 ± 16.6^{ab}	76.7 ± 29.8^{abc}
Numbers of species						
Herbs	9.8 ± 1.4^{a}	12.0 ± 2.3^{b}	11.0 ± 2.1^{ab}	12.4 ± 3.6^{ab}	10.0 ± 2.9^{ab}	12.2 ± 4.2^{ab}
Bryophytes	15.6 ± 2.4^{cd}	11.9 ± 2.8^{ab}	13.6 ± 3.9^{bc}	9.4 ± 2.4^{a}	18.8 ± 2.5^{de}	21.6 ± 3.9^{e}
Typical species	14.4 ± 1.1^{b}	13.5 ± 0.9^{b}	11.4 ± 1.7^{ab}	9.8 ± 1.9^{a}	13.4 ± 2.7^{b}	14.0 ± 4.1^{b}

Means and standard deviations are presented. Different letters in rows indicate significant differences at $p \leqslant 0.05$.

Table 3 – The results of repeated measures ANOVA

	Tested variables	*F*	*p*
Cover of herb layer	Plot type	5.11	0.02
	Time	38.63	$<10^{-4}$
	Plot type × time	23.48	$<10^{-4}$
Cover of moss layer	Plot type	118.21	$<10^{-6}$
	Time	6.39	0.023
	Plot type × time	1.94	n.s.
Cover of typical species	Plot type	3.61	0.05
	Time	13.27	0.002
	Plot type × time	22.01	$<10^{-4}$
Number of herb species	Plot type	0.13	n.s.
	Time	12.95	0.003
	Plot type × time	0.25	n.s.
Number of bryophyte species	Plot type	16.26	0.0002
	Time	2.90	n.s.
	Plot type × time	4.71	0.026
Number of typical species	Plot type	4.05	0.039
	Time	1.58	n.s.
	Plot type × time	1.50	n.s.

Plot type, time and the interaction of plot type and time were tested as explanatory variables for particular dependent variables.

The results were rather different for herbs and bryophytes. Whereas species composition of herbs did not differ very much between dead canopy and clearcuts in the first year, bryophytes, as organisms sensitive to disturbance (Fenton et al., 2003), responded to the salvage logging immediately, resulting in differences between dead canopy and clearcuts already in the first year. Dynesius and Hylander (2007) found reduced numbers of liverwort and forest bryophyte species in clearcuts, and these were evident even 30–50 years after clearcutting. Waterlogged spruce forests, with only partly dead canopy and more moisture, showed less changes both in the herb and moss layers. The important finding of our study was that successional trends over the five years studied were quite different in clearcuts than in dead canopy forests. The sudden lack of tree layer in clearcuts would, no doubt, lead to a severe change in microclimatic conditions (Chen et al., 1995; Fenton and Frego, 2005), which many forest species may not survive (Hannerz and Hånell, 1997). Pioneer species, such as *Juncus effusus*, *Agrostis capillaris*, *Epilobium angustifolium*, and *Taraxacum* sect. *Ruderalia*, occurred in bare sites after salvage logging in our case. All of these species are common in temperate forests after various disturbances (Brunet et al., 1996). These species are characterized by having a persistent seed bank or effective dispersal by wind (Pykälä, 2004). Soil disturbance caused by logging operations can facilitate their establishment, as was found by Fischer (1992) and Fischer et al. (1990) when comparing cleared and uncleared windthrow areas. A very slow process of regeneration of the original ground layer vegetation can be expected in clearcuts, together with the growth of a new tree layer (Jonášová and Prach, 2004). The regeneration time of forest ground layer vegetation after a severe disturbance depends on the type of forest, but may often require several decades (e.g Duffy and Meier, 1992; Godefroid et al., 2005).

