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Deadwood anisotropic facilitation on seedling establishment after a stand-replacing wildfire in Aosta Valley (NW Italy)

Raffaella Marzano[a*], Matteo Garbarino[a], Enrico Marcolin[b], Mario Pividori [b], Emanuele Lingua[b]

[a] University of Torino, Department DISAFA, via L. da Vinci, 44, I-10095 Grugliasco (TO), Italy; raffaella.marzano@unito.it; matteo.garbarino@unito.it;
[b] University of Padova, Department TESAF, viale dell'Università, 16, I-35020 Legnaro (PD), Italy; ; enrico.marcolin@unipd.it; mario.pividori@unipd.it; emanuele.lingua@unipd.it

*Corresponding author. Tel. +39 0116705552; fax +39 0116705556. E-mail address raffaella.marzano@unito.it

Abstract
The capacity of a forest ecosystem to recover following major disturbances depends on the regeneration characteristics of the species and the environment at the time of establishment, resulting from several interacting biotic and abiotic factors. At climatically stressed sites major drivers of recruitment are the presence of a seed source and the availability of 'safe sites' for germination, particularly in the harsh conditions resulting after a stand-replacing wildfire. Post-fire rehabilitation and restoration treatments can produce a deep ecological impact on recruitment processes, acting on biotic legacies and altering the variety and abundance of microsites.
Two common post-fire management strategies, salvage logging and the absence of any post-fire intervention, were contrasted in a burned area located in Aosta Valley (North-Western Italy) to identify main environmental variables affecting seedlings and to quantify the effect of shelter elements on tree recruitment. Our hypothesis is that post-fire burned wood management may greatly affect microhabitat suitability for seedling survival in an dry mountain *Pinus sylvestris* forest.
Regeneration density five years after the fire was still low, even though tree species recruitment started immediately following the disturbance. Differences in species composition were found among the investigated treatments. Regeneration density and diversity were positively associated with deadwood. An exception was represented by *Populus tremula*, regenerating mostly vegetatively, whose behaviour differed from the other tree species. Ground cover conditions contributed to patterns of seedling occurrence. The strong spatial association of seedlings with deadwood suggests that deadwood produces microsites that enhance establishment of regeneration. The relationship between nurse deadwood elements and regeneration was found to be highly anisotropic, as a consequence of the higher protection from radiation and reduced soil moisture loss in the shady sides of the shelter element. In this context post-fire management, particularly when removing burned wood, should be implemented with an understanding of its potential to affect the capacity of the ecosystem to restore, influencing both directly and indirectly recruitment.

Keywords
Post-fire restoration, Microsite amelioration, Nurse objects, Salvage logging, Italian Alps

1. Introduction

After a major disturbance natural regeneration of forest ecosystems results from the complex interactions between propagules and site factors (Kozlowski, 2002). Numerous scale related biotic and abiotic factors (Clark et al. 1998, 1999) influence current recruitment patterns, playing a role in determining future forest structure and composition (Barbeito et al., 2009) by affecting the initially established tree cohort. The type of regeneration (seed or sprouting) directly influences the spatial pattern of plants (Pardos et al., 2008). The successful establishment of a seedling depends on several processes, such as seed viability, dispersal, germination, the presence of symbiotic organisms (e.g., mycorrhizae), mortality factors due to seedling predation, competition, and abiotic stress (Nathan and Muller-Landau, 2000; Castro et al., 2004; Kipfer et al., 2009), whose impact is usually local and species-specific (Pardos et al., 2008). Mechanisms operating at small scales may in particular limit the abundance and performance of seedlings (Collins and Good, 1987).

Seedling establishment is a key component in plant distribution patterns (Harper, 1977). After germination, seedling mortality rates are usually high and the probability of long-term survival is strictly related to the physical habitat surrounding a seedling (Collins and Good, 1987). Preferential recruitment is associated with the availability of 'safe sites' for germination and is linked to the regeneration niche concept (Grubb, 1977). This is particularly evident in climatically stressed sites, where seedlings establishment is strongly limited by harsh conditions. Mature plants, shrubs, deadwood or rocks can play a positive role in ameliorating microsites along with surface microtopography (Castro et al., 2002; Resler et al., 2005; Franzese et al., 2009; Beghin et al., 2010; Legras et al., 2010). Especially in water stressed/limited environment these elements can reduce soil temperature (shading effect) and wind (less transpiration), and increase relative humidity (Flores and Jurado, 2003; Castro et al., 2011). Intra- or interspecific facilitation mechanisms and sheltering effects of abiotic elements are found to be determinant in tree seedling establishment and survivorship in arid environments (Callaway, 2007). In drought-stressed Mediterranean mountain ecosystems, already established vegetation has been often identified as one of the main factor favouring tree regeneration survival through direct protection against high radiation, high temperatures, and high transpiration rates (e.g. Callaway, 1995, 2007). After a stand-replacing fire, with no mature plants or shrubs remaining to facilitate seedling performance after germination, deadwood, rocks as well as surface microtopography may be critical to restoration patterns.

