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UNIVERSITÀ DEGLI STUDI DI TORINO

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

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25 **Keywords**

26 Salvage logging; tree regeneration; wind storm; insect outbreak; silviculture; *Picea abies* (L.) H.
27 Karst.

32 **Abstract**

33 The combined effects of a natural (i.e., insect outbreak or wind storm) and an anthropogenic (i.e.,
34 salvage logging) disturbance on stand dynamics, including tree regeneration, were studied to
35 assess the role of post-disturbance management practices following the most common
36 disturbances affecting the northern slopes of montane Norway spruce (*Picea abies* (L.) H. Karst.)
37 forests in the European Alps. The study areas were in two adjacent inner valleys of the Aosta
38 Valley Autonomous Region (western Italian Alps). Les Combes study area experienced an insect
39 (*Lymantria monacha* L.) outbreak that affected 91 ha in 1984-1990, while a wind storm impacted
40 70 ha in the other valley (Pariod study area) in 1990. Salvage logging took place in both study
41 areas two years after the natural disturbance occurrence (i.e., in 1991-1992 in Les Combes, and
42 in 1992-1993 in Pariod), and only dead trees were salvaged. Site characteristics, overstory and
43 understory trees, and coarse woody debris (CWD) data were collected during the summer of
44 2010 in 90 plots randomly distributed within disturbed portions and in control stands of the two
45 study areas. The variability of natural regeneration structure and composition in relation to
46 environment, forest structure, type of disturbance, and salvage logging were analyzed by
47 univariate (i.e., ANOVA and correlations) and multivariate (i.e., MRPP, PCA, and RDA)
48 analyses. Regeneration structure and composition were clearly different for the two disturbance
49 types. Individuals originated mainly from seed after the insect outbreak, while an important role
50 was played by advance regeneration in the windthrow area. Regeneration was more abundant
51 and rich in shade tolerant species (i.e., *Abies alba* Mill.) after the insect outbreak, while *Larix*
52 *decidua* Mill. and light demanding broadleaves were dominant after the windthrow. The two
53 major factors influencing post-disturbance regeneration were the amount of the residual
54 overstory and the amount and distribution of CWD. The presence of residual forest patches
55 facilitated regeneration establishment by reducing herb and shrub competition, and regulating the
56 light that penetrates to the ground. Woodpiles had a negative influence on regeneration in terms
57 of abundance and also influenced composition. On the contrary, scattered CWD facilitated the
58 establishment of new individuals by reducing competition with herbs and shrubs, reducing the
59 browsing impact and improving substrate moisture, especially for Norway spruce.

60

61 **1 Introduction**

62 Montane Norway spruce (*Picea abies* (L.) H. Karst.) forests cover a substantial area of the
63 European Alps (more than 150000 km² within the territory of the Alps of the Alpine Convention,
64 Skrøppa, 2003) and are the dominant forest type in the northern slopes of the inner Aosta Valley.
65 Landscapes in this region, even in remote areas, reflect centuries of human activities, particularly
66 timber extraction and livestock grazing, which have considerably changed forest vegetation from
67 natural conditions (e.g., Bastian and Bernhardt, 1993; Kräuchi et al., 2000; Spiecker, 2003; Motta
68 et al., 2006a; Bolli et al., 2007; Kulakowski et al., 2011). Human influence on these landscapes
69 began to diminish in the second half of the nineteenth century, when the economy and social
70 structure of alpine valleys underwent radical changes. A consequence of changes in land use in
71 the last 100 years has been an increase in forest surface and in growing stock that, at the
72 European scale, it is currently three times higher than in 1950 (Schellhaas et al., 2005). These
73 changes are associated with a general increase in spatial pattern homogeneity (Garbarino et al.,
74 2010) which, in turn, is associated with a loss in suitable habitat for some species and an increase
75 in susceptibility to major forest disturbances (Foster, 1988; Kulakowski and Veblen, 2002;
76 Hanewinkel et al., 2008; Kulakowski et al., 2011).