The disturbance caused by bark beetle outbreak itself appears to be very moderate compared to salvage logging: only partial needle loss occurred in the first year, while tree canopy became gradually more open in the following years due to continuing defoliation, breaking off of thin branches and later bigger branches and parts of trunks. Forest vegetation survived very well in such stands leaving pioneer species with almost no bare soil available for their establishment. Similarly, Bauer (2002), who studied dead spruce forests before and after bark beetle outbreak in Bayerischer Wald, found only few changes in the herb vegetation after three years of bark beetle outbreak. Allen et al. (2006) reached similar conclusions in boreal forests of white (*Picea glauca*) and black (*Picea mariana*) spruce after a widespread outbreak of spruce beetles. They found a few vegetation changes five years after the outbreak and suspected that relatively few changes would occur in the cover or diversity of herbaceous species unless a significant ground disturbance occurred. The presumption that pioneer vegetation will not prevail in dead spruce forests after bark beetle outbreak was also supported by Jehl (2001). Nevertheless, somewhat different results were obtained by Kupferschmid (2002) in Switzerland, where the vegetation changed due to invasion by *Rubus idaeus* shortly after tree death due to bark beetle attack. No comparable data are available in the case of waterlogged forests, which were supposed to be resistant to bark beetle attacks. Our results indicate that, although many trees in the waterlogged forests died, the forests experienced only minor changes in the herb and moss layers.

The severe effect of salvage logging was also reflected in the total cover of the herb and moss layers, which were the lowest in clearcuts at the start of the study. The greatest change of herb layer cover over time occurred in clearcuts, while herb layer cover remained almost unchanged under completely dead canopy of the mountain forests, which supports the findings of Allen et al. (2006) and Mayer et al. (2004). Dead branches and parts of dead trees, gradually breaking off and falling down, could prevent expansion of herbs. The same phenomenon was described by Bauer (2002) from dead spruce forests in Bayerischer Wald. There was not so much litter material in waterlogged spruce forests, where many trees survived, so the effect of a more open canopy resulted only in a slight increase of herb layer cover.

The total numbers of herb species did not differ among the plot types and only slightly increased during the observation period in all of the plots. This small increase was due to the establishment of some pioneer species. In dead canopy and waterlogged stands only a few such species established with negligible cover over time after the disturbance. Bauer (2002) in dead spruce forest and Jehl (2001) in uncleared windthrow stand presented similar results. In clearcuts, more pioneer species established but the total number of species was counterbalanced by extinction of some typical forest species.

A different situation was found for bryophytes. The cover was the lowest in clearcuts, where bryophytes evidently did not survive the disturbance represented by forestry intervention. An immediate drastic decline of moss cover was reported by Hannerz and Hånell (1997) after clearcutting and by Jalonen and Vanha-Majamaa (2001) even after single-tree selection system of felling. Some decrease of bryophytes cover also occurred under dead canopy and in waterlogged forests during the observation period, which is a common phenomenon under decreased tree layer cover (Vacek et al., 1999). On the other hand, falling parts of branches and trees in dead stands, which prevent grass expansion and form a very structured terrain, can be expected to preserve microsites with moist and shady microclimate where bryophytes could survive (Jonsson and Esseen, 1990).

The number of bryophytes was the lowest in clearcuts and decreased both under dead canopy and in clearcuts over time after the disturbance. Similarly, Uotila and Kouki (2005) reported a decreased number of liverwort species due to cuttings and management in boreal forests. The number of bryophytes increased in waterlogged forests in our case. The reason can be that reduction in the tree canopy was not severe enough to cause local extinction in the original species, while it created conditions for new species to establish.

The cover of typical species of spruce forests, although different at the beginning of the study, was similar in all plots after five years. Only two typical forest species, the grass dominants *C. villosa* and *A. flexuosa*, exhibited a rapid increase in clearcuts. Both species could rapidly fill open sites after logging. The situation was different under dead canopy, where *A. flexuosa* decreased likely because of competition with *C. villosa*. *C. villosa* also increased at the expense of *A. flexuosa* in forests influenced by acid deposition (Malcová et al., 1999). Bauer (2002) found decreased *A. flexuosa* cover three years after bark beetle outbreak, but no change in the cover of *C. villosa*, which is in contrast to our findings.