An accurate description of early successional dynamics and the role that microhabitat plays in tree seedling establishment following a major disturbance may be of great importance to clarify restoration patterns aiding in defining ecologically adequate management strategies and silvicultural practices (Pardos et al., 2008; Legras et al., 2010). Post-fire management may greatly affect the resilience of the ecosystem, influencing recruitment both directly and indirectly (Beghin et al., 2010; Moreira et al., 2012). In this context we implemented two different post-fire management treatments within one large wildfire in the Western Italian Alps (Aosta Valley). Our objectives were (1) to analyse natural regeneration dynamics in a post-fire environment characterized by harsh conditions in terms of solar radiation and water availability; (2) to verify the impact of post-fire management (namely salvage logging) on seedling establishment and survival. We hypothesized that post-fire burned wood management would greatly influence the availability of sites for seedling survival. To address these issues we conducted an experimental study contrasting two common post-fire management practices, no intervention and conventional salvage logging (Beghin et al., 2010), to identify the main environmental variables affecting naturally established seedlings and to quantify the effect of shelter elements, particularly lying and standing deadwood, on tree recruitment.

2. Methods

2.1. Study site

The study site is located in the Aosta Valley Region (NW Italy), within the municipality of Verrayes, in an area named Bourra (45°46'21''N, 7°33'16''E), that was severely affected by a stand-replacing fire in March 2005. The wildfire, which is one of the biggest and more severe fire events ever experienced in the region, burned 257 ha, completely destroying 160 ha of an almost pure *Pinus sylvestris* stand. A post-fire salvage logging project was approved in December 2005; salvage logging operations started during autumn 2007. To contrast active management and non-intervention, one area salvaged (salvage logging - SL) according to the conventional post-fire management activities in the Region (Beghin et al. 2010) was compared to another one left untouched (passive management

- PM). Both areas have a surface of 5 ha; they are adjoining and were characterized by similar pre-fire conditions and total mortality of the previous stand. The altitude of the area ranges between 1650 m and 1800 m a.s.l. and the slope is facing south with an average inclination of 25°. The bedrock is ophiolite and schist and the soils are entisols (Soil Taxonomy USDA). The mean annual temperature is 5.6 °C and the mean annual precipitation is approximately 750 mm (less than 250 mm from June to August), with the driest month being February, coinciding with the main peak of the fire season. The tree vegetation consisted almost solely of dense even-aged *P. sylvestris* stands, with a sporadic presence of *Larix decidua* Miller, *Picea abies* L. Karst, *Quercus pubescens* Will., *Populus tremula* L., *Betula pendula* Roth.

2.2. Experimental design and field data collection

Field surveys were conducted in summer 2010 following two different approaches in order to capture regeneration patterns at different spatial scales (site and microsite). At site-scale we adopted a complete random design, locating on the ground 60 circular sample plots with a 6 m radius (about 113 m^2). Twenty plots were established within the salvaged area, the remaining in the unsalvaged area. Given the relative environmental homogeneity of the salvaged area, a lower number of plots (20) was considered sufficient. Site-scale collected parameters (Table 1) included UTM coordinates (submetric GPS device), regeneration characteristics (species, seed or sprout origin, root collar diameter - RCD, height, age), and ground cover. This latter was estimated to the nearest 5% and comprised litter, lying deadwood, bare soil, grasses, forbs, shrubs, and gravel. Game damage was assessed by counting regeneration presenting signs of browsing. The number of standing dead trees was also recorded in the unsalvaged area. Regeneration age was estimated in the field by counting the terminal bud scars (internodes) along the main stem. Topographic variables (slope, aspect, elevation) were computed from a DTM (1-m resolution) derived from LiDAR data acquired in June 2011.

