

# Influence of salvage logging on forest recovery following intermediate severity canopy disturbances in mixed beech dominated forests of Slovenia

Gal Fidej<sup>(1)</sup>, Andrej Rozman<sup>(1)</sup>,  
Thomas A Nagel<sup>(1)</sup>, Igor  
Dakskobler<sup>(2)</sup>, Jurij Diaci<sup>(1)</sup>

The practice of salvage logging dead and damaged timber following large high severity disturbances has raised much controversy, partly because of the negative ecological effects that such practices have on forest ecosystems. Many of the studies on salvage logging effects, however, have been done on sites damaged by large, severe disturbances. Less is known about the ecological consequences of salvage logging following intermediate severity disturbances that cause partial canopy damage at smaller scales. We examined the response of the herbaceous layer and tree regeneration to salvaged and non-salvaged treatments following small-scale intermediate severity disturbances in eight mixed beech (*Fagus sylvatica* L.) dominated forest stands in Slovenia. The cover and diversity of herbaceous vegetation, as well as the density and diversity of tree regeneration were similar between treatments across the study sites. The only notable differences between the treatments were that salvaged sites had a larger proportion of shade intolerant tree species in the regeneration layer, while non-salvaged sites tended to have a more well-developed regeneration layer in taller height classes. The results suggest that salvage logging following small-scale intermediate severity disturbances may not hinder forest recovery in mixed beech dominated forests.

**Keywords:** *Fagus sylvatica*, Forest Management, Intermediate Severity, Natural Disturbance, Regeneration, Salvage Logging

## Introduction

Salvage logging is often practiced following severe natural disturbances (e.g., fire, windthrow, insect outbreaks), primarily to recover financial losses from damaged timber (Lindenmayer et al. 2004). The potential negative effects of such practices on forest ecosystems have raised concerns among ecologists and resource managers. Much of the ecological literature indicates that salvage logging has a negative influence on forest recovery, ecosystem functions, and biodiversity (reviews in Lindenmayer & Noss 2006, Saint-Germain & Greene 2009). As such, the long-term ecological costs may outweigh short-term economic gains, particularly given that the ecological consequences of salvage logging are poorly

understood at longer time scales.

Much of the research that has examined the impact of salvage logging on forest ecosystems has been carried out following very large stand replacing fires, blow-downs, or barkbeetle outbreaks (Donato et al. 2006, Lindenmayer & Ough 2006, Jonasova & Prach 2008, Jonasova et al. 2010.), often in fire-prone regions or conifer dominated landscapes susceptible to large bark beetle outbreaks. As some authors pointed out, it is not surprising that completely salvaging severely damaged forests over large areas (e.g., 100-1000 ha) would have a substantial impact on forest ecosystems due to the large scale and cumulative impact of severe disturbance followed by salvage logging (Peterson & Leach

2008a, 2008b).

In many mesic, mixed temperate forests, however, disturbances that create large patches of near stand replacement are rare (Seymour et al. 2002), particularly those caused by fire and host-specific insects. In the temperate region of Europe, for example, where *Fagus sylvatica* is often dominant, forest dynamics is driven by relatively continuous small-scale mortality of canopy trees (i.e., gap dynamics) and periodic intermediate severity damage from wind, ice, or snow associated with more localized storm events (Nagel et al. 2013, 2014b). Such events may remove 20-30% of the canopy at stand scales (e.g. < 10 ha) and create very heterogeneous damage patterns, ranging from small scattered gaps to patches of several thousand m<sup>2</sup> (Woods 2004, Nagel & Diaci 2006).

Given that intermediate severity disturbances are relatively common, and that salvage logging is widely practiced on both private and public forestland in Europe, understanding the impact of these practices on forest ecosystems is warranted. Very few studies, however, have examined the effects of salvage logging on forest recovery following such disturbances in temperate forests. Peterson & Leach (2008a, 2008b) compared vegetation recovery in salvaged and non-salvaged sites following intermediate severity windthrow in a mixed forest of Tennessee, USA; while

□ (1) Biotechnical Faculty, University of Ljubljana, Ljubljana (Slovenia); (2) Slovenian Academy of Science and Arts, Jovan Hadži Institute of Biology, Ljubljana (Slovenia)

@ Gal Fidej ([gal.fidej@bf.uni-lj.si](mailto:gal.fidej@bf.uni-lj.si))

Received: Feb 24, 2015 - Accepted: Aug 27, 2015

**Citation:** Fidej G, Rozman A, Nagel TA, Dakskobler I, Diaci J (2016). Influence of salvage logging on forest recovery following intermediate severity canopy disturbances in mixed beech dominated forests of Slovenia. *iForest* 9: 430-436. - doi: [10.3832/ifor1616-008](https://doi.org/10.3832/ifor1616-008) [online 2016-01-07]

Communicated by: Emanuele Lingua

they found clear differences in microsite diversity and abundance between the two treatments, the density and diversity of herbs and tree seedlings did not show a detrimental response to salvaging. Lang et al. (2009) followed the long-term vegetation response to non-salvage and salvage treatments in a mixed forest damaged by severe wind in Wisconsin, USA. They found that the structure and composition of tree species on both treatments largely converged after 25 years, despite substantial damage to advance regeneration during salvage operations. Working in mixed forests throughout Switzerland, Kramer et al. (2014) examined the long-term response of tree regeneration to salvage and non-salvage treatments in large windthrow gaps. They found that the density and diversity of tree regeneration did not differ between treatments, presumably because salvage operations did not damage advance regeneration of late successional species, which dominated the forest recovery.

