Disturbance in boreal spruce forest - immediate dynamics from stand to understorey level

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Academic dissertation

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ABSTRACT

The immediate effects of two human-related vegetation disturbances, (1) green tree retention (GTR) patch felling and scarification by harrowing and (2) experimental understorey vegetation layer removal, were examined in boreal forest stands in Finland.

Effects of GTR patch felling and scarification on tree uprootings (I), on coarse woody debris (CWD) (II) and on epixylic plant community (III) were followed in upland and in paludified forest types. Uprootings increased considerably during 2-3 years after the fellings and were more frequent (47%) in the paludified than in the upland forest (13%). Scarification reduced 68% of the CWD in the felling area. Cover and especially species richness of epixylics declined in the both areas during 1-2 years after the felling. The increasing size of GTR patch correlated positively with the species richness.

Regeneration of understorey vegetation community (IV) and *Vaccinium myrtillus* and *Vaccinium vitis-idaea* (IV) after different removals of vegetation layers in an old-growth forest took four years. The regeneration occurred mainly by vegetative means and it was faster in the terms of species richness than in the cover. In the most severe treatment, recovery occurred merely by sexual reproduction. *V. myrtillus* recovered mainly by producing new shoots. *V. vitis-idaea* recovered faster than *V. myrtillus*, mainly by increasing length growth.

For ecological reasons, use of larger GTR patches on paludified biotope would be recommendable. In felling areas, scarification by harrowing could be replaced with some other spot-wise method. After moderate intensity level disturbance, recovery occurs rapidly by vegetative regrowth of the dominating species. High level of intensity may prevent the recovery of vegetation community for years, while enabling also the genetic regeneration of the initial species. Local anthropogenic-related disturbances are currently increasing and they can interact during temporally short times, which should be taken in to account in the future forest management plans.

Keywords: coarse woody debris, epixylics, green tree retention, growth form, understorey community, uprooting

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications:

I. Hautala, H. & Vanha-Majamaa, I. 2006. Immediate tree uprooting after retention-felling in a coniferous boreal forest in Fennoscandia. Canadian Journal of Forest Research 3: 3167-3172. DOI 10.1139/X06-193

II. Hautala, H., Jalonen, J., Laaka-Lindberg, S. & Vanha-Majamaa, I. 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodiversity and Conservation 13(8): 1541-1554.
DOI 10.1023/B:BIOC.0000021327.43783.a9

III. Hautala, H., Laaka-Lindberg, S. & Vanha-Majamaa, I. 2008a. Effects of retention felling on epixylic species in boreal spruce forests in southern Finland. Manuscript.

IV. Hautala, H., Tolvanen, A. & Nuortila, C. 2008b. Recovery of pristine boreal forest floor community after selective removal of understorey, ground and humus layers. Plant Ecology 194: 273-282. DOI 10.1007/s11258-007-9290-0

V. Hautala, H., Tolvanen, A. & Nuortila, C. 2001. Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understorey layers. Journal of Vegetation Science 12: 503-510. http://www.jstor.org/pss/3237002

The publications are referred to in the text by their roman numerals.

AUTHOR'S CONTRIBUTIONS

	I	II	III	IV	V
Original idea	IV-M, JJ	IV-M, JJ	IV-M, JJ	HH, AT	HH, AT
Field work	IV-M, JJ	HH,IV-M, JJ, SL-L	HH, IV-M, SL-L	HH, AT, CN	HH, AT, CN
Data processing	HH	HH	HH	HH, AT, CN	HH, AT, CN
Data analyses	HH	HH	HH	HH, AT, CN	HH, AT, CN
Article preparation	HH, IV-M	HH, IV-M, JJ, SL-L	HH, IV-M, SL-L	HH, AT, CN	HH, AT, CN

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CONTENTS

1 INTRODUCTION

1.1 Anthropogenic disturbances in boreal forests

Human activities, including forest management actions and increasing recreational usage are producing the great majority of disturbances in boreal forests today, while the significance of previously prevalent natural disturbances, such as forest fire, has decreased (Esseen et al. 1997). At the same time, biodiversity and resilience are considered to be very susceptible to the changes in disturbance regimes (Jentsch et al. 2002). In the context of this thesis, disturbance is examined as a physical event that destroys wholly or partially vegetation community with varying severity on spatially smaller (local) and on temporally shorter (few years) scale.

Locally, the human-related disturbances reach from the tree stand to the individual plant level. The most important current anthropogenic disturbance is removal of the tree layer, as it directly controls the carbon balance of boreal forests (Magnani et al. 2007). For understorey vegetation too, tree layer removal may even exceed the effects of local environment, including e.g. substrate availability (Økland et al. 2003).

During the last few decades, the most common tree layer removal method in boreal area has been clear-felling. During forest regeneration, especially in the early stages, clear-felling areas are unfavourable habitats for interior and later successional forest species. Due to the increasing evidence of negative effects of clear-felling on plant communities (e.g. Bergstedt & Milberg 2001; Jalonen & Vanha-Majamaa 2001; Haeussler et al. 2002; Norwegian Institute of Land Inventory 2003, Dynesius & Hylander 2007), new pro-environmental forest management methods, such as green tree retention (GTR) felling (see reviews by Vanha-Majamaa & Jalonen 2001 and Rosenvald & Lõhmus 2008), have been introduced recently. In GTR felling, some trees and their nearby environment are saved from fellings, either in a dispersed or in a patch form. The alleged main idea behind GTR methods is that they can both protect and sustain the initial biological and structural diversity found in the forests, while they simultaneously guarantee the desired economical objectives. Already Darwin & Wallace (1858) observed that "The same spot will support more life if occupied by very diverse forms. We see this in the many generic forms in a square yard of turf, and in the plants or insects on any little uniform islet,...". From the ecological point of view, the burning question is how to manage forests so that the increasing mosaic of clear-fellings, regeneration areas and unmanaged forest patches can be kept adequately functioning so that the long-term dispersal barriers for mature forest species can be prevented.

Retained forest patches should be able to maintain a sufficient level of habitat and niche structures needed e.g. for sessile and sensitive epixylic[1] species that depend largely or even totally on natural forest conditions. Vegetation dynamics in these isolated patches are more or less driven by edge-effects, more precisely 'adjacent opening effects' (Burton 2002), which in this thesis refers to the zone of influence of a clear-felling area in the adjoining forest. These effects change abiotic and biotic conditions of the edge area and they may reach several tens of metres into forest interior. In GTR patches, adjacent opening effects may increase susceptibility to windthrows on stand level or reduce abundance and diversity of the initial vegetation. It has been theorized that edge-effects may also interact with each

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[1] Species that use (dead) wood as their nesting/breeding site or for some other critical functions during their life cycle (definition of Stokland, 2007).

other. Currently, more estimates of impacts of edge-effects in fragmented forests are needed in order to understand the underlying mechanisms (Murcia 1995).

