

ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE

Katedra pěstování lesů

Fakulta lesnická a dřevařská



**Recruitment pattern of the regeneration following stand replacing
disturbance in Norway spruce dominated forests in the High Tatra
National Park**

(Regarding the changes in plant diversity after two distinct disturbance types)

Diplomová práce

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2013

Prohlašuji, že jsem diplomovou práci na téma

Recruitment pattern of the regeneration following stand replacing disturbance in
Norway spruce dominated forests in the High Tatra National Park

vypracovala samostatně pod vedením doc. Ing. Miroslava Svobody, PhD., a použila jen
prameny, které uvádím v seznamu použitých zdrojů.

Jsem si vědoma, že zveřejněním diplomové práce souhlasím s jejím zveřejněním dle
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výsledek její obhajoby.

V Praze dne 23. 4. 2013

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For his help and support I thank to my supervisor, Miroslav Svoboda.

Abstract

Questions addressed: How does the environmental gradient of plant communities influence the presence and growth of spruce regeneration? Does the anthropogenic disturbance cause the homogenization of landscape-pattern? Are the structural features of spruce regeneration and functional plant diversity influenced by deadwood legacies?

Methods applied: Establishment of permanent monitoring plots for long-term observation of changes in vegetation structure, spruce growth and mortality.

Conclusions: Man-induced and natural disturbance dynamics differ substantially in their severities. Dead wood buffer the environmental conditions on a stand after a disturbance. This top-down driven control influences plant composition and its relation to establishing tree regeneration. At least partial retention of deadwood helps to maintain biodiversity and promotes future forest regeneration.

Key words: Norway spruce, natural regeneration, plant diversity, natural disturbance, salvage-logging, dead wood, Shannon-Wiener index, beta-diversity, competition

Abstrakt

Otázky: Jak ovlivňuje environmentální daný rostlinnými společenstvy přítomnost a růst smrkového zmlazení? Způsobuje antropogenní disturbance homogenizaci v krajinném vzhledu? Je struktura a funkční rostlinná diverzita ovlivněna přítomností mrtvého dřeva?

Použité metody: Zřízení trvalých monitorovacích ploch pro dlouhodobé sledování vegetační sukcese, růstu smrků a jejich mortality.

Závěry: Antropogenní disturbance se od přírodní významně odlišuje v síle dopadu. Mrtvé dřevo zmírňuje nepříznivé klimatické výkyvy spojené s otevřením zápoje po disturbanci. Tento druh „top-down“ kontroly následně ovlivňuje složení rostlinných společenstev a jejich vztahy s rostoucí obnovou. Alespoň částečné ponechání dřevní biomasy napomáhá k zachování diverzity a podporuje samoobnovu lesa.

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1. Introduction

1.1. Past disturbance history in the Slovakian High Tatra Mts.

Combination of bad accessibility and little number of inhabitants preserved the primeval forests of High Tatra Mountains till the late 13th century. Continuous colonization and human-induced disturbance of forests started just in the modern period. It is of interest, that the new settlements were probably founded on forests clearings, which established by past windthrows (Fleischer et al. 2007). Major interventions to forest naturalness came up together with intensive sheep pasture by the end of the 16. century and took to till the end of 18. century. During the mining activities were extracted large amount of woods for the production of rock reinforcement and charcoal (Fleischer et al. 2007). Accidental logging continued thereafter.

The decisive change in management practices came at the time of declaration of the High Tatra National Park. The rotation period and regeneration period were prolonged, and practically no management was taken. However, this approach led just to the partial exclusion of forest interventions from the national park. Accidental loggings due to natural disturbance agents moved still steadily around 70 % (Fleischer and Chmiel 2010).

The first information about large-scale disturbance dynamics goes back to the beginning of 20th century (Fleischer and Chmiel 2010). Written sources inform about large-scale replanting, which followed after salvage-logging in the area. This statement is the first well-documented proof on windthrow dynamics in the Tatra region. The periodicity of naturally occurring wind disturbances was discovered thanks to dendrochronology. During the past 150 years occurred already four major disturbance events on Tatra slopes: between 1865-1879, afterwards in 1915-1924, in 1940-1949 and recently in 2004 (Zielonka et al. 2010).

After the last disturbance event in November 2004, large bark-beetle outbreak followed. Since remaining stands were already hardly damaged by immission deposition (Fleischer et al. 2007), the coincidence caused a large die-back of the main canopy. Accordingly was initiated the large-scale restructuring and recovery of the forest (Kulakowski and Bebi 2004).

Although the major proportion of calamity wood was extracted, some areas were left without an intervention (Fleischer, Homolová 2011). This offered the possibility to compare the followings of natural and human-induced disturbances on biodiversity and future forest development in the long-term run (Jonášová, Vávrová and Cudlín 2010; Budzáková et al. 2013).

1.2. Role of natural disturbance in reestablishment of forest naturalness

Every forest is already born complex and it is the history of disturbances, which precludes its future appearance.

Past large-scale plantations caused the establishment of dense single-layer and even-aged stands, with minimum of understory vegetation (Kuuluvainen 2002). However, due to structural homogeneity the stands became susceptible to insect, fungi and wind-disturbances, what contributed to the broad die-back of the forest. Early successional stands, that cover i.e. the major part of the Tatra slopes at the time, have been perceived as rather structurally simple in the past. This distorted perception of seral forest stages rose from previous deadwood-removal practices, dense tree plantations and vegetation control.

Nowadays, naturally developing stands have large variation in vertical and spatial structure of regeneration. The structure of seral stages in natural-forests remind of an old-growth forest in several ways. Dead wood belongs undoubtedly among the most important factors for structural differentiation of newly developing forest (Kuuluvainen 2002, Svoboda and Zenáhlíková 2009, Priewasser et al. 2012). Deadwood legacies as a compound of functional diversity control the microsites distribution and so the occurrence of tree regeneration. Great number of microsites created by downed stems contributes to increased structural heterogeneity and higher complexity of the future forest (Donato, Campbell, and Franklin 2012). Purely by the theory of chance, more heterogeneous stands will possess graters number of suitable microsites for forest regeneration.

Seedlings have evolved large number of adaptations on deadwood substrate and can take advantage from the presence of wooden legacies, which remain after a disturbance. Downed decaying stems and wooden debris provides the only source of nutrients and have suitable moisture conditions for spruce regeneration (Baier et al. 2006, Zielonka

2006, Bače et al. 2012). Rooting on decayed logs diminishes the competition from graminoids and tall herbs (Svoboda et al. 1952, Glončák 2009). Uprooted stems and slash buffer the soil evaporation and stabilize moisture conditions of the stand. They as well draw shade to the stand, and hinder to expansion of competitively strong grasses (Pyšek 1993, Jonášová and Prach 2008). This is important for the success of spruce recruitment, particularly in drier regions with rather continental climate.

Since the regeneration of heterogeneous stands is mostly concentrated and aggregated in suitable microsites (Kuuluvainen 1994, Hunziker and Brang 2005), the process of intraspecific competition accelerates the stem exclusion and so reduces the stocking (Krumm et al. 2012). Also the competition with surrounding vegetation will select for the most viable individuals (Brang 1996). Therefore, naturally established stands might in consequence have lower number of stems, as previously derived from the example of commercial forests (unless the clumps are distributed regularly on a stand). On the other hand, forests with less denser structure have greater stability and accommodate more species than fully stocked close-canopy stands (Svoboda et al. 1952, Muller and Butler 2010).

Donato, Campbell, and Franklin (2012) have already pointed at remarkable similarity of early-successional stages to an old-growth forest. Even forests, which did have fully natural developmental history before the disturbance, acquire structural attributes of an old-growth (Kulakowski and Bebi 2004) if left without an intervention. We suggest that a natural disturbance might predestine even a non-natural, monoculturally managed, forest to become an old-growth.

1.3. Followings of anthropogenic vs. natural disturbance regarding ecosystem stability and plant diversity

Removal of forest overstory alters the side conditions, particularly light regimes and connectedly soil moisture (Hais 2008). Light conditions vary dramatically if trees are death or alive, if they are still standing or enriching the soil by the progressive decomposition (Lindenmeyer, Burton and Franklin 2008). Deadwood remnants contribute to landscape patchiness, which enables both: persistence of old species together with occurrence of new pioneer and opened-space life-forms, and consequently leads to biodiversity increment (Holeksa 2003, Swanson et al. 2010). The joint effect of

light and heat after the opening of overstory creates opportunities for the release of understory vegetation and trees (Diaci, Pisek and Boncina 2005). Many species have evolved adaptations to natural stand-replacement. The growth of suppressed plants accelerates; germination from buried seeds and sprouting from rhizomes starts. Consequently, future stand development is determined by whether the pre-disturbance understory consisted of well-stocked tree regeneration or vigorous shrubs and herbs, which may constrain the tree-layer establishment or at least restrict its growth.

It has been already proven, that mountain coniferous forests accommodate the greatest number of species in their early developmental stages. Seral stages of naturally developing forests had even the greatest total diversity of saproxylic fungi, beetles, bryophytes, lichens, amphibians, birds, and small mammals, when compared to closed-canopy and partially opened stands (Pawson et al. 2006, Pouska et al. 2011, Muller and Butler 2010).

Ongoing logging on a stand contributes to decrease of its spatial and vertical heterogeneity. In all taxonomic groups, the most affected by anthropogenic disturbance are sedentary organisms with poor dispersal ability (Okland et al. 2003). Those which lack clonal growth ability and specialists with low rate of adaptability, for example associated with coarse woody debris.

Large logs, which diversify light and moisture conditions and so alter the tree growth, are replaced from a stand. Due to immediate release of suppressed trees (Svoboda et al. 2010) and shorter duration of snow cover (Cunningham et al. 2006) overall intensive growth of tree-plants follows. Vegetation richness and suitable microsites are reduced, as well as advanced regeneration and post-disturbance recruits are killed. Since the vegetation that evolves after a combination of disturbances (natural, followed by human) is in rule competitively stronger than former forest seedbed, smaller tree-seedlings use to be outcompeted. Moreover, because of small residual number of surviving trees due to former logging, stands are usually being artificially replanted by tree saplings. In this manner changes the heterogeneous structure of seral forests to homogeneous cultures (Kuuluvainen 2002).

Conservation of biodiversity requires that the management is as consistent as possible with natural disturbance regime. In accordance with the intermediate disturbance hypothesis, the highest species richness is present under intermediate rate and intensity of disturbance (Connell 1978 in Lindenmeyer, Burton and Franklin 2008). Some authors contend that anthropogenic disturbances may be alike to natural ones. Nevertheless, extent and periodicity of human induced interventions is considerably different from the natural developmental pathway. Salvage logging is frequently being compared to the combination of disturbances, since the natural and anthropogenic both follow in considerably short time span (Lindenmeyer and Noss 2006). While the natural disturbance will in rule lead to increment in abundance of species (Lehnert et al. 2013), additional stress caused by anthropogenic disturbance leads to its decline (Rumbaitis del Rio 2006).