Here we focus on the influence of salvage logging on forest recovery following small-scale intermediate severity disturbances in mixed beech dominated forests. Although beech dominated forests are widespread in Europe, very little attention has been given to the cumulative impact of disturbance and salvage logging in this forest type. We compared the structure and composition of regeneration in neighboring salvaged and non-salvaged areas at eight sites located throughout Slovenia. Many studies have focused on regeneration in beech dominated forests in Europe; these studies indicate that beech, one of the most shade tolerant species in the temperate zone, often forms a persistent bank of seedlings and saplings in the forest understorey, such that even after relatively large disturbances it is able to maintain dominance (Collet et al. 2008, Nagel et al. 2006, 2014b, Kramer et al. 2014). The success of beech during the regeneration stage is thought to limit recruitment opportunities of other more light demanding species, such as *Acer pseudoplatanus* L., *A. platanoides* Scop., *Fraxinus excelsior* L., *F. ornus* L. and

*Ulmus glabra* Huds. that coexist in these forest communities. We therefore hypothesized that release of regeneration that established prior to disturbances will dominate untreated areas, while salvaged areas will provide opportunities for recruitment of less shade tolerant species due to damage and burial of advance regeneration during logging operations. For the same reason, however, we hypothesized that forest recovery would be more rapid (i.e., taller regeneration) in non-salvaged areas.

## Methods

### Study area

This study was carried out in mixed beech dominated forest stands located throughout Slovenia. Beech dominated forest types make up about 70% of Slovene forest lands and are managed with continuous cover forestry practices that rely on natural regeneration. Salvage logging is almost always practiced following natural disturbances on both public and privately owned forest land. As such, it was difficult to find sites with adjacent salvaged and non-salvaged treatments. After extensive field reconnaissance, we identified 8 sites that included both treatments (Tab. 1, Fig. 1); the main reason for not entirely salvaging these areas were inaccessibility due to rugged terrain and lack of roads and skidding trails. The study sites were mainly damaged by wind disturbances (except two sites damaged by ice and snow) between 1993 and 2008. Sampling was carried out in 2012, such that forest recovery was well underway at the time of sampling. Based on visual estimates from high-resolution aerial photographs provided by the Slovenian Environment Agency, the severity of these disturbances varied between 25-75% canopy removal (Tab. 1).

Although beech was the dominant canopy species across the study sites, inventory data from the Slovenian Forest Service indicated that a number of other tree species were present in these stands. Those species that were relatively dominant compared to beech included *Picea abies* (L.) H.

Karst. (Norway spruce), *Acer pseudoplatanus* L. (sycamore maple), *Ostrya carpinifolia* Scop. (Hop Hornbeam), *Abies alba* Mill. (European silver-fir), *Fraxinus excelsior* L. (ash), *Quercus petraea* (Matt.) Liebl. (Cornish oak), *Fraxinus ornus* L. (manna ash), *Sorbus aria* (L.) Crantz (Whitebeam) and *Carpinus betulus* L. (European hornbeam).

Salvage operations were carried out in the same year or one year following the disturbances with motor-manual cutting and either tractor or cable crane skidding. Both skidding techniques damaged regeneration via removal of tree boles, while tractor skidding included additional damage depending on the surface area of skidding trails at a given site. However, of the three sites harvested with tractor skidding, the Jagrščce site was the only site where a new skidding trail was constructed; the other two sites used existing infrastructure.

### Field sampling

Within each of the broader disturbance areas, which often included scattered patches of damage within stands, we limited our sampling to disturbed patches that had adjacent non-salvaged and salvaged treatments. These patches ranged from 0.7 to 5.5 ha (Tab. 1). Each treatment within these patches was stratified into 4 approximately equal sized areas and a 100 m<sup>2</sup> sample plot was placed at a random location within each area. In each plot, we visually estimated the per cent cover of the herbaceous layer and tree regeneration following the Braun-Blanquet approach, i.e., regeneration cover estimates were divided into herb (< 0.5 m tall) and shrub (0.5-6 m tall) layers – Mucina et al. 2000). Additionally, we counted the number of woody stems for each tree species in the following height classes: (i) 20-50 cm; (ii) 51-130 cm; (iii) 131 cm of height up to 5 cm diameter at breast height (dbh); and (iv) dbh > 5 cm. This last class included pole size trees typically between 5 and 10 cm dbh, which occurred at low densities in some plots. For each woody stem we categorized browsing damage in 3 classes: (i) up to 10%

**Tab. 1** - Site characteristics of the eight disturbance areas with adjacent non-salvaged and salvaged treatments. Species are listed according to their abundance in the surrounding stands. (FS): *Fagus sylvatica*, (OC): *Ostrya carpinifolia*, (FO): *Fraxinus ornus*, (FE): *Fraxinus excelsior*, (AP): *Acer pseudoplatanus*, (QP): *Quercus petraea*, (PT): *Populus tremula*, (CB): *Carpinus betulus*, (PA): *Picea abies*, (AA): *Abies alba*. (SA): *Sorbus aria*. (lim): limestone, (dol): dolomites, (sil): intrusions of silicates. Disturbance class: (1): 0-25%, (2): 25-50%, (3): 50-75%, (4): 75-100% of disturbed canopy.

No.	Site	Main tree species	Bedrock	Year of disturbance	Slope (°)	Disturbance type	Elevation (m)	Exposure	Size (ha)	Disturbance Class	Salvage Technique
1	Bohor	FS, OC, FO, SA, AP	dol & lim + sil	2008	34	wind	300-460	S	5.5	2	tractor
2	Črmošnjice	FS, AP, QP, PT, CB	dol	2006	32	ice	700-830	NE	1.3	2	cable crane
3	Kosmate doline	FS, PA, AP, AA	dol	1993	25	wind	1250-1300	NW-N	0.7	3	tractor
4	Lesično	FS, OC, AP, PA, FO	dol & lim + sil	2008	29	wind	400-500	NW	1.1	2	cable crane
5	Nemškarica	FS, AA, PA, AP, FE	dol	2006	36	wind	610-750	N-NE	1.5	3	cable crane
6	Jagrščce	FS, OC, FE, PA, CB	dol	2007	38	snow	270-380	E-NE	1.5	3	tractor
7	Zadlog	FS, PA, AP, OC, FE	dol	2006	36	wind	700-750	N	1.1	2	cable crane
8	Zala	FS, PA, AA, AP, FE	dol & lim	2005	36	wind	400-500	N-NE	1	2	cable crane