According to the equilibrium theory of island biogeography of MacArthur & Wilson (1967), dynamic interplay of colonization and extinction defines the observation that number of species increases with the size of the area. In boreal forest management, it is already known that very small GTR patches do not support the species continuum (Jalonen & Vanha-Majamaa 2001). Study of larger areas could reveal whether or not increasing patch size can foster a more balanced dynamic interplay of colonization and extinction processes, i.e. that the number of surviving species would be higher in larger GTR patches.

Current metapopulation theory for fragmented landscapes by Hanski & Ovaskainen (2003) provides a modeling opportunity to examine the survival of species living within and among fragmented populations. However, the classical metapopulation models are not of the greatest value for studying smaller patch nets (Hanski 2004). It has also been suggested that single population approaches instead of metapopulation approaches could be used for the majority of plant species (Harrison & Ray 2002). It has been theorized that the survival of plant species depends mainly upon the reproductive characteristics and dispersal abilities of each respective species. During adverse conditions, clonally reproducing plants may form the most stable populations. With more short-lived species, it depends upon their dispersal ability whether they can sustain metapopulations (Eriksson 1996). When studying the survival of epixylic plant communities in retention fellings, more local and single population approaches could be used to test what real immediate effects in the abundance and diversity of the epixylic species can be seen in the isolated patches, such as GTR patches. To date, vegetation field studies on this subject are virtually lacking.

Windthrows, where single or several trees uproot due to allogenic (mainly extreme winds) or autogenic (mainly fungal infection and insect attacks, Qinghong & Hytteborn 1991) factors, contribute significantly to the creation of natural small-scale heterogeneity of boreal spruce (*Picea abies* L.) forest vegetation. In the absence of large-scale disturbances, this gap disturbance type is very important in those forest types that rarely experience fire (Kuuluvainen 1994; McCarthy 2001; Gromtsev 2002; Harper et al. 2003). In old-growth spruce forests, fungal infection comes often first and wind acts then as a contributing factor (Fraver et al. 2008). Forest fires are nowadays suppressed and delimited and the forested landscape of Fennoscandia consists mainly of a mosaic of thinned even-aged small stands and larger clear-felling areas, which together increase the likelihood for wind damages. Also, future scenarios predict that the likely decreasing vitality of spruce forests due to climate change can lead to rapid increase in the number of windthrows in boreal areas (Schlyter et al. 2006). Windthrow is typically launched by altered stand conditions after clear-felling. The susceptibility of a forest stand to windthrow depends upon the combination of different factors, including e.g. age, size, shape and placement of the stand, main direction of the forest edge, the soil and forest biotope type, the felling method and the former fertilization (Laiho 1987; Mayer 1989; Kalinin 1991; FRBC Proj. 1999; Ruel 2000; Burton 2002). A single tree uprooting causes a local gap with a characteristic pit and mound -pattern among the understorey vegetation. Windthrow usually changes the local microclimatic conditions (Schaetzl et al. 1989), but it may also destroy adjacent living and dead wood.

Coarse woody debris (CWD[2]) is nowadays susceptible to anthropogenic disturbances, while it tops among the most important biodiversity key structures in the taiga biome (Esseen et al. 1997). For example in Finland, 20-25% of the forest-dwelling species has been estimated to be dependent on dead wood (Siitonen 2001). Currently, high levels of CWD are met only in a small area of protected northern forests, while level of CWD in managed forests e.g. in southern Finland is over 90% lower if compared to the old-growth forests (Siitonen 2001). Until these days, CWD has been systematically removed from the managed boreal forests in fear of pathogen or insect outbreaks (Kimmins 1997; Fridman & Walheim 2000). The role of CWD is threatened also after clear-felling, when abiotic conditions along with quality of the remaining CWD deteoriorate untenable for sensitive and demanding forest interior specialists (Esseen et al. 1997). The clear-felling area is also often treated mechanically in order to enhance the regeneration of tree seedlings and planted trees. In these treatments forest floor is disturbed to some degree so that the mineral soil is exposed. Along with understorey vegetation and saplings, also dead wood structures and epixylic species may be affected during these actions. As great number of species depend on CWD, adequate survival of CWD (qualitatively and quantitatively) in the clear-felling areas over the regeneration phase probably largely determines if it is possible to save a prominent part of the boreal forest biodiversity from isolation, destruction and possible extinction.

Understorey vegetation of boreal forests is under increasing small-scale human-related wearing pressure created by factors such as maintenance of over-large moose and reindeer populations (Persson et al. 2000; Suominen & Olofsson 2000), forest roads, trails of forestry machinery (Sumners & Archibold 2007) and recreational human trampling (Hamberg et al. 2008; Kangas et al. 2007). The occurrence of these small-scale gap disturbances is often sporadic, although they can be locally very intensive. Natural small-scale disturbances are common in the forests that have escaped fires for longer time (Kuuluvainen 1994) and they enhance fine-scale heterogeneity e.g. by affecting temporarily on interspecific plant community dynamics by lowering the abundance of initial species and bringing in weaker competitors. The nonequilibrium intermediate disturbance hypothesis by Connell (1978) predicts that disturbances increase diversity by preventing competitive exclusion. According to this theory, in boreal forest understorey vegetation, disturbances of intermediate severity should then lead to greatest diversity in vegetation. Additionally, very low severity disturbance should disturb plant community only temporarily, while high severity disturbance should change the community composition permanently by removing the dominant clonally reproducing dwarf shrubs *Vaccinium myrtillus* and *Vaccinium vitis-idaea*. Their effective regeneration is based on rejuvenation from an abundant bud bank (Tolvanen 1994).