The numbers of typical spruce forest species per plot were the lowest in clearcuts at the start of the study and decreased further over the observation period. This demonstrates the negative effect of salvage logging. Some studies have documented increased diversity after clearcutting in boreal forests (Pykälä, 2004). These forests are adapted to naturally regenerate after large-scale destruction of the tree layer, mostly by fire and uprooting, when the soil is disturbed and patches of bare soil occur (Bergeron et al., 2001). Nevertheless, natural disturbances in the studied mountain spruce forests seem to be different; they typically do not experience severe soil disturbance at a large-scale and likely lack the species adapted to this type of disturbance. This may explain why we did not observe any pronounced increase in species number in clearcuts.

5. Conclusions

The results suggested that natural disturbance, represented by bark beetle outbreak, had a smaller effect on ground layer vegetation than additional anthropogenic disturbance in the form of salvage logging. Most forest herb and bryophyte species survived quite well after bark beetle outbreak under dead canopy if it remained, with pioneer species rarely colonizing these areas. In clearcuts, bryophytes decreased or even disappeared, while competitive grasses and some pioneer species expanded. Waterlogged forests experienced only minor changes in both herb and moss layers over time after bark beetle outbreak. The moss layer appeared to be more sensitive to disturbances and more species rich than the herb layer in the mountain spruce forests. Forests affected by a large bark beetle outbreak and left without interventions most likely will not develop via a pioneer stage of succession in contrast to clearcuts. Instead, they immediately regenerate. This conclusion is also supported by the fast natural regeneration of tree species observed in plots without salvage logging (Jonášová and Prach, 2004). Our results indicate that no intervention in spruce forests attacked by bark beetle is a much better option for the preservation of species composition and restoration of these forests than any forestry measures. Moreover, no drastic forestry intervention should be allowed in the core zone of the national park.

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Appendix I

Mean covers of herb species per 400 m^2 plot in each type of plot and years. Covers lower than 1% are denoted by "+", the absence of a species is denoted by a dot

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Typical spruce forest species						
Avenella flexuosa	26.0	15.0	16.9	26.5	2.8	6.5
Calamagrostis villosa	27.4	40.7	20.4	49.6	1.3	3.4
Dryopteris dilatata	2.1	2.5	+	+	+	+
Homogyne alpina	+	1.0	.	.	+	+
Luzula sylvatica	9.1	3.0	4.7	3.4	.	.
Lycopodium annotinum	+	+	1.0	+	+	+
Oxalis acetosella	+	2.9	+	+	+	+
Trientalis europea	+	1.5	+	.	+	+
Vaccinium myrtillus	14.2	10.0	1.5	2.0	25.3	30.0
Vaccinium vitis-idea	.	+	.	.	+	+
Other species						
Agrostis canina	.	.	.	.	+	+
Agrostis capillaris	.	.	+	.	.	.
Athyrium distentifolium	+	+	.	.	.	.
Bistorta major	.	+	.	.	.	.
Carex canescens	.	.	+	2.5	+	1.1
Carex echinata	.	.	.	3.5	1.2	2.1
Carex nigra	+	+	.	.	+	+
Deschampsia cespitosa	.	.	.	+	.	+
Epilobium angustifolium	+	+	+	+	.	+
Epilobium montanum	.	.	.	.	.	+
Eriophorum vaginatum	.	.	.	.	8.4	8.5
Galium harcynicum	+	1.3	+	+	.	+
Hieracium sp.	.	.	.	+	.	.
Juncus effusus	.	.	.	+	.	.
Juncus filiformis	.	.	.	+	+	.
Juncus squarrosus	.	.	.	+	.	.
Maianthemum bifolium	+	+	+	+	.	.
Molinia coerulea	.	.	.	.	5.0	5.6
Nardus stricta	.	.	.	.	+	+
Polygonatum verticillatum	+	+	+	.	.	.
Prenanthes purpurea	.	+	.	.	.	.
Rubus idaeus	+	+	+	1.3	.	+
Rumex acetosella	.	.	+	+	.	.