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

88 Wind storms and insect outbreaks are two common disturbances affecting forests in the
89 European Alps (Schellhaas et al., 2003; Büntgen et al., 2009). Large-scale windthrow may impact
90 thousands of hectares of mature forests (Bründl and Rickli, 2002; Wohlgemuth et al., 2002;
91 Zielonka et al., 2010), and leave legacies of advance regeneration, which can contribute to the
92 persistence of shade-tolerant species within the forest (Schönenberger, 2002). Typical

93 microstructures such as pits and mounds, and the exposed mineral soil caused by windthrow
94 create heterogeneity in microsites at the ground level (Ulanova, 2000). Moreover, fallen coarse
95 woody debris plays an important role in creating suitable microhabitat especially for the
96 establishment of shade-tolerant species (Zielonka, 2006; Svoboda et al., 2010). In contrast, insect
97 outbreaks may result in patchy mortality of both overstory and understory trees, and leave more
98 standing dead trees (Müller et al., 2008). Surviving trees and the complex spatial pattern of light
99 distribution may also contribute to higher levels of seed production and thereby influence
100 regeneration (Dai, 1996; Jonášová and Matějková, 2007).

101 Despite the importance of large-scale disturbances in Europe, most studies have focused on the
102 role of intermediate- and small-scale disturbances in forest dynamics (e.g., Nagel and Diaci,
103 2006; Svoboda et al., 2010; Bottero et al., 2011). For spruce forests in the Italian Alps several
104 studies have explored stand-scale dynamics, especially in the eastern part of the mountain range
105 (e.g., Motta et al., 2002; Motta et al., 2006a), but there is limited information on landscape-scale
106 disturbances in this important forest type in the western Alps.

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

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

124 This combination of disturbances gave us the opportunity to examine the influence of two
125 different types of high severity natural disturbance on forest regeneration, including their
126 interaction with a second disturbance represented by salvage logging. Within this overarching
127 framework, we specifically addressed the following questions: (1) what is the influence of
128 residual canopy cover and coarse woody debris on post-disturbance forest regeneration
129 establishment and growth? (2) What is the combined effect of the natural disturbances and
130 subsequent management on tree regeneration? (3) Are the medium-term effects of salvage
131 logging on forest dynamics dependent on the type of the preceding natural disturbance?
132
133

134 **2 Material and methods**

135 **2.1 Study area**

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

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

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

154 Reports document that both study areas underwent the same management since the late 19th
155 century. Management altered the stand structure, the spatial patterns of vegetation types and age
156 classes, and resulted in quite dense stands with limited CWD accumulation and unfavorable
157 conditions for natural regeneration establishment (Motta et al., 2010; Castagneri et al., 2012).
158 The Les Combes study area (*LM* for *Lymantria monacha* disturbance) occupies 91 ha (45° 40'
159 N, 7° 9' E), and elevation ranges from 1367 m a.s.l. and 1733 m a.s.l. (Fig. 1). It was severely
160 affected by a nun moth outbreak in 1984-1990. The outbreak ended in 1991. The main species
161 defoliated were Norway spruce, silver fir, European larch and Scots pine. Differences in severity
162 of attack (i.e., percentage of trees killed by the insect) created a complex pattern of dead to
163 lightly damaged trees across the landscape, with mortality, represented by tree volume, ranging
164 from 15 to 85% (forest inventory records, Corpo Forestale Aosta Valley Autonomous Region,
165 1994).

166 The second study area, Parriod (*WD* for wind disturbance) occupies 70 ha (45° 40' N, 7° 11' E)
167 with an elevation ranging from 1400 m a.s.l. to 1744 m a.s.l. (Fig. 1). It was not affected by the
168 defoliator outbreak (forest inventory records, Corpo Forestale Aosta Valley Autonomous Region,
169 1994). The storm Vivian in 1990 heavily impacted 15 ha of the 70 ha total area, and created three
170 large gaps (i.e., > 0.4 ha) with nearly 100% windthrow. These gaps were surrounded by less
171 severely disturbed forest where mortality ranged from 33 to 54% (forest inventory records,
172 Corpo Forestale Aosta Valley Autonomous Region, 1994). Both study areas were salvage logged
173 and included portions of forest disturbed by a natural agent (wind or *Lymantria monacha*), and
174 areas where no disturbance occurred.