1.2 Green tree retention patch felling and mechanical soil preparation

In GTR patch felling, patches of initial forest are set aside from the fellings. The basic idea is to preserve part of the initial structural and biological diversity of the forest area unchanged in the patches over the forest regeneration phase, which is around 80-130 years between southern and northern boreal forests (Esseen et al. 1997). It has been believed that such patch retention can be carried out so that it resembles the natural disturbance regime of

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[2] Downed woody material, diameter > 10 cm (definition of Lofroth, 1998), logs throughout this thesis.

a boreal forest, where patches of initial stand survive following forest fire. Under boreal conditions, this kind of imitation could be realized, for example, if the patches were located in those spruce forest stands which under natural conditions remain more or less unburned after forest fires. Paludified spruce forests (i.e. swamp forests) represent such a forest type. It has been generally recognized that they sustain much higher structural and biological diversity than more common spruce forest types (Segerström 1997; Hörnberg et al. 1998; Vanha-Majamaa & Jalonen 2001; Korpela 2004). In Finland, this forest type has been subjected to heavy drainage in recent decades (Korpela 2004). Due to the fire resistance and long continuum of old trees, there is also more CWD available (Segerström 1997), more likely the number of epixylic species is higher, the understorey vegetation has developed for longer time and the species composition of vegetation of this forest type may differ from the surrounding, more common upland forests. All of the aforementioned processes probably contribute to the ß-diversity at the larger landscape level. One deficiency of GTR studies on sustaining biodiversity, hitherto, is that the influence of forest type is poorly studied (Rosenvald & Lõhmus 2008). To fulfill their ecological task, GTR patches should be large enough to prevent the edge-effects and guarantee the microclimatic conditions of the forest interior adequate for the most sensitive and sessile species. Additionally, the shape of GTR patches should (more or less) resemble a circle, where the ratio of edge vs. area is smaller than in a rectangle. Also local abiotic conditions, including e.g. soil characteristics, slope of the area and exposure to extreme winds also partly determine the function of a GTR patch. According to the meta-analysis of Rosenval & Lõhmus (2008) on GTR effects, GTR nearly always improves habitat and lifeboating for most of the organisms, excluding bryophytes and vascular plants. GTR study of Jalonen & Vanha-Majamaa (2001) from Finland showed that currently used size of GTR patches is not adequate for survival of understorey species. Concerning tree seedlings and saplings, studies done on *Pinus sylvestris* stands in Finland, have revealed that patch retention has generally negative effects on the growth (Valkonen et al. 2001; 2002) and productivity (Ruuska et al. 2008) of the stands. The negative effects are smaller, if retention trees represent deciduous species (Valkonen et al. 2003).

Mechanical soil preparation is practiced commonly in the clear-felling areas of Finland today. Since the 1980's, around 120000 hectares of regeneration areas are prepared annually, which is nearly the same amount of forest that is being clear-felled simultaneously (Finnish Statistical Yearbook of Forestry 2006). Mechanical soil preparation exposes mineral soil and releases nutrients for tree seedlings, which leads to increased number of saplings especially on spruce-dominated lands (Hyppönen et al. 2002). Soil preparation may also simultaneously disturb and deplete understorey vegetation (Karlsson et. al 2002) and dead wood. The latter can have other indirect consequences: Reduction of CWD affects directly on the amount of epixylics, but also on the future substrate of logs as 'stepping-tones' for epixylic plant species during the forest regeneration phase. This may cause long-term and even fatal dispersal barrier for the sessile species.

1.3 Understorey vegetation removal and wearing

Boreal spruce forest understorey vegetation consists typically of remarkably thick and abundant field, ground and humus layers, which are regulated by allogenic (e.g. disturbances) and autogenic (e.g. inter- and intraspecific competition) dynamics. Occasional replacement of vegetation via disturbance releases space and resources and the canopy then forms the only barrier e.g. for light (Lieffers et al. 1999).

Anthropogenic imprints like hiking paths, lichen picking sites, forestry trails and other similar disturbances that affect the understorey vegetation of uncut boreal spruce forests are often relatively narrow and small, although their spatial and temporal intensity and severity may be high, e.g. in forests near urban areas (Malmivaara et al. 2002, Hamberg et al. 2008). If the disturbance is severe enough, all of the vegetation along with the regeneration propagules may be completely destroyed throughout both the organic and mineral soil horizons. Significant local community changes are also possible (Hamberg et al. 2008).

This type of disturbance has its natural analogues e.g. in animal browsings, burrowings, diggings and small tree uprootings. However, animal activity rarely leads to the removal of the entire understorey vegetation, while tree uprooting usually creates exposed mineral soil patches (at the scale of a square meter to an acre) within the understorey vegetation. Anthropogenic activity can create small-scale patch disturbances of all intensity and severity classes.

1.4 Aims of the thesis

This thesis includes two anthropogenic regimes:

The first is GTR patch felling combined with mechanical soil preparation by scarification (harrowing). This felling method is believed to be more ecological, as it spares patches of the original forest and it has been thought that sensitive forest species could survive in the patches over the forest regeneration period. To meet both ecological and economical goals, GTR felling could be a potential management solution for heavily utilized forest areas, such as southern Finland. Scarification is a commonly used post-felling treatment, which should enhance regeneration of trees. The ecological effects of the two former methods on the ecological key elements, such as CWD and species depending on it, are still largely unknown. Additionally, it is not known how stable GTR patches are to extreme winds or what is the effect of location (biotope type) and size of the patches for the initial environment within them.

The second is an experimental understorey vegetation removal, which was designated so that it was possible to imitate small-sized understorey disturbances, such as recreational trampling or animal browsing by controlling the severity of disturbance. The importance of this disturbance type in previously unmanaged forests has increased rapidly lasting recent decades due to human encroachment and forest fragmentation. The effects of the severity of this disturbance on composition and regeneration of initial understorey vegetation are largely unknown. Knowledge of this aspect of succession could help e.g. in the designation of ecologically sustainable tourist trails and herding areas.

The effects of both disturbance regimes on boreal spruce forest vegetation structures were examined over short (immediate) and small-sized (local) scales. The basic idea behind the whole study was that disturbances are not merely discrete events, but that they also can interact between the examined levels, i.e. disturbance at the tree stand level can lead to disturbance at the understorey vegetation level.

Study I presents how GTR patch felling affects tree uprooting in two different spruce forest biotopes. Study II examines the effects of GTR patch felling and scarification on CWD. Study III follows survival of the epixylic community (including vascular plants, mosses and lichens) after GTR patch felling and scarification. Here, it was thought that the basic prerequisites for epixylic species include decent environmental conditions (as defined by stability of tree layer and size of patch) and growing substrate (CWD) availability. Study IV examines regeneration of the understorey vegetation community after different removals

of vegetation layers and study V presents the regeneration of two dominant understorey vascular species (deciduous *V. myrtillus* and evergreen *V. vitis-idaea*) after different removals of vegetation layers and artificial seed-sowing.