of lateral shoots browsed; (ii) terminal shoot browsed and/or <50% of lateral shoots browsed; and (iii) terminal shoot and majority of lateral shoots browsed. As an additional indicator of regeneration recovery, we also measured the height of the five tallest individuals in the regeneration layer present in the plot. Finally, we recorded environmental conditions in each plot, including elevation, slope aspect and inclination, relief (i.e., flat, convex, concave), rockiness (% cover), skidding trails (% cover), coarse woody debris (% CWD cover), and erosion (% cover of eroded surface).

The effects of treatment and site factors (elevation, slope, CWD and rockiness) on vegetation cover, regeneration densities, diversity, and height were analyzed with mixed-effects models. These models allow nested error structures as the sample plots were nested within eight sites. Models for tree regeneration density were built with generalized mixed-effects models (GLMMs - Fournier et al. 2012) using a negative binomial distribution, while models for vegetation cover and diversity were built with linear mixed-effects models (LMMs - Pinheiro et al. 2013). To meet the assumptions of normality and linearity variables were transformed if necessary. For model diagnostics, both model confidence intervals of parameters and analyzed sets of graphical summaries proposed by Robinson & Hamann (2011) and Zuur et al. (2009) were examined. Data were analyzed using R Version 3.0.2 (R Development Core Team 2013).

## Results

### Vegetation cover and density

Herbaceous cover and tree regeneration density varied among the 8 study sites. For example, total regeneration density (for both treatments and height classes combined at each site) ranged from 767 to 35467 stems  $\text{ha}^{-1}$ , respectively. There was, however, a significant decrease in regeneration density with elevation ( $p = 0.020$ ). With respect to the salvaged and non-salvaged treatments pooled across the 8 sites, the cover of herbaceous vegetation was similar between treatments ( $p = 0.877$  - Fig. 2), while total tree regeneration density (all height classes combined) was higher on salvaged sites, though this difference was not significant ( $p = 0.059$  - Fig. 2). A Spearman's bivariate analysis revealed that regeneration density was also negatively related with CWD cover ( $\rho = -0.29$ ), but this was not significant in the GLMM model. The average cover of CWD was 19% in non-salvaged and 6% in salvaged treatments ( $p < 0.001$ ). Evidence of erosion was minimal, with an average cover of 4% in both treatments. We found significant differences ( $p = 0.009$ ) in shrub layer coverage between sites that were harvested with tractor (about 20%) and those with cable crane (about 40%).

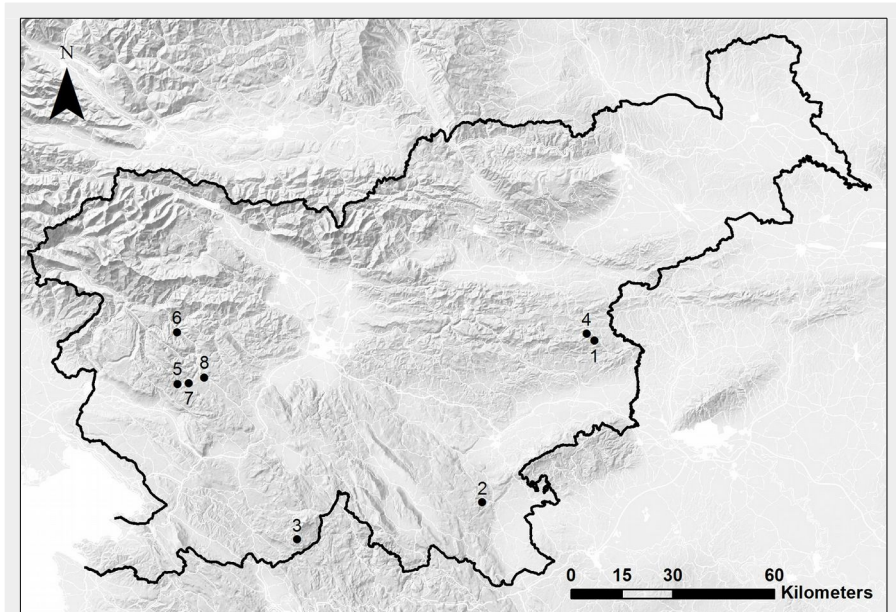


Fig. 1 - Map of Slovenia showing the eight study sites. The number of each study site corresponds with those listed in Tab. 1.