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

182

183 **2.2 Sampling design**

184 Site selection was firstly based on photointerpretation of a high resolution (50-cm) grayscale
185 aerial orthoimage (IGM, 1992) and forest inventory maps (Corpo Forestale Aosta Valley
186 Autonomous Region, 1984, 1994).
187 Through on-screen photointerpretation each study area was classified in two categories: forest
188 areas > 0.2 ha affected by either the wind storm or the insect outbreak, and homogeneous patches
189 of dense forest, which had not been affected by the disturbances analyzed in this study. Hence,
190 dense forest patches were identified as controls (i.e., undisturbed forest) for each of the two
191 natural disturbances (wind storm and *Lymantria monacha*).
192 A stratified random sample was applied to locate sample plots in each patch (either disturbed or
193 undisturbed), with a minimum distance of 25 m between plots and 100 m from the edge of each
194 polygon to avoid the edge influence on both abiotic and biotic processes (Chen et al., 1992;
195 Harper et al., 2005).
196 A total of 90 circular plots were established (45 in *LM* and 45 in *WD*). In *LM* 15 plots were
197 located in undisturbed forest patches (i.e., not disturbed by the insect outbreak and the following
198 salvage logging) and 30 plots in disturbed ones (i.e., affected by the insect outbreak and the
199 following salvage logging). In *WD* 10 plots were established in each of three blowdown patches
200 (openings > 0.4 ha affected by the wind storm and the following salvage logging); 15 plots were
201 established in dense undisturbed forest patches (i.e., not disturbed by the wind storm and the
202 following salvage logging) at a minimum distance of 250 m from the centroids of the openings,
203 in SW and NE direction.

204

205 **2.3 Data collection**

206 Data, relating to topographic characteristics, overstory and understory trees, and coarse woody
207 debris (CWD) were collected on the 90 temporary plots during the summer of 2010. Site
208 characteristics (location, elevation, aspect, slope steepness, slope position, and slope
209 configuration) were record on each 6 m radius plot. On each plot, diameter at breast height
210 (DBH) was measured for trees ≥ 7.5 cm DBH. In addition, ages were determined from cores
211 collected at 0.5 m height from the largest (DBH) trees (two for each species, from trees ≥ 7.5 cm
212 DBH) on each plot (total sample size = 105 cores). Coarse woody debris remaining after salvage
213 logging was used as a proxy measure of the impact and severity of the salvage logging. This
214 simplification was made because no data on the volume of deadwood logged were available, and

215 the amount and characteristics of CWD in pre-disturbance forests were comparable across the
216 two study areas (Corpo Forestale Aosta Valley Autonomous Region, 1984). Coarse woody
217 debris was classified as standing dead trees or snags (height ≥ 1.3 m and DBH ≥ 7.5 cm), stumps
218 (height < 1.3 m and diameter at the top > 7.5 cm), and downed logs (length > 1 m) (Motta et al.,
219 2006b). Woodpiles (side lengths > 1 m), were also recorded. The decay rate of CWD was
220 classified using a categorization made of five classes for logs and snags, and four for stumps
221 (Sollins, 1982; Motta et al., 2006b).

222 A subplot of 3 m radius was established within each plot to measure regeneration (DBH < 7.5
223 cm), and tree canopy cover and microhabitat cover types. Regeneration was grouped in three size
224 classes: seedlings < 0.3 m height (R1), saplings 0.3 m $<$ height < 1.3 m (R2), and regeneration
225 higher than 1.3 m with a DBH < 7.5 cm (R3). For each size class the species, height, seed or
226 vegetative origin, ground cover type, browsing damage, and distance from upslope CWD, which
227 could potentially limit snow accumulation and late-lying snowpacks (Rochefort et al., 1994),
228 were recorded. For regeneration class R3, DBH was recorded, and cross-sections were cut at the
229 root-shoot interface to reconstruct the age structure of the post-disturbance regeneration from the
230 biggest three or four individuals for each species in this size class (total sample size = 131 cross-
231 sections). A pilot study determined that DBH and age were significantly correlated (Spearman's
232 $\rho = 0.822$, $P < 0.01$), and that this correlation was higher than the one between height and age.
233 Therefore, DBH was used to identify individuals presumed to be the oldest. Forest floor
234 microhabitat cover types were classed as CWD, patches of herbs, mosses, shrubs, bare soil, rocks
235 or litter. The percent cover of each type was visually estimated on each subplot.
236 Increment cores and cross-sections were air-dried (and the cores glued to wooden mounts) prior
237 to sanding. Ring widths were measured using the LINTABTM measuring system, with a
238 measurement precision of 0.01 mm, and analyzed by the Time Series Analysis Program
239 TSAPWinTM (Rinntech, Heidelberg, Germany, 2003). For cores missing the pith by less than
240 approximately 15 mm, the missing years in the innermost part of the core were estimated using a
241 geometric procedure (Motta and Nola, 2001).