In the GTR studies (I-III) it was hypothesized that immediately after felling and scarification, (I) the number of uprootings increases depending on the forest biotope and on the size of the GTR patch, (II) that the amount of CWD is reduced through direct scarification or indirect uprooting disturbances, depending on species and decay class of the logs and (III) that the cover and species richness of epixylic vegetation change in the felling area and also in the GTR patches due to the felling-related disturbances. In these studies, it was also examined whether equilibrium theory of island biogeography of MacArthur & Wilson (1967), which predicts that increasing size of an island correlates with species diversity, can be applied to increasing size change of GTR patches. The purpose of these studies was also to increase much needed knowledge on edge-effects in fragmented forests (Murcia 1995) and respectively, still exiguous knowledge on influence of forest type on biodiversity in GTR studies (Rosenwald & Lõhmus 2008). As the setting of the study had a smaller-scale and more local approach and because the studied species represented epixylics with relatively low dispersal abilities over clear-cuts, the studies also produced new basic data, which can be utilized in studying metapopulations.

In the understorey vegetation removal studies (IV-V) it was hypothesized (IV) that the recovery of dominating species depends strongly on the availability of the reproductive organs and that the recovery of different plant growth forms is related to the removals of specific vegetation layers and that after a severe disturbance the community composition of recovered plant community differs the most in comparison with the untreated vegetation and (V) that the recovery rates of *V. myrtillus* and *V. vitis-idaea* differ mainly due to their different growth forms and that the experimental seed-sowing of the two *Vaccinium*-species increases the number of their seedlings, especially in exposed mineral soil habitats. In these studies, it was examined whether the intermediate disturbance hypothesis (Connell 1978) applies to small-sized disturbance in a boreal forest understorey vegetation community under natural conditions. Here, different plant layer removals and their combinations along a continuum represented the severity of disturbance.

By examining boreal forest vegetation components and structures on five different levels (tree stand, CWD, epixylics, understorey plant community, understorey plant population), an extensive picture of immediate effects of the most common smaller-scale anthropogenic disturbances and their interacting relationships in a boreal forest stand could be created. The conclusions of this thesis can be directly applied in to the practical use of various forest professionals, who plan and carry out sustainable management and restoration operations in boreal forests.

2 MATERIALS AND METHODS

2.1 Study areas and sampling

The data of this thesis was collected from two separate areas: The GTR patch felling study area was located in the southern boreal vegetation zone at Heinävesi, middle Finland (62°25' N; 28°37' E). During the last half of the 20th century, the time of the most intense forest management in the history of Finland, forests of the area have been conventionally used, i.e. they have been thinned regularly to some degree and part of the dead trees have been removed from the forests, which has led eventually to more even-aged structure of the remaining mature forest stands. The forests represent the most typical type of managed forests met in southern Finland. As the area of unmanaged forests is almost negligible and e.g. the amount of CWD is very low in the southern and middle Finland, examination of alternative and restorative forest management methods are very much needed in this part of the country.

The study area was first biotope-mapped in 1997 in order to distinguish the different *Myrtillus*-type spruce forest biotopes. Around 200 ha of mature mesic spruce forest were mapped before the fellings. In this mapping, clearly defined and homogenous biotopes were distinguished from the mapped forest. Minimum size of a biotope was between 100 and 300 m^2. Of the sampled biotopes, from an area of 100 m^2, the following variables were measured: vegetation type, distance of the area to the biotope edge, medium length of trees, topography, slope, soil type, amount of ditches, peat layer thickness, humus layer thickness, level of mire water, cover of tree and shrub layer, branch litter cover, amount of decaying wood and basal area of trees. Understorey vegetation (species cover) was also assessed from four randomized 1 m^2 sample sites per each sampled biotope. Through the mapping procedure, five different forest and peatland biotopes were determined. The selection was based on ordination analysis of the understorey vegetation (Global Non-metric Multi-dimensional Scaling, GNMDS) and fitting of environmental vectors (amount of decaying wood, basal area of *Pinus sylvestris*, basal area of *Populus tremula*, cover percentage (%) of branch litter, humus layer thickness, peat layer thickness) to the ordination patterns. The selected biotopes differed significantly from upland forest types according to the following environmental variables: 1. amount of decaying wood (m^3/ha), 2. basal area of *Pinus sylvestris*, 3. basal area of *Populus tremula*, 4. branch litter cover percentage (%), 5. mor layer thickness (cm) and 6. peat layer thickness (cm), On the basis of this, the locations of the GTR patches were chosen. Two biotopes were included: Paludified spruce forest (11 patches) and typical drier upland spruce forest (8 patches), from where the shape and the size of the patches were measured. The edges of the paludified GTR patches were set to coincide with the natural edges of the biotope patches. Due to practical limitations, upland GTR patches were left relatively small. The mean size of GTR patch was 0.2 ha (between 0.09 and 0.55 ha) on paludified biotope and on upland biotope 0.06 ha (between 0.03 and 0.09 ha) (I; Vanha-Majamaa & Jalonen 2001).

After site marking and selection, the logs (CWD) along with the 200 cm^2 sized epixylic study plots on the logs were chosen and marked. The study plots were located on both ends and in the middle of the logs. At each location there were three study plots, one on top and two on either side of the logs (Figure 1). The number of study plots (between 6 and 15) on each log depended on length of the log. Pre-treatment data, which included number of living trees (I), location and size data of CWD (II) and cover and species number of epixylic vegetation (III), was collected from the GTR patches during 1998. The

surroundings of the GTR patches were felled during spring of 1999 and they were mechanically harrowed with a disc trencher during autumn 1999. Post-treatment data, which included number of living and uprooted trees (I, 1999-2001), visual estimation (with aid of pre-treatment length and log description data) of CWD damage percentage (II, 1999-2000) and cover and species number of epixylic vegetation (III, 1999-2000), was collected from the clear-felling areas and the GTR patches.

The understorey vegetation removal study area was located in the northern boreal vegetation zone in a mesic spruce forest at Oulanka National Park, Kuusamo, northern Finland (66°20' N; 29°20' E). The forest stand represents the most primeval type of *Hylocomium-Myrtillus* -spruce forest in Finland. As the forests here are in their (practically) natural state, the possible anthropogenic side-effects could be minimized and with the executed experiment it was possible to predict similar natural disturbances, like recreational human trampling or reindeer browsing in the forest.

