

Article

Salvage-Logging after Windstorm Leads to Structural and Functional Homogenization of Understory Layer and Delayed Spruce Tree Recovery in Tatra Mts., Slovakia

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Abstract: Stand-replacing disturbance and post-disturbance salvage-logging influence forest succession in different ways; however, limited knowledge regarding how salvage-logging affects vegetation patterns compared to natural development of forest ecosystems is still lacking. In this study, we described the diversity pattern of understory vegetation and tree regeneration in mountain spruce forest of Tatra Mountains, northern Slovakia, where a high severity windstorm affecting over 10,000 ha occurred in 2004. The area was consequently subjected to salvage-logging. We asked how the species composition, vegetation diversity, and its spatial heterogeneity were modified by severe salvage-logging. Vascular plants, deadwood coverage, and tree species densities were monitored on non-intervention (NI; $n = 108$) and salvage-logged (SL; $n = 95$) experimental plots (spatially nested design, sample plot area 3.14 m²) six and seven years after disturbance, respectively. The NI sites were structurally more diverse with post-windstorms legacies such as deadwood and pit and mound topography being recorded. The NI plots contained more late-successional plant and moss species that are commonly found in the pre-disturbance forest. The NI plots were also more diverse in terms of alpha- and beta-diversity with abundant natural regeneration of Norway spruce (*Picea abies* (L.) Karst). The structure of SL site was more homogeneous and its species composition shifted towards being dominated by grasses, although the site accommodated a higher number of plant species due to newly established pioneer plant- and tree species. The retreat of late-successional species in favour of grasses can lead to structural and functional homogenization of habitat and to delayed succession towards establishment of spruce forest. We conclude that the removal of wind-disturbance legacies significantly diverts natural successional pathways. We recommend avoiding salvage-logging in protected areas since large-scale application of salvage-logging reduces beta-diversity of the landscape.

Keywords: large-scale disturbance; salvage-logging; plant diversity; homogenization; successional pathway; deadwood

1. Introduction

In temperate conifer-dominated forests in the Northern Hemisphere, disturbances caused by strong winds together with bark-beetle outbreaks are important drivers of forest ecosystem composition, structure, and functioning [1–3]. Increasing frequency of severe windstorms [4] coupled with a century-old tradition of coniferous-oriented monoculture forestry has resulted in an increased extent and higher severity of storm events [3]. Historically, salvage-logging in central Europe has been used to reduce timber losses and curb bark beetle outbreaks to protect neighbouring undisturbed stands. However, studies focusing on natural successional processes following large wind disturbances are still rather limited. With increased risk of extreme storm events and bark beetle population gradation related to climate change [5], the role of salvage-logging in successional processes and biodiversity will become increasingly important. The main focus of foresters tends to be on post-disturbance species composition and future forest appearance [6–8].

Successional pathways and biodiversity are designed by post-disturbance forest composition and structure [9]. Tree, herb, and moss abundance and diversity are influenced by the live and dead tree composition and structure [10], and salvage-logging may thus change successional pathways. Non-intervention (NI) stands affected by windstorms are characterized by well-preserved pit and mound topography and abundant deadwood in the form of stems and snags [11,12], which may enhance the recruitment of tree seedlings and preserve the biological legacy of tree spatial patterns [13]. Deadwood can protect vegetation from snow gliding and erosion [14,15], encourage seed accumulation in tree wells in winter [13], provide nutrients to regeneration, and reduce the competition from highly competitive vegetation [16]. Deadwood can also form a buffer against soil evaporation and can retain soil moisture [17–19].

Some studies examined the successional pathways of areas subjected to salvage-logging and compared them to post-disturbance areas that receive no management [6,20]. Since the basic principle of biodiversity conservation and ecosystem management is to carry out interventions that are as consistent as possible with natural disturbance regimes [21,22], natural disturbances can increase species diversity [23], while additional stress caused by salvage-logging may lead to its decline [2,24]. Hewitt et al. [25] and Clavel et al. [26] described how diversity declines with increasing stress-level; i.e., how low rates of stress lead to random loss of rare species. If the stress increases, well-adapted specialists are replaced by stronger generalists, which leads to habitat homogenization and consequently to a decline in community functioning and ecosystem resilience [27–29].

Salvage-logging is applied extensively in many central European national parks irrespective of stand and landscape conditions [20,30]. If salvage-logging is not too extensive, or is carried out on a small scale, such intervention may be considered as beneficial for tree recruitment due to unlimited spread of seeds, perturbed surface as optimal seed bed, improved light conditions, and local increases in temperature [6,31]. However, salvage-logging is often applied throughout large wind-disturbed areas, which results in low amounts of deadwood, damage to advanced natural regeneration [32], and site perturbation (e.g., forest floor damage, reduction in pit and mound features). If desirable tree species do not regenerate in affected areas, competing species, such as grasses, invade the site and impede the establishment of spruce seedlings for a long time [33–35]. In severely damaged stands in central European mountain systems, highly-competitive grasses often dominate sites and restrict the establishment of other herb and tree species [36]. Species diversity therefore declines with only a few competitively strong species prevailing [26].

In November 2004, a large storm event, Bora, blew down extensive areas in the Tatra National Park in Slovakia. This led to a bark beetle outbreak affecting the total area of 12,600 ha with a total damage of 2.03 million m³ of timber [37] with around 165,000 m³ of timber left untreated [38]. Although the large-scale wind disturbances are part of the historical range of variability in the mountain forests in the High Tatras [39,40], the majority of the affected timber is commonly salvage-logged with the minority being left intact without any intervention applied [41]. The areas where any interventions have been absent are therefore believed to form an important ground for comparison of both natural and

human-influenced successional pathways. We hypothesized that after a large-scale wind disturbance, salvage-logged areas would show different successional pathways compared to non-intervention areas. The following questions were therefore proposed:

- (i) Will patterns of alpha and beta-diversity differ between non-intervention and salvage-logged sites?
- (ii) Will the late successional species be more prominent on the non-intervention site in comparison to the salvage-logged site?

2. Materials and Methods

2.1. Study Area

The study was conducted in Tatra National Park, which is located in the High Tatra Mountains in Slovakia. The climate of the mountain range is continental, with the mean annual precipitation of 864 mm (temperature peaks in June and July) and the mean annual temperature of 4.7 °C that ranges between −5.6 °C in January and 14.4 °C in July [39]. Forest soils are mainly dystic cambisols [42] and the vegetation is classified as spruce forest with *Vaccinium myrtillus* of the order *Piceion excelsae* and fir, fir-spruce forests (*Abietion albae* and *Vaccinio-Abietion*) [43]. The study sites are located within the altitude ranging between 1100 and 1400 m.

The area subjected to the study is dominated by secondary forests that had been managed in the past with only a small proportion of the areas being considered as primary forests. With the establishment of the National Park in 1949, the management practices were revised in order to extend the rotation and regeneration periods to create structurally diverse and resilient forests, although salvage-logging was still extensively applied in the National Park due to concerns about bark beetle outbreaks [37].

In November 2004, a large-scale catastrophic windthrow occurred leaving only scattered groups of individual living trees and solitaire living trees. The majority of the affected stands comprised of spruce (72.4%, average age 79 years) with the remainder consisting of Scots pine (9.6%, average age 75 years), larch (7.1%, average age 78 years), silver fir (2.4%, average age 80 years), alder (4.3%, average age 53 years), and birch (2.9%, average age 33 years [44]).

In an attempt to prevent a bark beetle outbreak, salvage-logging following the storm event was applied. Although stumps and branch biomass remained in the salvage-logged areas, large woody biomass was removed from 70% to 90% of the affected area with a help of large machinery. Impacts of the salvage-logging resulted in reduced pit and mound topography related to tree uprootings from the storm event, redistribution of remaining dead biomass material, and intensive and extensive soil surface perturbation and soil compaction. Nonetheless, the lack of empirical studies on post-disturbance forest regeneration encouraged the retention of 100 ha of windthrow forest (site dominated by a large number of broken and uprooted trees) where no salvage-logging was carried out.