242

243 **2.4 Data analysis**

244 The data in this study were of three main types: regeneration structure and composition,
245 overstory structure and composition, and topographic and environmental variables collected in

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

267 The variability of natural regeneration structure and composition in relation to explanatory
268 variables (i.e., environment, forest structure, and type of disturbance) were analyzed by
269 redundancy analysis (RDA) using Canoco[®] (Ter Braak and Šmilauer, 1998). This direct gradient
270 analysis is a constrained ordination method used to explore the variability explained by the
271 explanatory variables and their correlation with regeneration structure and composition variation.
272 The statistical significance of the relation with explanatory variables was evaluated with the
273 Monte Carlo permutation test. The analysis of growth increments of post-disturbance
274 regeneration was performed for the main species (i.e., Norway spruce, European larch and silver
275 fir). Mean annual increments aligned to the cambial age were analyzed in order to compare
276 growing patterns of regeneration established after the two disturbances. Differences in growth

277 trends were analyzed with ANOVA tests by SPSS[®] version 19.0 owing to the homoscedasticity
278 of variance and the normal distribution of residuals.
279 Finally, the influence of coarse woody debris remaining after salvage logging on regeneration
280 structure and composition was analyzed by Spearman's ρ correlations.

281

282

283 **3 Results**

284 **3.1 Forest structure**

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

290 In both areas, the disturbed plots were significantly different from the undisturbed ones ($LM p =$
291 0.05 , $WD p = 0.009$, MRPP test), with a low within-group homogeneity ($LM A = 0.03$, $WD A =$
292 0.05 , MRPP test). The separation between the undisturbed forest and LM was lower ($T = -1.94$)
293 than the one with WD ($T = -3.59$). The main differences found between LM and WD concerned
294 residual trees, residual canopy cover, and regeneration. Residual overstory density (expressed as
295 basal area) was variable, but greater in LM . All conifer species were attacked by the nun moth,
296 but the most damaged was Norway spruce. In contrast, the density of trees > 7.5 cm DBH in WD
297 mainly consisted of advance regeneration and individuals established immediately after the wind
298 storm. This result is also confirmed by the low mean DBH (7.9 cm), just above the 7.5 cm
299 threshold, and the young age of the individuals (Table 2).

300

301 **3.2 Post-disturbance regeneration**

302 Post-disturbance regeneration of five tree species was found in disturbed portions of each study
303 area. In WD silver fir was absent, whereas larch and Norway spruce were abundant (Table 2).
304 Though highly variable, the total amount of regeneration, including all three size classes, was
305 more abundant in LM (12680 individuals per ha) than WD (9691 individuals per ha).
306 Regeneration was mainly from seed (96.6%) with only a few individuals of mountain ash and
307 aspen from vegetative reproduction (3.4%). In LM regeneration class R3 had a mean age of 12

308 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
309 DBH. R3 mean height in *LM* (2.8 m) was not significantly different ($p = 0.15$, T-test) from the
310 one in *WD* (2.5 m).

311 The incidence of ungulate browsing on the regeneration was 12.9%. Silver fir and Norway
312 spruce were the most affected species (41.8%), followed by larch (26.5%), and mountain ash
313 (19.4%). European aspen and silver birch were less damaged by browsing.