Hewitt et al. (2010) and Clavel, Julliard and Devictor (2010) jointly describe how diversity declines depending on the stress-level: low rates of stress lead to random loss of rare species. If the stress increases, well-adapted specialists are being replaced by stronger generalists. In effect, the spatial distribution of persisting species will be “reshuffled” (Clavel, Julliard and Devictor 2010). As for following of diversity loss, landscape will homogenize. Community functioning and ecosystem resilience will weaken (Peterson, Allen, Holling 1998, Bengtsson et al. 2000).

Based on previous disturbance-biodiversity lemma, we may reciprocally estimate the severity of each disturbance type (anthropogenic vs. natural) according to the level of landscape homogeneity and species diversity. However, biological studies using this approach are sparse up to date (Uotila and Kouki 2005).

1.4. Influence of stand characteristics on future regeneration of mountain spruce forest

As already mentioned, soil moisture and light attenuation belong to the main driving factors for presence and growth of spruce germinants. Nevertheless, presence and density of forest regeneration is driven by a number of factors. To one of the most important belongs dispersal ability of seeds (Kantor et al. 1975, Jonášová et al. 2006), given by the distance from the forest edge (Hanssen 2003) and maternal trees (Svoboda

and Wild, unpublished data). Terrain roughness (Kuuluvainen, Kalmari 2003) causes trapping of seeds during their snow-gliding, what leads to local aggregated growth of germinants (Baier, Meyer and Goettlein 2007). For the presence and spatial distribution of natural regeneration are very important even climatic events, like duration of snow coverage (Cunningham et al. 2006) or moisture conditions on a stand (Diaci, Pisek and Boncina 2005).

Except for variables mentioned above, most decisive for successful recruitment is the microenvironment of seedlings, created by their surrounding vegetation (Vodde et al. 2011, Korpel' et al. 1991). Namely dead wood (in form of litter, decaying logs, or stumps) has already been recognized as favourable microsite for regeneration, but the knowledge on interactions of seedlings with surrounding vegetation is sparse up to date. Nevertheless, it gains crucial importance mainly in areas, which lack sufficient deadwood legacies suited for spruce recruitment.

Surrounding vegetation indicates and modifies the environment perceived by seedlings (Hunziker and Brang 2005). Adaptive, competitive or facilitative interactions may take a role (Holeksa 2003, Kupferschmid and Bugmann 2005). To the date it has been largely unexplored, how precisely affects vegetation composition the seedling growth and mortality.

Some vegetation species have common niches, or share the same microhabitats as spruce seedlings. However, having the same environmental requirements often precludes competition and death of seedlings (Svoboda et al. 1952). Generally, the regeneration tends to aggregate on places, which stand for either favourable microsities or competitively less-stronger surroundings. Competitive interactions influence the growth of seedlings and density of regeneration. Knowledge on the interaction between vegetation and spruce seedlings might help to predict, how dense and structured will be the future, newly establishing forest.

Many authors have already tried to distinguish favourable from less favourable conditions for spruce regeneration, according to number of surviving seedlings and annual increment. Future reading will give a brief overview about the current knowledge on this issue. However, it should be noticed, that there is a lot of contradiction in studies dealing with this topic, attributable to differing stand conditions

or experimental design (Atlegrim and Sjoeborg 1996, Frak and Ponge 2002, Chrimes, Lundqvist and Atlegrim 2004).

After a disturbance, simultaneous acceleration in growth of spruce and vegetation follows and aboveground competition takes place. Until tree seedlings overgrow surrounding herbs and graminoids, they have to compete for light (Bače et al. 2012). Kupferschmidt and Bugmann (2005) report that *Rubus* species does not hinder to spruce growth, in case seedlings are present prior to the disturbance. This may also be truth for herb *Epilobum angustifolium*, which typically appears on stands rich on nitrogen (Hangs, Knight, Van Rees 2003), like wooden debris and litter, and accommodate quite large number of advanced regeneration (Michalová 2012). On the other hand, other early-successional species of tall herbs (*Athyrium distentifolium*) are considered dangerous for regeneration: they accumulate dense leaf-litter, which restricts the light attenuation and causes a major die-back of seedlings (Holeksa, Zielonka and Zywiec 2012).

Below-ground competition for resources endangers young trees before their root system is not sufficiently developed. Dense roots of surrounding vegetation might disable young seedlings to reach the mineral soil, and cause their desiccation by intensive water-uptake (Nilsson and Orlander 1999, Okland et al. 2003). Due to belowground competition, *Vaccinium* shrubs are disentangled with sufficient number of seedlings (Holeksa, Zielonka and Zywiec 2012). But while *Vaccinium* spreads to newly opened areas by a slow rate (Kirchner, Kathke and Bruelheide 2011), expansion of graminoids is much quicker process. Grasses (mainly species *Luzula sylvatica*, *Avenella flexuosa* and *Calamagrostis villosa*) create dense root carpets and strongly compete for water as well as for nutrients. They inhabit mostly places with full light irradiation and account for the major die-back in spruce regeneration (Korpeľ 1991). In declining stands and on clear-cut areas, the grasses *Calamagrostis villosa* and *Avenella flexuosa* gain the dominance, while reducing species diversity of herbal layer and eliminating characteristic and rare species of former community (Emmer et al. 1998).

2. Study questions

As already mentioned, salvage-logging might alter the future development of stand, and modify its future structure. Questions particularly addressed in this study are:

A) Is there any difference in plant diversity between men-induced and natural disturbance? Does the anthropogenic disturbance cause the homogenization of landscape-pattern?

B) Are the structural features of spruce regeneration and functional plant diversity influenced by deadwood legacies?

C) How does the environmental gradient of plant communities influence the presence and growth of spruce regeneration?

3. Materials and methods

3.1. Study area

The study was conducted in the mountain forest of Slovakian High Tatras, in the areas affected by the windthrow by the end of 2004. Annual precipitation is 864 mm, with highest peak in June and July and its minimum in October and February (Zielonka et al. 2010). Average temperature is 4.7°C, with minimum in January (-5.6°C) and maximum in July (14.4°C; Zielonka et al. 2010).

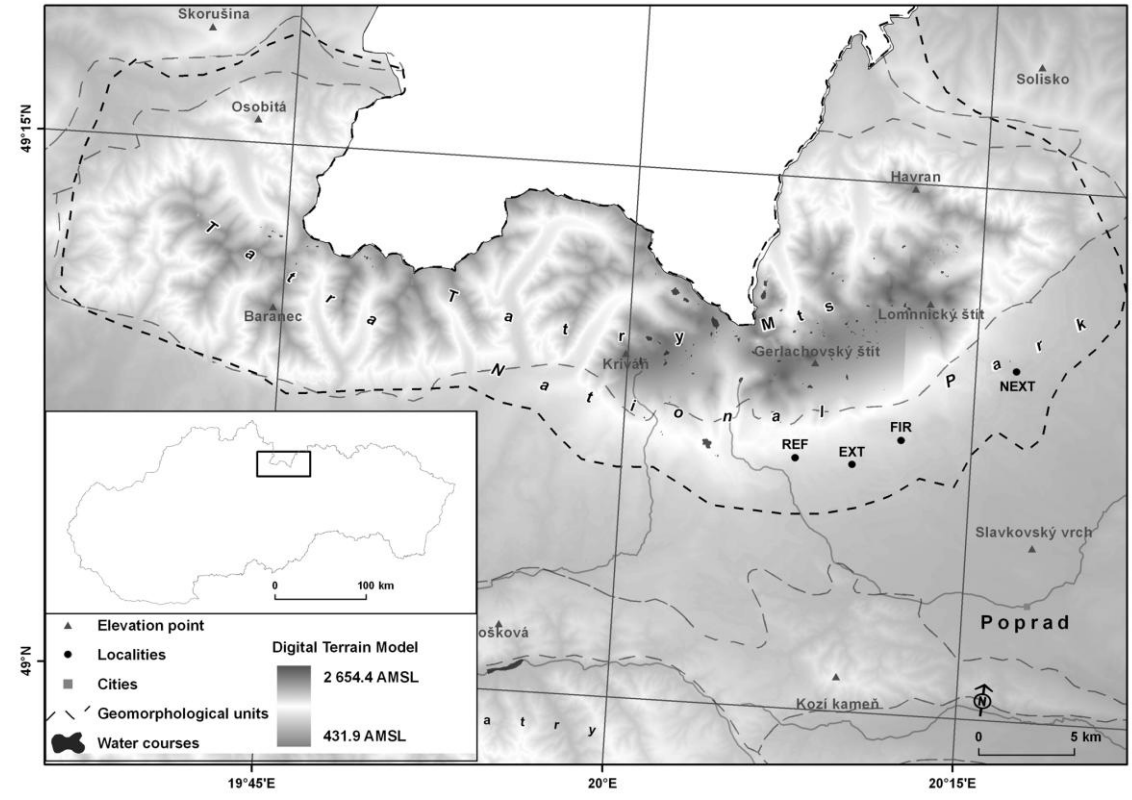
The data were collected in 2010-2012 on sites representing the post-windstorm non-management treatment and the salvage-logging treatment. Monitoring localities were chosen by researchers from the Institute of National Forests of TANAP (**Fig 1.**). The localities had similar geological and topological conditions, as well as similar forest type (Fleischer, Homolová 2011), but varied in the management approach. While the non-intervention locality accommodates large number of broken and uprooted timber, the second locality was extracted with harvester mechanization. Both localities spread over 100 ha, approximately.

The non-intervention locality (non-extracted, hence NEX) is situated in average elevation of 1100 a. s. l. (WGS 84 coordinates: N 49.180, E 20.251). The average slope is 5%, with the south-eastern exposure. Prevailing soil type is podzolic cambisol, from the geological viewpoint originates the bedrock from Wurm glaciation. The pre-windstorm composition of tree canopy consisted of Norway spruce from 70 % and of European larch from 30 % (Fleischer, Homolová 2011).