2.2. Sampling Design

Two 100 ha sites of comparable forest type (i.e., larch-spruce forest; [41]) with similar geological, topological, topographical, climatological, and hydrological conditions were subjected to this study (non-intervention site (hereafter NI) coordinates: 20°15.2002' E, 49°09.5749' N; salvage-logged site (hereafter SL) coordinates: 20°09.7729' E, 49°07.2791' N; [41]). Eleven experimental plots (six in the NI site and five in the SL site) were established during the summer 2010 and 2011, i.e., six and seven years after the wind disturbance, respectively. Their location was randomly generated (at least 10 m from the forest edge) and their position was permanently marked. Each experimental plot comprised of twenty nested subplots ($r = 1$ m) that were placed every 10 m along two transects perpendicular to each other. The experimental plots were evenly stratified to account for environmental heterogeneity (Figure 1).

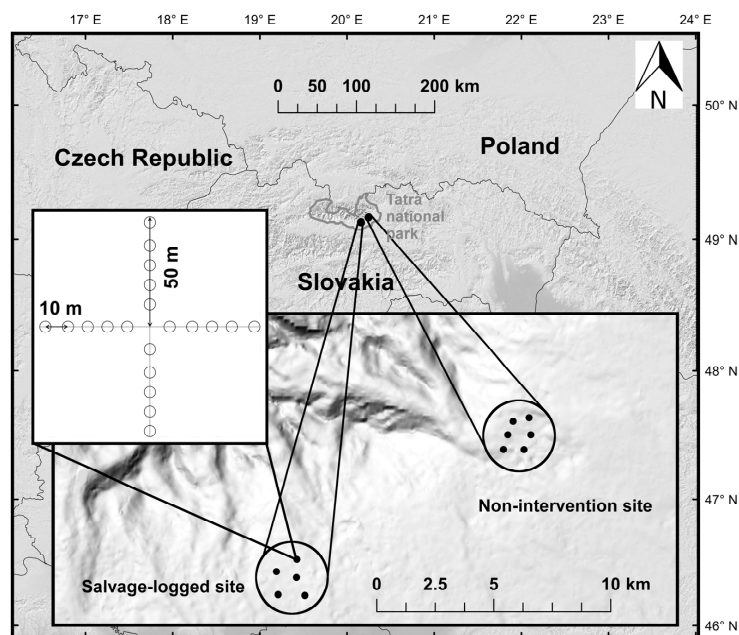


Figure 1. Sampling design: six and five experimental plots are located in the non-intervention and the salvage-logged sites found in the Tatra National Park (Slovakia), respectively. Each experimental plot is comprised of twenty circular subplots of $r = 1$ m (area: 3.14 m^2) that are arranged along two perpendicular transects.

The abundance of plant species and deadwood was recorded for each subplot. The present deadwood was classified into the following categories: stump (including the root plate), twigs litter, branches, downed stems, and standing snags. Quantities of individual deadwood categories, vascular plants, and mosses were recorded as proportion (%) of the plot cover. The frequency, non-zero median, and maximum cover of plant species and deadwood were recorded for each plot, species richness was calculated specifically for each subplot. All regeneration (i.e., trees ≤ 1.5 m in height) were counted in each subplot; trees > 1.5 m in height were considered as advanced natural regeneration and were excluded from the analyses. Pre- and post-disturbance natural regeneration was not distinguished due to the imprecise definitions of true seedling/sapling ages. Seventeen of the total 220 subplots were excluded since they were placed on, for example, brook, forwarding trail, peat bog, etc. (due to random allocation) and such locations were not considered to be resembling true forest conditions.

2.3. Statistical Analyses

Detrended correspondence analysis was used to detect spatial heterogeneity of the vegetation composition. Prior to analyses, the data representing deadwood and plant cover were transformed using square-root transformation that was performed in order to reduce the importance of common species whose presence was rather abundant [45]. Reducing the weight of rare species was not conducted. Euclidean distance was used as the dissimilarity measure to compare sample plots [45] since the species were considered linearly distributed along the environmental gradient [46].

Differences in species richness between experimental sites were explored using species accumulation curves according to Kindt's exact method [47]. Two species groups, i.e., "early successional species", appearing early after disturbance, and "late successional species", growing under conditions of closed-canopy, were distinguished following the classifications of Ellenberg [48] and Chytrý et al. [49].

Species diversity within (alpha-) and between (beta-) sites was described using functional species groups based on the dispersal types and life-strategies (i.e., trees, grasses, herbs, and mosses). The sites were compared using Shannon-Wiener index and species richness. Both measures were calculated for

all functional species groups and compared between sites using the non-parametric Kruskal-Wallis test. Beta-diversity was calculated using Euclidean distance for each site and the differences in beta-diversity between sites were compared with the permutation test for multivariate homogeneity using 999 iterations.

Non-metric dimensional scaling analysis was performed to detect differences in species composition and deadwood amounts for both NI and SL sites. Meanwhile the species matrix contained 22 species variables and 203 subplots, the environmental matrix comprised of seven items (one nominative variable for sites and six numerical variables for Ellenberg values) and 203 subplots. The numbers of spruce stems per experimental plot (i.e., natural regeneration of spruce) were also added to the species data in order to address the affinity to habitat preferences. The species data were square-rooted, centred, and scaled. The data for sites and Ellenberg values, on the other hand, were tested against canonical axes with permutation test (1999 iterations). Ellenberg indicator scores were obtained for vascular plants as the unweighted average values per subplot. Species significantly resident on NI or SL sites were estimated using indicator values for each site and species according to the frequencies of their occurrence. Finally, tree regeneration density between sites was compared using the Kruskal-Wallis test.

Statistical analyses of species abundances and frequencies were carried out using the programme JUICE [50]. Additional analyses were performed with R software (R Foundation for Statistical Computing, Vienna, Austria) with the indices and multivariate analyses being calculated with the help of the package “vegan” [51].

3. Results

Late-successional species were recorded to dominate the NI site (Table 1; the full version can be seen in Supplementary Materials) with the most frequently occurring species being *Vaccinium myrtillus* (L.) and *Dryopteris dilatata* (Hoffm.) A. Gray and tree seedlings of spruce (*Picea abies* (L.) Karst). The NI site had a higher frequency of mosses; e.g., *Sphagnum*, *Hylocomium*, and *Pleurozium*. The grass species *Avenella flexuosa* (L.) was also recorded to be more frequent, although having a lower coverage compared to the SL site. The presence of deadwood was common on the NI site, as demonstrated by high frequencies in all categories with the exception for the category ‘stump’.

Table 1. The frequency, the cover of plant species and deadwood categories, for subplots in non-intervention (NI) ($n = 108$) and salvage-logged (SL) ($n = 95$) sites are presented. Although all deadwood categories are included, species that occurred on 30 or more subplots of the NI site are shown. Values for all species are included in the Supplementary Materials.