Appendix I – *continued*

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Soldanella montana	+	+	.	+	.	.
Streptopus amplexifolius	.	+	.	.	.	.
Taraxacum sect. *Ruderalia*	.	+	.	+	.	.

Appendix II

Mean covers of bryophyte species per 400 m^2 plot in particular types of plots and years. Covers lower than 1% are denoted by "+", the absence of a species is denoted by a dot

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Typical spruce forest species						
Bazzania trilobata	+	.	.	.	8.0	6.0
Calypogeia azurea	.	.	.	.	+	+
Calypogeia integristipula	+	+	.	.	+	+
Dicranodontium denudatum	+	+	+	+	5.3	3.3
Dicranum scoparium	3.8	2.2	3.6	1.2	3.7	5.0
Lepidozia reptans	+	+	+	+	4.1	2.0
Lophozia lycopodioides	+	+	+	+	+	+
Polytrichastrum formosum	9.7	5.0	4.2	1.9	4.7	6.8
Polytrichum commune	1.1	+	+	+	3.5	4.8
Sphagnum girgensohnii	2.7	1.8	+	.	5.0	5.0
Tetraphis pellucida	+	+	+	+	+	+
Other species						
Anastrepta orcadensis	.	.	.	.	+	+
Bazzania tricrenata	.	.	.	.	.	+
Blepharostoma trichophyllum	+	.	.	+	.	+
Calypogeia neesiana	+	.	.	.	.	.
Cephalozia bicuspidata	+	.	.	.	+	+
Cephalozia leucantha	.	.	.	.	+	.
Cephalozia lunulifolia	+	+	.	.	+	+
Ceratodon purpureus	.	.	+	.	.	.
Chiloscyphus profundus	+	+	.	.	.	+
Dicranella heteromalla	.	.	+	+	.	+
Dicranum fuscescens	1.6	+	2.2	.	+	1
Dicranum montanum	+	+	+	+	+	+
Funaria hygrometrica	.	.	+	+	.	.
Herzogiella seligeri	.	.	.	.	.	+
Hylocomium splendens	.	.	.	.	+	.
Hypnum cupressiforme	+	+	+	+	+	+
Jungermannia sphaerocarpa	.	.	.	.	.	+
Lophozia attenuata	+	+	+	.	+	+
Lophozia floerkei	.	+	+	.	.	+
Lophozia hatcheri	+	.	.	.	.	.
Lophozia longidens	.	.	.	.	+	.
Lophozia longiflora	+	+	+	.	+	+
Lophozia ventricosa	+	+	+	+	+	+

(continued on next page)

Appendix II – *continued*

	Dead canopy		Clearcut		Waterlogged	
	1997	2002	1997	2002	1998	2002
Marchantia polymorpha	.	.	+	.	.	.
Mylia anomala	.	.	.	.	+	+
Mylia taylorii	.	.	.	+	+	+
Oligotrichum hercynicum	.	.	+	.	.	.
Plagiothecium curvifolium	+	+	+	+	.	+
Plagiothecium denticulatum	+	.	.	.	.	+
Plagiothecium undulatum	.	.	+	.	.	.
Pohlia nutans	+	.	+	.	.	+
Polytrichastrum longisetum	.	.	+	.	+	+
Polytrichum juniperinum	.	.	+	1.1	+	.
Polytrichum strictum	.	.	.	.	.	+
Ptilidium ciliare	+	+	.	.	+	+
Ptilidium pulcherrimum	+	+	+	+	+	+
Ptilium crista-castrensis	.	.	.	.	+	+
Racomitrium microcarpon	.	.	+	+	.	.
Rhytidiadelphus loreus	+	+	.	+	+	.
Sanionia uncinata	.	.	.	.	+	.
Sphagnum capillifolium	.	.	+	.	1.4	1.0
Sphagnum denticulatum	.	.	+	+	.	.
Sphagnum fallax	.	.	.	.	2.4	2.0
Sphagnum magellanicum	.	.	.	.	6.0	5.6
Sphagnum palustre	.	.	.	.	+	+
Warnstorfia fluitans	.	.	.	.	.	+

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