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The interacting ecological effects of large-scale disturbances and salvage logging on montane spruce forest regeneration in the western European Alps

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Abstract

The combined effects of a natural (i.e., insect outbreak or wind storm) and an anthropogenic (i.e., salvage logging) disturbance on stand dynamics, including tree regeneration, were studied to assess the role of post-disturbance management practices following the most common disturbances affecting the northern slopes of montane Norway spruce (*Picea abies* (L.) H. Karst.) forests in the European Alps. The study areas were in two adjacent inner valleys of the Aosta Valley Autonomous Region (western Italian Alps). Les Combes study area experienced an insect (*Lymantria monacha* L.) outbreak that affected 91 ha in 1984-1990, while a wind storm impacted 70 ha in the other valley (Parriod study area) in 1990. Salvage logging took place in both study areas two years after the natural disturbance occurrence (i.e., in 1991-1992 in Les Combes, and in 1992-1993 in Parriod), and only dead trees were salvaged. Site characteristics, overstory and understory trees, and coarse woody debris (CWD) data were collected during the summer of 2010 in 90 plots randomly distributed within disturbed portions and in control stands of the two study areas. The variability of natural regeneration structure and composition in relation to environment, forest structure, type of disturbance, and salvage logging were analyzed by univariate (i.e., ANOVA and correlations) and multivariate (i.e., MRPP, PCA, and RDA) analyses. Regeneration structure and composition were clearly different for the two disturbance types. Individuals originated mainly from seed after the insect outbreak, while an important role was played by advance regeneration in the windthrow area. Regeneration was more abundant and rich in shade tolerant species (i.e., *Abies alba* Mill.) after the insect outbreak, while *Larix decidua* Mill. and light demanding broadleaves were dominant after the windthrow. The two major factors influencing post-disturbance regeneration were the amount of the residual overstory and the amount and distribution of CWD. The presence of residual forest patches facilitated regeneration establishment by reducing herb and shrub competition, and regulating the light that penetrates to the ground. Woodpiles had a negative influence on regeneration in terms of abundance and also influenced composition. On the contrary, scattered CWD facilitated the establishment of new individuals by reducing competition with herbs and shrubs, reducing the browsing impact and improving substrate moisture, especially for Norway spruce.

1 Introduction

Montane Norway spruce (*Picea abies* (L.) H. Karst.) forests cover a substantial area of the European Alps (more than 150000 km^2 within the territory of the Alps of the Alpine Convention, Skrøppa, 2003) and are the dominant forest type in the northern slopes of the inner Aosta Valley. Landscapes in this region, even in remote areas, reflect centuries of human activities, particularly timber extraction and livestock grazing, which have considerably changed forest vegetation from natural conditions (e.g., Bastian and Bernhardt, 1993; Kräuchi et al., 2000; Spiecker, 2003; Motta et al., 2006a; Bolli et al., 2007; Kulakowski et al., 2011). Human influence on these landscapes began to diminish in the second half of the nineteenth century, when the economy and social structure of alpine valleys underwent radical changes. A consequence of changes in land use in the last 100 years has been an increase in forest surface and in growing stock that, at the European scale, it is currently three times higher that in 1950 (Schellhaas et al, 2005). These changes are associated with a general increase in spatial pattern homogeneity (Garbarino et al., 2010) which, in turn, is associated with a loss in suitable habitat for some species and an increase in susceptibility to major forest disturbances (Foster, 1988; Kulakowski and Veblen, 2002; Hanewinkel et al., 2008; Kulakowski et al., 2011).

Centuries of human activity, including the more recent changes in land use, have also certainly influenced the natural disturbance regimes. The occurrence of natural disturbances in stands and landscapes altered by anthropogenic activities (e.g., fire suppression, timber harvesting, and grazing) modifies outcomes for ecosystem structure and function (Zumbrunnen et al., 2009; Kulakowski et al., 2011). The concept of a natural fire regime in the European Alps is, for example, problematic. Most of the forest fires in the Valle d'Aosta region are currently winter fires, principally important on low elevation southern slopes of the lower valley, and are mainly caused by human activity (Beghin et al., 2010; Zumbrunnen et al., 2011); in the same time there is a small percentage of summer lightning fires in the higher montane and subalpine belts (Cesti et al. 2005) that could potentially play an important role in the natural disturbance regime (Tinner et al., 2005; Carcaillet et al., 2009).

Wind storms and insect outbreaks are two common disturbances affecting forests in the European Alps (Schelhaas et al., 2003; Büntgen et al., 2009). Large-scale windthrow may impact thousands of hectares of mature forests (Bründl and Rickli, 2002; Wohlgemuth et al., 2002; Zielonka et al., 2010), and leave legacies of advance regeneration, which can contribute to the persistence of shade-tolerant species within the forest (Schönenberger, 2002). Typical microstructures such as pits and mounds, and the exposed mineral soil caused by windthrow create heterogeneity in microsites at the ground level (Ulanova, 2000). Moreover, fallen coarse woody debris plays an important role in creating suitable microhabitat especially for the establishment of shade-tolerant species (Zielonka, 2006; Svoboda et al., 2010). In contrast, insect outbreaks may result in patchy mortality of both overstory and understory trees, and leave more standing dead trees (Müller et al., 2008). Surviving trees and the complex spatial pattern of light distribution may also contribute to higher levels of seed production and thereby influence regeneration (Dai, 1996; Jonášová and Matějková, 2007).

Despite the importance of large-scale disturbances in Europe, most studies have focused on the role of intermediate- and small-scale disturbances in forest dynamics (e.g., Nagel and Diaci, 2006; Svoboda et al., 2010; Bottero et al., 2011). For spruce forests in the Italian Alps several studies have explored stand-scale dynamics, especially in the eastern part of the mountain range (e.g., Motta et al., 2002; Motta et al., 2006a), but there is limited information on landscape-scale disturbances in this important forest type in the western Alps.