	Non-Intervention Site						Salvage-Logged Site			
	Functional Group	Successional Stage	Frequency	Median Cover (%)	Maximum Cover (%)	Frequency per Subplot	Frequency	Median Cover (%)	Maximum Cover (%)	Frequency per Subplot
Species										
<i>Avenella flexuosa</i>	Grass	Early	89	20	85	10	75	25	85	6
<i>Epilobium angustifolium</i>	Herb	Early	78	10	95	9	82	15	70	6
<i>Calamagrostis villosa</i>	Grass	Early	73	29	100	9	79	34	100	6
<i>Vaccinium myrtillus</i>	Herb	Late	63	11	60	10	46	10	75	7
<i>Picea abies</i>	Tree	Late	56	3	80	10	20	5	25	7
<i>Sphagnum</i> sp.	Moss	Late	54	5	70	10	3	3	5	9
<i>Hylocomium</i> sp.	Moss	Late	50	2	20	10	3	3	5	9
<i>Rubus idaeus</i>	Herb	Early	35	10	55	9	40	5	55	7
<i>Pleurozium</i> sp.	Moss	Late	32	2	60	10	19	3	30	8
<i>Dryopteris dilatata</i>	Herb	Late	30	3	25	11	6	5	5	9
Deadwood										
Stems			95	10	60	9	14	5	20	7
Branches			85	5	55	9	30	5	95	6
Litter			32	2	9	10	3	3	3	8
Stumps			14	10	60	10	19	5	50	7
Snags			14	2	3	10	0			

The SL site was characterized by higher occurrence and median cover of grass species *Calamagrostis villosa* (Chaix) J. F. Gmel. and *A. flexuosa*. Pioneer species such as *Rubus idaeus* (L.) and *Epilobium angustifolium* (L.) were more frequently occurring at the SL site. Deadwood occurrence at the SL site was, however, much lower than in the case of the NI site with the exception of the category “stump”.

The total species richness on the NI site was represented by 29 species with the significant majority of the species comprised of late-successional specialists (Figure 2; shown by the lower pair of curves where only late-successional species are plotted). The average number of species per plot on the NI site was 6.8, which was greater in comparison to the mean of 5.4 species that were recorded on the SL site. Nonetheless, the total number of species occurring on the SL site clearly exceeded the species richness on the NI site as the total number of recorded species on the former site was 35.

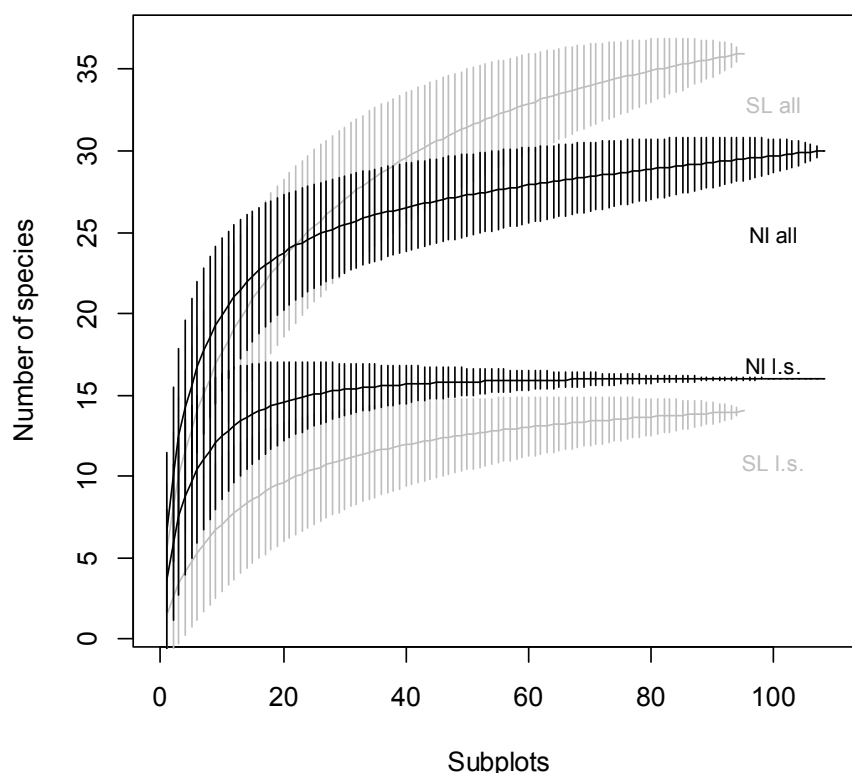


Figure 2. Species accumulation curves [47] for salvage-logged (SL) and non-intervention (NI) sites using two species groups; i.e., late successional species (l.s.) and all species (all). Vertical lines indicate confidence intervals estimated by the first order jack knife method; i.e., “all” refers to all species used while “l.s.” indicates late successional species.

Shannon-Wiener index values (S.-W.; $\chi^2 = 7.16$, $p = 0.007$) were significantly greater on the NI site as opposed to the SL site (Figure 3). Although the same significant difference was recorded for the group of mosses (species richness: $\chi^2 = 62.34$, $p < 0.001$, S.-W.: $\chi^2 = 42.45$, $p < 0.001$), the SL site was significantly richer in grass species (species richness: $\chi^2 = 8.17$, $p = 0.004$, S.-W.: $\chi^2 = 3.91$, $p = 0.05$). Herb (species richness: $\chi^2 = 0.86$, $p = 0.35$, S.-W.: $\chi^2 = 0.01$, $p = 0.91$) and tree species (species richness: $\chi^2 = 3.83$, $p = 0.05$, S.-W.: $\chi^2 = 0.09$, $p = 0.76$) did not show any significant trends in alpha-diversity between the tested sites.

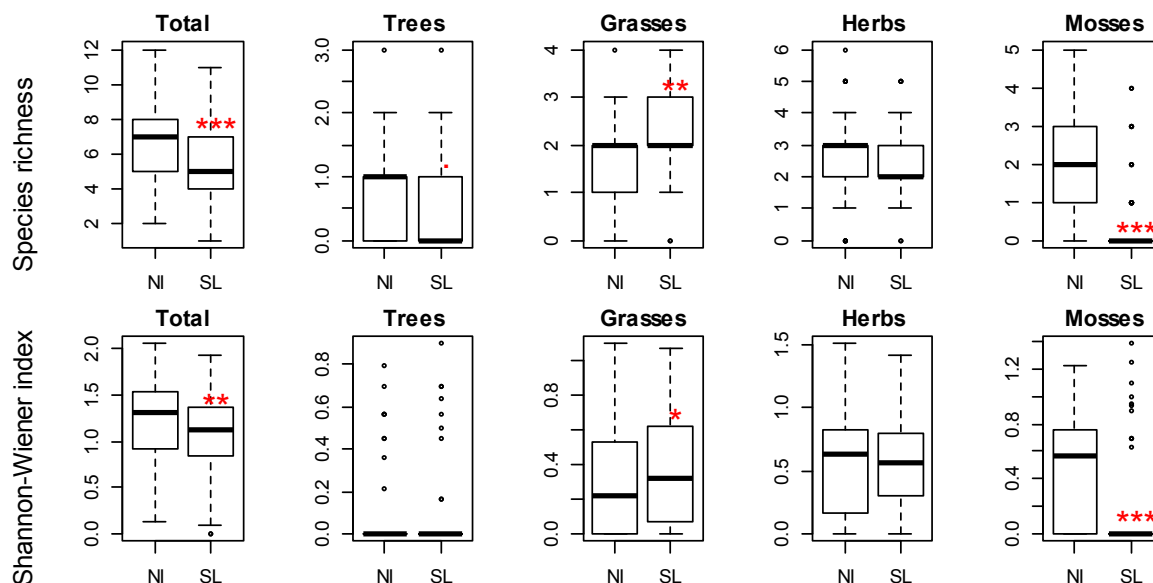


Figure 3. Boxplots presenting comparisons of species richness (top row) and Shannon-Wiener index (bottom row) for all species pooled together (i.e., Total), for tree species, and for individual plant functional groups for both NI and SL sites (statistical significance: “****” $p < 0.001$, “***” $p < 0.01$, “**” $p < 0.05$, “*” $p < 0.1$).