The experiment consisted of 50 square plots (sized 0.5 m^2) on the forest floor. The plots were experimentally disturbed during spring of 1994 in the following way: (a) control, (b) removal of the ground layer, (c) removal of the field layer, (d) removal of both the ground and field layers and (e) removal of both the ground and field layers and humus layer down to the mineral soil. After the initial removal, ramet densities of *V. myrtillus* and *V. vitis-idaea*, were recorded. The study period was five years (1994-1999) during which recovery of the understorey vegetation community (IV) and recovery of the two most common field layer species, *V. myrtillus* and *V. vitis-idaea* (V), were measured in terms of cover (IV, V), species numbers (IV), shoot length and relative growth rate (V) from the plots. Cover was estimated using the point-frequency method (100 random points on a plastic disc with 400 drilled holes), where first touches with both field and ground layer were recorded. Study V included also an experimental sowing of *V. myrtillus* and *V. vitis-idaea* seeds to the plots. The seeds, 500 from *V. myrtillus* berries and 400 from *V. vitis-idaea* fruiting ramets from the area were collected, dried and mixed during September 1994 and sowed one month later. On each disturbance treatment, 5 plots were sowed with 200 seeds and 5 plots were left as control. The number of seedlings was counted before and a year after the seed-sowing (V).
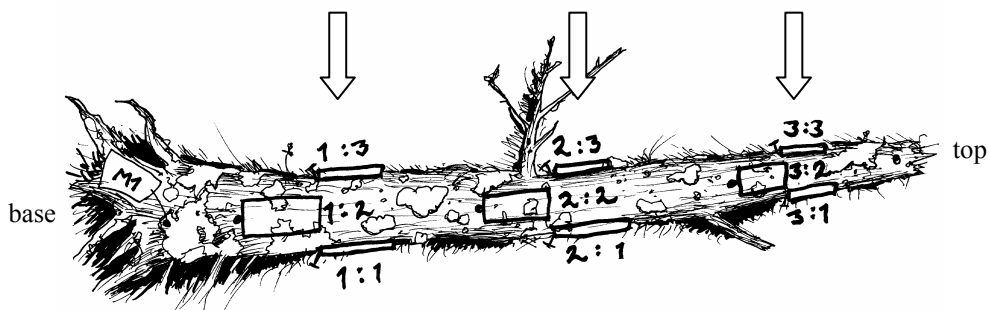
Figure 1. Location of epixylic study plots on a log (III).

Table 1. Timetable of the thesis studies I-V.

	I (uprootings)	II (CWD)	III (epixylics)	IV (understorey)	V (*Vaccinium*)
1994	-	-	-	choosing site, treatments, measuring cover and species numbers	choosing site, treatments, measuring ramets and cover, seedling counting
1995	-	-	-	measuring cover and species numbers	measuring ramets and cover, seedling counting
1997	biotope-mapping, GTR patch marking	biotope-mapping, CWD marking	biotope-mapping, CWD marking	measuring cover and species numbers	measuring cover
1998	collection of pre-treatment data (living tree variables)	collection of pre-treatment data	epixylic study plot marking, collection of pre-treatment data	measuring plant cover and species numbers	measuring cover
1999	felling (spring), collection of post-felling data, scarification (autumn),	felling (spring), collection of post-felling data, scarification (autumn),	felling (spring), collection of post-felling data, scarification (autumn),	measuring cover and species numbers	measuring cover
2000	collection of post-scarification data	collection of post-scarification data	collection of post-scarification data	-	-
2001	post-treatment data (uprootings and tree size variables)	-	-	-	-

2.2 Statistical methods

Statistical analyses were performed with SPSS (I, II, III, IV, V) and for illustrations, SigmaPlot (I, II, III, IV,V) software was used. The following analytical methods were used in the studies I-V: A linear regression analysis to check dependence of vegetation variables on the GTR patch traits (I, II, III), an independent-samples t-test to check differences between the biotopes (I), a paired-samples t-test to check differences between the years (I, II), a Wilcoxon's signed-ranks test to check differences between the years (I, III), repeated-measures ANOVA to check interactions between the time and the disturbance variables (II), 1-way ANOVA to check differences between the biotopes and the differences between the vegetative traits (II, V), factorial ANOVA to check differences between the disturbance treatments (IV, V), Tukey's HSD-test for pairwise comparisons (VI), Tukey's B test for pairwise comparisons (V), arithmetic (I, II, III) and logarithmic transformation (I, II, III, IV, V).

3 RESULTS

3.1 Uprooted trees

In this study, it was hypothesized that the number of uprootings increases soon depending on the forest biotope (I). According to the pre-treatment comparison, neither the number of living tree numbers, nor the basal area differed between the paludified and upland spruce forest types before the treatments. Before the treatments, average number of living trees was around 809 trees/ha on the paludified biotope and around 725 trees/ha on upland biotope. In both treatments, the two most common tree species were *Picea abies* and *Betula pubescens*. After the 1st year, there was a small, but non-significant uprooting percentage difference between the two biotopes. The percentage shares of the uprooted trees were low (paludified: 7%; upland: 2%). By the end of the 2nd and 3rd year, the numbers of uprootings had increased considerably in comparison with the 1st post-treatment year. By then, the uprooting percentage was around four times higher in the paludified biotope (3rd year: 47%) than in the upland biotope (3rd year: 13%). The highest recorded amount of uprooted trees in a single (paludified) green-tree retention GTR patch, was around 727 trees/ha. The highest within-species uprooting rate was recorded for *P. abies* in paludified biotope, around 47% of the trees had uprooted. Uprooting rate did not correlate with patch shape. There was an increasing trend, however statistically non-significant, of dependence between increasing size of GTR patch and decreasing amount of uprootings. The original hypotheses was verified as true (I).

3.2 Coarse woody debris

In this study, it was hypothesized that the amount of CWD reduces soon to some extent through direct or indirect disturbances, while depending on the respective species and decay class of the logs. Pre-treatment comparison revealed that the paludified biotope had over seven times higher volume of initial CWD than the upland biotope: 15.6 m^3/ha on paludified and 2.2 m^3/ha on upland biotope. During the 1st year felling operations, 8% of the initial volume of CWD was depleted from the felling area. On the contrary, during the 2nd year scarification, 68% of CWD was destroyed or disappeared from the felling area. Between times, 20% of CWD was depleted from the GTR patches. The greatest total losses occurred for the deciduous (76%) and the highly decayed (88%) logs in the felling area. Respectively, of the individual species, the greatest loss of CWD was recorded for *Populus tremula*, 72%, and of the individual decay classes, for class 5, 90%, both in the felling area. During the study, 33% of the logs disappeared during the study, if these logs are included on the total loss, 81% of the initial volume of CWD had disappeared after the scarification. There was no significant connection between remaining CWD and the distance to the patch edge. The original hypotheses was verified, although the amount of depleted CWD in the felling area after scarification surpassed expectations (II).