The salvage-logged (extracted: EXT) area extends in an average elevation of 1260 m a. s. l. (WGS coordinates: N 49.121, E 20.164), average slope steepness refers to 5-10 %. Slopes are southwards oriented. The soil types are cambisols and podzols, the bedrock is moraine form Donau-Mindel era. Before the windbreak, canopy consisted of Norway spruce from 90 % and 10 % created European larch (Fleischer, Homolová 2011). After the windstorm, the management priority was to remove the calamity wood as quick as possible to and so to prevent a bark-beetle outbreak. For that reason followed the total extraction of wooden biomass, except for discrete piles of branches and stumps. The pit-mound topography was destroyed as well. During logging

operations experienced the soil surface major disturbance, what lead to partial destruction of advanced regeneration on the stand.

Fig 1. Map of study localities (from Budzáková et al. 2013)



Study area refers to “EXT” for extracted, and “NEX” (in the picture depicted as NEXT) for non-extracted locality.

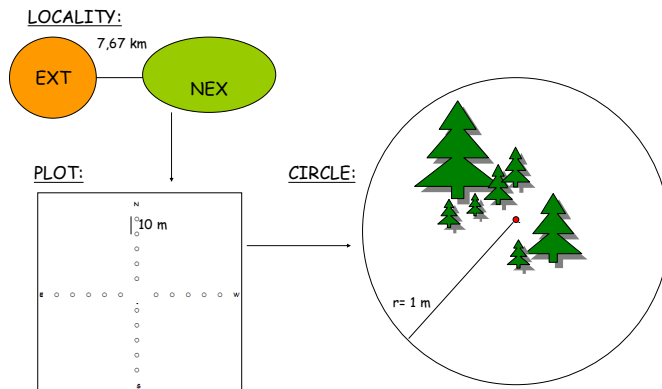
3.2. Sampling design

Permanent observation plots were established during seasons 2010 and 2011. In order to account for total environmental heterogeneity in each locality, plots were evenly distributed within localities and nested-sampling design was applied. Centers of plots were recorded with the GPS (GARMIN Company, model eTrex Venture). Altogether 21 plots were founded; 10 in EXT and 11 in NEX locality. Subplots for data-sampling were created on two radial axes from plot center.

Each of radial transects contained 5 subplots and the distance between closest-neighboring subplots was 10 m. Since there were 4 transects (on two radial axes), every plot accommodated 20 sampling points (Fig. 2.). The size of each subplot was 3.14 m²

(radius 1 m). These subplots served as basic units for the phytocenological research and estimation of deadwood presence. Their total number was 220.

Fig. 2. The study area and the design of permanent observation plots



In each circle was estimated coverage of vegetation and dead wood. The vegetation was recognized up to the species level in case of trees, shrubs and forbs, herbs and grasses. Mosses were described only at the genera level. Recorded tree species were *Picea abies*, *Larix decidua*, *Betula pendula*, *Salix caprea*, *Pinus sylvestris* and *Sorbus aucuparia*; graminoids *Avenella flexuosa*, *Calamagrostis villosa*, *Calamagrostis arundinacea*, *Luzula luzuloides*, *Luzula sylvatica*, *Juncus effusus*, *Carex canescens*, *Carex ovalis*; shrubs belonged to species *Calluna vulgaris*, *Rubus idaeus*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*; herbal layer was created by *Epilobium angustifolium*, *Oxalis acetosella*, *Maianthemum bifolium*, *Dryopteris dilatata*, *Athyrium distentifolium*, *Melampyrum pratense*, *Homogyne alpina*, *Senecio ovatus*, *Solidago virgaurea*, *Galeopsis speciosa*, *Urtica dioica*, *Cirsium palustre*, *Veronica officinalis* and mosses of genera *Dicranum*, *Hylocomium*, *Hypnum*, *Plagiomnium*, *Pleurozium*, *Polytrichum* and *Sphagnum*. The nomenclature of mosses was unified after Kremer and Muhle (1998), the nomenclature of vascular plants was confirmed after Kubát et al. (2002). Thereafter was recorded the amount of dead wood, distinguished to categories of “litter”, “downed log”, “stump”, “snag” and “branches”, each of them in percentage of circular plot. Frequencies of plants and wooden legacies, their median coverage, maximal coverage

and richness were calculated with the use of JUICE programme (Tichý 2002). The result is shown in the **Attachment 1**.

Because of strong monodominance of Norway spruce in middle European coniferous forests, the sampling was particularly focused on spruce regeneration. Remnant spruce trees, that exceeded the size of 1.5m, were excluded from the data analysis. Nonetheless, such trees were present only in a few releves from NEX. We measured tree height (in mm), diameter at stem base (in mm) and estimated the age by counting of year-whorls and scars (Niklasson 2002 in Zielonka 2006). Next season, we checked for mortality and recorded the annual height increment. The data were used for explicit estimation of suitable growth conditions (Michalová 2012).

3.4. Statistical evaluation of the data

Analyses were performed with the use of CANOCO for Windows 4.5 (Ter Braak 1998) and R 2.13.2 (R Development Core Team 2010). Package “vegan” was used for biodiversity assessment (Oksanen et al. 2013). Package “nlme” (Pinheiro et al. 2011) served for linear mixed-effect models. The “lme4” library (Bates, Maechler and Bolker 2012) was applied for generalized mixed-effect models (Poisson and binomial error structure). Because run of this package required an upgraded version of R software, the analysis was provided in new version of R 2.15.2 software (R Core Team 2012).

Data on species coverage were recorded in percentage. Therefore, square-root transformation was performed prior to the analyses. In this manner was reduced the importance of excessively common species (Krebs 1999). Fit of models was verified by visualization of residual regression graphs. The dispersion was inspected in case of Poisson and binomial error distribution.

A) *Is there any difference in plant diversity between men-induced and natural disturbance? Does the anthropogenic disturbance cause the homogenization of landscape-pattern?*

To access the spatial heterogeneity in vegetation composition between management treatments, we first inspected the length of the environmental gradient for each separate locality using *Detrended Correspondence Analysis* (Hill and Gauch 1980) in CANOCO programme (Lepš and Šmilauer 2000). Weight of rare species was not reduced. For both localities, the length of environmental gradient did not exceed 4 SD (Lepš and Šmilauer 2000). The changes in species composition were therefore considered linear on the environmental gradient. Because of that, dissimilarity in vegetation composition between samples could have been expressed by Euclidean distance (Krebs 1999).

The R-package “vegan” was implemented to describe the similarity in vegetation patches, so to compute the beta-diversity of localities. Plants, which have similar spreading and life-strategies (*sensu* Tilman 1997), were divided to following functional groups: trees, shrubs, graminoids, herbs and mosses. With functions “vegdist” and “betadisper” was calculated the mean beta-diversity for each locality, using Euclidean distance between samples (within-group variance stands for difference between each two samples). Beta-diversity between localities was compared by *analysis of variance* (ANOVA).

Species richness was compared between localities as well. For species richness we used the non-parametric *Shannon-Wiener index* (Krebs 1999). It is suited for estimation of both species richness and evenness of communities, and places most weight on rare species in samples. Shannon-Wiener values were calculated for each plant group (package “vegan”), and compared between localities with *analysis of variance* (ANOVA). The homogeneity of variances was inspected with the *Bartlett test* prior to ANOVA. If significant difference was proved, the non-parametric *Kruskal-Wallis test* was performed (Lepš 1996).

To inspect how fast and to which extend raises the overall number of species with the increasing number of samples (to address alpha- and beta-diversity), species accumulation curves were constructed (“vegan” package). For the construction of curves was called the *Kindt’s exact method* (Kindt et al. 2006). Confidential intervals

were estimated with the first-order jack-knife. *Wilcoxon paired test* was applied to examine the difference in species accumulation between particular disturbance types (localities).

These analyses were performed for quantification of biodiversity changes after two distinct disturbance severities.

B) Are the structural features of spruce regeneration and functional plant diversity influenced by deadwood legacies?

Next, we wanted to determine the influence of dead wood on plant richness and spruce growth. Plant richness was expressed as *Shannon-Wiener index* for each functional plant group (mosses, herbs, grasses, shrubs and trees). Dead wood served as explanatory variable, and was divided in two separate groups: total dead wood and dead lying stems. Finally we calculated the *variation coefficient* (standard deviation of heights standardized by mean height in each sample). With the use of the variation coefficient (response variable) we wanted to address, if spruce seedlings exhibit more heterogeneity in height distribution, when environmental conditions are modified by differing amounts of dead wood (explanatory variable).

First we calculated *partial redundancy canonical analysis* (RDA), where both plot and locality were separated to covariables (Lepš and Šmilauer 2000). The split-plot design was chosen. Species data were centered and scaling was focused on inter-species distances. After that we fitted the species response curves on deadwood amounts in the CanoDraw (implemented application of the CANOCO software).

However, there was no reason to expect overall linear trend in the response of diversity to deadwood amounts. For that reason, *locally weighted linear regression* was called (Cleveland and Devlin 1988 in Lepš and Šmilauer 2000, Hastie and Tibshirani 1990 in Lepš and Šmilauer 2000). Values obtained from this regression have lower variability than real observed data, so the technique belongs to the smoother regression models. For fitting of model are used only such predictive values, which are reasonably close to the predicted point. The predictor is being divided into certain fractions, so-called “bands”. The greatest prediction weights obtain those points, which are the

closest to center of each band. The significance of resultant model was tested through analysis of variance (Leps and Smilauer 2000).

C) How does the environmental gradient of plant communities influence the presence and growth of spruce regeneration?

Second part of the study was to judge the qualitative effect of plant diversity and deadwood legacies on the presence and growth of spruce regeneration. Since the species response to environmental gradient was linear, first we applied the *principal component analysis* (PCA) in CANOCO. The square-root transformed species data were centered and the scaling was focused on inter-sample distances. With the use of CanoDraw programme (implementation of CANOCO) we restricted the appearance of the species (plants and woods) that were either too rare or their variability was sparsely explained by environmental gradients on first two canonical axes (Lepš and Šmilauer 2000). After that we extracted the sample scores, from the first and second canonical axis respectively, and used them as explanatory variables for spruce growth and presence in the univariate analyses (in the R environment).

Data on vegetation communities were recorded at the sample level, whereas parameters of spruce seedlings were taken for each individual separately. We calculated the median value of height and annual increment per each sample and so avoided pseudoreplication. Median height increment was used for response variable in the analysis. To find out, if some ecological gradient influences the increment rate of spruce seedlings significantly, *linear mixed-effect models* were involved. Mixed-effect models are generally used when pseudoreplications can arise, due to hierarchically nested design of data sampling. In such cases is the error structure common and therefore cannot be treated as independent (Crawley 2007).

Because the absolute growth increment is given by the size of a tree as well, the absolute tree-height was added to a covariate. Increment together with the height of seedlings stood for fixed (tested) effects, and plot nested in locality were attributed to random effects.