### Vegetation composition and height structure

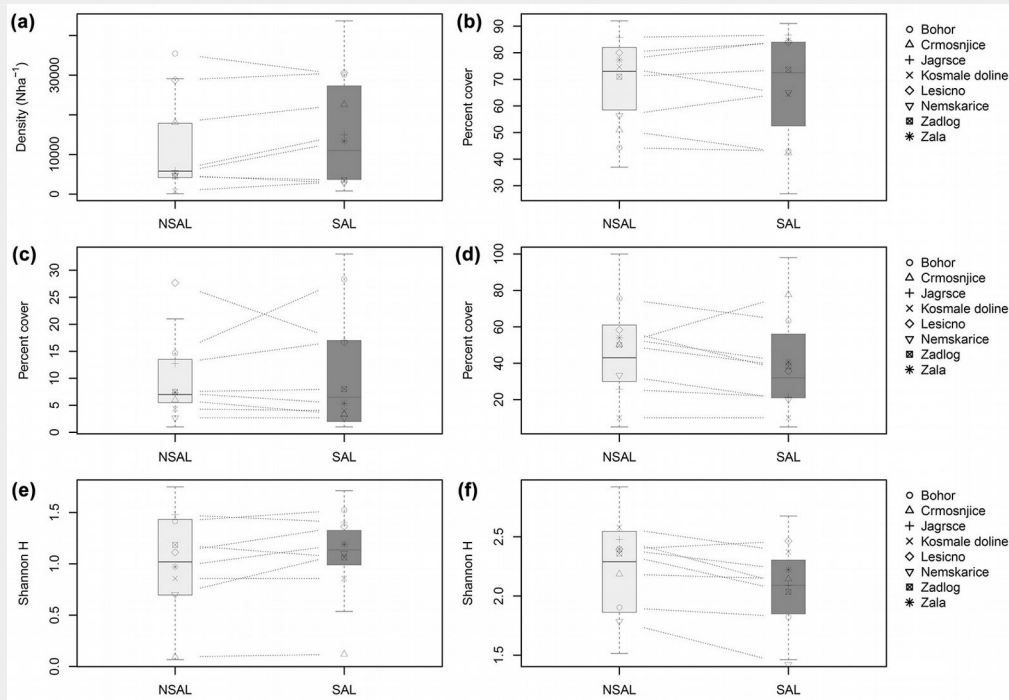
A total of 237 herbaceous species and 25 tree species were encountered across the 8 sites, but there were fewer species that dominated each site. For tree species, there were typically about 4-6 species that made up > 90% of the individuals across the sites. The Shannon index for herbaceous diversity was marginally higher on non-salvaged sites ( $p=0.023$ ), while for trees species (for all height classes combined) it was higher on salvaged sites, though not significant ( $p=0.200$  - Fig. 2).

We documented considerable variability in the height structure of tree regeneration by species across the sites and treatments, patterns which are useful for interpreting successional pathways (Fig. 3). To simplify our interpretation, we divided tree species into three shade tolerance categories based on Ellenberg's indicator values (EIV) for light (Ellenberg 1988): (i) tolerant (EIV < 4); (ii) intermediate (EIV = 4); and intolerant (EIV > 4). Contrary to our expectations, shade tolerant species, namely *Fagus sylvatica*, *Carpinus betulus*, and *Abies alba*, were not dominant across the study sites (44% of stems), nor were they clearly dominant in non-salvaged sites (47% in non-salvaged versus 41% in salvaged - Fig. 3, Fig. 4). However, they were more abundant in taller regeneration height classes (60% of the two tallest height classes). There were no significant differences between treatments with regard to either the combined cover ( $p=0.072$ ) or density ( $p=0.110$ ) of these three shade tolerant species. It is worth noting, however, that these shade tolerant species made up a higher proportion of the regeneration layer in non-salvaged treatments, although this was not significant (Fig. 4).