At microsite-scale we adopted a matched case-control design, where seedlings were actively located and 20x20 cm quadratic plots (microsites) were centred on them. Microsites with seedlings (cases) were then matched with microsites without seedlings (controls) for comparison. Controls were always positioned one meter east from their case. Sprout-origin regeneration was excluded from this analysis. Microsite-scale parameters were recorded in 720 microsites, representing 360 matched pairs of cases and controls. Besides collecting the seedling (if present) characteristics, as described above, the parameters that were used to characterize microsites were (1) seedbed type, classified as litter, rotten wood, bare soil, grasses, forbs, shrubs, and gravel; (2) presence and relative position (distance, azimuth) of standing or lying deadwood elements within one meter from the microsite centre; (3) presence and relative position of rock elements (minumum height 10 cm) within one meter from the microsite centre. Microsites position was recorded with a submetric GPS device to allow further monitoring.

2.3. Data analysis

Multivariate statistical analyses (ordination, grouping, and regression methods) were combined to assess the impact of environmental variables and post-disturbance management on tree regeneration. A nonparametric group comparison procedure (MRPP) was used to test the effects produced by different post-disturbance management options on tree species composition. The variability of natural regeneration structure at site-scale (6 variables x 60 plots) in relation to management type and environmental factors (13 variables x 60 plots) (Table 1) was analysed through redundancy analysis (RDA) (Rao, 1964; ter Braak and Prentice, 1988). Redundancy analysis is an extension of principal component analysis and was used to investigate the variability explained by the explanatory variables and their correlation with regeneration structure variation. Redundancy analysis was performed using Canoco® (ter Braak and Smilauer, 1998), while MRPP was performed using the PC-ORD statistical package (McCune and Mefford, 1999). The statistical significance of all ordination analyses was tested by the Monte Carlo permutation method based on 10,000 runs with randomized data.

Conditional logistic regression analysis for matched-pairs data (Breslow, 1982) was used to relate the occurrence (case) and absence (control) of seedlings to microsite variables. The within-pair differences in all variables were calculated, resulting in a constant value of 1 for the response variable "seedling occurrence" and a set of new potential explanatory variables that are the differences between the case and the control for each matched pair (Gibbons et al., 2008). The probability of occurrence of a seedling as related to differences in the variables characterizing matching microsites pair is expressed by odds ratio values (OR). Odds ratios (OR = p/(1-p), with p = proportion of an event, i.e., a seedling present) were calculated by comparing proportions of microsites with and without seedlings. The conditional logistic regression was performed using the SPSS 17 statistical package.

3. Results

3.1. Regeneration structure and composition at site-scale

Tree regeneration ranged between 0 and 8319 seedlings ha^{-1}, averaging 558 ha^{-1} (± 242) in passive management plots, 702 ha^{-1} (± 355) in salvaged plots. Sprouts accounted for 77% and 82 % of the total regeneration in PM and SL respectively. The estimated age of the regeneration ranged from 1 to 5 years. Mean diameter and height of sprout-origin regeneration were respectively 0.74 (±0.04) cm and 49.06 (±2.10) cm. Seedling mean diameter was 0.73 (±0.05) and mean height was 35.51 (±3.09). Damage from wild ungulate browsing was observed on 44% of regeneration individuals, thus affecting height values. No statistically significant differences were found (χ^2 test; $p < 0.05$) among management types and species. The management type emerged as an influential factor only for seedling species composition (MRPP: T = -2.128, p < 0.05). Considering each species separately, *P. sylvestris* and *Larix decidua* relative abundances were higher in passive management sites (Table 2). Most sprouter species, particularly *Populus tremula*, *Quercus pubescens* and *Sorbus aria* were more abundant in salvaged plots.

The role of environmental and management factors on the structure of regeneration of tree species was analysed through direct gradient analysis. Redundancy analysis of regeneration structure related to the examined management options and environmental variables is shown in Fig. 1. The first and second axes accounted for 19.9 and 3.1% of the total variation, respectively. Density, diversity, and maximum age of tree seedlings were positively associated to lying and standing deadwood. Regeneration density of 'other trees' (all tree species except *P. tremula*) was weakly and negatively associated to sites with abundant bare soil, gravel, litter, and shrub cover at the ground. *Populus tremula* density was uncorrelated to 'other trees' density and seemed not influenced by the presence of deadwood.

3.2. Microsite influence on seedling occurrence

Three hundred and sixty matched pairs of microsites with and without seedlings were measured in the salvage logging and the untreated area. The root collar diameter of measured seedlings ranged from 0.1 to 3.2 cm with a mean of 0.84 cm (± 0.02). Seedling height ranged from 6 to 134 cm with a mean of 38.57 cm (± 1.09). The most abundant measured species were *Pinus sylvestris* (15%), *Salix caprea* (15%), *Quercus pubescens* (14%), *Larix decidua* (13%), and *Populus tremula* (11%). The other measured species accounting for 31% of the total amount of seedlings were *Betula pendula*, *Sorbus aucuparia*, *Sorbus aria*, *Prunus avium*, *Populus alba*, *Fraxinus excelsior*, *Juniperus communis*, and *Corylus avellana*.