In Aosta valley the management of forests affected by high severity disturbances (i.e., disturbances that kill most of both the overstory and understory, and leave only a few scattered individuals survive) often includes the removal of damaged trees (i.e., salvage logging), in order to recover economic value and prepare the site for tree regeneration (Beghin et al., 2010). As a consequence, there are few disturbed sites left to natural stand development. Logging potentially interacts with the prior natural disturbance, affecting ecosystem processes and enhancing the differences between post-logged forests and natural forests through time (Noss and Lindenmayer, 2006; Kneeshaw et al., 2011).

Two different high severity disturbances (i.e., a wind storm and an insect outbreak) in adjacent inner valleys of the Aosta Valley Autonomous Region have provided an opportunity to examine the influence of disturbance, and disturbance interactions, on forest dynamics. The winter storm Vivian in 1990 was a catastrophic wind storm that blew down more than 50 million cubic meters of wood across the Alps (Wohlgemuth et al., 2002). Severe nun moth (*Lymantria monacha* L.) outbreaks occurred in European forests in the last decades (Watt et al., 1997). In the same period as storm Vivian an outbreak of the nun moth occurred in the Aosta Valley Autonomous Region (bib). Both the windthrow and defoliation events were followed by salvage logging in the next two years.

This combination of disturbances gave us the opportunity to examine the influence of two different types of high severity natural disturbance on forest regeneration, including their interaction with a second disturbance represented by salvage logging. Within this overarching framework, we specifically addressed the following questions: (1) what is the influence of residual canopy cover and coarse woody debris on post-disturbance forest regeneration establishment and growth? (2) What is the combined effect of the natural disturbances and subsequent management on tree regeneration? (3) Are the medium-term effects of salvage logging on forest dynamics dependent on the type of the preceding natural disturbance?

2 Material and methods

2.1 Study area

The present study was conducted in two adjacent SW-NE oriented inner valleys, approximately one kilometer apart, located in the southwest part of the Introd municipality (Graie Alps, Aosta Valley Autonomous Region, Italy).

Both areas are in the "endalpic district" (Del Favero, 2004) characterized by a continental climate. Average annual precipitation is approximately 705 mm (maximum in October and minimum in January). Mean annual temperature is 4.3 °C (maximum in July and minimum in January) at the nearest meteorological station (Rhêmes-St-Georges, 1200 m a.s.l.). The bedrock is silicate, schists are the predominant rocks, and soils are classified as entisols (Soil Taxonomy USDA).

Norway spruce is the dominant tree species, and European larch (*Larix decidua* Mill.) and silver fir (*Abies alba* Mill.) are common associates. Other tree species are mainly located in gaps or in localized xeric soil patches and include Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), European aspen (*Populus tremula* L.), goat willow (*Salix caprea* L.), mountain ash (*Sorbus aucuparia* L.), and sycamore maple (*Acer pseudoplatanus* L.). The understory vegetation cover is usually < 30% and mainly composed of *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L., *Rubus idaeus* L., *Luzula nivea* (L.) DC., *Melampyrum sylvaticum* L., *Oxalis acetosella* L., *Pyrola uniflora* L., and *Chamerion* (formerly *Epilobium*) *angustifolium* L. Holub in openings.

Reports document that both study areas underwent the same management since the late 19th century. Management altered the stand structure, the spatial patterns of vegetation types and age classes, and resulted in quite dense stands with limited CWD accumulation and unfavorable conditions for natural regeneration establishment (Motta et al., 2010; Castagneri et al., 2012).

The Les Combes study area (*LM* for *Lymantria monacha* disturbance) occupies 91 ha (45° 40' N, 7° 9' E), and elevation ranges from 1367 m a.s.l. and 1733 m a.s.l. (Fig. 1). It was severely affected by a nun moth outbreak in 1984-1990. The outbreak ended in 1991. The main species defoliated were Norway spruce, silver fir, European larch and Scots pine. Differences in severity of attack (i.e., percentage of trees killed by the insect) created a complex pattern of dead to lightly damaged trees across the landscape, with mortality, represented by tree volume, ranging from 15 to 85% (forest inventory records, Corpo Forestale Aosta Valley Autonomous Region, 1994).

The second study area, Parriod (*WD* for wind disturbance) occupies 70 ha (45° 40' N, 7° 11' E) with an elevation ranging from 1400 m a.s.l. to 1744 m a.s.l. (Fig. 1). It was not affected by the defoliator outbreak (forest inventory records, Corpo Forestale Aosta Valley Autonomous Region, 1994). The storm Vivian in 1990 heavily impacted 15 ha of the 70 ha total area, and created three large gaps (i.e., > 0.4 ha) with nearly 100% windthrow. These gaps were surrounded by less severely disturbed forest where mortality ranged from 33 to 54% (forest inventory records, Corpo Forestale Aosta Valley Autonomous Region, 1994). Both study areas were salvage logged and included portions of forest disturbed by a natural agent (wind or *Lymantria monacha*), and areas where no disturbance occurred.

Salvage logging occurred in 1991-1992 in Les Combes (*LM*), and in 1992-1993 in Parriod (*WD*). Adopting the same management criteria, only standing dead trees were cut in both areas. The actual removal of the windthrow and insect-killed trees varied across each area depending on the number of dead trees (i.e., from few individuals to nearly 100% dead trees), the economics of removal, and proximity to roads. The "salvage" treatment varied from near complete removal to piling of the dead ttrees. The result was different amounts and distribution of coarse woody debris remaining after salvage logging.