3.3 Epixylic vegetation

In this study, it was hypothesized that the cover and species richness of epixylic vegetation is affected to some extent in the felling area and also in the GTR patches. Pre-treatment comparison showed that the initial cover and the number of species were slightly higher in the paludified biotope (GTR patches) than in the upland biotope (felling area). During the

study period, of all species groups, bryophytes had the highest covers and species numbers. In the beginning of the study, the most common species were *V. myrtillus* (1%, in vascular plants), *Pleurozium schreberi* (19%, in mosses), *Ptilidium pulcherrinum* (2%, in liverworts) and *Cladonia coniocraea* (1%, in lichens). After the felling, the cover and species diversity of almost all epixylic species groups declined rapidly in the both areas (the highest drops in the RTGs: cover of mosses, -15%; number of liverwort species, -20%; in the felling areas: cover of mosses, -28%; numbers of liverwort species, -30%), while the amount of dead and/or dying vegetation and felling-related litter increased in the both areas. After scarification, the cover and number of species continued to decline in the felling area (the highest drops: cover of mosses, -4%; number of moss species, -50%), while correspondingly in the GTR patches, the covers remained around the same (the highest increment: lichens, 0.5%), but the species numbers declined still (the highest drop: mosses, -14%). The increasing size of a GTR patch correlated positively with the total species numbers, but not with the total cover. The original hypotheses was verified (III).

3.4 Understorey vegetation

In this study, it was hypothesized that the recovery of dominant species depends strongly on the availability of the reproductive organs and that the recovery of different plant growth forms is related to the removal of specific vegetation layers and that after a severe disturbance the community composition of regenerating plant community differs the most in comparison with the untreated vegetation. In the removal treatments where the humus layer was not disturbed, the cover of both ground and field layers recovered to the initial level during four years mainly due to rapid regeneration of the dominant dwarf shrubs. In the 5th year after the disturbance cover was over 85%. Recovery was generally faster in terms of species numbers than cover. In the humus layer removal treatment, regeneration of vegetation was very slow and it occurred mainly by sexual reproduction, while the community composition of the treatment differed considerably from the others: 62% of the cover consisted of graminoids. The most rapidly regenerating species were *V. myrtillus*, *V. vitis-idaea*, *Hylocomium splendens*, *Pleurozium schreberi* and *Polytrichum commune*. Seedlings of tree species were recorded only on disturbed plots. All of the regenerated species in the experiment represented the members of initial community. In the study, especially high cover and species diversity during 1998 could be connected to rainy weather conditions during that year. The original hypotheses was verified (IV).

3.5 *Vaccinium myrtillus* and *Vaccinium vitis-idea*

In this study, it was hypothesized that the recovery rates of *V. myrtillus* and *V. vitis-idaea* differ mainly due to their different growth forms and that the experimental seed-sowing of the two *Vaccinium*-species increases the number of their seedlings especially on bare mineral soil habitat. Deciduous plants, which renew leaves annually, have generally greater reproduction capacity, mostly due to their abundant belowground resources (Karlsson 1985). Evergreen plants retain green leaves throughout the winter period, and for example, *V. vitis-idaea* regenerates more slowly from disturbance than *V. myrtillus* (Tolvanen & Laine 1997). In the beginning of the study, around 294 ramets/m^2 and 132 ramets/m^2 of *V. myrtillus* and *V.vitis-idaea*, respectively, were recorded from the plots. New ramet production during the 1st and 2nd year was rapid for the both species, and it increased in a pattern consistent with the severity of the initial disturbance (A, B, C, D). After disturbance,

the mean current shoot length decreased for the both species. Cover of evergreen *V. vitis-idaea* returned to the level occurring in controls after one year in the treatment where only the field layer was removed. The rapid regeneration took place by efficient production of new ramets, while in the other treatments regeneration took four years. This was faster than with deciduous *V. myrtillus*, which recovered fully in four years. The former species responded to damage with increased length growth of shoots, while the latter concentrated on increased production of annual shoots. During the first year after severe disturbance (removal of the field and ground layers), ramet mortality was high (around 35% for the both species) if compared to the control (around 0% for the both species). In the most severe treatment, regeneration of both species was exiguous. Experimental seed-sowing produced the highest number of *Vaccinium*-seedlings when the humus layer was removed (sown: 149 seedlings/m^2; unsown: 6 seedlings/m^2), although the mortality of seedlings after the first winter increased considerably in this treatment. In contrast to the original hypotheses, no growth form –related differences in the recovery rate between the species were found (V).

4 DISCUSSION

4.1 Green tree retention patch felling and scarification

Location of GTR patches on boreal forest landscape significantly affects short-term vegetation structure dynamics within the patches. This thesis also shows that local epixylic species dynamics in single patches are very intense in the beginning phases of regeneration (III). It is possible that metapopulation dynamics in the very beginning of regeneration period may be shadowed by the local dynamics, which supports the view of Harrison & Ray (2002), who argued that using metapopulation dynamics is not always appropriate in case of plants. The paludified forest type sustains significant amount of biological and structural diversity, but the sum of other characteristics of this biotope, e.g. wet and stony soil and the flat root structure of the dominant tree species (*P. abies*), endanger the trees to very extensive windthrow disturbance after indirect anthropogenic disturbance, i.e. clear-felling of adjacent areas (I). Generally, moist forest sites are known to be very susceptible to uprooting (see survey of Ilisson et al. 2004). Also mature, old-growth-like stands seem to be more susceptible to wind damage at high tree removal rates (Coates 1997). Even though the mean size of the GTR patches was almost 10 times higher than the average size currently used in Finland, the patches came in for excessive windthrows during the 2nd year since the felling (I). The magnitude of tree uprootings was almost 40 times higher than the normal tree mortality rates in these forests, which are under 1% (Jonsson 2000; Siitonen et al. 2000; Rouvinen et al. 2002; Fraver et al. 2008). Still, the wind speeds measured from the area during the study period were normal and no strong storms were officially recorded from the study area (I), although some local observations of strong winds were made during that time (II). It is known that windthrows may show large variation over time (Jonsson & Dynesius 1993). There was a small trend between increasing GTR patch size and decreasing number of uprootings, which may indicate that the GTR patch size used in this study was near the possible threshold level, above which the effect could be much more pronounced.

If it is decided that trees are to be preserved within the paludified patches, it seems possible to sustain and even restore CWD over the forest regeneration phase due to the high uprooting susceptibility of trees (II). This is in accordance with the stochastic equations based on computer simulation by Ranius et al. (2003), in which retention of small productive areas leads to an acceptable continuum of CWD. Clear-felling operations alone do not destroy high quantities of CWD from the felling areas, especially if the fellings are done during the period of snow cover. For the continuum of initial CWD, the most crucial defining factor seems to be the scarification of clear-felling area. Harrowing with disc-trencher proves to be very devastating, as the great majority of the initial CWD (especially the deciduous and highly decayed logs) either gets destroyed or will be buried under the soil (II). Additionally, during harrowing it is not always possible to bypass the downed logs even though the regulations could advise to do so. Further, the damaged logs are also possibly prone to degradation due to the desiccation and temperature extremes in the felling area.