If the presence of seedlings is given by the environmental gradient (expressed through the sample scores from canonical ordination) was tested with use of *generalized mixed-effect models* with quasibinomial error distribution (package “lmer”). The dependence of counts of seedlings on the gradient was examined through the model with discrete probability distribution and quasipoisson error structure. Both models belong to the family of *generalized mixed-effect models*, and were preferred over binomial and Poisson distribution because of overdispersion in the response variability (accomplished in R 2.15.2). Generalized mixed-effect models are fitted using the Laplace scheme, which resolves the problem of non-normal probability distribution (Crawley 2007). In both cases, plot nested in locality was added to the random effect of the model variability, in order to account for joint structure of errors due to the spatial design.

4. Results

A) *Is there any difference in plant diversity between men-induced and natural disturbance? Does the anthropogenic disturbance cause the homogenization of landscape-pattern?*

Beta diversity had generally greater means and dispersion in the non-extracted locality. Total beta-diversity, as well as the beta-diversity of trees, herbs and mosses was higher in non-intervention area. In opposite, the spatial heterogeneity in grass species tended to be higher on extracted plots. Shrub species distribution did not show any trend (Fig. 3-8., Table 1.).

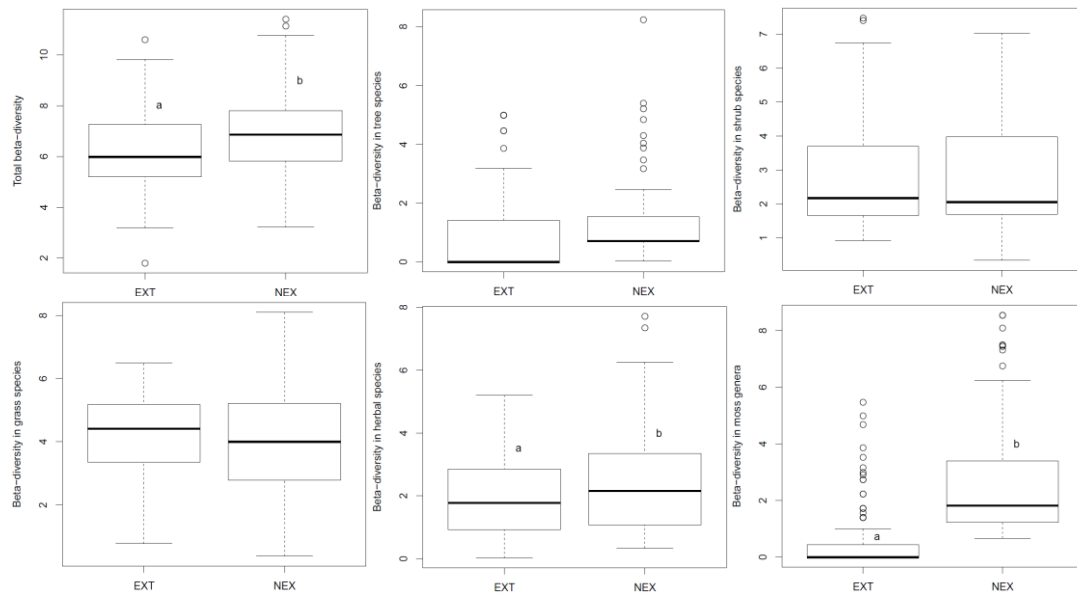


Fig. 3-8. Differences in beta-diversity of plant functional groups between localities. Left to right: total beta-diversity, diversity of tree species, shrubs, grasses, herbs and mosses. Significant differences between groups are marked with alphabetical symbols in the graphs. Species data were square-rooted prior to the analysis. Index of beta-diversity was calculated as Euclidean distance between each two samples in the locality. The horizontal lines in boxplots stand for medians; the bottom and top of the box show the 25th and 75th percentiles, respectively. Whiskers show either the range upper and lower values, or 1.5 times the interquartile range. Outliers are plotted individually.

Table 1. Beta-diversity differences of functional plant groups between two distinct management types (localities).

<i>method</i>	<i>expalnatory</i>	<i>response</i>	F	DF	p
betadisper, anova	locality	total beta-div.	9.80	1, 197	0.002
betadisper, anova	locality	trees' beta-div.	2.69	1, 197	<i>n.s.</i>
betadisper, anova	locality	shrubs' beta-div.	0.14	1, 197	<i>n.s.</i>
betadisper, anova	locality	grasses' beta-div.	0.83	1, 197	<i>n.s.</i>
betadisper, anova	locality	herbal beta-div.	5.97	1, 197	0.015
betadisper, anova	locality	mosses' beta-div.	72.52	1, 197	<0.001

Shannon's diversity index (species richness of relevés) was higher in non-intervention area for the total diversity and herbal species, as well as for mosses. Higher proportion of grasses was found in the extracted locality. Species diversity in shrubs and trees did not differ among localities (**Fig. 9-14.**, **Table 2.**).

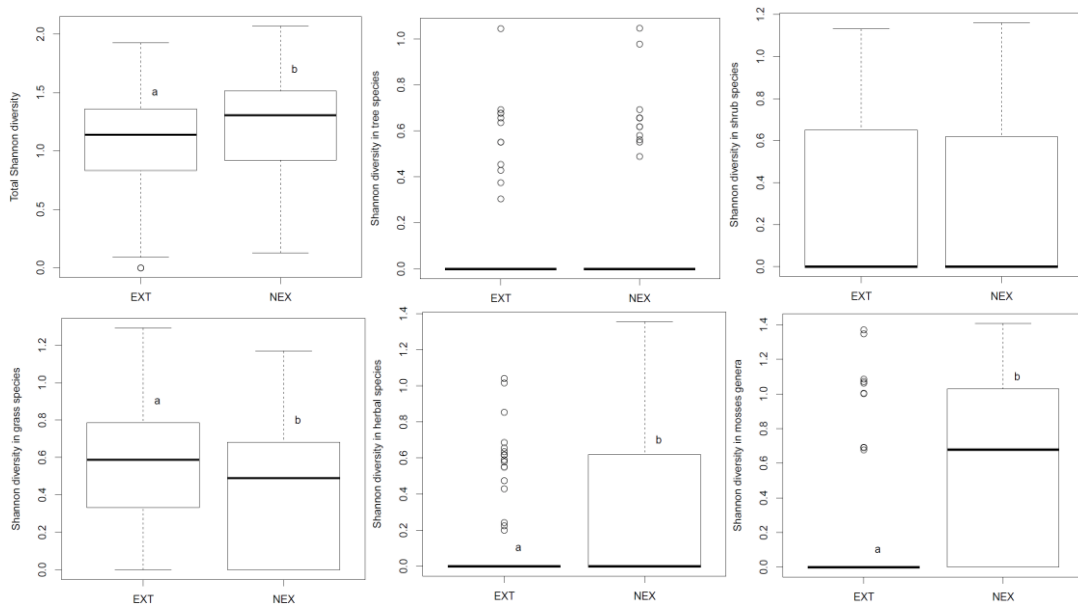


Fig. 9-14. Differences in Shannon's diversity of plant functional groups between localities. Left to right: total beta-diversity, diversity of tree species, shrubs, grasses, herbs and mosses. Significant differences between groups are marked with alphabetical symbols in the graphs. Species data were square-rooted prior to the analysis. Shannon index was calculated for each plant functional group and sample. Afterwards the values were compared between localities. The horizontal lines in boxplots stand for medians; the bottom and top of the box show the 25th and 75th percentiles, respectively. Whiskers show either the range upper and lower values, or 1.5 times the interquartile range. Outliers are plotted individually.

Table 2. Shannon’s diversity of functional plant groups between two distinct management types (localities).

<i>method</i>	<i>explanatory</i>	<i>response</i>	F	DF	p
anova	locality	total Shannon div.	5.70	1, 197	0.018
anova	locality	trees' Shannon div.	0.00	1, 197	<i>n.s.</i>
anova	locality	shrubs' Shannon div.	1.10	1, 197	<i>n.s.</i>
anova	locality	grasses' Shannon div.	6.45	1, 197	0.012
Kruskal-Wallis	locality	herbal Shannon div.	chi-sq.: 17.26	1	<0.001
Kruskal-Wallis	locality	mosses' Shannon div.	chi-sq.: 55.45	1	<0.001

According to the results of *Bartlett test* (not shown) was chosen parametric test of differences in means and variances between groups (*analysis of variance*) or the non-parametric *Kruskal-Wallis test*.

Slower accumulation of species and steadier increase in number of species by adding of samples in non-intervention locality refers to greater beta-diversity on larger scale. On extracted plots reached the number of species faster the inflection point and the number of species increased just slowly after that. This can be a following of greater patchiness and sharper borders between plant communities on the extracted locality (**Fig. 15**).

Because of overall low plant diversity on both localities has the Wilcoxon signed rank test shown no significant difference the areas ($p= 0.51$).

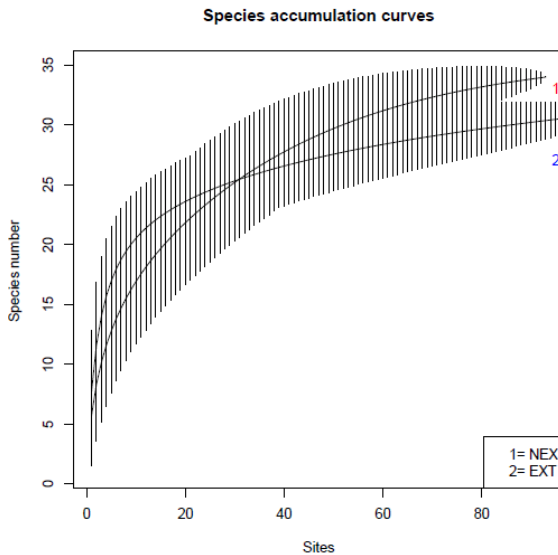


Fig. 15. Species accumulation curves calculated for two localities. The curve 1-„NEX“ shows the response accumulation on non-extracted locality, while 2-“EXT” shows the course for extracted area. Vertical lines are confidential intervals, estimated with the use of the first order jack knife method.

B) Are the structural features of spruce regeneration and functional plant diversity influenced by deadwood legacies?

The proportion in species richness increased for herbs with deadwood amounts. The same was truth for mosses, with the optimum of coverage by median deadwood totals. Coverage of grasses and shrubs dropped with wood presence. There was visible underdispersion in the tree species diversity connected to deadwood portion. This was given by clumped distribution of tree seedlings, with many places (circles) lacking the tree regeneration, and low species diversity. Total species richness was not significantly connected with dead wood. No significant differentiation of heights in spruce regeneration with increasing amounts of wood was detected (**Fig. 21.**, **Table 3.**).