2.2 Sampling design

Site selection was firstly based on photointerpretation of a high resolution (50-cm) grayscale aerial orthoimage (IGM, 1992) and forest inventory maps (Corpo Forestale Aosta Valley Autonomous Region, 1984, 1994).

Through on-screen photointerpretation each study area was classified in two categories: forest areas > 0.2 ha affected by either the wind storm or the insect outbreak, and homogeneous patches of dense forest, which had not been affected by the disturbances analyzed in this study. Hence, dense forest patches were identified as controls (i.e., undisturbed forest) for each of the two natural disturbances (wind storm and *Lymantria monacha*).

A stratified random sample was applied to locate sample plots in each patch (either disturbed or undisturbed), with a minimum distance of 25 m between plots and 100 m from the edge of each polygon to avoid the edge influence on both abiotic and biotic processes (Chen et al., 1992; Harper et al., 2005).

A total of 90 circular plots were established (45 in *LM* and 45 in *WD*). In *LM* 15 plots were located in undisturbed forest patches (i.e., not disturbed by the insect outbreak and the following salvage logging) and 30 plots in disturbed ones (i.e., affected by the insect outbreak and the following salvage logging). In *WD* 10 plots were established in each of three blowdown patches (openings > 0.4 ha affected by the wind storm and the following salvage logging); 15 plots were established in dense undisturbed forest patches (i.e., not disturbed by the wind storm and the following salvage logging) at a minimum distance of 250 m from the centroids of the openings, in SW and NE direction.

2.3 Data collection

Data, relating to topographic characteristics, overstory and understory trees, and coarse woody debris (CWD) were collected on the 90 temporary plots during the summer of 2010. Site characteristics (location, elevation, aspect, slope steepness, slope position, and slope configuration) were record on each 6 m radius plot. On each plot, diameter at breast height (DBH) was measured for trees ≥ 7.5 cm DBH. In addition, ages were determined from cores collected at 0.5 m height from the largest (DBH) trees (two for each species, from trees ≥ 7.5 cm DBH) on each plot (total sample size = 105 cores). Coarse woody debris remaining after salvage logging was used as a proxy measure of the impact and severity of the salvage logging. This simplification was made because no data on the volume of deadwood logged were available, and the amount and characteristics of CWD in pre-disturbance forests were comparable across the two study areas (Corpo Forestale Aosta Valley Autonomous Region, 1984). Coarse woody debris was classified as standing dead trees or snags (height ≥ 1.3 m and DBH ≥ 7.5 cm), stumps (height < 1.3 m and diameter at the top > 7.5 cm), and downed logs (length > 1 m) (Motta et al., 2006b). Woodpiles (side lengths > 1 m), were also recorded. The decay rate of CWD was classified using a categorization made of five classes for logs and snags, and four for stumps (Sollins, 1982; Motta et al., 2006b).

A subplot of 3 m radius was established within each plot to measure regeneration (DBH < 7.5 cm), and tree canopy cover and microhabitat cover types. Regeneration was grouped in three size classes: seedlings < 0.3 m height (R1), saplings 0.3 m < height < 1.3 m (R2), and regeneration higher than 1.3 m with a DBH < 7.5 cm (R3). For each size class the species, height, seed or vegetative origin, ground cover type, browsing damage, and distance from upslope CWD, which could potentially limit snow accumulation and late-lying snowpacks (Rochefort et al., 1994), were recorded. For regeneration class R3, DBH was recorded, and cross-sections were cut at the root-shoot interface to reconstruct the age structure of the post-disturbance regeneration from the biggest three or four individuals for each species in this size class (total sample size = 131 cross-sections). A pilot study determined that DBH and age were significantly correlated (Spearman's $\rho = 0.822$, $P < 0.01$), and that this correlation was higher than the one between height and age. Therefore, DBH was used to identify individuals presumed to be the oldest. Forest floor microhabitat cover types were classed as CWD, patches of herbs, mosses, shrubs, bare soil, rocks or litter. The percent cover of each type was visually estimated on each subplot.

Increment cores and cross-sections were air-dried (and the cores glued to wooden mounts) prior to sanding. Ring widths were measured using the LINTAB™ measuring system, with a measurement precision of 0.01 mm, and analyzed by the Time Series Analysis Program TSAPWin™ (Rinntech, Heidelberg, Germany, 2003). For cores missing the pith by less than approximately 15 mm, the missing years in the innermost part of the core were estimated using a geometric procedure (Motta and Nola, 2001).

2.4 Data analysis

The data in this study were of three main types: regeneration structure and composition, overstory structure and composition, and topographic and environmental variables collected in the field and derived from a 10-m resolution digital elevation model (DEM). Topographic variables, included elevation, aspect, slope steepness, and the combination of site characteristics in indices as solar radiation, heat load, and soil wetness index (Basist et al., 2006). Aspect as circular data (degrees) were transformed to linear data following a method based on the interaction of slope and aspect to indicate the relative solar radiation (Clark, 1990). A method based on least-squares multiple regression using trigonometric functions of slope, aspect, and latitude was used to estimate an index of heat load (McCune and Keon, 2002). The soil wetness index represents the amount of water in the top few centimeters of the soil or the water intercepted by crowns, in presence of a dense canopy cover (Basist et al., 2006). Differences in stand structure between undisturbed, windthrown and logged, and defoliated and logged plots were tested through Multi-response Permutation Procedure (MRPP). This test permitted evaluation of differences between and homogeneity within groups (Zimmerman et al., 1985). Principal Components Analyses (PCA) and Spearman's ρ correlations were used to explore the correlation structure of variables, identify key factors and minimize multicollinearity among independent variables, and discard redundant variables (Jolliffe, 1972, 1973). The smaller subsets of variables included the most highly (> 0.7) correlated variables within each of the significant (P-value < 0.01) Principal Components. Correlations between the remaining variables were tested by Spearman's ρ correlations, and only those showing a Spearman's $\rho < 0.7$ were retained for further analysis. MRPP and PCA were performed using the PC-ORD version 5 statistical package (McCune and Mefford, 1999), and Spearman's ρ correlations by SPSS® version 19.0.