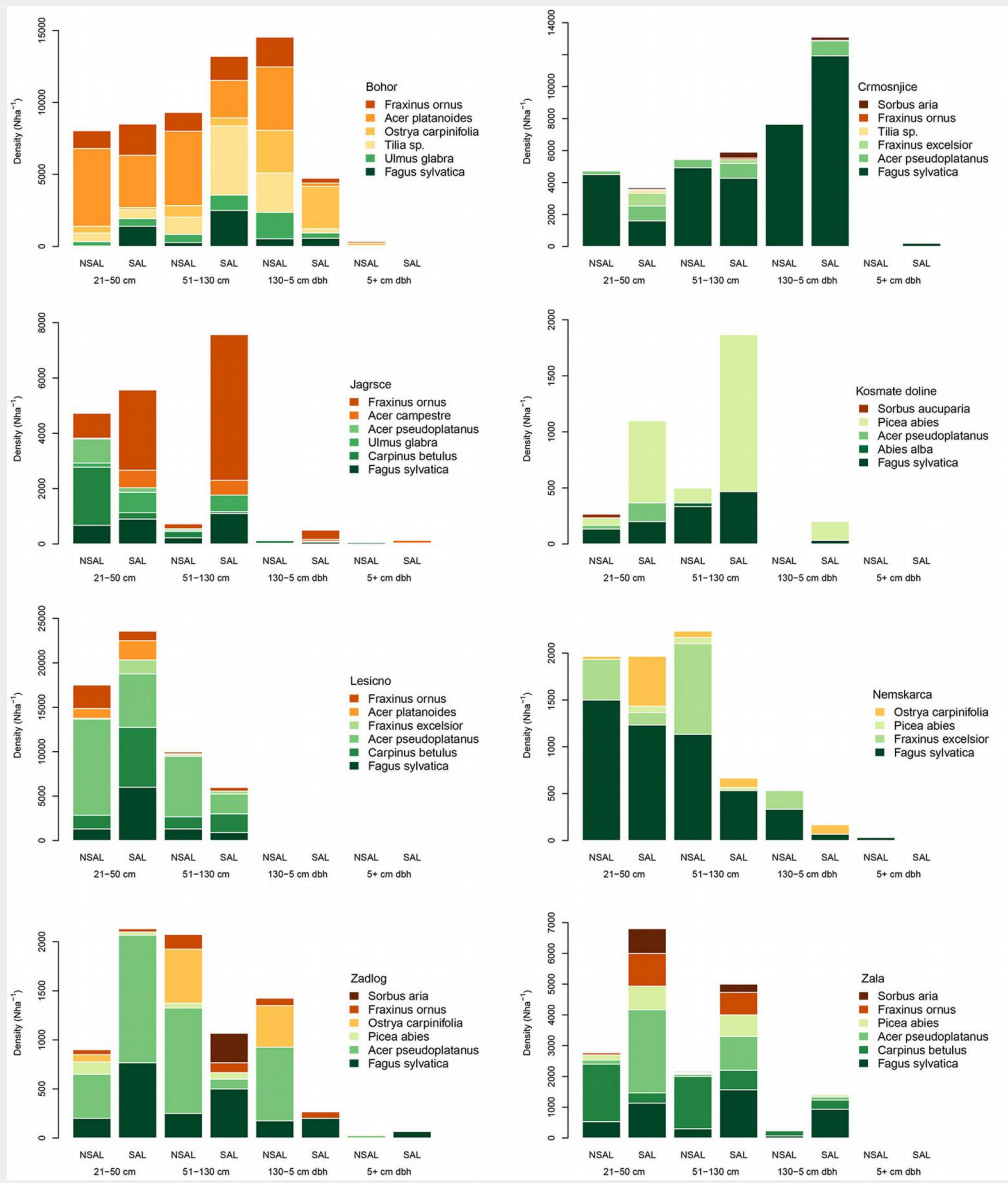
Less shade tolerant tree species, espe-

cially species like *Acer pseudoplatanus*, *A. platanoides*, *Fraxinus excelsior* and *F. ornus*, were equally or more abundant than shade tolerant species across the height classes, but the patterns between the salvaged and non-salvaged treatments were variable (Fig. 3). At some sites, there was a general trend toward higher densities of less shade tolerant species in the salvaged treatment (e.g., Črmošnjice, Zala), while the opposite pattern was found on other sites (e.g., Zadlog). Nevertheless, we did find that shade intolerant species made up a larger proportion ( $p = 0.013$ ) of the regeneration layer in salvaged (36 %) compared to non-salvaged sites (23 % - Fig. 4). This was consistent across all height classes. The proportion of tree species with intermediate shade tolerance was similar between treatments, but decreased with increasing height classes in both treatments.

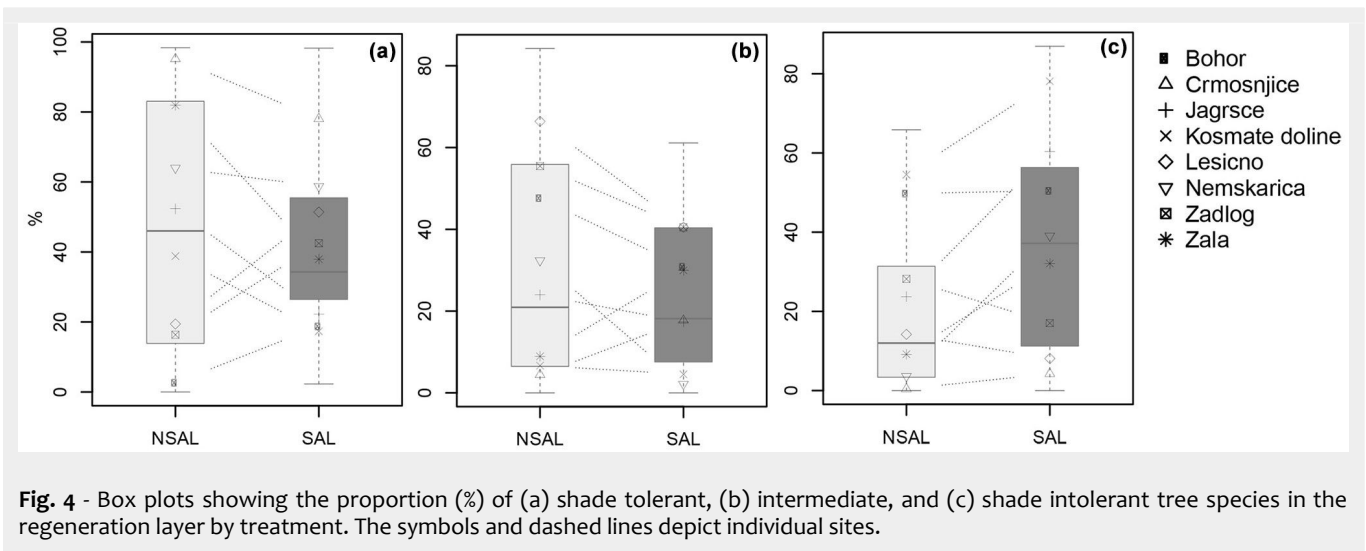
There was also no clear pattern with regard to the overall height structure of the regeneration layer between treatments. On sites with a well developed layer of regeneration in the  $H > 131$  cm and  $\text{dbh} < 5$  cm class, for example, some sites had a higher overall density in non-salvaged treatments (i.e., Bohor, Nemškarica, Zadlog), while others had a higher density in the salvaged treatment (i.e., Črmošnjice, Zala). Overall, stems in the two smaller classes combined had a higher density in salvaged treatments ( $p = 0.038$ ). Likewise, the Braun-Blanquet cover estimates indicated that the combined cover of the moss and herb layer was higher in salvaged sites (78%) when compared to non-salvaged (72%), while the combined cover of the shrub and tree layer was higher in non-salvaged sites (46% vs. 40%); none of these differences were statistically significant ( $p = 0.170$ ,  $p = 0.164$ ). The overall mean height of the tallest stems was marginally taller in



**Fig. 2** - Box plots of: (a) tree regeneration density (all height classes combined); (b) herb per cent cover; (c) tree and shrub cover in the herb layer; (d) tree and shrub cover; (e) tree regeneration diversity; and (f) herb diversity in non-salvaged and salvaged treatments for the eight study sites combined. The symbols and dashed lines depict individual sites.



**Fig. 3** - Density of tree species in the regeneration layer by height class and treatment. Only the six most abundant tree species, which made up > 90% of the total stems, are shown for each site.



**Fig. 4** - Box plots showing the proportion (%) of (a) shade tolerant, (b) intermediate, and (c) shade intolerant tree species in the regeneration layer by treatment. The symbols and dashed lines depict individual sites.

non-salvaged (189.0 cm;  $n=106$ ) compared to salvaged treatments (167.1 cm;  $n=95$  –  $p=0.060$ ). Browsing damage on regeneration was relatively low across the sites (80 % of the regeneration was classified in the category with  $< 10\%$  of lateral shoots browsed) and significantly higher ( $\chi^2$ ,  $p=0.000$ ) on salvaged sites.