The conditional logistic regression analysis for matched-pairs on presence-absence of tree seedlings demonstrated the importance of deadwood as a facilitative element (Table 3). Recruitment was highly associated with specific locations of surrounding deadwood. The proximity of at least one element of deadwood (stump, log or snag) within 1 m increased the probability of successful establishment and survival of tree seedlings. Azimuth locations of seedlings with respect to deadwood were highly nonuniform (χ^2 test; p < 0.05). Seedling regeneration pattern thus evidenced a marked anisotropy. In particular seedlings occurred significantly more often than by chance when deadwood elements were located on west (odds ratio [OR] = 3.6), south (OR = 2.6), east (OR = 2.5), and north (OR = 1.9) azimuth quadrants (Table 3). All the other explanatory variables (Table 4) used in the model emerged as not significantly ($p > 0.05$) affecting the occurrence or absence of tree seedlings. A further stratification involving separately the matched-pair data of seedling species did not produce any significant model. Analysing seedling species data and pooled deadwood presence/absence data nevertheless revealed a significant and positive ($\chi^2 = 4.58$; $p < 0.05$) influence of deadwood elements on *P. sylvestris* seedlings.

4. Discussion

Regeneration density five years after the fire was still low even though tree species recruitment started immediately. Resprouts dominated the regeneration layer and higher densities of regenerating stems were observed in particular for *P. tremula*. *Populus tremula* is able to produce both stump sprouts and root suckers, and this reproductive strategy is very effective in maintaining the population under severe disturbance or stressful condition (Hamberg et al., 2011). Root suckers are specialized in efficiently and quickly encroaching a wide underground space after a high severity disturbance (Homma et al., 2003). The high production of juveniles from suckering, producing dense clonal thickets, could balance the high browsing pressure since aspen is a preferred species by ungulates (Hamberg et al., 2011; de Chantal and Granström, 2007; Myking et al., 2011). Browsing of regeneration was actually rather high, affecting the height of sprout-origin individuals (data not shown). Despite the short time since post-fire interventions, management strategies proved to produce an immediate influence on regeneration species composition. Facultative sprouters (e.g. *P. tremula* and *Q. pubescens*), showing a preference for salvage logged areas, confirmed the high resilience of these species in harsher post-fire conditions due to their main regeneration strategy. On the contrary obligate seeders, namely those conifer species (*P. sylvestris* and *L. decidua*) that were present in the pre-fire stand, although less abundant in absolute numbers, were favoured by leaving deadwood on site. Regeneration was in fact positively associated with deadwood. Its density and species diversity were higher when lying and/or standing deadwood were present. This positive effect proved to be essential from the first post-fire growing season, as demonstrated by a stronger association for older seedlings (i.e. seedlings established in the harsher early post-fire environment). The removal of dead or damaged trees by salvage logging strongly reduces the availability of biological legacies (Lindenmayer, 2006). Furthermore salvage harvesting can produce ground disturbance affecting vegetation development (Macdonald, 2007). The presence of patches of standing dead trees could moreover favour tree recruitment by providing perching sites for frugivore birds, potentially improving species richness in the regeneration layer (McClanahan and Wolfe, 1993; Rost et al., 2009; Castro et al., 2009).

Ground cover conditions contributed to patterns of seedling occurrence. Regeneration was most successful in sites where the amount of bare soil, litter, gravel or shrub species was reduced. In our dry site with a water stress condition, even pioneer conifer species (*P. sylvestris* and *L. decidua*) did not thrive on exposed mineral soil in open sites available in the salvaged area, preferring safe sites close to deadwood. The facilitative effect of shrubs on tree seedling establishment and survival commonly seen in dry sites (see Callaway, 2007) is not evident in our site probably because in this short post-fire period they are both competing for colonizing the burned area. We might expect future evidence of this facilitative role when shrubs cover will be higher, as found in other studies (Castro et al., 2004; Gómez-Aparicio et al., 2004) and in an older burned area having similar site conditions in the same region (Beghin et al., 2010). An exception was represented by *P. tremula*, the most abundant species in the regeneration layer, whose behaviour differed from the other regenerating tree species, being uncorrelated to the presence of deadwood. *Populus tremula* proved to successfully encroach grass cover dominated sites. The fast growth of *Populus* root suckers undoubtedly provided a competitive advantage for light with the grass layer (Homma et al., 2003; Myking et al., 2011). Similar results were found by Beghin et al. (2010) with the sprouting ability of this broadleaved species providing an explanation for its widespread presence in areas characterized by a dominance