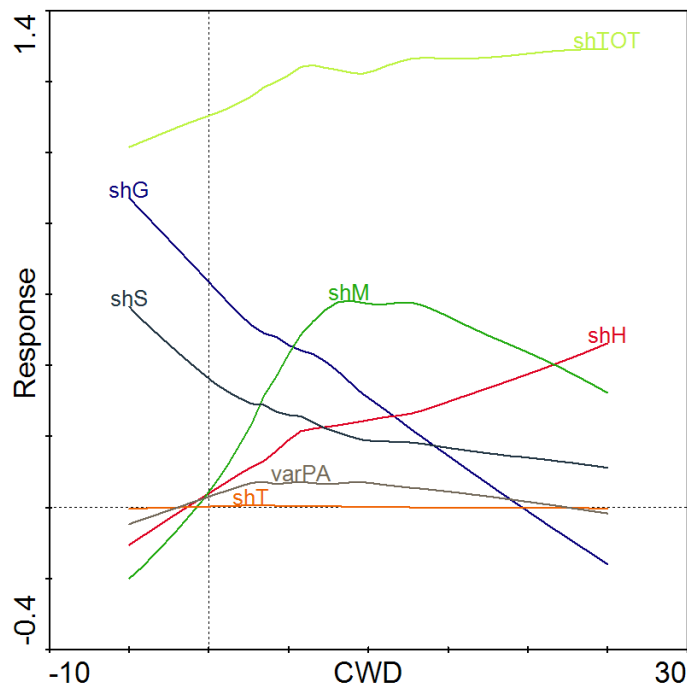


Fig. 21. Species response curves to deadwood amounts (*CWD*). Explanation of abbreviations: *shTOT*= total Shannon diversity, *shT*= Shannon diversity of tree species, *shS*= Shannon diversity of shrub species, *shG*= Shannon diversity of graminoids, *shH*= Shannon diversity of herbal species, *shM*= Shannon diversity of moss genera, *varPA*= variation coefficient of height distribution in sample. The curves are results of weighted linear regression estimations.

Table 3. Response of Shannon's diversity in functional plant groups and in height variation of spruce on deadwood amounts.

<i>method</i>	<i>explanatory</i>	<i>response</i>	F	DF	p
partial RDA, locally weighted LR	dead wood	total Shannon div.	1.82	3.4, 199	<i>n.s.</i>
partial RDA, locally weighted LR	dead wood	trees' Shannon div.	585.29	3.4, 199	<0.001
partial RDA, locally weighted LR	dead wood	shrubs' Shannon div.	4.13	3.4, 199	0.005
partial RDA, locally weighted LR	dead wood	grasses' Shannon div.	17.6	3.4, 199	<0.001
partial RDA, locally weighted LR	dead wood	herbal Shannon div.	22.19	3.4, 199	<0.001
partial RDA, locally weighted LR	dead wood	mosses' Shannon div.	18.25	3.4, 199	<0.001
partial RDA, locally weighted LR	dead wood	variation coef. of height distribution of P.A.	0.78	3.4, 199	<i>n.s.</i>

Effect of the nested sampling design (plot in locality) was separated prior to the regression, with the use of *partial redundancy analysis* (RDA).

C) How does the environmental gradient of plant communities influence the presence and growth of spruce regeneration?

The non-intervention locality (samples are marked with red crosses) was characterized by more heterogeneous plant community and presence of deadwood legacies. Vegetation composition consisted of shade-tolerant species, like *Oxalis acetosella* (Ellenberg 1992) and also had major coverage of moss species. Extracted locality was characterized by abundant grass-species presence (*Luzula luzuloides*, *Calamagrostis villosa*, *Avenella flexuosa*), as well as pioneer tree regeneration (Michalová 2012). The transition step was created by a pioneer, nitrogen demanding species typically inhabiting stands with decomposing wooden biomass, *Epilobium angustifolium* (Olšovská, Křižová and Šoltés 2009). A typical pioneer species after large-scale disturbances (Kupferschmid and Bugmann 2005) is also the shrub *Rubus idaeus*, which, however, was rather ubiquity, without any observed specific environmental preferences (its optimum is not plotted in the graph).

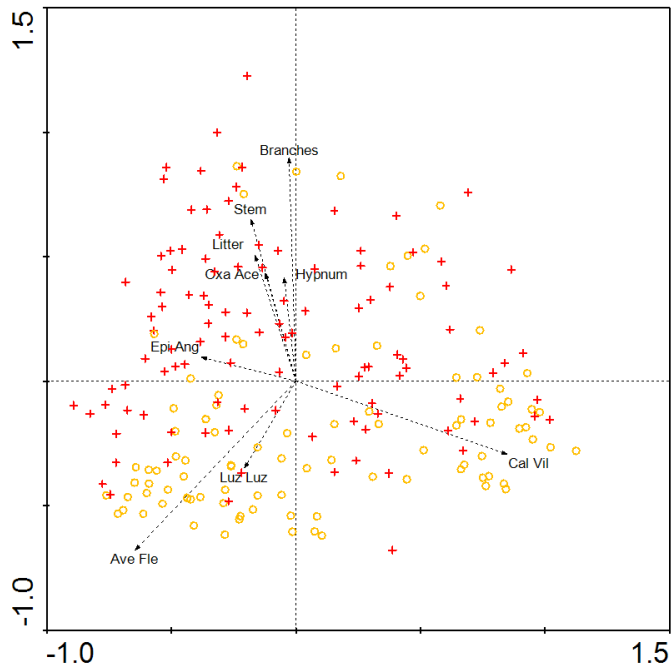


Fig. 16. PCA ordination of plant species. Particular samples are coloured according to their locality identity, *orange circles* stand for extracted areas, and *red crosses* belong to non-intervention plots. Species data were square-root transformed and centred prior to the analysis. The scaling was focused on inter-sample distances. First canonical axes accounts for 27% of total explained variability, the second axis explains 15.4%. Appearance of species in the graph was conditioned by at least 10% fit to the explained variability of first two canonical axes (Leps and Smilauer 2000).
 Explanation of abbreviations: *Ave Fle*= *Avenella flexuosa*, *Cal Vil*= *Calamagrostis villosa*, *Epi Ang*= *Epilobium angustifolium*, *Luz Luz*= *Luzula luzuloides*, *Oxa Ace*=*Oxalis acetosella*.

Graphs below depict the relation of spruce counts on biotic-environmental gradient. From the both graphs is obvious, that the greatest number of seedlings was attributed to the non-intervention locality (samples coloured green). Numerous regeneration was present in the vicinity of deadwood biomass (“branches”, “stem”, “litter”) and the amounts of seedlings decreased towards to denser proportion of graminoids (especially *Calamagrostis villosa*). Pure effect for both axes was separated by subtraction of the common variance explained by their interaction. Random effect of plot in locality was separated too. The first canonical axes explained the amount of spruce regeneration as follows: $b_{ax1} = -1.2632$, $t_{ax1} = -7.356$, $p_{ax1} = <0.001$ (Fig. 17). The second canonical axis refers to $b_{ax2} = -0.8905$, $t_{ax2} = -3.356$, $p_{ax2} = <0.001$ (Fig. 18).

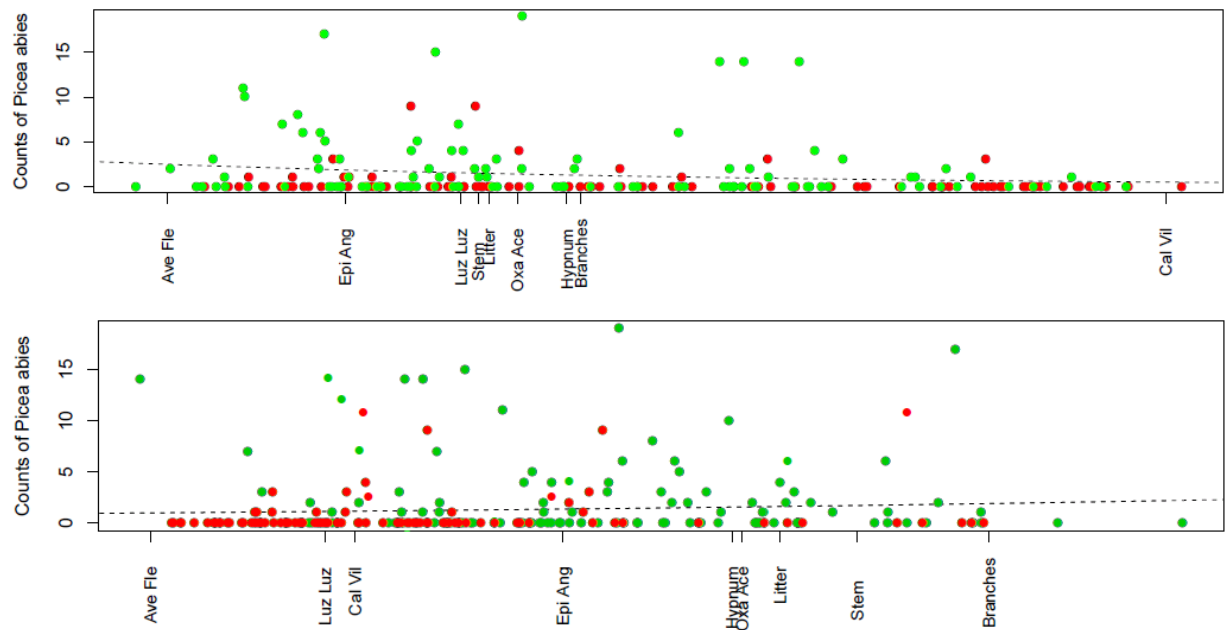


Fig. 17 and Fig. 18. Dependence of spruce regeneration number on the biotical-environmental gradient. Explanatory variables are scores extracted from the PCA ordination, respectively from the first and second axis. Species scores have been linearly rescaled, in order to correspond with the range of sample scores. The position of each species on the x-axis refers to its environmental optimum. Resultant models were fitted by generalized mixed-effect models with quasipoisson error structure. Data samples are coloured according to their locality identity, whereas *green* stands for non-intervention, and *red* stands for extracted stands.

Explanation of abbreviations: *Ave Fle*= *Avenella flexuosa*, *Cal Vil*= *Calamagrostis villosa*, *Epi Ang*= *Epilobium angustifolium*, *Luz Luz*= *Luzula luzuloides*, *Oxa Ace*=*Oxalis acetosella*.