Beta-diversity was also recorded to be higher on the NI site ($F_{(1,197)} = 10.25$, $p = 0.003$; Figure 4). This difference was significant for mosses ($F_{(1,197)} = 75.67$, $p < 0.001$), marginally significant for trees ($F_{(1,197)} = 3.13$, $p = 0.08$), and non-significant for herbs ($F_{(1,197)} = 1.98$, $p = 0.15$) and grasses ($F_{(1,197)} = 0.84$, $p = 0.39$).

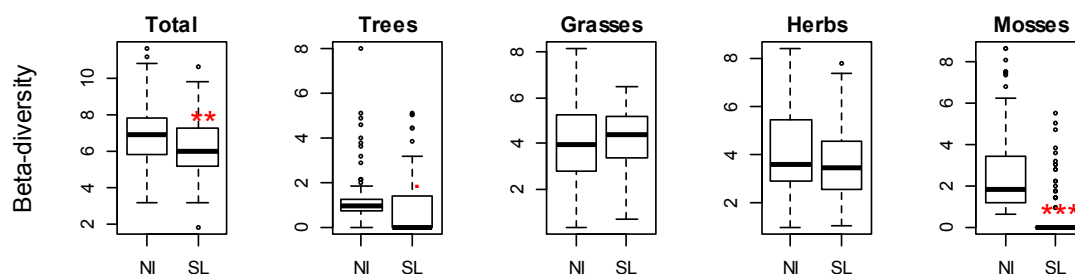


Figure 4. Boxplot comparisons of beta diversity for all species pooled together (i.e., Total), for tree species, and for individual plant functional groups for both NI and SL sites (statistical significance: “****” $p < 0.001$, “***” $p < 0.01$, “**” $p < 0.05$, “*” $p < 0.1$, “ ” not significant).

NI and SL significantly differed in species composition ($r^2 = 0.203$; $p < 0.001$), as both communities were distinctively distributed at the opposite site of the ordination space (Figure 5). Structurally diverse downed stems, branches, and other types of deadwood created the heterogeneity of habitats on the NI site. Species such as *Oxalis acetosella* (L.) that are typical for forest understorey dominated the vegetation composition on the NI site along with naturally regenerating spruce. Moss communities formed by *Dicranum* sp., *Hypnum* sp., *Plagiomnium* sp., *Pleurozium* sp., *Polytrichum* sp., and *Sphagnum* sp. were recorded to be highly abundant.

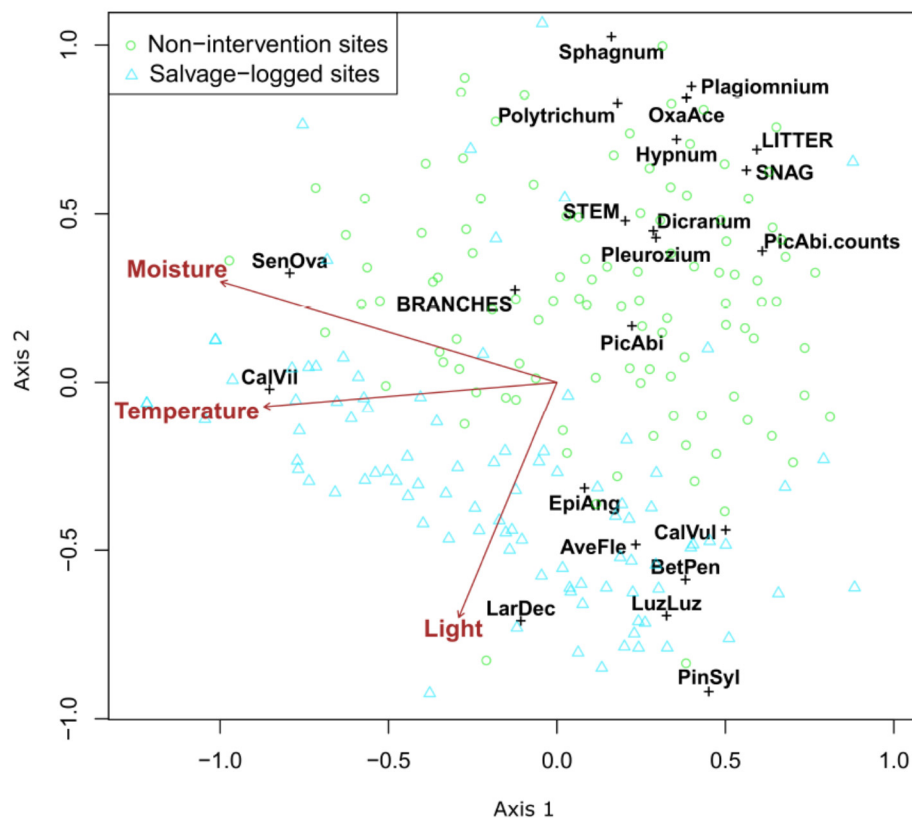


Figure 5. Non-metric multidimensional scaling (NMDS) ordination of vegetation and deadwood legacies on NI and SL sites. Vectors show passively projected Ellenberg indicator values where only those with $r^2 > 0.2$ and p -value < 0.001 are shown. The vector orientation shows the direction of the gradient with its length being proportional to the correlation between the variable and the ordination. Acronyms follows: “Ave fle” *Avenella flexuosa*, “Bet pen” *Betula pendula*, “Cal vil” *Calamagrostis villosa*, “Cal vul” *Calluna vulgaris*, “Epi ang” *Epilobium angustifolium*, “Gal bif” *Galeopsis bifida* (Boenn.), Lar dec *Larix decidua*, “Luz” *Luzula luzuloides*, “Oxa ace” *Oxalis acetosella*, “Pic abi” *Picea abies*, “Pica abi (counts)” —number of stems of *P. abies* natural regeneration per subplot, “Pin syl” *Pinus sylvestris*, and “Sen ova” *Senecio ovatus* (G. Gaertn. B. Mey. Et Scherb.) Willd.

According to the Ellenberg values, the SL site was characterized by higher light levels ($r^2 = 0.15$; $p < 0.001$) and temperature ($r^2 = 0.20$; $p < 0.001$) as opposed to the NI site. The SL site accommodated for much lower cover of downed stems and other deadwood types with grasses, in particular *C. villosa* that dominated the site, and whose presence was positively associated with the moisture gradient ($r^2 = 0.29$; $p < 0.001$). Light-demanding tree species *Betula pendula* (Roth), *Pinus sylvestris* (L.), and *Larix decidua* (Mill.) also showed closer association to the SL site. While *Calluna vulgaris* (L.) and *Luzula luzuloides* (Lam.) Dandy et. Wilmott. were found on rather freely-drained locations with sufficient light predominantly on the SL site, *A. flexuosa* was more frequent on the NI area, but more abundant on the SL site where it showed a patchy presence (Table 1). The nitrogen demanding pioneer species such as *E. angustifolium* indicated a transition step between fully stocked forests and clearcut stands. Ellenberg indicators for continentality ($r^2 = 0.02$; $p = 0.09$), nutrients ($r^2 = 0.03$; $p = 0.07$), and soil reaction ($r^2 = 0.001$; $p = 0.91$) were not significantly attributed to the species composition.

Meanwhile the SL site was dominated by light-demanding and early-successional vegetation species, the NI site hosted species typical for forest understorey, as based on the indicator value analyses (Table 2).

Table 2. Species significantly indicative of either SL (salvage-logged) or NI (non-intervention) site.