The variability of natural regeneration structure and composition in relation to explanatory variables (i.e., environment, forest structure, and type of disturbance) were analyzed by redundancy analysis (RDA) using Canoco® (Ter Braak and Šmilauer, 1998). This direct gradient analysis is a constrained ordination method used to explore the variability explained by the explanatory variables and their correlation with regeneration structure and composition variation. The statistical significance of the relation with explanatory variables was evaluated with the Monte Carlo permutation test. The analysis of growth increments of post-disturbance regeneration was performed for the main species (i.e., Norway spruce, European larch and silver fir). Mean annual increments aligned to the cambial age were analyzed in order to compare growing patterns of regeneration established after the two disturbances. Differences in growth trends were analyzed with ANOVA tests by SPSS® version 19.0 owing to the homoscedasticity of variance and the normal distribution of residuals.

Finally, the influence of coarse woody debris remaining after salvage logging on regeneration structure and composition was analyzed by Spearman's ρ correlations.

3 Results

3.1 Forest structure

Forest structure and environmental data collected in undisturbed stands in the two study areas showed no significant differences (p = 0.627, MRPP test) (Table 1). Norway spruce was the dominant species and ranged from 57% to 100% of total stand basal area. Regeneration mainly consisted of shade tolerant species (70-100% of individuals). Larch regeneration was absent and regeneration of light demanding broadleaves was restricted to small openings.

In both areas, the disturbed plots were significantly different from the undisturbed ones (*LM* p = 0.05, *WD* p = 0.009, MRPP test), with a low within-group homogeneity (*LM* A = 0.03, *WD* A = 0.05, MRPP test). The separation between the undisturbed forest and *LM* was lower (T = -1.94) than the one with *WD* (T = -3.59). The main differences found between *LM* and *WD* concerned residual trees, residual canopy cover, and regeneration. Residual overstory density (expressed as basal area) was variable, but greater in *LM*. All conifer species were attacked by the nun moth, but the most damaged was Norway spruce. In contrast, the density of trees > 7.5 cm DBH in *WD* mainly consisted of advance regeneration and individuals established immediately after the wind storm. This result is also confirmed by the low mean DBH (7.9 cm), just above the 7.5 cm threshold, and the young age of the individuals (Table 2).

3.2 Post-disturbance regeneration

Post-disturbance regeneration of five tree species was found in disturbed portions of each study area. In *WD* silver fir was absent, whereas larch and Norway spruce were abundant (Table 2). Though highly variable, the total amount of regeneration, including all three size classes, was more abundant in *LM* (12680 individuals per ha) than *WD* (9691 individuals per ha).

Regeneration was mainly from seed (96.6%) with only a few individuals of mountain ash and aspen from vegetative reproduction (3.4%). In *LM* regeneration class R3 had a mean age of 12 years with a mean DBH of 2.5 cm; in *WD* this class had a mean age of 8 years and 2.5 cm mean DBH. R3 mean height in *LM* (2.8 m) was not significantly different (p = 0.15, T-test) from the one in *WD* (2.5 m).

The incidence of ungulate browsing on the regeneration was 12.9%. Silver fir and Norway spruce were the most affected species (41.8%), followed by larch (26.5%), and mountain ash (19.4%). European aspen and silver birch were less damaged by browsing.

3.2.1 Regeneration structure

The influence of forest structure, environment, and disturbance type on the structure of natural regeneration of tree species was analyzed through direct gradient analysis (RDA, Table 3). A clear separation between the two disturbance types emerged from all the ordination analyses performed.

Redundancy analysis of natural regeneration structure related to forest structure and disturbance type is shown in Fig. 2. The first and second axes accounted for 15.7 and 5.7% of the total variation, respectively. Regeneration of all size classes (R1, R2, and R3) was more abundant in *LM* and positively associated with the presence of light demanding tree species as broadleaves and European larch. Seedlings (R1) were positively associated with older and more dense forest patches (bigger DBH m, DBH sd, BA, and age), especially in *LM*. Regeneration structure in both *LM* and *WD* appeared to be uncorrelated with logs, snags, and stumps, but was negatively correlated with woodpiles.

Redundancy analysis of natural regeneration structure related to environmental variables and disturbance type is shown in Fig. 3. The first and second axes accounted for 13.4 and 3.0% of the total variation, respectively. Regeneration (R1, R2, and R3) tended to be more abundant at lower elevation and where herbs were less important, but both these two environmental variables were independent from the type of natural disturbance. Seedlings (R1) and saplings (R2) in *LM* were positively associated with the presence of shrubs.

3.2.2 Regeneration composition

Direct gradient analyses of the influence of forest structure, environment, and disturbance type on the tree species composition of post-disturbance natural regeneration (RDA, Table 3) highlighted differences in regeneration composition mainly due to the disturbance type.

Redundancy analysis of natural regeneration composition related to forest structure and disturbance type is shown in Fig. 4. The first and second axes accounted for 9.6 and 6.8% of the total variation, respectively. All silver fir regeneration size classes were positively associated with mature silver fir patches and greater total stand basal area, and were found in *LM* only. In contrast, all size class of European larch regeneration were more abundant in *WD*. Broadleaf regeneration was independent of the disturbance type, and positively associated with larches and residual snags in both *LM* and *WD*. Stumps and woodpiles appeared to be uncorrelated with regeneration composition in both *LM* and *WD*, while logs were positively correlated with European larch and Norway spruce.