## Discussion

While we found substantial variability in vegetation structure and composition among sites and between salvaged and non-salvaged treatments within individual sites, we did not identify compelling differences between salvaged and non-salvaged treatments pooled across the study sites. Salvaged treatments on many of the study sites had marginally higher species diversity in the regeneration layer and a higher proportion of shade intolerant tree species than in non-salvaged treatments, yet there was no clear evidence that release of shade-tolerant advance regeneration dominated non-salvaged treatments. Therefore, we found limited support for our first hypothesis. Our second hypothesis, that salvaged treatments would be less advanced in their development due to damaged advance regeneration, also received only partial support. On the whole non-salvaged treatments had marginally higher cover, density, and heights within the taller regeneration classes.

Although we do not have data on the pre-disturbance forest structure and composition, national forest service inventory plots indicate that beech was dominant in the canopy across most of the sites (60-90% of canopy layer), except Kosmate doline, where spruce was co-dominant. The higher tree species diversity found in the study areas (relative to their abundance in the canopy), regardless of treatment type, suggests that increased light levels following the natural disturbance events facilitated recruitment of less shade-tolerant species. Although we cannot distinguish stems that were present as advance regeneration

prior to disturbance from those that established afterwards, the height structure data indirectly suggest that both pathways were important for the recovery process. It is also important to note that the study areas varied in time since disturbance, yet disturbances in all but one site (Kosmate doline – a cold, high elevation site with slower development) were within a four year span, such that recovering forests were likely within similar stages of development.

Several reasons may explain the lack of a clear treatment effect. First, given that we focused on intermediate severity wind disturbances that damaged relatively small areas, it is reasonable to assume that much of the soil, herbs, and advance tree regeneration were left intact, except for vegetation crushed by fallen trees. Furthermore, the salvage operations were also relatively moderate and relied on existing skidding trails and forest roads, such that much of the soil and vegetation on these sites likely remained relatively undamaged. This is well exemplified by the low cover of eroded bare soil across the sites, which averaged only 4% in both treatments. In a large study of damage to regeneration resulting from tractor skidding and cable crane harvesting across 51 stands in Slovenia, the average amount of damaged regeneration was 21 and 16%, respectively (Košir 2008). This suggests that both extraction techniques in this study (tractor skidding and cable crane) were unlikely to have caused a substantial amount of residual stand damage. In contrast, harvester machines, which are often employed for large-scale salvage operations, drive over a larger portion of a given stand, which could result in greater residual damage to soils and regeneration (Surakka et al. 2011).

A second reason may be that environmental differences between neighboring treatments were more important drivers of vegetation recovery than treatment. Because it was difficult to find study sites with neighboring salvaged and non-salvaged treatments throughout beech forests

in Slovenia, we were unable to control for variation in site conditions between treatments, such as small differences in slope aspect and steepness or soil conditions, which were likely to confound treatment effects. For example, in a large-scale study on the influence of salvage logging on forest recovery across Swiss forests, Kramer et al. (2014) found that site factors (i.e., soil pH and ground vegetation) were more important than treatment.

Although we did not find substantial differences in vegetation structure and composition between treatments, the trends in the pooled data set provide some support for our predictions. Both the density and diversity of tree regeneration were slightly higher in salvaged treatments, while there was evidence of a more well-developed regeneration layer in non-salvaged areas. It seems likely that removal of coarse woody debris, which may act as a physical barrier to regeneration, coupled with less competition from taller advance regeneration, enabled establishment and recruitment of a wide range of tree species in the salvaged areas. The higher cover of taller stems in the non-salvaged area may be ecologically important because these individuals are likely to form the next canopy layer and may shade out many of the stems in the lower layers.

Differences in the cover and composition of herbs were less clearly related to treatment, perhaps because they respond more to underlying differences in site conditions. A number of studies have indicated that a dense herb layer may develop following disturbance to the forest canopy, which may inhibit tree regeneration during early stages of forest recovery (Wohlgemuth et al. 2002, Jonasova & Prach 2008, Kelemen et al. 2012). The relatively low density of tree regeneration across the study sites, with an overall average of 13770 stems  $ha^{-1}$ , provides indirect evidence of this. For comparison, published regeneration densities from unmanaged beech dominated forests in Europe, where smaller scale gap dynamics drive regeneration dynamics, are

often substantially higher (Drösser & Von Lupke 2007, Rozenberger et al. 2007, Hobi et al. 2014).

One of the more surprising findings was the low level of browsing damage to regeneration across the study sites. The density of red deer in Slovenia is high, with more than 10 deer km<sup>2</sup> in some regions (Nagel et al. 2014a). Moreover, compared to species of *Fagus sylvatica* and *Carpinus betulus* regeneration, many of the less shade tolerant tree species in the regeneration layer, particularly *Acer pseudoplatanus*, *A. platanoides*, *Ulmus glabra*, *Fraxinus excelsior* and *F. ornus* are highly preferred browse species (Gill 1992). We did observe lower levels of browsing in non-salvaged treatments, which some authors attribute to physical barriers provided by downed trees (Relva et al. 2009, Bottero et al. 2013).