Species	Site	Indicator Value	p-Value	Frequency
<i>Calamagrostis villosa</i>	SL	0.50	0.004	150
<i>Luzula luzuloides</i>	SL	0.32	0.001	50
<i>Larix decidua</i>	SL	0.20	0.001	26
<i>Melampyrum pratense</i>	SL	0.06	0.046	8
<i>Carex canescens</i>	SL	0.04	0.05	4
<i>Picea abies</i>	NI	0.42	0.001	83
<i>Pleurozium</i> sp.	NI	0.35	0.001	63
<i>Dicranum</i> sp.	NI	0.29	0.002	53
<i>Polytrichum</i> sp.	NI	0.21	0.001	23
<i>Hypnum</i> sp.	NI	0.21	0.003	38
<i>Oxalis acetosella</i>	NI	0.19	0.001	20
<i>Sphagnum</i> sp.	NI	0.13	0.003	18
<i>Hylocomium</i> sp.	NI	0.13	0.003	16
<i>Plagiomnium</i> sp.	NI	0.09	0.013	11

P. abies was recorded to be the most abundant tree species on both tested sites; i.e., 8611 stems ha⁻¹ on NI site and 3118 stems ha⁻¹ on SL site (Figure 6). However, the density was significantly higher at the NI site ($\chi^2 = 25.99$, $p < 0.001$). Although more light demanding species occurred on the SL site, statistically significant difference was found only for *Larix decidua* Mill. was ($\chi^2 = 9.59$, $p = 0.002$).

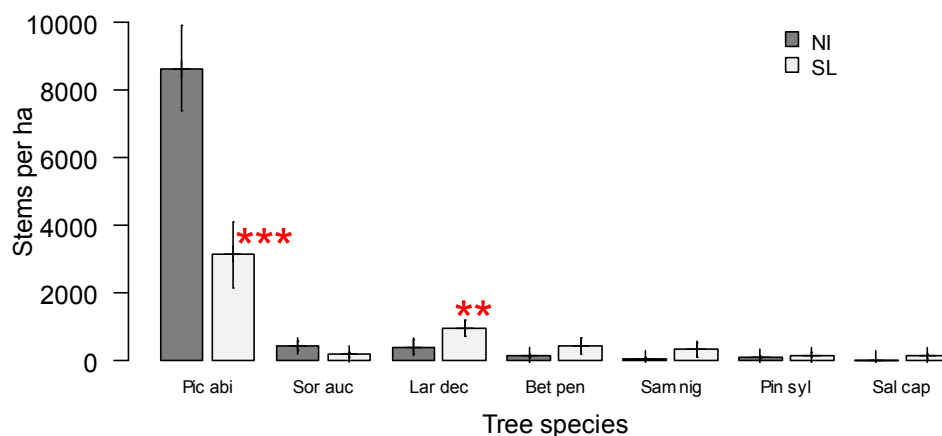


Figure 6. Bar plots representing counts (stems/ha) of natural tree regeneration for NI and SL sites (statistical significance: “***” < 0.001 , “**” < 0.01 , “ ” not significant). Acronyms used: “Bet pen” *Betula pendula*, “Lar dec” *Larix decidua*, “Pic abi” *Picea abies*, “Pin syl” *Pinus sylvestris*, “Sal cap” *Salix caprea* (L.), “Sam nig” *Sambucus nigra* (L.), and “Sor auc” *Sorbus aucuparia* (L.).

4. Discussion

A higher number of species was observed on the SL site when compared to the NI site following a severe windstorm event in 2004. However, increased species diversity on the SL sites was boosted by the establishment of species typically found on sites after clearcutting (e.g., grasses). This is associated with the loss of other species, particularly mosses that are characteristic of late-successional forests. The species richness between the two researched stands differed as higher species richness of shade-tolerant species was found on the NI site in comparison to the SL stands where grasses and pioneer species prevailed. The natural regeneration of spruce was more abundant and widely distributed on the NI site where it exhibited a pattern of lower densities of early-successional tree species.

We detected strong cumulative severity of salvage-logging operations. The species composition shift, decreased beta-diversity, and deadwood removal jointly causing late-successional species to

decline indicated a strong severity effect of salvage-logging. Such findings are consistent with those of Rumbaitis del Rio [2] who examined the effect of windthrow and salvage-logging on herbaceous vegetation in subalpine forests of northwestern Colorado and found that vegetation cover and species diversity were reduced in salvage-logged areas in comparison to areas where the windthrow was not followed by any intervention. Nonetheless, this cumulative severity effect was not observed in all related studies. For instance, salvage-logging was reported to have no negative impact on seedling density, species richness, or diversity in mixed oak–pine forest of North America [52]. The differences could be attributed to different impacts of logging operations on soil conditions in different ecosystems. The impact in temperate broadleaved forests could be smaller than in the case of montane coniferous forest on shallow soils [52].

Our results—based on a spruce stand effected solely by large-scale and severe windstorm—show that natural regeneration could take place without major shifts in plant species composition. However, a similar pattern was also observed after a large-scale bark beetle outbreak [53,54]. Although this shows that both severe wind and insect disturbances have similar influences on plant communities, both disturbance types are largely different from salvage-logging in terms of their effect on plant community. It is important to note that salvage-logging practices in mountain spruce forest pose more severe impacts on the ecosystem than windstorms. Lindenmayer et al. [24] stated increased solar radiation, soil disruption and compaction, removal of deadwood and uprooted root plates, homogenization of pit and mound topography, etc. as the major consequences of salvage-logging; such effects are therefore likely to lead to major shifts in plant species composition in European mountain spruce forests as supported by the current study.

The most favourable conditions for facilitating the natural regeneration of spruce are vegetation communities that are commonly found on forest floor under full canopy. Retaining deadwood is also considered to be positive, as supported by the findings from the experimental plots where sufficient post-disturbance deadwood was found and thus accommodated for considerable amounts of regeneration. Lying logs probably created a buffer to intensive evapotranspiration [17–19]. Humid and shady conditions do not allow for extensive expansion of grasses to such microsites [55], thereby preventing intensive interspecific competition. In addition, lying stems and snags as well as the presence of specific microtopography—typical post-disturbance legacies—create features promoting heterogeneity in height distribution and spatial randomness of tree regeneration [7,13]. Although natural regeneration of spruce was recorded on the salvage-logged stands in our study, its densities were smaller in comparison to the site where no intervention was carried out, though still more abundant than other tree species. Jonášová et al. [56] observed a similar pattern and attributed the lower number of spruce saplings at the salvage-logged sites to the lack of post-disturbance recruitment. Some of the established saplings and seedlings were destroyed mechanically by uprooting, by fallen stems caused by the wind disturbance, and importantly by the salvage-logging operation itself [56].

A major proportion of spruce regeneration was found to be accompanied by mosses and *Oxalis acetosella*. Since *O. acetosella* is indicative of shady conditions prevailing under closed forest canopy [48], where light demanding competitive forbs or grasses are excluded by shade, the germination and early growth of shade-tolerant tree species is thus favoured. Some authors consider mosses to be an unsuitable seedbed due to their susceptibility to desiccation during seasonal droughts [16,57,58]. Although Brang [59] described the occurrence of *O. acetosella* as an unfavourable seedbed, other studies found it suitable for natural regeneration (e.g., Hanssen [35] and Hanssen [60]). However, it is important to note that the abovementioned survival studies only refer to the behaviour of germinants and seedlings in the first years following their germination that are characteristic of increased mortality of spruce regeneration due to their insufficiently developed root system [16,61,62].

Salvage-logging on our experimental sites significantly reduced the species richness and the moss cover. Such findings are consistent with Jonášová and Prach [20] who also reported that salvage-logging following bark beetle outbreak decreased the cover of mosses. One of the possible explanations for this is the increased solar radiation on the salvage-logged site, which results in a decrease in species

sensitive to light. This results in greater environmental filtering for e.g., shade-bearing bryophytes due to the reduced retention of deadwood that is crucial for their survival [63]. Mosses thrive in the shade of lying logs, but their occurrence tends to decrease when the deadwood is removed. In such a case, moss species are replaced by more light-demanding species [20]. Such a shift in moss species composition was also confirmed by Thorn et al. [63] in a study that focused on salvage-logging after windthrow.