Redundancy analysis of natural regeneration composition related to environmental variables and disturbance type is shown in Fig. 5. The first and second axes accounted for 7.8 and 3.7% of the total variation, respectively. Aspect was independent of the disturbance type and positively correlated with all broadleaf species, which were more abundant at lower elevations in both *LM* and *WD*. Silver fir in *LM* was positively correlated with the presence of litter.

3.2.3 Regeneration growth increments

Post-disturbance regeneration of Norway spruce (*LM* sample size = 20 cross-sections, *WD* sample size = 22 cross-sections) and European larch (*LM* sample size = 27 cross-sections, *WD* sample size = 38 cross-sections) had comparable ring width annual increments (Fig. 6) for the first ten years following disturbance, regardless of the disturbance type ($p = 0.26$, ANOVA test) (Table 4). In the subsequent decade, however, differences in ring widths were found between regeneration in *WD* and *LM* ($p < 0.01$, ANOVA test). Growth in *LM* ranged from 0.6 to 1.6 mm, and was slightly decreasing. In contrast, regeneration in *WD* ranged from 1.7 to 4.4 mm, showed an increasing trend, and had a mean value 60% greater than *LM* (Table 4). Silver fir was not represented in the graph because few individuals were present in *LM*. Its growth trend was in line with those of Norway spruce and European larch in *LM*, and ranged from 0.7 and 1.3 mm during the first decade and 0.8 and 1.5 mm during the subsequent one.

3.2.4 Influence of salvage logging on regeneration

The amount of coarse woody debris following the salvage logging operations was similar among *LM* and *WD*, and had a mean volume of 120 m^3 per hectare (Table 2). Logs and stumps made up 64.4% of the volume of deadwood, while snags were found only in areas where wood was not piled, and were less important (c.a. 1% in volume). The amount of deadwood in both disturbed areas was strongly conditioned by the presence of woodpiles, which represented 34.7% of the total CWD volume, and were found in 17% of the plots. Downed logs left on the forest floor had a mean diameter at half-length of 16.6 cm, while snags had 18.8 cm mean DBH.

Overall, the height of regeneration (R1, R2, R3) was negatively correlated to upslope CWD distance in *WD* (Spearman's ρ = -0.504, $P < 0.01$), with browsed individuals being furthest deadwood.

On those plots where woodpiles were present, the majority of deadwood (80.6%) was stacked. The abundance of regeneration class R3 was negatively correlated to the presence of woodpiles (Spearman's ρ = -0.291, $P < 0.05$). This deadwood component also had a negative effect on the density of larch and silver fir seedlings (R1) density (Spearman's ρ = -0.618, and -0.279, $P < 0.01$, respectively).

In contrast, logs were the most common element of CWD (63.2% in volume) in plots where deadwood was not stacked. In these areas the average ground cover for CWD was less than 10% and emerged as being a preferential germination substrate of seedlings after litter, and the most important surface for Norway spruce establishment (40% of spruce regeneration established on CWD). Indeed, Norway spruce seedlings (R1) were positively correlated to deadwood (Spearman's ρ = 0.427, $P < 0.01$), logs in particular (Spearman's ρ = 0.396, $P < 0.01$).

The amount of coarse woody debris in undisturbed plots had a mean volume of 24 m^3 per hectare (Table 1), and the ground cover for CWD was 12%. Logs and stumps made up 90.5% of the volume of deadwood, while snags were less important (9.5% in volume), and no woodpiles were found. Downed logs had a mean diameter at half-length of 18.5 cm, while snags had 13.9 cm mean DBH.

4 Discussion

Analysis of the mosaic of disturbance severity, and assessment of pre-disturbance forest composition and structure provided valuable insight into the contrasting influences of two different natural high-severity disturbance types and their interactions with a common post-disturbance treatment. The two study areas are very closely matched in terms of their proximity to one another, environmental conditions, and land management histories. Within the same time frame, both areas were impacted by high severity natural disturbances and subsequent salvage logging.

4.1 Pre-disturbance forest composition and structure

In both study areas Norway spruce was the dominant tree species in the overstory. European larch and silver fir were common associates, while light demanding broadleaves were sporadic and mainly located in small gaps. The understory vegetation cover was usually < 30% and composed of species associated with montane forests, soils of medium fertility, and shaded conditions. Tree regeneration was not abundant and mainly consisted of shade tolerant species, while light demanding conifers and broadleaves were restricted to openings.

4.2 Post-disturbance dynamics

The two major factors influencing post-disturbance regeneration were the amount of residual overstory and the amount and distribution of CWD. Post-disturbance forest density and cover, of course, were lower than in the pre-disturbance forest. There were, however, important differences between the two types of natural disturbance. In the area impacted by the wind storm, residual trees consisted of only a few stable overstory individuals, mainly with good root anchorages, and patches of advance regeneration of Norway spruce. In contrast, in the area impacted by insect defoliation, residual forest density and cover were variable and generally higher. Nun moth feeds mainly on needles and male cones of conifers (*Picea, Pinus, Abies,* and *Larix* spp.), with a preference for Norway spruce and Scots pine in European forests (Lipa and Glowacka, 1995). Due to the high severity of the outbreak, in the study area all the conifers were attacked, with a slight preference for Norway spruce.