It is difficult to make broad generalizations regarding the influence of salvage logging on forest recovery across forest types and disturbance regimes. While there is clear evidence of the negative effects of salvaging on regeneration in some circumstances (e.g., large-scale high severity disturbance and salvaging – Donato et al. 2006, Jonasova et al. 2010), the evidence is less clear following a combination of intermediate severity disturbance and salvage logging (Peterson & Leach 2008a, Lang et al. 2009, D'Amato et al. 2011, Kramer et al. 2014). It is important to note that we focused on the influence of salvage logging on vegetation in this study. There is overwhelming evidence that salvage logging has a negative influence on a number of other structures and functions of forest ecosystems. For example, salvaging large amounts of dead coarse wood removes key food and habitat for species dependent on these biological legacies (Franklin et al. 2000, Lachat et al. 2013). Given the low volume of dead wood across managed forests in Europe (FOREST EUROPE/UNECE/FAO 2011), refraining from salvage logging some post-disturbance sites should be advised in forests managed for multiple functions, such as many publicly owned forest lands in Europe that integrate both ecological and economic functions. On private land, however, where owners often have a vested interest in recovering value from downed wood following disturbances, our study suggests that salvage logging may not hinder forest development following small-scale intermediate severity disturbances in mixed beech dominated forests.

### Acknowledgements

The study was supported by the applied project "Ecological restoration of natural disturbances in forests" (L4-4091) as well as by the Pahernik foundation. We thank students from the Department of Forestry, University of Ljubljana (Slovenia) that conducted the field work. We also thank the Slovenian Forest Service for help with identifying suitable research sites. Finally, we

are grateful to Aleš Poljanec who provided the data from the Slovenian Forest Service inventory for the research sites.

### References

- Bottero A, Garbarino M, Long JN, Motta R (2013). The interacting ecological effects of large-scale disturbances and salvage logging on montane spruce forest regeneration in the western European Alps. *Forest Ecology and Management* 292: 19-28. - doi: [10.1016/j.foreco.2012.12.021](https://doi.org/10.1016/j.foreco.2012.12.021)
- Collet C, Piboule A, Leroy O, Frochot H (2008). Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest. *Forestry* 81: 135-150. - doi: [10.1093/forestry/cpn004](https://doi.org/10.1093/forestry/cpn004)
- Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2006). Post-Wildfire logging hinders regeneration and increases fire risk. *Science* 311: 352-352. - doi: [10.1126/science.1122855](https://doi.org/10.1126/science.1122855)
- Drösser L, Von Lupke B (2007). Stand structure, regeneration and site conditions in two virgin beech forest reserves in Slovakia. *Allgemeine Forst Und Jagdzeitung* 178: 121-135.
- D'Amato AW, Fraver S, Palik BJ, Bradford JB, Patty L (2011). Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecology and Management* 262: 2070-2078. - doi: [10.1016/j.foreco.2011.09.003](https://doi.org/10.1016/j.foreco.2011.09.003)
- Ellenberg H (1988). *Vegetation ecology of central europe*. Cambridge University Press, New York, USA, pp. 753. [online] URL: <http://books.google.com/books?id=LQNxbuyPxawC>
- FOREST EUROPE/UNECE/FAO (2011). *State of Europe's Forests 2011. Status and trends in sustainable forest management in Europe*. Ministerial Conference on the Protection of Forests in Europe, FOREST EUROPE Liaison Unit, Oslo, Norway, pp. 344. [online] URL: [http://www.foresteurope.org/documentos/State\\_of\\_Europes\\_Forests\\_2011\\_Report\\_Revised\\_November\\_2011.pdf](http://www.foresteurope.org/documentos/State_of_Europes_Forests_2011_Report_Revised_November_2011.pdf)
- Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27: 233-249. - doi: [10.1080/10556788.2011.597854](https://doi.org/10.1080/10556788.2011.597854)
- Franklin JF, Lindenmayer DB, MacMahon JA, McKee A, Magnusson J, Perry DA, Waide R, Foster DR (2000). Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. *Conservation Biology in Practice* 1: 8-16. - doi: [10.1111/j.1526-4629.2000.tb00155.x](https://doi.org/10.1111/j.1526-4629.2000.tb00155.x)
- Gill RMA (1992). A review of damage by mammals in north temperate forests: 1. Deer. *Forestry* 65: 145-169. - doi: [10.1093/forestry/65.2.145](https://doi.org/10.1093/forestry/65.2.145)
- Hobi ML, Commarmot B, Bugmann H (2014). Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science* 26: 323-336. - doi: [10.1111/jvs.12234](https://doi.org/10.1111/jvs.12234)
- Jonasova M, Prach K (2008). The influence of bark beetles outbreak vs. salvage logging on

ground layer vegetation in Central European mountain spruce forests. *Biological Conservation* 141: 1525-1535. - doi: [10.1016/j.biocon.2008.03.013](https://doi.org/10.1016/j.biocon.2008.03.013)

Jonasova M, Vavrova E, Cudlin P (2010). Western Carpathian mountain spruce forest after a windthrow: natural regeneration in cleared and uncleared areas. *Forest Ecology and Management* 259: 1127-1134. - doi: [10.1016/j.foreco.2009.12.027](https://doi.org/10.1016/j.foreco.2009.12.027)

Kelemen K, Mihók B, Gálhidy L, Standovár T (2012). Dynamic response of herbaceous vegetation to gap opening in a central European beech stand. *Silva Fennica* 46: 53-65. - doi: [10.14214/sf.65](https://doi.org/10.14214/sf.65)

Košir B (2008). Damage to young forest due to harvesting in shelterwood systems. *Croatian Journal of Forest Engineering* 29: 141-153. [online] URL: <http://hrcak.srce.hr/32190?lang=en>

Kramer K, Brang P, Bachofen H, Bugmann H, Wohlgemuth T (2014). Site factors are more important than salvage logging for tree regeneration after wind disturbance in Central European forests. *Forest Ecology and Management* 331: 116-128. - doi: [10.1016/j.foreco.2014.08.002](https://doi.org/10.1016/j.foreco.2014.08.002)

Lachat T, Ecker K, Duelli P (2013). Population trends of *Rosalina alpina* (L.) in Switzerland: a lasting turnaround? *Journal of Insect Conservation* 17: 653-662. - doi: [10.1007/s10841-013-9549-9](https://doi.org/10.1007/s10841-013-9549-9)