After subsequent salvage-logging, plant species richness may increase due to germination of pioneer and ruderal species [64] as well as due to the contemporary invasion of many species in places that are transiently free of competition, which is also supported by our study. Nevertheless, grasses, particularly *C. villosa*, colonized most of the areas in our study that experienced soil damage due to logging operations or that were free of any vegetation. The life history traits of grasses include adaptability to acidic mineral soil, large and deep root systems that allow grasses to resist to drought and, to certain extent, to pathogens and herbivores [55]. *C. villosa* has high indicator values for soil moisture according to Ellenberg [48]. Nevertheless, *C. villosa* accumulates water and nutrients in its dense root-system thereby preventing other species to benefit from growth and effectively suffocating them in the upper soil layer [55].

Management Implications

This study indicates that salvage-logging after large windstorm events can alter early successional pathways compared to non-intervention areas. In the case of applying no intervention, the species composition is likely to be similar to the conditions prior to the disturbance, although the spatial and structural heterogeneity increases. The salvage-logging causes shift in species composition, as the conditions following the logging operation facilitate the dominance of more light-demanding and pioneer species. Kramer et al. [6] stated different regeneration patterns following salvage-logging, with more abundant natural regeneration occurring on plots where the timber was at least partially extracted. This may be explained by the fact that the plot was located nearby a seed source, but also by the existence of seedbank that was created by more diverse composition of the former forest; i.e., spruce and European beech (*Fagus sylvatica* L.). If the logging operation is carefully performed and avoids damaging the advanced natural regeneration, the survival of formerly established seedlings and small trees is thus favoured [6]. The importance of supporting advanced regeneration in order to restore the forest stand following a large-scale windthrow event was also concluded by other studies (e.g., [56,65]).

In order to promote structural heterogeneity and to preserve advanced natural regeneration after large-scale windthrow, we recommend careful execution of the logging operations where patches of snags and lying stems are retained [6]. Although Newton et al. [66] considered salvage-logging to be beneficial for higher regularity in the spatial pattern of tree regeneration, on our sites, on the other hand, the dead stems seemed to have fulfilled the function of spatial separator for groups of naturally regenerating individuals and therefore contributed towards increased differentiation in height distribution. The post-disturbance structural heterogeneity in height and spatial distribution was reported to be even higher in forest than undergone natural development following natural disturbance [9].

5. Conclusions

The stand where no intervention was applied showed greater heterogeneity in species distribution with the major differences attributed to deadwood structures, which differentiated environmental conditions along the light and moisture gradient. Evidence for decreased structural heterogeneity in the salvage-logged stands was found as the total alpha- and beta-diversity was lower compared to the non-intervention area.

The presence of deadwood seems to sustain the structural conditions of the former spruce forest with plots where no timber extraction was carried out following the path towards earlier re-establishment of spruce forest. Competition from grasses and the damage to ground vegetation, tree regeneration, and forest floor caused by logging operations likely contributed to the reduced

natural regeneration of spruce and promoted the regeneration of pioneer tree species on salvage-logged sites by exposing mineral soil and allowing increased light levels to reach the forest floor. Surprisingly, spruce was the most frequently naturally regenerating tree species on the salvage-logged site, though less frequent than on the non-intervention site. Pioneer tree species were found to be more abundant on salvage-logged sites.

The complete extraction of timber from disturbance-affected sites not only reduces the microsite diversity that generally favours natural regeneration of spruce spatially as well as temporally, but it also encourages the spread of grasses such as *C. villosa* that eventually impede the natural regeneration of spruce. In order to promote the structural diversification in forest stands and to sustain the biodiversity and successful natural regeneration of spruce in the continental mountain forests of the Carpathian Mountains, based on our findings, we recommend at least a partial retention of deadwood in the case that salvage-logging is applied.

Nomenclature: Kubát et al. ([67]; vascular plants), Kremer and Mühle ([68]; mosses at genera level).

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/8/3/88/s1, Table S1: Complete list of plant species.

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Author Contributions: Z.M. designed the experiments; Z.M. and R.B. performed the experiments; Z.M. and T.W. analyzed the data; each of the authors wrote the paper.

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Abbreviations

The following abbreviations are used in this manuscript:

NI non-intervention
SL salvage-logged

References

1. Čada, V.; Morrissey, R.C.; Michalová, Z.; Bače, R.; Janda, P.; Svoboda, M. Frequent Severe Natural Disturbances and Non-Equilibrium Landscape Dynamics Shaped the Mountain Spruce Forest in Central Europe. *For. Ecol. Manag.* **2016**, *363*, 169–178. [CrossRef]
2. Rumbaitis del Rio, C.M. Changes in Understory Composition Following Catastrophic Windthrow and Salvage Logging in a Subalpine Forest Ecosystem. *Can. J. For. Res.* **2006**, *36*, 2943–2954. [CrossRef]
3. Seidl, R.; Schelhaas, M.; Lexer, M.J. Unraveling the Drivers of Intensifying Forest Disturbance Regimes in Europe. *Glob. Chang. Biol.* **2011**, *17*, 2842–2852. [CrossRef]
4. Usbeck, T.; Wohlgemuth, T.; Dobbertin, M.; Pfister, C.; Bürgi, A.; Rebetez, M. Increasing Storm Damage to Forests in Switzerland from 1858 to 2007. *Agric. For. Meteorol.* **2010**, *150*, 47–55. [CrossRef]
5. Lindner, M.; Maroschek, M.; Netherer, S.; Kremer, A.; Barbati, A.; Garcia-Gonzalo, J.; Seidl, R.; Delzon, S.; Corona, P.; Kolström, M.; et al. Climate Change Impacts, Adaptive Capacity, and Vulnerability of European Forest Ecosystems. *For. Ecol. Manag.* **2010**, *259*, 698–709. [CrossRef]
6. Kramer, K.; Brang, P.; Bachofen, H.; Bugmann, H.; Wohlgemuth, T. Site Factors are More Important than Salvage Logging for Tree Regeneration After Wind Disturbance in Central European Forests. *For. Ecol. Manag.* **2014**, *331*, 116–128. [CrossRef]
7. Bače, R.; Svoboda, M.; Janda, P.; Morrissey, R.C.; Wild, J.; Clear, J.L.; Čada, V.; Donato, D.C. Legacy of Pre-Disturbance Spatial Pattern Determines Early Structural Diversity Following Severe Disturbance in Montane Spruce Forests. *PLoS ONE* **2015**, *10*, e0139214. [CrossRef] [PubMed]