The logs are best preserved in the GTR patches, where microclimatic conditions are also supposedly milder (II). The better recovery of epixylics in the GTR patches vs. the felling area suggests that the post-felling windthrows may even enhance microclimate in the forest interior patches (III), as uprooted trees often package in to tight agglomerations and piles (H. Hautala, personal observation). It has been observed earlier also that windthrows can

enhance spruce regeneration (Drobyshev 2001) and increased amount of dead wood in the clear-felling area can improve abundance of polypores (Selonen et al. 2005). On the other hand, frequent uprootings in GTR patches can consume a considerably large portion of the initial CWD by crushing and breaking it into pieces, which may lead to unilateral accumulation of new CWD.

Clear-felling causes immediate and steep declines of epixylic species in the felling area (III). Further, microclimatic extremes and deterioration of the logs as growing substrate in the clear-felling area will present new challenges even for the most tolerant epixylic bryophyte species. Also, the depletion of CWD during the soil harrowing correlates directly with the quantitative decrease of epixylics especially in the clear-felling area, which supports the view of Newmaster et al. (2007), according to whom displacement of CWD, along with organic layers during site preparation, is the main cause for the decline in species richness. It has been observed earlier that soil preparation has also other negative ecological consequences, like delays in the growth of field layer vegetation (Karlsson et al. 2002) and potentially facilitating the invasion of ruderals (Haeussler et al. 2002).

The immediate microclimatic edge-effects caused by clear-felling reach also the interior of GTR patches and seem to lead to a decline in cover for all epixylic species groups (III). According to the informal climate data recorded during summer of 2003, there were no notable temperature and air humidity differences between the edges and the interior of the GTR patches. It has been estimated that the edge-effects from clear-felling area (i.e. 'the adjacent opening effects') can extend several tens of meters into the boreal forest interior (Burton 2002; Harper & Macdonald 2002; Moe & Jonsson 2003). In modern forestry, it is often not understood that preserving particular areas of initial forest from felling does not necessarily mean that equivalent areas of 'unchanged initial forest' are preserved for the future. Instead, adjacent opening effects may diminish greatly the value of preserved forest (Murcia 1995). Liverworts, as well as certain common forest interior vascular plants, are especially sensitive to edge-effects, which according to this thesis, seem to be transient for the most of the epixylics (III). However, larger GTR patch size seems to correlate positively with the species diversity (III), which means that the proportion of edge-effects may decrease at some level already at this size-scale of GTR patches. The former result is also supported by statistically non-significant observation, according to which, there are less uprootings in larger GTR patches (I). These observations support the classical view of MacArthur & Wilson (1967), where increasing island size correlates with increasing number of species due to the more balanced interplay of community dynamics in the larger islands. However, the increasing number of epixylic species with the increasing size of GTR patch immediately after the isolation most likely results from the enhanced local conditions (microclimate, aided by increased tree uprooting) than colonization from outside. As felling areas during the first years seem to be unsuitable for epixylic species, it is probable to local dynamics outcompete possible effects of metapopulation dynamics, at least in the beginning.

In order to sustain the initial conditions with minimal change, the size of GTR patches should still be notably larger than the size used in this thesis in order to guarantee their full ecological function (I, II, III). Generally, small patch size leads usually to functional reductions and to transformation of GTR patches into edge habitats (Esseen 1994; North et al. 1996; Halpern & McKenzie 2001; Jalonen & Vanha-Majamaa 2001; Bradbury 2004; Halpern et al. 2005). It has been estimated that the threshold size of a GTR patch could be around 1 ha (Esseen 1994), also for key habitats in general (Pykälä 2007). Then, it would be possible to attain the state of 'core area', where the retained patch is free of the edge-

effects from surrounding habitats (Ohman 2000). The current practice in Fennoscandia is to leave 5-10 trees/ha (Vanha-Majamaa & Jalonen 2001), which is most likely inadequate in an ecological sense. For urban areas, Hamberg et al. (2008) recommend that size of forest fragments should be at least 2-3 ha. In Finland, one current problem is also the poor implementation of forest legislation and thus the poor fulfilling of biodiversity targets (Pykälä 2007), like retention of trees.

In practice, it is not always possible to estimate or imitate locally the initial forest's natural disturbance regime to the full extent, as there are many factors involved in it, including e.g. biotope variation, disturbance history and earlier forest management actions which all have affected the present state of the forest stand. Executing management actions according to the presumed disturbance regime of the area is certainly better option than to ignore completely what has happened historically. Even single-tree retention can sometimes be a better option than clear-felling (see Atlegrim & Sjöberg 1996). By leaving retention trees into the fire-refugia biotopes, it is possible to more closely mimic the natural disturbance regimes, where smaller islands often remain unburned for a longer period than larger islands (see Wardle et al. 1997).

4.2 Understorey vegetation removal

Boreal spruce forest understorey plant growth forms respond individually to the removal of single vegetation layers and their respective combinations (IV). In general, response of vegetation to the different intensities of disturbance fits well with the intermediate disturbance hypothesis of Connell (1978). The main evidence of this is as follows: 1. the number of species was greatest after moderately intensity of disturbance, 2. after low intensity disturbance, the plant community returned rapidly to its initial state, where dwarf shrubs dominate in the vegetation, and 3. after high intensity disturbance, community composition had changed very significantly and there was no sign of healthy recovery even five years after the disturbance.

Due to the characteristically thick and 'packed' structure of undisturbed understorey vegetation layers in boreal spruce forest, competition for released resources, such as growth space, is rigid and regeneration after low and moderately severe disturbance is restricted to the vegetative growth of the dominant clonal dwarf shrubs, *V. myrtillus* and *V. vitis-idaea* (IV, V). Removal of a specific layer or a growth form releases resources for an existing layer or for another growth form, respectively. For example, a dense ground layer suppresses growth of the field layer to some extent. Generally, mosses seem to recover slower than vascular plants (IV), which is in accordance with the results of Rydgren et al. (1998). The same trend has been recognized also in the heavily trampled urban boreal forests (Malmivaara et al. 2002). Mosses recover mainly by growing new segments or lateral shoots (Salemaa et al. 2008), while their main competitors, dwarf shrubs, can reallocate effectively resources from their belowground storages into the regeneration of new ramets. For tree seedling regeneration, some level of disturbance seems to be necessary (IV).