Post-disturbance regeneration was more abundant and rich in light demanding species than in the pre-disturbance forest in both study areas. It was also true that regeneration was generally more abundant after the insect attack than the windthrow. In general, residual forest cover and composition strongly influenced regeneration structure and composition. European larches and light demanding broadleaves were the tree species under which regeneration was more abundant

(???). Seedlings < 0.3 m height, of silver fir mainly, were primarily found under dense residual forest patches, in the presence of litter and mosses, and where the herb layer was not dominant. In contrast, all size classes of European larch regeneration were more abundant after the wind disturbance (*WD*). Despite better light conditions for regeneration establishment in gaps (Spies and Franklin, 1989), herbaceous competition was a limiting factor for regeneration establishment, especially for shade tolerant species. Seeds tended to germinate under residual forest patches instead of in openings created by the wind storm (WD) or the insect attack (LM). Post-disturbance regeneration increment patterns were comparable between *LM* and *WD* for the first decade post-disturbance. In the subsequent decade, regeneration in *WD* showed an increasing growth trend, while regeneration in *LM* slightly decreased, probably because of less favorable light conditions. The forest canopy cover influences the quantity and quality of the light that penetrates to the ground (Anderson, 1966). Reduced radiation may be essential for the germination and early survival of spruce seedlings; however, high radiation could accelerate the growth of established seedlings (Dai, 1996). Light amount was adequate for regeneration in both *LM* and *WD* for the first decade after the disturbance occurrence. In the subsequent decade, however, the higher canopy cover in *LM* was associated with reduced growth of seedlings and saplings. The higher amount of light available to the ground in the windthrow area is also reflected in a higher proportion of pioneering species (e.g., larch).

Our results also provide evidence for the important role of CWD in facilitating the establishment of new individuals by reducing competition with herbs and shrubs, and improving substrate moisture (Harmon et al., 1986; Kuuluvainen et al., 2002; Brang et al., 2003). CWD appears to be especially important for the establishment of Norway spruce (Motta et al., 2006a; Svoboda et al., 2010). Major natural disturbances generally provide an important pulse of biological legacies such as large-diameter standing dead trees and large pieces of coarse woody debris, which supply habitat and nutrients for a wide range of organisms (Harmon et al., 1986). Because of the salvage logging, in our study sites only small size elements of deadwood were left standing or on the ground, and often grouped in woodpiles. Large-diameter elements were removed mainly because of their higher economic value. Even with the implementation of salvage logging, the amount of deadwood in *LM* and *WD* was higher than in undisturbed stands. Nevertheless, the deadwood was concentrated spatially and covered a small portion of the ground. Woodpiles were found to have a negative influence on regeneration in terms of abundance and also influenced composition. The artificial assemblage of deadwood in woodpiles (i.e., blocks > 1 m^3 volume) physically inhibited regeneration establishment and growth. For our study sites, salvage logging had the effect of reducing the amount of favorable germination sites reducing the total volume of deadwood, and assembling the remaining in a not suitable component for regeneration establishment. In fact, areas where woodpiles were not present and, thus, deadwood was scattered, CWD emerged as a preferential substrate for germination of Norway spruce acting as nurse logs (Hofgaard, 1993). In our study the incidence of browsing was high only on preferred species (e.g., silver fir). Browsing can play an important role in forest dynamics after the disturbance (e.g., preventing the establishment or reducing the abundance of selected species, and reducing height growth of trees) (Didion et al., 2009), and some impacts might be strongly underestimated (Motta, 2003). Post-disturbance CWD left on the ground can play an important role in limiting the browsing pressure on tree regeneration (Kupferschmid and Bugmann, 2005). In our study sites browsing damage was more severe on regeneration farther away from CWD, suggesting how deadwood lying on the ground may offer mechanical protection to seedlings (Long et al., 1998; de Chantal et al., 2009).

Recent studies raised questions concerning the ecological role of salvage logging and its appropriateness as a post-disturbance management (e.g., McIver and Starr, 2000; Lindenmayer et al., 2008). It has been suggested, for example, that salvage logging may amplify unfavorable natural and topographic conditions (Lindenmayer et al., 2008), particularly on marginal sites where even small changes in the microclimate and substrate may compromise regeneration success. Our results suggest that even on mesic sites, salvage logging, and in particular the way it is implemented, may have substantial impacts on the structure and composition of post-disturbance regeneration.

The main management concern in leaving dead wood after natural disturbances or salvage logging, in Norway spruce forests, is the potential development of bark beetle (*Ips typographus*) outbreaks (Wermeliger, 2004). For this reason in managed forests where there is a potential risks for bark beetle outbreaks, the amount of dead wood should be maintained above a landscape threshold value critical for the biodiversity conservation (Müller and Bütler, 2010) but, in the same time, it is necessary to monitor the bark beetle density (e.g. using pheromone traps) in the years following the disturbance event. This problem could be diminished in the next future by the transformation of the current monospecific or Norway spruce dominated stands in more natural mixed stands (Spiecker, 2003) that are less affected by bark beetle outbreaks, more resilient and could host a higher value of dead wood.

5 Conclusions

Our analysis explored regeneration dynamics following the most common disturbances affecting the northern slopes of montane Norway spruce forests in the European Alps (i.e., wind storms and insect outbreaks) and their interactions with a common post-disturbance treatment, salvage logging. Post-disturbance regeneration composition and structure were mainly influenced by the amount and distribution of residual canopy cover and CWD, which reflected the medium-term outcomes of the combined effect of the type of natural disturbance and subsequent salvage logging on forest dynamics. Type and intensity of post-disturbance management practices may influence forest stand development for decades (Fischer and Fischer, 2012). If deadwood removal following salvage logging could limit potential risks of European spruce bark beetle (*Ips typographus* L.) attacks in disturbed Norway spruce forests (Flot et al., 2002; Wermelinger, 2004), the importance of CWD remaining, even after salvage logging, for regeneration and post-disturbance forest dynamics is currently underestimated (Müller et al., 2008). The gathering of CWD strongly influences tree regeneration especially immediately after the disturbance event. If woodpiles have a negative influence on forest regeneration, hindering the establishment of new seedlings and subtracting important germination substrates such as logs, on the other hand scattered large snags and logs play an important role in protecting tree regeneration from browsing and, thus, their conservation is advised.