8. Kulakowski, D.; Seidl, R.; Holeksa, J.; Kuuluvainen, T.; Nagel, T.A.; Panayotov, M.; Svoboda, M.; Thorn, S.; Vacchiano, G.; Whitlock, C.; et al. A Walk on the Wild Side: Disturbance Dynamics and the Conservation and Management of European Mountain Forest Ecosystems. *For. Ecol. Manag.* **2016**. [[CrossRef](#)]
9. Donato, D.C.; Campbell, J.L.; Franklin, J.F. Multiple Successional Pathways and Precocity in Forest Development: Can some Forests be Born Complex? *J. Veg. Sci.* **2012**, *23*, 576–584. [[CrossRef](#)]
10. Franklin, J.F. Preserving Biodiversity: Species, Ecosystems, Or Landscapes? *Ecol. Appl.* **1993**, *3*, 202–205. [[CrossRef](#)] [[PubMed](#)]
11. Ulanova, N.G. The Effects of Windthrow on Forests at Different Spatial Scales: A Review. *For. Ecol. Manag.* **2000**, *135*, 155–167. [[CrossRef](#)]
12. Kupferschmid, A.D.; Brang, P.; Schönenberger, W.; Bugmann, H. Predicting Tree Regeneration in Picea Abies Snag Stands. *Eur. J. For. Res.* **2006**, *125*, 163–179. [[CrossRef](#)]
13. Wild, J.; Kopecký, M.; Svoboda, M.; Zenáhlíková, J.; Edwards-Jonášová, M.; Herben, T. Spatial Patterns with Memory: Tree Regeneration After stand-replacing Disturbance in Picea Abies Mountain Forests. *J. Veg. Sci.* **2014**, *25*, 1327–1340. [[CrossRef](#)]
14. Baier, R.; Meyer, J.; Göttlein, A. Regeneration Niches of Norway Spruce (*Picea Abies* [L.] Karst.) Saplings in Small Canopy Gaps in Mixed Mountain Forests of the Bavarian Limestone Alps. *Eur. J. For. Res.* **2007**, *126*, 11–22. [[CrossRef](#)]
15. Büttler, R.; Lachat, T.; Schlaepfer, R. *Grundlagen Für Eine Alt-Und Totholzstrategie Der Schweiz*; Laboratorium für Ökosystemmanagement (GECOS): Lausanne, Switzerland, 2005.
16. Holeksa, J.; Zywiec, M.; Parusel, J.; Szewczyk, J.; Zielonka, T. *Subalpine Spruce Forests in the Babia Góra National Park. Structure, Production, Coarse Woody Debris and Regeneration Processes of Norway Spruce Natural Forest in National Nature Reserves Babia Hora and Pilsko*; Technical University in Zwolen: Zwolen, Poland, 2008; pp. 49–96.
17. Stevens, V. *The Ecological Role of Coarse Woody Debris: An Overview of the Ecological Importance of CWD in BC Forests*; Ministry of Forests, Research Program: Victoria, BC, Canada, 1997.
18. Bottero, A.; Garbarino, M.; Long, J.N.; Motta, R. The Interacting Ecological Effects of Large-Scale Disturbances and Salvage Logging on Montane Spruce Forest Regeneration in the Western European Alps. *For. Ecol. Manag.* **2013**, *292*, 19–28. [[CrossRef](#)]
19. Marzano, R.; Garbarino, M.; Marcolin, E.; Pividori, M.; Lingua, E. Deadwood Anisotropic Facilitation on Seedling Establishment After a Stand-Replacing Wildfire in Aosta Valley (NW Italy). *Ecol. Eng.* **2013**, *51*, 117–122. [[CrossRef](#)]
20. Jonášová, M.; Prach, K. The Influence of Bark Beetles Outbreak vs. Salvage Logging on Ground Layer Vegetation in Central European Mountain Spruce Forests. *Biol. Conserv.* **2008**, *141*, 1525–1535. [[CrossRef](#)]
21. Keeton, W.S. Managing for Late-successional/old-Growth Characteristics in Northern Hardwood-Conifer Forests. *For. Ecol. Manag.* **2006**, *235*, 129–142. [[CrossRef](#)]
22. Keeton, W.; Chernyavskyy, M.; Gratzer, G.; Main-Knorn, M.; Shpylchak, M.; Bihun, Y. Structural Characteristics and Aboveground Biomass of old-growth spruce–fir Stands in the Eastern Carpathian Mountains, Ukraine. *Plant Biosyst.* **2010**, *144*, 148–159. [[CrossRef](#)]
23. Lehnert, L.W.; Bässler, C.; Brandl, R.; Burton, P.J.; Müller, J. Conservation Value of Forests Attacked by Bark Beetles: Highest Number of Indicator Species is found in Early Successional Stages. *J. Nat. Conserv.* **2013**, *21*, 97–104. [[CrossRef](#)]
24. Lindenmayer, D.B.; Burton, P.J.; Franklin, J.F. *Salvage Logging and Its Ecological Consequences*; Island Press: Washington, DC, USA, 2012.
25. Hewitt, J.; Thrush, S.; Lohrer, A.; Townsend, M. A Latent Threat to Biodiversity: Consequences of Small-Scale Heterogeneity Loss. *Biodivers. Conserv.* **2010**, *19*, 1315–1323. [[CrossRef](#)]
26. Clavel, J.; Julliard, R.; Devictor, V. Worldwide Decline of Specialist Species: Toward a Global Functional Homogenization? *Front. Ecol. Environ.* **2011**, *9*, 222–228. [[CrossRef](#)]
27. Lockwood, J.L.; Pimm, S.L. Biological Diversity: Species: Would any of them be Missed? *Curr. Biol.* **1994**, *4*, 455–457. [[CrossRef](#)]
28. Peterson, G.; Allen, C.R.; Holling, C.S. Ecological Resilience, Biodiversity, and Scale. *Ecosystems* **1998**, *1*, 6–18. [[CrossRef](#)]
29. Bengtsson, J.; Nilsson, S.G.; Franc, A.; Menozzi, P. Biodiversity, Disturbances, Ecosystem Function and Management of European Forests. *For. Ecol. Manag.* **2000**, *132*, 39–50. [[CrossRef](#)]