314

315 **3.2.1 Regeneration structure**

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

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

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

334

335 **3.2.2 Regeneration composition**

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

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

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

353

354

355 **3.2.3 Regeneration growth increments**

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

367

368 **3.2.4 Influence of salvage logging on regeneration**

369 The amount of coarse woody debris following the salvage logging operations was similar among
370 *LM* and *WD*, and had a mean volume of 120 m³ per hectare (Table 2). Logs and stumps made up
371 64.4% of the volume of deadwood, while snags were found only in areas where wood was not
372 piled, and were less important (c.a. 1% in volume). The amount of deadwood in both disturbed
373 areas was strongly conditioned by the presence of woodpiles, which represented 34.7% of the
374 total CWD volume, and were found in 17% of the plots. Downed logs left on the forest floor had
375 a mean diameter at half-length of 16.6 cm, while snags had 18.8 cm mean DBH.

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

379 On those plots where woodpiles were present, the majority of deadwood (80.6%) was stacked.
380 The abundance of regeneration class R3 was negatively correlated to the presence of woodpiles
381 (Spearman's $\rho = -0.291$, $P < 0.05$). This deadwood component also had a negative effect on the
382 density of larch and silver fir seedlings (R1) density (Spearman's $\rho = -0.618$, and -0.279 , $P <$
383 0.01 , respectively).

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

390 The amount of coarse woody debris in undisturbed plots had a mean volume of 24 m³ per hectare
391 (Table 1), and the ground cover for CWD was 12%. Logs and stumps made up 90.5% of the
392 volume of deadwood, while snags were less important (9.5% in volume), and no woodpiles were
393 found. Downed logs had a mean diameter at half-length of 18.5 cm, while snags had 13.9 cm
394 mean DBH.

395

396

397 **4 Discussion**

398 Analysis of the mosaic of disturbance severity, and assessment of pre-disturbance forest
399 composition and structure provided valuable insight into the contrasting influences of two

400 different natural high-severity disturbance types and their interactions with a common post-
401 disturbance treatment. The two study areas are very closely matched in terms of their proximity
402 to one another, environmental conditions, and land management histories. Within the same time
403 frame, both areas were impacted by high severity natural disturbances and subsequent salvage
404 logging.

405

406 **4.1 Pre-disturbance forest composition and structure**

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

413

414 **4.2 Post-disturbance dynamics**

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

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

431 (???). Seedlings < 0.3 m height, of silver fir mainly, were primarily found under dense residual
432 forest patches, in the presence of litter and mosses, and where the herb layer was not dominant.
433 In contrast, all size classes of European larch regeneration were more abundant after the wind
434 disturbance (*WD*). Despite better light conditions for regeneration establishment in gaps (Spies
435 and Franklin, 1989), herbaceous competition was a limiting factor for regeneration
436 establishment, especially for shade tolerant species. Seeds tended to germinate under residual
437 forest patches instead of in openings created by the wind storm (*WD*) or the insect attack (*LM*).
438 Post-disturbance regeneration increment patterns were comparable between *LM* and *WD* for the
439 first decade post-disturbance. In the subsequent decade, regeneration in *WD* showed an
440 increasing growth trend, while regeneration in *LM* slightly decreased, probably because of less
441 favorable light conditions. The forest canopy cover influences the quantity and quality of the
442 light that penetrates to the ground (Anderson, 1966). Reduced radiation may be essential for the
443 germination and early survival of spruce seedlings; however, high radiation could accelerate the
444 growth of established seedlings (Dai, 1996). Light amount was adequate for regeneration in both
445 *LM* and *WD* for the first decade after the disturbance occurrence. In the subsequent decade,
446 however, the higher canopy cover in *LM* was associated with reduced growth of seedlings and
447 saplings. The higher amount of light available to the ground in the windthrow area is also
448 reflected in a higher proportion of pioneering species (e.g., larch).
449 Our results also provide evidence for the important role of CWD in facilitating the establishment
450 of new individuals by reducing competition with herbs and shrubs, and improving substrate
451 moisture (Harmon et al., 1986; Kuuluvainen et al., 2002; Brang et al., 2003). CWD appears to be
452 especially important for the establishment of Norway spruce (Motta et al., 2006a; Svoboda et al.,
453 2010). Major natural disturbances generally provide an important pulse of biological legacies
454 such as large-diameter standing dead trees and large pieces of coarse woody debris, which
455 supply habitat and nutrients for a wide range of organisms (Harmon et al., 1986). Because of the
456 salvage logging, in our study sites only small size elements of deadwood were left standing or on
457 the ground, and often grouped in woodpiles. Large-diameter elements were removed mainly
458 because of their higher economic value. Even with the implementation of salvage logging, the
459 amount of deadwood in *LM* and *WD* was higher than in undisturbed stands. Nevertheless, the
460 deadwood was concentrated spatially and covered a small portion of the ground. Woodpiles were
461 found to have a negative influence on regeneration in terms of abundance and also influenced