As a consequence leaving portions of disturbed forests results in more complex habitat conditions that enhance forest resilience speeding up the regeneration processes and increases landscape heterogeneity and natural biodiversity in managed forests.

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Tables

Table 1

		LM		***WD***	
	Units	Mean	Sd	Mean	Sd
Aspect	degrees	324	14.3	329	12.3
Slope	degrees	26.2	5.4	26.6	4.4
Trees	stems/ha	429	180.4	451	208.5
CC%	%	80	20	80	20
Pab%	%	70	20	90	20
Aal%	%	10	10	10	10
Lde%	%	20	10	10	10
DBH me	cm	35	5.6	29.9	5
BA tot	m^2/ha	49.2	14.3	55	21.5
Age ma	years	148.1	3.9	120.1	18.2
Age me	years	137.7	7.1	109.3	20.6
CWD	m^3/ha	24	5.1	23.6	7.6
Reg Pab	%	30	40	40	20
Reg Aal	%	70	40	40	20
Reg bro	%	0	0	20	30

Table 1. Mean values (mean) and standard deviations (Sd) of 30 control plots (undisturbed forests) in relation to the two study areas (*LM, WD*). Trees = number of trees > 7.5 cm DBH; CC% = trees canopy cover; Pab%, Aal%, Lde% = ratio of Norway spruce, silver fir, European larch expressed in percentage of basal area; DBH me = mean DBH of trees; BA tot = basal area of trees; Age ma = maximum age of trees; Age me = mean age of trees; CWD = volume of CWD; Reg Pab, Reg Aal, Reg bro = ratio of Norway spruce, silver fir, broadleaves regeneration (R1, R2, R3) expressed in percentage of total number per hectare.

Table 2

		LM (*Lymantria monacha* outbreak and logging)		***WD*** (Wind storm and logging)	
	Units	Mean	Sd	Mean	Sd
Trees	stems/ha	408.3	311.7	229.9	312
CC%	%	40	30	10	20
Pab%	%	40	40	50	40
Aal%	%	20	30	0	0
Lde%	%	20	30	20	20
Psy%	%	10	20	0	0
Bro%	%	10	20	30	40
DBH me	cm	22.9	12.1	7.9	7.4
BA tot	m^2/ha	17.9	12.7	2.9	3.7
Age ma	years	106.6	80.5	20.1	24.4
Age me	years	84	60.6	16	17.7
CWD	m^3/ha	133.6	280.8	107.5	114
R1	stems/ha	8083	16181	4350	8683
R2	stems/ha	3089	2465	4032	3747
R3	stems/ha	1508	1920	1309	2177
Reg Pab	%	28	22	47	24
Reg Aal	%	30	30	0	0
Reg bro	%	16	21	15	20
Reg Lde	%	24	24	38	27
Reg Psy	%	2	7	0	0

Table 2. Mean values and standard deviations (Sd) of plots pertaining to the two study areas (*LM*, 30 plots; *WD*, 30 plots). Trees = number of trees > 7.5 cm DBH; CC% = trees canopy cover; Pab%, Aal%, Lde%, Psy%, Bro% = ratio of Norway spruce, silver fir, European larch, Scots pine, broadleaves expressed in percentage of basal area; DBH me = mean DBH of trees; BA tot = basal area of trees; Age ma = maximum age of trees; Age me = mean age of trees; CWD = volume of CWD; R1 = number of seedlings < 0.3 m height; R2 = number of saplings 0.3 m < height < 1.3 m; R3 = number of individuals higher than 1.3 m with a DBH < 7.5 cm; Reg Pab, Reg Aal, Reg bro, Reg Lde, Reg Psy = ratio of Norway spruce, silver fir, broadleaves,

European larch, Scots pine regeneration (R1, R2, R3) expressed in percentage of total number per hectare.

Table 3

Data used	Variable tested	Explained variability (%)	Correlation 1st axis	*p*
Regeneration structure				
All plots	Environment and Disturbance	14.5	0.651	< 0.001
All plots	Forest structure and Disturbance	15.7	0.665	0.01
Regeneration composition				
All plots	Environment and Disturbance	7.8	0.820	0.01
All plots	Forest structure and Disturbance	9.6	0.850	< 0.001

Table 3. Summary of ordination analyses (RDA) of natural regeneration structure and natural regeneration composition in relation to environment (elevation, expo, soil, herbs, litter, mosses, rocks, shrubs), forest structure (DBH mean, DBH standard deviation, basal area, basal area of Norway spruce, silver fir, European larch, Scots pine, broadleaves, age mean, CWD volume, woodpiles, logs, snags, stumps), and type of disturbance (windthrow, insect outbreak). The explained variability indicates the percentage of the total variability in species data that can be explained by each group of environmental variables. The correlation of the first axis is the

species–environment correlation for the first RDA axis.