30. Mikoláš, M.; Tejkal, M.; Kuemmerle, T.; Griffiths, P.; Svoboda, M.; Hlásny, T.; Leitão, P.J.; Morrissey, R.C. Forest Management Impacts on Capercaillie (Tetrao Urogallus) Habitat Distribution and Connectivity in the Carpathians. *Landsc. Ecol.* **2017**, *32*, 163–179. [CrossRef]
31. White, P.S.; Jentsch, A. The search for generality in studies of disturbance and ecosystem dynamics. In *Progress in Botany: Genetics Physiology Systematics Ecology*; Springer: Berlin/Heidelberg, Germany, 2001; pp. 399–450.
32. Lindenmayer, D.; Noss, R. Salvage Logging, Ecosystem Processes, and Biodiversity Conservation. *Conserv. Biol.* **2006**, *20*, 949–958. [CrossRef] [PubMed]
33. Nilsson, U.; Örlander, G. Water Uptake by Planted Picea Abies in Relation to Competing Field Vegetation and Seedling Rooting Depth on Two Grass-Dominated Sites in Southern Sweden. *Scand. J. For. Res.* **1999**, *14*, 312–319. [CrossRef]
34. Karlsson, M.; Nilsson, U.; Örlander, G. Natural Regeneration in Clear-Cuts: Effects of Scarification, Slash Removal and Clear-Cut Age. *Scand. J. For. Res.* **2002**, *17*, 131–138. [CrossRef]
35. Hanssen, K.H. Effects of Seedbed Substrates on Regeneration of Picea Abies from Seeds. *Scand. J. For. Res.* **2002**, *17*, 511–521. [CrossRef]
36. Dovčiak, M.; Hrivnák, R.; Ujházy, K.; Gömöry, D. Seed Rain and Environmental Controls on Invasion of Picea Abies into Grassland. *Plant Ecol.* **2008**, *194*, 135–148. [CrossRef]
37. Jankovič, J.; Celer, S.; Caboun, V.; Fleischer, P.; Gubka, K.; Hlavac, P.; Chromek, I.; Juleny, J.; Kamensky, M.; Koren, M. *Projekt Revitalizácie Lesných Ekosystémov Na Území Vysokých Tatier Postihnutom Veternou Kalamitou Dňa 19. 11. 2004*; Národné Lesnícke Centrum: Zvolen, Slovakia, 2007.
38. Vakula, J.; Zúbrik, M.; Brutovský, D.; Gubka, A.; Ferenčík, J.; Kaštier, P. *Forest Conservation Project of High Tatra National Park After Windstorm of November 2004*; National Forest Centre, Forest Research Institute: Zvolen, Slovakia, 2007.
39. Zielonka, T.; Holeksa, J.; Fleischer, P.; Kapusta, P. A tree-ring Reconstruction of Wind Disturbances in a Forest of the Slovakian Tatra Mountains, Western Carpathians. *J. Veg. Sci.* **2010**, *21*, 31–42. [CrossRef]
40. Janda, P.; Trotsiuk, V.; Mikoláš, M.; Bače, R.; Nagel, T.A.; Seidl, R.; Seedre, M.; Morrissey, R.C.; Kucbel, S.; Jaloviar, P.; et al. The Historical Disturbance Regime of Mountain Norway Spruce Forests in the Western Carpathians and its Influence on Current Forest Structure and Composition. *For. Ecol. Manag.* **2016**. [CrossRef]
41. Fleischer, P.; Homolová, Z. Long-Term Research on Ecological Condition in the Larch-Spruce Forests in High Tatras After Natural Disturbances. *Lesnícky Časopis For. J.* **2011**, *57*, 237–250.
42. Gömöryová, E.; Střelcová, K.; Škvařina, J.; Bebej, J.; Gömöry, D. The Impact of Windthrow and Fire Disturbances on Selected Soil Properties in the Tatra National Park. *Soil Water Res.* **2008**, *3*, 574–580.
43. Budzáková, M.; Galvánek, D.; Littera, P.; Sibik, J. The Wind and Fire Disturbance in Central European Mountain Spruce Forests: The Regeneration After Four Years. *Acta Soc. Bot. Pol.* **2013**, *82*. [CrossRef]
44. Koreň, M. Vetrová Kalamita 19. Novembra 2004–Nové Pohľady a Konsekvencie. *Tatry* **2005**, *44*, 6–29.
45. Krebs, C. *Ecological Methodology*, 2nd ed.; A. Wesley Longman: New York, NY, USA, 1999.
46. Lepš, J.; Šmilauer, P. *Mnohorozměrná Analýza Ekologických Dat*; Biologická Fakulta Jihočeské Univerzity v Českých Budějovicích: České Budějovice, Czech Republic, 2000.
47. Kindt, R.; van Damme, P.; Simons, A. Patterns of Species Richness at Varying Scales in Western Kenya: Planning for Agroecosystem Diversification. *Biodivers. Conserv.* **2006**, *15*, 3235–3249. [CrossRef]
48. Ellenberg, H.; Weber, H.E.; Düll, R.; Wirth, V.; Werner, W.; Paulißen, D. *Zeigerwerte von Pflanzen in Mitteleuropa*; Verlag Erich Goltze KG: Göttingen, Germany, 1992.
49. Chytrý, M.; Kučera, T.; Kočí, M.; Grulich, V.; Lustyk, P. *Katalog Biotopů České Republiky*; Agentura Ochrany Přírody a Krajiny ČR: Praha, Czech Republic, 2001.
50. Tichý, L.; Bruehlheide, H. JUICE, Software for Vegetation Classification. *J. Veg. Sci.* **2002**, *13*, 451–453.
51. Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Wagner, H. Package vegan: Community ecology package. R package version 2.2-0. 2014. Available online: <http://cran.rproject.org/web/packages/vegan/> (accessed on 14 January 2014).
52. Peterson, C.J.; Leach, A.D. Limited Salvage Logging Effects on Forest Regeneration After moderate-severity Windthrow. *Ecol. Appl.* **2008**, *18*, 407–420. [CrossRef] [PubMed]
53. Fischer, A.; Fischer, H.S.; Kopecký, M.; Macek, M.; Wild, J. Small Changes in Species Composition Despite Stand-Replacing Bark Beetle Outbreak in Picea Abies Mountain Forests 1. *Can. J. For. Res.* **2015**, *45*, 1164–1171. [CrossRef]

54. Zeppenfeld, T.; Svoboda, M.; DeRose, R.J.; Heurich, M.; Müller, J.; Čížková, P.; Starý, M.; Bače, R.; Donato, D.C. Response of Mountain Picea Abies Forests to stand-replacing Bark Beetle Outbreaks: Neighbourhood Effects Lead to self-replacement. *J. Appl. Ecol.* **2015**, *52*, 1402–1411. [[CrossRef](#)]
55. Pyšek, P. Dominant Species Exchange during Succession in Reclaimed Habitats: A Case Study from Areas Deforested by Air Pollution. *For. Ecol. Manag.* **1992**, *54*, 27–44. [[CrossRef](#)]
56. Jonášová, M.; Vávrová, E.; Cudlín, P. Western Carpathian Mountain Spruce Forest After a Windthrow: Natural Regeneration in Cleared and Uncleared Areas. *For. Ecol. Manag.* **2010**, *259*, 1127–1134. [[CrossRef](#)]
57. Zielonka, T.; Piątek, G. The Herb and Dwarf Shrubs Colonization of Decaying Logs in Subalpine Forest in the Polish Tatra Mountains. *Plant Ecol.* **2004**, *172*, 63–72. [[CrossRef](#)]
58. Valkonen, S.; Maguire, D.A. Relationship between Seedbed Properties and the Emergence of Spruce Germinants in Recently Cut Norway Spruce Selection Stands in Southern Finland. *For. Ecol. Manag.* **2005**, *210*, 255–266. [[CrossRef](#)]
59. Brang, V.P. Ansainungunst Und Verteilung Der Direktstrahlng in Schlitzförmigen Bestandesöffnungen Zwischenalpiner Fichtenwälder. *Schweiz. Z. Forstwes.* **1996**, *147*, 761–784.
60. Hanssen, K.H. Natural Regeneration of Picea Abies on Small Clear-Cuts in SE Norway. *For. Ecol. Manag.* **2003**, *180*, 199–213. [[CrossRef](#)]
61. Mori, A.; Mizumachi, E. Season and Substrate Effects on the First-Year Establishment of Current-Year Seedlings of Major Conifer Species in an Old-Growth Subalpine Forest in Central Japan. *For. Ecol. Manag.* **2005**, *210*, 461–467. [[CrossRef](#)]
62. Macek, M.; Wild, J.; Kopecký, M.; Červenka, J.; Svoboda, M.; Zenáhlíková, J.; Brůna, J.; Mosandl, R.; Fischer, A. Life and Death of Picea Abies After bark-beetle Outbreak: Ecological Processes Driving Seedling Recruitment. *Ecol. Appl.* **2016**. [[CrossRef](#)] [[PubMed](#)]
63. Thorn, S.; Bässler, C.; Bernhardt-Römermann, M.; Cadotte, M.; Heibl, C.; Schäfer, H.; Seibold, S.; Müller, J. Changes in the Dominant Assembly Mechanism Drive Species Loss Caused by Declining Resources. *Ecol. Lett.* **2016**, *19*, 163–170. [[CrossRef](#)] [[PubMed](#)]
64. Wohlgenuth, T.; Kull, P.; Wüthrich, H. Disturbance of Microsites and Early Tree Regeneration After Windthrow in Swiss Mountain Forests due to the Winter Storm Vivian 1990. *For. Snow Landsc. Res.* **2002**, *77*, 2.
65. Waldron, K.; Ruel, J.; Gauthier, S.; De Grandpré, L.; Peterson, C.J. Effects of post-windthrow Salvage Logging on Microsites, Plant Composition and Regeneration. *Appl. Veg. Sci.* **2014**, *17*, 323–337. [[CrossRef](#)]
66. Newton, M.; Fitzgerald, S.; Rose, R.R.; Adams, P.W.; Tesch, S.D.; Atzet, T.; Powers, R.F.; Skinner, C. Comment on “Post-wildfire logging hinders regeneration and increases fire risk”. *Science* **2006**, *313*, 615a. [[CrossRef](#)] [[PubMed](#)]
67. Kubát, K. *Klíc Ke Kvetene České Republiky*; Česká Geografická Společnost: Praha, Czech Republic, 2002; Volume 1, 927p.
68. Kremer, P.; Muhle, H. *Lišejníky, Mechorosty, Kaprad'orosty*; Ikar: Praha, Czech Republic, 1998.



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