462 composition. The artificial assemblage of deadwood in woodpiles (i.e., blocks > 1 m³ volume)
463 physically inhibited regeneration establishment and growth. For our study sites, salvage logging
464 had the effect of reducing the amount of favorable germination sites reducing the total volume of
465 deadwood, and assembling the remaining in a not suitable component for regeneration
466 establishment. In fact, areas where woodpiles were not present and, thus, deadwood was
467 scattered, CWD emerged as a preferential substrate for germination of Norway spruce acting as
468 nurse logs (Hofgaard, 1993). In our study the incidence of browsing was high only on preferred
469 species (e.g., silver fir). Browsing can play an important role in forest dynamics after the
470 disturbance (e.g., preventing the establishment or reducing the abundance of selected species,
471 and reducing height growth of trees) (Didion et al., 2009), and some impacts might be strongly
472 underestimated (Motta, 2003). Post-disturbance CWD left on the ground can play an important
473 role in limiting the browsing pressure on tree regeneration (Kupferschmid and Bugmann, 2005).
474 In our study sites browsing damage was more severe on regeneration farther away from CWD,
475 suggesting how deadwood lying on the ground may offer mechanical protection to seedlings
476 (Long et al., 1998; de Chantal et al., 2009).

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

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

493 natural mixed stands (Spiecker, 2003) that are less affected by bark beetle outbreaks, more
494 resilient and could host a higher value of dead wood.

495

496

497 **5 Conclusions**

498 Our analysis explored regeneration dynamics following the most common disturbances affecting
499 the northern slopes of montane Norway spruce forests in the European Alps (i.e., wind storms
500 and insect outbreaks) and their interactions with a common post-disturbance treatment, salvage
501 logging. Post-disturbance regeneration composition and structure were mainly influenced by the
502 amount and distribution of residual canopy cover and CWD, which reflected the medium-term
503 outcomes of the combined effect of the type of natural disturbance and subsequent salvage
504 logging on forest dynamics. Type and intensity of post-disturbance management practices may
505 influence forest stand development for decades (Fischer and Fischer, 2012). If deadwood
506 removal following salvage logging could limit potential risks of European spruce bark beetle (*Ips*
507 *typographus* L.) attacks in disturbed Norway spruce forests (Flot et al., 2002; Wermelinger,
508 2004), the importance of CWD remaining, even after salvage logging, for regeneration and post-
509 disturbance forest dynamics is currently underestimated (Müller et al., 2008). The gathering of
510 CWD strongly influences tree regeneration especially immediately after the disturbance event. If
511 woodpiles have a negative influence on forest regeneration, hindering the establishment of new
512 seedlings and subtracting important germination substrates such as logs, on the other hand
513 scattered large snags and logs play an important role in protecting tree regeneration from
514 browsing and, thus, their conservation is advised.

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

518

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Tables

Table 1

	Units	<i>LM</i>		<i>WD</i>	
		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.

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Table 2

	Units	<i>LM</i> (<i>Lymantria monacha</i> outbreak and logging)		<i>WD</i> (Wind storm and logging)	
		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

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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,

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

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746 **Table 3**

Data used	Variable tested	Explained variability (%)	Correlation 1st axis	<i>p</i>
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

747

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

755 species–environment correlation for the first RDA axis.

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762 **Table 4**

	<i>WD</i>	<i>LM</i>
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)

763

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

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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

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

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

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

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

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