Fig 19. shows the probability of presence of spruce recruits and plants. Since interaction of both axes was subtracted, the pure effect of both axes was examined. Only the first canonical axes had significant effect on the presence of spruce regeneration:

$b_{ax1} = -0.97710$, $t_{ax1} = -2.745$, $p_{ax1} = 0.006$. The result of the test for the second canonical axis was not significant $b_{ax2} = -0.06435$, $t_{ax2} = -0.133$, $p_{ax2} = 0.894$ (not plotted).

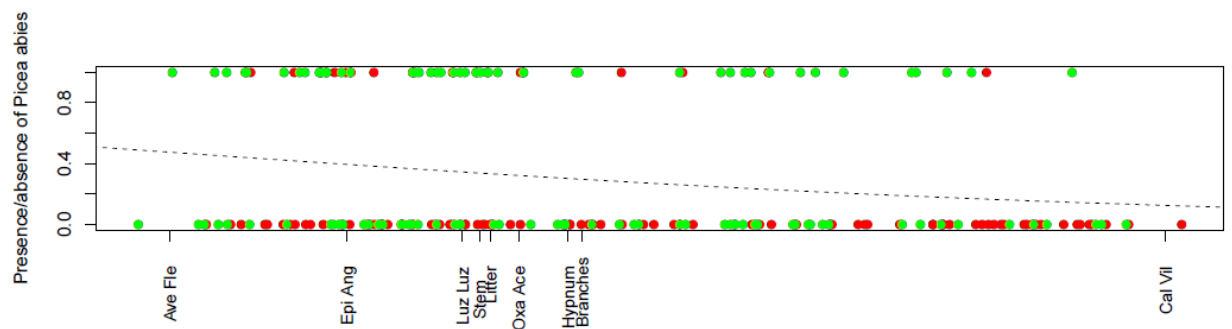


Fig 19. Dependence of spruce regeneration presence on the biotical-environmental gradient. The predictor was extracted from the PCA ordination scores of the first ordination axis. Species scores have been linearly rescaled, in order to correspond with the range of sample scores. The model was fitted by generalized mixed-effect models with quasibinomial error structure. Data samples are coloured according to their locality identity. *Green* stands for non-intervention and *red* refers to extracted stands.

Explanation of abbreviations: *Ave Fle*= *Avenella flexuosa*, *Cal Vil*= *Calamagrostis villosa*, *Epi Ang*= *Epilobium angustifolium*, *Luz Luz*= *Luzula luzuloides*, *Oxa Ace*=*Oxalis acetosella*.

Net annual increment disregards the effect of tree size. The growth rate declines towards the shady conditions of NEX (white circles), which is characterized by deadwood components and shade-tolerant vegetation. Also the net increment was somewhat higher in the extracted locality. The exception is *Calamagrostis villosa*, which seems to slower the spruce growth, probably by its competitive effect. The analyses were performed by the same procedure as mentioned above and the pure effect of canonical axes was tested. While the first canonical axis proved to be important, the second axis did not have any significant meaning: $b_{ax1} = -2.445181$, $t_{ax1} = -2.927327$, $p_{ax1} = 0.0047$; $b_{ax2} = -1.629660$, $t_{ax2} = -1.442580$, $p_{ax2} = 0.1539$. **Fig. 20.** depict significant results of the analyses.

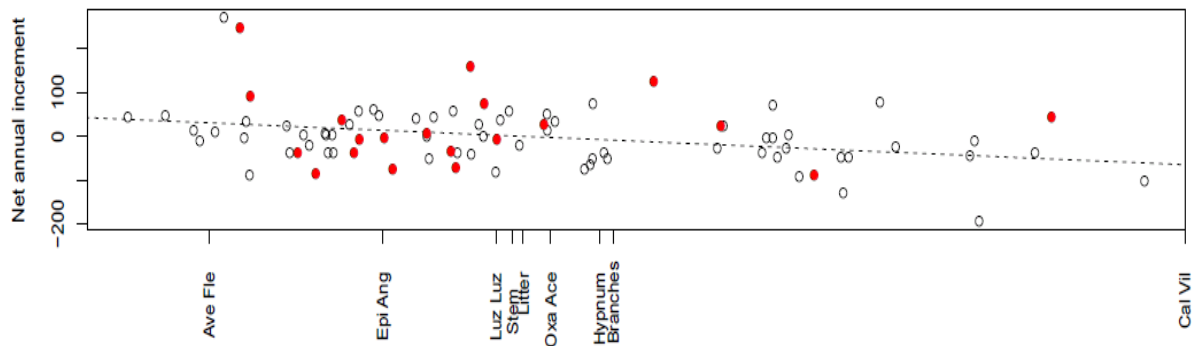


Fig. 20. Dependence of annual growth increment on biotical-environmental gradient. Upper graph depicts the residual growth increment without the effect of height. Lower graph shows the absolute annual growth increment. Explanatory variables are scores extracted from the PCA ordination, respectively from the first and second axis. Species scores have been linearly rescaled, in order to correspond with the range of sample scores. The model was fitted by linear mixed-effect models. Data samples are coloured according to their locality identity. *White* stands for non-intervention, while *red* refers to extracted stands. Explanation of abbreviations: *Ave Fle*= *Avenella flexuosa*, *Cal Vil*= *Calamagrostis villosa*, *Epi Ang*= *Epilobium angustifolium*, *Luz Luz*= *Luzula luzuloides*, *Oxa Ace*=*Oxalis acetosella*.

5. Discussion

5.1. Discussion on analytical methods and results

A) *Is there any difference in plant diversity between men-induced and natural disturbance? Does the anthropogenic disturbance cause the homogenization of landscape-pattern?*

The species accumulation curve (**Fig. 15.**) shows sharper contrasts between particular plant-communities on EXT, ergo discrete patchy distribution of species (Krebs 1999). Meanwhile, the diversity in the extracted area is slightly lower than in NEX. This means that particular plant communities start to repeat over space.

Quick development of vegetation in EXT causes the saturation of niches (Begon, Harper and Townsend 1997). Graminoids are usually the most frequent and abundant group to expand to extracted localities (**Fig. 16.**; Korpel' et al. 1991, Pyšek 1992). They frequently use phalanx spreading strategy to protect themselves against the interspecific competition. By creating of aggregates of their own species, spatial arrangement in vegetation becomes aggregated and patchy too.

Rest of vegetation in EXT was created by remnant species, prevailingly composed of shrubs from the genus *Vaccinium*, together with some moss genera (e.g. *Pleurozium*, Michalová 2012). Kirchner, Kathke and Bruelheide (2011) pointed at possible coexistence of the shrub *Vaccinium myrtillus* together with the common weed-grass *Calamagrostis villosa* on clear-cuts, in spite of the strong interspecific competition.

On shallow soils grew clumps of *Calluna vulgaris*, a shrub which is exclusively adapted to shallow and acid soils with lacking humus layer and creates distinct patches there (Svoboda et al. 1952, Olšavská, Křižová and Šoltés 2009).

Epilobium angustifolium is known for its strong demand for nutrients (Ellenberg 1992, Hangs, Knight and Van Rees 2002), so it frequently roots on deadwood residues. However, the dead wood was retained in EXT just in the form of distinct piles of branches, what caused its patchy occurrence. All of the previously discussed points explain the aggregated pattern in vegetation in EXT.

The locality NEX did not allow for such extensive expansion of graminoids, thanks to lower light attenuation (Pyšek 1992). For the same reason, local moss communities did not disappear. *Epilobium angustifolium* disposed over wider range of suitable sites, while another frequent pioneer species, *Rubus idaeus*, did not show any preferences in its occurrence. The transition between samples on shorter distances was more fluent and changes in diversity more continuous. Clumped distribution of species, due to deterioration of habitats through lying stems, was not stated in NEX. This brings an alternative solution to the forefront: lying stems rather buffer environmental conditions than separate plant niches.

Slower increase in the number of species in NEX suggests that the ecotones were wider – changes in species composition were continuous and steadier. The NEX locality has even a larger number of species. Because the change in species composition was slower, the greater total diversity in NEX can be reflected just on a wider spatial scale.

It is obvious that the interpretation of results might be badly affected by the choice of scale (Peterson, Allen and Holling 1998, Bengtsson et al. 2000, Chalcraft 2013). If insufficiently large areas had been sampled, the results could have been completely different, as the species accumulation curves would not have even crossed.

Smart et al. (2006) claim, that the rare species are the first to disappear after a major disturbance. Their occurrence is mostly random and frequencies are low, so they can be easily replaced by some common and abundant species.

In our study, the situation turned out to be slightly different. Rare species (like *Carex canescens*, *Carex ovalis*, *Juncus effusus*, *Urtica dioica*, or *Veronica officinalis*; see **Table 1.**) were more frequent in EXT (**Table 1.**). The new scarce species appeared probably after the timber extraction, in following of changes in water-regime and locally waterlogged places. The other group of rare-species consisted of pioneer trees (e.g. *Salix caprea*, *Betula pendula*, *Larix decidua*). So in opposite: beta-diversity EXT was subsidized by presence of newly-settled rare species.

Anyway, the total beta-diversity was higher in NEX locality (**Fig. 3.**). Probable explanation for it can be the disappearance of common species from EXT, which still

remained dominant in NEX (**Table 1.**). Significant departure of species from EXT was mainly noticed for herbs and mosses (in their beta-, as well as alpha- diversity; see **Fig. 3. and 8.** and **Fig. 9. and 14.**). Okland et al. (2003) reported, that after clear-cutting, the worst affected species are those with shallow root system, which is the case of mosses and many herbal species. Budzáková et al. (2013) also described the affection of mosses to NEX locality.

The only group with higher species richness and beta-diversity in the EXT locality was the one of grasses. This is a typical post-disturbance phenomenon, referred to the replacement of canopy and deadwood legacies (Korpeľ et al. 1991, Uotila and Kouki 2005, Jonášová and Prach 2008). Expanding graminoids from rule on suppress and exclude the other, less competitive species (Pyšek 1993).

Generally we can assume that loss of species richness leads to decline in total beta-diversity (Smart et al. 2006). For some plant groups, the decline in beta-diversity was not significant. This can be explained by a wider range of factors. Beta diversity is calculated from distances between all combinations of samples. After that the centroids of sample-distances are compared between localities with ANOVA. The clumping effect prolongs the distance between particular samples, therefore the average beta-diversity rises. Meanwhile the variance remains low, if the total diversity is small in the area. This was the case of the EXT locality.

The situation in NEX locality was different. For the change in species composition was rather continuous, the variation around the mean beta-diversity was higher. Due to unequal variances of both localities, the differences obtained from ANOVA (analysis of variance) might have been insignificant. Nevertheless, valuable information can be obtained merely by visualization of estimated effects.