Lang KD, Schulte LA, Guntenspergen GR (2009). Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. *Forest Ecology and Management* 259: 56-64. - doi: [10.1016/j.foreco.2009.09.042](https://doi.org/10.1016/j.foreco.2009.09.042)

Lindenmayer DB, Noss RF (2006). Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation Biology* 20: 949-958. - doi: [10.1111/j.1523-1739.2006.00497.x](https://doi.org/10.1111/j.1523-1739.2006.00497.x)

Lindenmayer DB, Ough K (2006). Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. *Conservation Biology* 20: 1005-1015. - doi: [10.1111/j.1523-1739.2006.00501.x](https://doi.org/10.1111/j.1523-1739.2006.00501.x)

Lindenmayer D, Foster DR, Franklin JF, Hunter ML, Noss RF, Schmiegelow FA, Perry D (2004). Salvage harvesting policies after natural disturbances. *Science* 303: 1303. [online] URL: [http://www.californiachaparral.com/images/Lindenmayer\\_et\\_al\\_Salvage\\_Harvesting\\_Science\\_2004.pdf](http://www.californiachaparral.com/images/Lindenmayer_et_al_Salvage_Harvesting_Science_2004.pdf)

Mucina L, Schaminée JHJ, Rodwell JS (2000). Common data standards for recording relevés in field survey for vegetation classification. *Journal of Vegetation Science* 11: 769-772. - doi: [10.2307/3236581](https://doi.org/10.2307/3236581)

Nagel TA, Diaci J (2006). Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. *Canadian Journal of Forest Research* 36: 629-638. - doi: [10.1139/x05-263](https://doi.org/10.1139/x05-263)

Nagel TA, Svoboda M, Diaci J (2006). Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. *Forest Ecology and Management* 226: 268-278. - doi: [10.1016/j.foreco.2006.01.039](https://doi.org/10.1016/j.foreco.2006.01.039)

Nagel TA, Svoboda M, Panayotov M (2013). Natural disturbances and forest dynamics in temperate forests of Europe. In: "Integrative Approaches as an Opportunity for the Conserva-

- tion of Forest Biodiversity". European Forest Institute, Joensuu, Finland, pp. 116-123.
- Nagel TA, Diaci J, Jerina K, Kobal M, Rozenbergar D (2014a). Simultaneous influence of canopy decline and deer herbivory on regeneration in a conifer-broadleaf forest. *Canadian Journal of Forest Research* 45: 266-275. - doi: [10.1139/cjfr-2014-0249](https://doi.org/10.1139/cjfr-2014-0249)
- Nagel TA, Svoboda M, Kobal M (2014b). Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications* 24: 663-679. - doi: [10.1890/13-0632.1](https://doi.org/10.1890/13-0632.1)
- Peterson CJ, Leach AD (2008a). Limited salvage logging effects on forest regeneration after moderate-severity windthrow. *Ecological Applications* 18: 407-420. - doi: [10.1890/07-0603.1](https://doi.org/10.1890/07-0603.1)
- Peterson CJ, Leach AD (2008b). Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry* 81: 361-376. - doi: [10.1093/forestry/cpn007](https://doi.org/10.1093/forestry/cpn007)
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2013). "nlme": Linear and nonlinear mixed effects models. R package version 3.1-113, CRAN, pp. 335. [online] URL: <http://cran.r-project.org/web/packages/nlme/nlme.pdf>
- R Development Core Team (2013). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL. [online] URL: <http://www.R-project.org/>
- Relva MA, Westerholm CL, Kitzberger T (2009). Effects of introduced ungulates on forest understorey communities in northern Patagonia are modified by timing and severity of stand mortality. *Plant Ecology* 201: 11-22. - doi: [10.1007/s11258-008-9528-5](https://doi.org/10.1007/s11258-008-9528-5)
- Robinson AP, Hamann JD (2011). *Forest analytics with R: an introduction*. Springer-Verlag, New York, USA, pp. 354.
- Rozenbergar D, Mikac S, Anic I, Diaci J (2007). Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech-fir forest reserves in South East Europe. *Forestry* 80: 431-443. - doi: [10.1093/forestry/cpm037](https://doi.org/10.1093/forestry/cpm037)
- Saint-Germain M, Greene DF (2009). Salvage logging in the boreal and cordilleran forests of Canada: integrating industrial and ecological concerns in management plans. *The Forestry Chronicle* 85 (1): 120-134. - doi: [10.5558/tfc85120-1](https://doi.org/10.5558/tfc85120-1)
- Seymour RS, White AS, DeMaynadier PG (2002). Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155 (1-3): 357-367. - doi: [10.1016/S0378-1127\(01\)00572-2](https://doi.org/10.1016/S0378-1127(01)00572-2)
- Surakka H, Siren M, Heikkinen J, Valkonen S (2011). Damage to saplings in mechanized selection cutting in uneven-aged Norway spruce stands. *Scandinavian Journal of Forest Research* 26 (3): 232-244. - doi: [10.1080/02827581.2011.552518](https://doi.org/10.1080/02827581.2011.552518)
- Wohlgemuth T, Kull P, Wüthrich H (2002). Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. *Forest, Snow and Landscape Research* 77: 17-47. [online] URL: <http://www.wslf.ch/dienstleistungen/publikationen/pdf/4706.pdf>
- Woods KD (2004). Intermediate disturbance in a late-successional hemlock- northern hardwood forest. *Journal of Ecology* 92 (3): 464-476. - doi: [10.1111/j.0022-0477.2004.00881.x](https://doi.org/10.1111/j.0022-0477.2004.00881.x)
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009). *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York, USA, pp. 574. - doi: [10.1007/978-0-387-87458-6](https://doi.org/10.1007/978-0-387-87458-6)