Table 4

	WD	*LM*
Years 1-9		
European larch	0.89 ± *0.05* (38)	0.88 ± *0.05* (27)
Norway spruce	0.97 ± *0.08* (22)	1.09 ± *0.10* (20)
Silver fir	\	1.22 ± *0.09* (10)
Years 10-20		
European larch	2.01 ± *0.15* (38)	1.23 ± *0.10* (27)
Norway spruce	2.23 ± *0.25* (22)	1.17 ± *0.07* (20)
Silver fir	\	1.24 ± *0.08* (10)

Table 4. Mean ring width increments (mm), standard errors (in italics), and sample size (i.e., number of cross-sections, in brackets) of post-disturbance regeneration main species (European larch, Norway spruce and silver fir) during the first nine years and the last decade after the disturbances (*LM*, *Lymantria monacha* disturbance, and *WD*, wind disturbance) occurrence.

Figure captions

Fig. 1. Location of the Aosta Valley Autonomous Region, Italy, in the western Alps (black contour of the lower frame). Country names follow to the ISO 3166-1-alpha-2 code. The study area (*LM*, *Lymantria monacha* disturbance and logging, and *WD*, wind disturbance and logging), Aosta Valley Autonomous Region, is shown in the enlargement in the right upper part of the picture.

Fig. 2. Redundancy analysis (RDA of 60 plots) of natural regeneration structure in relation to forest structure and disturbance type. The explained variability of the first two axes is reported in brackets. Forest structure variables correlations outside of range -0.2 – 0.2, and sample fit range from 4 to 100% were chosen as thresholds to display variables in the graph for its better understanding. Dashed arrows are the natural regeneration structure variables (Age = mean age; AgeDs = standard deviation of age; DBHm = mean DBH; DBHds = standard deviation of DBH; Hm = mean height; Hds = standard deviation of height; Rich = richness; De = number of individuals per hectare. Structure variables refer to regeneration life stages 1 = seedlings R1, 2 = saplings R2, 3 = regeneration R3). Full line arrows are the forest structure variables (Abies = relative dominance of silver fir; Age = mean age of trees > 7.5 cm DBH; BA = basal area; Broad = relative dominance of broadleaves; DBH m = mean DBH; DBH sd = DBH standard deviation; Larix = relative dominance of European larch; Woodpile = woodpiles volume). Triangular dots represent the two disturbances (*LM* = *Lymantria monacha* disturbance and logging, *WD* = wind disturbance and logging).

Fig. 3. Redundancy analysis (RDA of 60 plots) of natural regeneration structure in relation to environment and disturbance type. The explained variability of the first two axes is reported in brackets. Environmental variables correlations outside of range -0.2 – 0.2, and sample fit range

from 4 to 100% were chosen as thresholds to display variables in the graph for its better understanding. Dashed arrows are the natural regeneration structure variables (Age = mean age; AgeDs = standard deviation of age; DBHm = mean DBH; DBHds = standard deviation of DBH; Hm = mean height; Hds = standard deviation of height; Rich = richness; De = number of individuals per hectare. Structure variables refer to regeneration life stages 1 = seedlings R1, 2 = saplings R2, 3 = regeneration R3). Full line arrows are the environmental variables (Elevation = elevation; Herbs = herbs cover; Litter = litter cover; Mosses = mosses cover; Rocks = rocks cover; Shrubs = shrubs cover; Soil = soil cover). Triangular dots represent the two disturbances (*LM* = *Lymantria monacha* disturbance and logging, *WD* = wind disturbance and logging).

Fig. 4. Redundancy analysis (RDA of 60 plots) of natural regeneration composition in relation to forest structure and disturbance type. The explained variability of the first two axes is reported in brackets. Forest structure variables correlations outside of range -0.2 – 0.2, and sample fit range from 4 to 100% were chosen as thresholds to display variables in the graph for its better understanding. Dashed arrows are the natural regeneration composition variables (relative dominance of the species AA = silver fir, AP = sycamore maple, LD = European larch, PA = Norway spruce, PS = Scots pine, PT = European aspen, SA = mountain ash. Composition variables refer to regeneration life stages 1 = seedlings R1, 2 = saplings R2, 3 = regeneration R3). Full line arrows are the forest structure variables (Abies = relative dominance of silver fir; Age = mean age of trees > 7.5 cm DBH; BA = basal area; DBH sd = DBH standard deviation; Larix = relative dominance of European larch; Log = logs volume, Snag = snags volume). Triangular dots represent the two disturbances (*LM* = *Lymantria monacha* disturbance and logging, *WD* = wind disturbance and logging).

Fig. 5. Redundancy analysis (RDA of 60 plots) of natural regeneration composition in relation to environment and disturbance type. The explained variability of the first two axes is reported in brackets. Environmental variables correlations outside of range -0.2 – 0.2, and sample fit range from 4 to 100% were chosen as thresholds to display variables in the graph for its better understanding. Dashed arrows are the natural regeneration composition variables (relative dominance of the species AA = silver fir, BP = silver birch, LD = European larch, PA = Norway spruce, PS = Scots pine, PT = European aspen, SC = goat willow. Composition variables refer to regeneration life stages 1 = seedlings R1, 2 = saplings R2, 3 = regeneration R3). Full line arrows are the environmental variables (Elevation = elevation; Expo = relative solar insolation index,

Clark 1990; Herbs = herbs cover; Litter = litter cover; Mosses = mosses cover; Rocks = rocks cover). Triangular dots represent the two disturbances (*LM* = *Lymantria monacha* disturbance and logging, *WD* = wind disturbance and logging).

Fig. 6. Mean ring width increments (mm) of post-disturbance regeneration main species (Norway spruce, Pab, and European larch, Lde). Full lines represent wind disturbance and logging (*WD*) site, while dashed lines refer to the *Lymantria monacha* disturbance and logging (*LM*) site. Norway spruce sample size was of 20 cross-sections in *LM*, and 22 in *WD*. European larch sample size was of 27 cross-sections in *LM*, and 38 in *WD*.