Although graminoids had greater beta- and alpha diversity (higher average Shannon-Wiener index; see **Fig. 6.** and **Fig. 12.**) in EXT locality, the dispersion in beta-diversity was greater in the NEX locality. This is in accordance with the formerly explained effect of clumped distribution of vegetation. Particularly interesting was the group of trees. Low species richness (**Fig. 4.**) together with relatively high beta-diversity (**Fig. 10.**) indicated, that the arrangement of trees was aggregated and spatially random.

Clumping effect also increased the sample-heterogeneity (beta-diversity) of herbs and mosses in EXT, since both groups disposed over low species richness (**Fig. 7-8.** and **Fig. 13-14.**).

To sum up, the number of species decreased in the intervention EXT locality, when compared to non-managed NEX area, mainly because of reduction in the pre-disturbance species. However, the homogenization in beta-diversity in EXT locality was observable only on wider spatial scale, because of aggregated pattern (discrete composition) of species, which accounts for higher dissimilarity of communities.

C) Are the structural features of spruce regeneration and functional plant diversity influenced by deadwood legacies?

Alpha-diversity (measured by Shannon-Wiener index; **Fig. 21.**) of graminoids and shrubs declined with increasing amounts of coarse wood debris. On the contrary, diversity of herbs showed the positive trend. Mosses diversity increased sharply with the dead wood amounts to the medium factor-level, than it started to drop. This is in accordance with previous findings regarding the Shannon's diversity of particular functional groups of plants. Non-intervention locality was richer on herbal species as well as moss genera, and their diversity was in positive relation to coarse woody debris. Extensive growth of graminoids was hindered by the buffering-effect of logs and other wooden legacies.

Trees showed significantly positive response to deadwood occurrence. However, they overall diversity was low and their presence was scarce and aggregated, when compared to normal probability distribution. This invokes serious doubt about the correctness of applied model, in this particular case.

We precluded that greater amount of deadwood legacies can contribute to the differentiation in growth rate of spruce seedlings, so that the final forest would obtain more heterogeneous horizontal structure. In order to test the hypothesis, we used the variation coefficient, as for the standardized measure of height differentiation within each sample. However, no significant proof for structural differentiation was found. **Fig.**

21. shows the positive trend in structural differentiation of regeneration to wooden legacies; up to the intermediate level of the factor.

To conclude, the plant diversity is significantly affected by the amounts of dead wood. Herbs and mosses tend to retain higher coverage when compared to graminoids, which are rather disentangled with shady and moist conditions created by deadwood legacies.

B) How does the environmental gradient of plant communities influence the presence and growth of spruce regeneration?

In this question the qualitative features of species composition for spruce growth exhibition was examined. Rare species were involved in the analysis, to design the environmental gradient from sample scores. For the final interpretation were included only those species, which had the optimum on the gradient. The scaling was focused on inter-sample distances, so each species served as indicator for certain environmental conditions.

With respect to drawbacks regarding the data sampling (see *Discussion on data sampling*), here we interpret dependence of spruce density, presence and size on vegetation composition.

Plots inhabited by graminoids were, as stated before, prevailingly adjacent to the salvage-logged area. They accommodated lower counts of seedlings in total (Michalová 2012). Competitive relationships of graminoids played just partial role, because the major proportion of regeneration might have been destroyed by hasty salvage-logging already (Lindenmeyer, Burton and Franklin 2008). Nonetheless, graminoids are being considered for the major hindrance to successful forest establishment (Korpel' 1991). Especially in dryer periods they speed up the soil evaporation by the significant water-uptake (Saccone et al. 2009). Dense root system disables the rooting to newly establishing seedlings (Pyšek 1993). *Calamagrostis sp.* is known for its ability to exploit soil nitrogen, and to outcompete coniferous seedlings (Hangs, Knight and Van Rees 2002). Places with dominant coverage of *Calamagrostis villosa* and *Avenella flexuosa* eliminate characteristic and rare species and lower the herbal diversity as well (Emmer et al. 1998). The uniform areas experience faster snow melting, while

infiltration into soil is lowered. In this way a large proportion of precipitation is lost from the site (Pyšek 1993). Microclimatic extremes in temperature on the stands lead to strengthen die-back of spruce regeneration, which is in its seral stages vulnerable to unbalanced environmental conditions (Hais 2008, Michalová 2012). However, literature refers about the ability of older seedlings to survive in the competitive environment of graminoids (*Avenella flexuosa*), particularly by allocation of root biomass to other soil layers (Nilsson and Orlander 1999). When seedlings are rooting sufficiently deep already, they take up water and nutrients from different soil layer (Nilsson and Orlander 1999). Bigger trees have a nurse effect for newly establishing regeneration (Hrivnák and Ujházy 2005, Dovčiak et al. 2008). However, the presence of young regeneration seems to be disentangled from abundant grass cover (Michalová 2012). Following problematic was already addressed in Michalová (2012).

In our results, lower densities of regeneration were found namely in the connection with *Calamagrostis villosa* (**Fig. 17.** and **Fig. 18.**). However, the total (gross) annual increment was the highest. This can be prescribed to the effect of canopy opening and release from suppression, because the light attenuation is highest on opened stands (**Fig. 21.**). When discounting the prior size of seedlings from increments (we obtain net annual increment), the growth rate seems to weaken by *Calamagrostis villosa* (**Fig. 20.**). This may indicate the below-ground competition for resources (Hangs, Knight and Van Rees 2002).

Over more favorable conditions disposed the pioneer vegetation. Species typically appearing after major disturbances, in the secondary succession, are *Epilobium angustifolium* (**Fig. 17.** and **Fig. 18.**) and *Rubus idaeus* (not plotted in graph). *Rubus idaeus* enters quickly to stands, which were formerly densely stocked and had lower covered of grasses. If the forest floor contained sufficient advanced regeneration, seedlings were able to win in the competition with this species (Kupferschmid and Bugmann 2005).

Budzáková et al. (2013) and Šebeň and Bošeľa (2011) claim in their studies, that density of spruce seedling is negatively affected by the succession of *Epilobium angustifolium*. Our founding was in contrast with former conclusions. This herb commonly grows on deadwood remnants, like decomposing bark. Seedlings, which germinated on the coarse woody debris immediately after the disturbance, or even

before it, were able to coexist with this species (Michalová 2012). The disapproval might erase from the study design, concretely from choice of sampling area. *Epilobium angustifolium* is one of the first herbal species to appear on plots with majorly disturbed top-soil, which are rich on nitrogen (Ellenberg 1992, Hangs, Knight and Van Rees 2002). To the other studies were also included fire-burned plots, and a very large number of salvage-logged areas (Šebeň and Bošel'a 2011). We assume the advanced regeneration of spruce was lacking there already, because of the disturbance history of these areas. Since both mentioned studies on natural regeneration were taken just a couple of years after the disturbance, the lack on regeneration in establishing *Epilobium* carpets could have been coincidental.

Major proportion of regeneration was found in the company of mosses and *Oxalis acetosella* (**Fig. 17.** and **Fig. 18.**). Since *Oxalis acetosella* frequently occurs under closed canopy (Ellenberg 1992), this part of the environmental gradient can be attributed to close –forest stands. Some authors find mosses for unsuitable seed-bed, because they tend to desiccate during seasonal drought periods (Zielonka, Piatek 2004, Valkonen, Maguire 2005, Saniga et al. 2008). Brang (1996) describes *Oxalis acetosella* as unfavorable too. Other authors find the seedbed favorable for the presence of regeneration (Hanssen 2002, Hanssen 2003, Jonášová, Vávrová and Cudlín 2010). However, the survival-studies were concerning exclusively the germinants and seedlings in the first years after their germination, which are characteristic for increased mortality (Mori and Mizumachi 2005, Saniga et al. 2008). The results in our study were concerning mostly the advanced regeneration, which was rooted sufficiently deep to withstand dryer periods.

On the other hand, the regeneration in here tended to be of lower size (**Fig. 21.**). The ecology of the vegetation composed by shade-tolerant species suggests that the seedlings were growing under closed-canopy, created by lying stems, which slowed their growth-rate. Same is the truth for higher abundances of stems and branches (**Fig. 21.**).

Nonetheless, samples with sufficient deadwood accommodated considerable amount of seedlings (**Fig. 17.** and **Fig. 18.**). Lying logs probably created a buffer to intensive evapotranspiration and threat stabilized the moisture conditions on the stand (Michalová 2012). Humid and shady conditions do not allow for extensive expansion of graminoids

to such microsites (Pyšek 1993), and so prevent the competition. Litter and woody debris represents a good seedbed in relation to nutrients content (Kuuluvainen 1994, Baier et al. 2006). Dead wood serves as favorable seedbed and growth substrate (Zielonka and Piatek 2004, Baier et al. 2006), and is also crucially important for biodiversity maintenance (Pawson et al. 2006, Keeton et al. 2010, Muller and Butler 2010). To the date a large number of studies underlined the importance of dead wood in forests (Narukawa et al. 2003, Motta et al. 2006, Bače et al. 2012). For practical management reasons is recommended at least its partial retention on the stand (Priewasser et al. 2012, Tikkanen et al 2012).

5.2. Discussion on data sampling

Only two comparative areas were chosen in order to look for their intrinsic variability. This was the consequence owing to the fact that in the region of High Tatra National Park was retained only one non-salvaged locality (**Fig. 15.**). Nevertheless, the whole area was relatively poor from the diversity viewpoint, so 100 ha large localities could sufficiently represent the ecology of salvaged versus non-extracted stands after the disturbance.

Nested design for the data sampling allowed for the movement in difficult terrain conditions and provided information over the spatial heterogeneity within each locality. On the other hand, there was significant amount of variation attributed to the plot-level (the hierarchical structure within localities) in the non-intervention area (Michalová 2012). This suggests that the sampling did not enclose all environmental heterogeneity available within locality. There is a fair reason to assume, that adding of similar localities would enhance the environmental variability to some extent.

Suitability of microsites for the presence of spruce natural regeneration was derived from the actual presence and density of seedlings. However, the influence of plant composition on the presence of seedlings shall be evaluated with respect. Especially in the very first years after the opening of the canopy follows the quick turn-over in the vegetation composition (Goldblum 1997, Kupferschmid and Bugmann 2005). The absence of regeneration could have been caused by the competition with the current vegetation or by some formerly present species.

Besides the competition does not affect small and bigger seedlings equally, but clearly is size-dependent (Castagneri et al. 2008, Peltoniemi and Mäkipää 2011). Bigger seedlings are more resistant to interspecific competition from the understory vegetation (Korpel' et al. 1991). The vegetation in the vicinity of older seedlings can either be considered for tolerable, or even indifferent in regard to spruce phenotype and survival.