If disturbance removes plant regenerative organs and the organic horizons the soil, i.e. environmental conditions represent a state of primary succession, the regeneration of vegetation is very slow and pioneers consist mainly of graminoid tillers, seedlings and bryophytes, the latter of which can rejuvenate on mineral soil from their vegetative fragments (IV). It is genetically important that the exposure of mineral soil in boreal spruce forest floor enables the sexual reproduction of plants, while the gaps also allow a

'reasonable chance' for the reproduction of weaker competitors, such as annual herbs. Also trampling routes in urban boreal forests (Hamberg et al. 2008) and other analogous disturbance regimes, like raking (Lindholm & Nummelin 1983) can produce similar results. Eventually, small gaps will close largely via the resprouting of dwarf shrubs and also partly by the inward growth of mosses (Frego 1996) from the outer edges. Additionally, in small gaps, plant species composition even after severe disturbances consists almost entirely of the same species that have previously persisted in the undisturbed community (IV, V), which is in contrast to the results of Jonsson (1993) and Jonsson & Esseen (1998). Small-sized, mechanical disturbance does not also seem to introduce new pioneer species that often born after forest fire or soil preparation after clear-felling (Haeussler et al. 2002; Frey et al. 2003). The reason for this may be simply low light availability. Species richness often correlates with high light availability (Liira et al. 2007; Hart & Chen 2008).

In *V. myrtillus* and *V. vitis-idaea*, almost any kind of mechanical disturbance from low to moderate severity leads to increased vegetative production of new ramets and cover (V), which clearly demonstrates that these species are well-adapted to herbivory, as shown earlier by the extensive work of Tolvanen (1994). It is already known that *V. vitis-idaea* recovers better from e.g. experimental tamping (Kellomäki & Saastamoinen 1975). However, according to this thesis, the recovery growth strategies seem to differ between the deciduous and evergreen growth forms which is in accordance with earlier studies (Karlsson 1985; Salemaa et al. 1999). Deciduous *V. myrtillus* can rapidly diverge into new ramets, a feature of which can be thought as an effective advantage against e.g. animal browsing, while evergreen *V. vitis-idaea* invests in growing length of the ramets (V). This latter investment, however, may be partly caused also by the forest type: In moist spruce forests, thick and shady understorey vegetation causes relatively greater competition within the community than in drier boreal forest types, where *V .vitis-idaea* usually dominates.

After severe small-sized understorey disturbance, deciduous and evergreen growth forms rely merely on sexual reproduction instead of otherwise prevalent vegetative recovery (V). Sexual reproduction of *V. myrtillus* and *V. vitis-idaea* seems to be limited both by the poor availability of bare mineral soil substrate and seeds in the boreal forest floor. For this reason, severe disturbance, which removes all existing plant layers up to the mineral soil, is imperative for the maintenance of adequate local genetic diversity of the populations of these species (IV, V). One shortcoming of bare mineral soil patches is that they do not seem to offer much shelter for the new seedlings, which then may be exposed to temperature changes, small floodings or alternatively become easy forage for herbivores in the beginning phases.

5 CONCLUSIONS AND IMPLICATIONS FOR PRACTICAL SILVICULTURE

Results gained in this thesis present new ecological data from less well-known effects of smaller-scale disturbances on different levels of vegetation dynamics in boreal forests. The findings also support some well-known ecological theories. Green-tree retention (GTR) studies showed that increasing island size correlates with increasing number of species and that the local initial vegetation dynamics are very strong, while understorey vegetation removal studies supported strongly the intermediate disturbance hypothesis.

The GTR patch felling studies of this thesis were executed in forest stands which have represented typical Finnish forest management histories, including e.g. occasional thinning, fertilization and removal of dead wood during recent decades. Most of the current forest stands in Finland and elsewhere in Scandinavia have been treated in a similar way. Thus, the lessons learned here can be applied also to the larger boreal forest zone within Fennoscandia.

GTR patch felling, with a larger patch size than currently used in Finnish forestry, seems to preserve and even restore elements of the initial vegetation. Therefore, this felling method has clear ecological advantages in comparison to e.g. clear-felling and dispersed GTR felling, where the immediate effects of e.g. microclimate change are much more pronounced. The GTR patches should be located according to the set local objectives of the respective management plans. In order to ensure the initial biological and structural diversity in the retained forest area, it is recommended to locate the GTR patches principally in those stands where initial biological and structural diversity is already prominent. Paludified forest patches among upland spruce forest are reasonable for this purpose as: (a) they are prone to uprooting, which assures the flow of new CWD during the forest regeneration process, (b) they have naturally high initial abundance and diversity of the most important ecological key resource in boreal forests, CWD and species diversity connected to it, (c) they also function often as forest aqueducts, and (d) they are easy to recognize and delimit without advanced expert knowledge. However, the size of the patches should be significantly larger than the current voluntary standards call for. According to this thesis, if size of the GTR patches is at least 10 times larger than the current practice, higher species richness can be maintained.

If the objectives of the local management plans demand preserving of existing CWD, use of less destructive methods than scarification should be recommended for the felling areas. Along with more localized options, such as mounding, one method could be e.g. prescribed burning, which also resembles better the natural boreal disturbance dynamics. However, the effects of the other available methods on CWD, including currently increasing stump removal, are still largely unknown and more future research should be directed toward understanding their ecological effects.

Even though the understorey vegetation of natural spruce forest can rejuvenate rapidly from small-scale disturbances by vegetative means of the dominating plants, the intensity of the initial disturbance is, as it ultimately defines the speed of recovery. The forest floor withstands well moderately severe disturbance, which is typically created by animals and light trails, for example. High severity disturbances that remove the entire vegetation layer, such as single tree uprootings typical for moist natural spruce forests, are nowadays mainly affiliated with modern foresty practices. Infrequent small-sized high severity disturbances form an essential part in the natural cycle of boreal spruce forest stand dynamics. These disturbances enable the maintenance of small-scale heterogeneity through the occasional

establishment and maintenance of weaker competitors and enabling the sexual reproduction of the initial forest floor species. In sensitive areas, where natural small-scale disturbance dynamics are functioning properly, excessive scarification of the forest floor should be avoided.

This thesis has shown that the boreal forest disturbances function within different vascular and non-vascular plant groups and they can interact (for example: felling increases the number of uprootings, which affects CWD and additionally epixylics) even over short temporal scales and thus it would always be useful to estimate the extent of this interaction in e.g. local forest usage and management plans in order to prevent unwanted side-effects.

Prior to modern times, boreal forest disturbance dynamics had certain temporal and spatial regimes to which forest-dwelling species had adapted over thousands of years. Today, the most common natural and anthropogenic disturbances are increasingly interactive and due to this we may witness in the near future different types of related extreme phenomenon, such as catastrophic windthrows and massive insect outbreaks. Whether it is possible to achieve a situation where ecological and economical goals can both be fulfilled satisfactorily in these forests, which are part of the world's largest terrestrial biome, depends upon our choices and actions.

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