The death of seedlings is also attributable to some other unmeasured factors, e.g. animal browsing (Smit, Gusberti and Muller-Scharer 2006), biotical pests (Alvarez-Loayza and Terborgh 2011), or a longer dry period with the combination of unsuitable substrate (Diaci, Pisek and Boncina 2005). This should be bared in mind by interpretation of results based on the field observation.

The focus should be paid mainly on young germinants, or eventually on seedlings immediately after the canopy opening, by the time of rapid vegetation exchanges. Small-sized seedlings tend to die more frequently in developing dense vegetation, or even fail to germinate. Graminoids usually acquire dominance on cleared forest stands, and mechanically suppress root-establishment of young spruces (Korpel' 1991). Even competition for resources (Baier et al. 2006) and light (Shropshire et al. 2000) plays somewhat greater role in the initial stages of seedlings' life. Therefore, the density, growth rate and mortality of small seedlings can be considered for relevant indicators of microsites' suitability.

The tree height was used for estimation of tree size, although age of seedlings was also recorded in the field. Both variables were significantly correlated (data not shown), but posterior analyses detected some disparities in the year-counting and age estimation. Hence, the height of seedlings was evaluated as more exact proxy-variable.

One another restriction on interpretation of field observations is the general randomness of occurrence of regeneration (Szwagrzyk and Szewczyk 2008) and its clumped distribution. A reason may be the dispersal within a limited distance from maternal trees (Hanssen 2003, Hauru, Niemi and Lehvavirta 2012, Svoboda and Wild, unpublished data) and the terrain geomorphology (Brang 1996, Baier, Meyer and Gottlein 2007). So the absence of seedlings does not necessarily stand for unfavorable growth conditions. Randomness of occurrence also contributes to great dispersion and

large unexplained variance in the data. However, on the salvage-logged stands and in the windthrow area, no information concerning the exact position of potential seed-trees for improvement of the final model was available.

To prevent any misinterpretation of relations between plants and seedlings, the most straightforward seem to be sowing-experiments (Brang 1996). Anyway, because of long life-span and slow growth of spruce, in this way could be observed only the germination and short-term survival of regeneration. Observational studies provide the information on annual increment according to several vegetation types, and enable the separation of age-dependent mortality from interspecific exclusion for large number of age-classes. This might bring important knowledge for forest practice. Therefore, the studies of similar type should be performed.

To look for the homogenization in species composition, concern should be taken to the proportion of rare species (Smart et al. 2006), since they are the first to disappear in case of biotope degradation (Hewitt et al. 2010; Lyons and Schwartz 2001). Besides, they serve as sensitive indicators for more detailed differentiation between particular habitats (Hooper et al. 2005).

To underline the importance of rare species, Shannon-Wiener index was in charge for the calculation of sample heterogeneity. We preferred it over associated Simpson's index, which on contrary places the most weight on common species (Krebs 1999).

The Euclid distance between two random samples for estimation of heterogeneity (beta-diversity) was preferred over any standardized measure of heterogeneity. The decision was taken because of greater total coverage of vegetation in the extracted area. Non-extracted locality accommodated large amounts of dead wood, therefore had lower total percentage of plant cover.

Since we used the information on total cover of species, it was necessary to square-root the data on absolute abundances. In this manner we put equal weights on species. If we had used an index based on the sound presence of species (not abundances), rare species would obtain much greater weights as they did by the current procedure. However, this would distort the real picture.

Addressing the plants diversity is just one part of a more complex issue, and the choice of other study organisms can bring different or even more significant results. It is generally recommended to sample the data for several groups of organisms, or to focus data-collection on so-called functional diversity (*sensu* ecosystem diversity; Peterson, Allen and Holling 1998, Ares, Neill and Puettmann 2010). The decision to study the diversity of plants was made with regard to the second aim of the study, which is to describe the spruce growth surroundings. Except for plant composition, in each releve was also recorded the amount of dead wood. It is already known, that deadwood legacies are closely related to plant communities' composition (Zielonka and Piatek 2004, Uotila and Kouki 2005, Michalová 2012). Therefore, some authors attribute the joint description of dead wood and vegetation to functional-diversity assessment (Kuuluvainen 2002, Lindenmeyer, Burton and Franklin 2008).

6. Conclusion

Expected homogenization in plant species distribution occurred on salvage-logged stands (EXT locality). Plant communities on salvage-logged stands were supposedly more expansive, and so their protection against interspecific competition caused their aggregated distribution. Because of that, the beta-diversity between particular two closely-related samples tended to be higher. On the other hand, communities started to repeat over space. Lower total species richness referred to lower beta diversity of the EXT locality. To conclude, beta diversity decreased on the salvage-logged stand, when compared to non-managed locality (NEX). Distribution of species in non-extracted locality was more continuous. This suggests that lying stems rather buffer environmental conditions than separate plant niches.

Number of plant species was influenced by deadwood amounts. While former closed-canopy vegetation preferred shady and moist conditions, graminoids expanded rapidly to timber-extracted areas.

The places mostly preferred by seedlings referred to moist and shadier conditions of former canopy. Importantly, retained deadwood seems to sustain favorable conditions ever after the stand-replacing disturbance. Both, competition from graminoids and logging operations, contribute to damages on regeneration. The negative following of complete timber extraction is the die-back of regeneration. For the sake of biodiversity conservation and successful forest regeneration, at least partial retention of deadwood has to treat in common forestry practice.

7. References

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Attachment 1. Data on species frequencies, median coverages, maximal coverages and average species richness for **non-intervention locality (top)** and **extracted locality (bottom)**.

SAMPLE RECORDINGS	NON-INTERVENTION LOCALITY			
	Frequency	Med. Cover (%)	Max. cover (%)	Aver. Rich.
<i>Litter</i>	32	5	75	10
<i>Stem</i>	97	10	60	9
<i>Stump</i>	14	10	60	9
<i>Branches</i>	86	5	55	9
<i>Snag</i>	19	1	3	9
<i>Picea abies</i>	63	3	80	10
<i>Sambucus nigra</i>	0 *	*	*	
<i>Larix decidua</i>	6	1	2	11
<i>Betula pendula</i>	4	5	5	10
<i>Salix caprea</i>	1	2	2	9
<i>Pinus sylvestris</i>	2	0.1	0.1	10
<i>Sorbus aucuparia</i>	10	0.5	3	11
<i>Calamagrostis villosa</i>	71	20	95	9
<i>Avenella felxuosa</i>	89	14	98	9
<i>Vaccinium myrtillus</i>	64	10	65	10
<i>Vaccinium vitis-idaea</i>	15	2	20	10
<i>Calluna vulgaris</i>	17	1	45	10
<i>Epilobium angustifolium</i>	80	10	70	9
<i>Luzula luzuloides</i>	13	4	10	10
<i>Rubus idaeus</i>	26	5	25	10
<i>Athyrium distentifolium</i>	6	5	5	11
<i>Dryopteris dilatata</i>	14	1	3	11
<i>Oxalis acetosella</i>	20	3	25	11
<i>Melampyrum pratense</i>	1	5	5	11
<i>Maianthemum bifolium</i>	12	0.1	3	11
<i>Senecio ovatus</i>	3	0.1	0.1	11
<i>Homogyne alpina</i>	7	1	5	12
<i>Luzula sylvatica</i>	0 *	*	*	
<i>Galeopsis speciosa</i>	0 *	*	*	
<i>Calamagrostis arundinacea</i>	0 *	*	*	
<i>Urtica dioica</i>	1	2	2	10
<i>Cirsium palustre</i>	0 *	*	*	
<i>Veronica officinalis</i>	0 *	*	*	
<i>Mycelis muralis</i>	1	1	1	6
<i>Carex canescens</i>	0 *	*	*	
<i>Carex ovalis</i>	0 *	*	*	
<i>Juncus effusus</i>	0 *	*	*	
<i>Dicranum sp.</i>	42	1	20	10
<i>Pleurozium sp.</i>	50	2	75	10
<i>Hylocomium sp.</i>	15	1	20	9
<i>Hypnum sp.</i>	32	0.5	5	11
<i>Polytrichum sp.</i>	23	2	40	10
<i>Sphagnum sp.</i>	15	7	35	10
<i>Plagiomnium sp.</i>	10	1	20	11

SAMPLE RECORDINGS	EXTRACTED LOCALITY			
	Frequency	Med. Cover (%)	Max. cover (%)	Aver. Rich.
<i>Litter</i>	3		10	9
<i>Stem</i>	14		5	7
<i>Stump</i>	20		5	7
<i>Branches</i>	30		5	6
<i>Snag</i>	0 *		*	*
<i>Picea abies</i>	20		5	8
<i>Sambucus nigra</i>	2		2	6
<i>Larix decidua</i>	20		1	7
<i>Betula pendula</i>	4		3	7
<i>Salix caprea</i>	2		1	8
<i>Pinus sylvestris</i>	4		1	7
<i>Sorbus aucuparia</i>	4		0.5	7
<i>Calamagrostis villosa</i>	79		25	6
<i>Avenella felxuosa</i>	73		27	7
<i>Vaccinium myrtillus</i>	53		5	7
<i>Vaccinium vitis-idaea</i>	8		4	7
<i>Calluna vulgaris</i>	14		2	8
<i>Epilobium angustifolium</i>	82		10	6
<i>Luzula luzuloides</i>	37		2	7
<i>Rubus idaeus</i>	30		5	7
<i>Athyrium distentifolium</i>	4		1	9
<i>Dryopteris dilatata</i>	4		1	7
<i>Oxalis acetosella</i>	0 *		*	*
<i>Melampyrum pratense</i>	7		2	7
<i>Maianthemum bifolium</i>	12		0.1	7
<i>Senecio ovatus</i>	4		0.5	6
<i>Homogyne alpina</i>	2		8	7
<i>Luzula sylvatica</i>	2		2	8
<i>Galeopsis speciosa</i>	4		13	6
<i>Calamagrostis arundinacea</i>	3		5	6
<i>Urtica dioica</i>	2		3	7
<i>Cirsium palustre</i>	1		1	6
<i>Veronica officinalis</i>	1		1	9
<i>Mycelis muralis</i>	0 *		*	*
<i>Carex canescens</i>	4		0.5	8
<i>Carex ovalis</i>	1		3	6
<i>Juncus effusus</i>	1		0.1	6
<i>Dicranum sp.</i>	11		0.5	8
<i>Pleurozium sp.</i>	13		1	8
<i>Hylocomium sp.</i>	1		4	7
<i>Hypnum sp.</i>	6		2	9
<i>Polytrichum sp.</i>	0 *		*	*
<i>Sphagnum sp.</i>	3		3	8
<i>Plagiomnium sp.</i>	1		0.1	11