of grasses, where reduced germination limited establishment of tree species dependent on sexual reproduction.
Analysing regeneration at the microsite level, the probability of a seedling was always higher when a deadwood element was present. The strong spatial association of tree seedlings with deadwood suggests that deadwood produces microsites that enhance establishment of seedlings. The presence of abiotic shelter elements can potentially provide safe microsite conditions for recruitment, without producing competition dynamics with the seedlings. Nurse objects can enhance both seedling establishment and survival (Coop and Schoettle, 2009; Resler et al., 2005; Castro et al., 2011). They can efficiently act as traps for wind-dispersed seed, and provide shading, resulting in reduced evaporation and higher soil moisture (Flores and Jurado, 2003; Carlucci et al., 2011). With water being a critical resource in xeric environments, microsites where microclimatic conditions help in conserving water can play a key role for tree seedling growth and development (Legras et al., 2010). Several studies have reported reduced growth and survival of tree species associated with low soil moisture (e.g. Conard and Radosevich, 1982; Germaine and McPherson, 1999). In our study area, characterized by low winter temperatures, the beneficial effect of deadwood material could also result in holding higher soil temperatures during night, thus affecting winter seedling survival, as found by Castro et al. (2011). The positive anisotropic relationship that we found between seedlings and deadwood was also evidenced in other harsh environments where shield effects were produced by shrubs or live trees (Kitzberger et al., 2000; Haase, 2001; Lingua et al., 2008). In xeric woodlands direct protection from radiation and the effects of shade on soil water availability are among the main factors facilitating the establishment of regeneration, with seedlings preferentially occurring on shady sides of the shelter elements (Kitzberger et al., 2000; Callaway, 2007; Beghin et al., 2010; Castro et al., 2011), in microsites protected in the sunniest hours. On average, seedlings occurred four times more often than would be expected under the assumption of a random distribution if a deadwood element was present westward. Besides the shadow effect, in this case the positive anisotropic relationship is probably also related to seed trapping. The main wind direction in our study site is east-west, and the live edge of untouched forest is bordering east, thus westward deadwood elements are obstacle that can trap wind-dispersed seed (Pounden et al., 2008). In our site only deadwood showed a positive effect on tree regeneration probably because rocks were generally small and single, not providing enough shadow. Seedbed characteristics did not prove to have a significant influence on seedling establishment/survival at microsite level. *Pinus sylvestris* was the species whose presence was more correlated with deadwood. Its seedling are known to be dependent on a sufficient water supply (Hille and den Ouden, 2004), consequently a stable soil moisture regime in the initial stages of recruitment is essential for their survival. *Pinus sylvestris* regeneration is therefore more likely to have taken advantage of the shelter effect provided by deadwood elements. Despite the facilitative effect produced by deadwood, *P. sylvestris* regeneration 5 years after the fire was still very scarce. The species has no cone serotiny (Tapias et al., 2004). Its winged seeds are typically dispersed by wind in a period of about 2 or 3 weeks after cone opening in early spring (Debain et al., 2007), thus benefitting from spring rains (Debain et al., 2005). Good seed production usually occurs every 4-6 years (Lanner, 1998). Variation in seed production and quality between years is higher in harsh environments (Karlsson and Örlander, 2000). Cones and seeds of *P.sylvestris* show a very limited resistance to fire (Habrouk et al., 1999), thus after a stand-replacing fire the only potential sources for regeneration are unburned edges or green islands. Despite its pioneer attributes, a difficulty of *P. sylvestris* to germinate after fire has been observed (Retana et al., 2002), together with a limited capacity of recolonization from the unburned edge due to limited dispersal distances (Vilà-Cabrera et al., 2012). Foreseen changes in fire regimes worldwide (Dale et al., 2001; Cary, 2002; Flannigan et al., 2005; Westerling et al., 2006) and specifically in the Mediterranean Basin (Pausas and Fernández-Munõz, 2012) will probably increase the vulnerability of pine stands to fire. The forthcoming scenario calls for a full understanding of post-disturbance tree recruitment processes; in particular, knowledge on severe crown fires' effects needs to be further explored (Marzano et al., 2012). A recent rise in crown fire occurrence in *P. sylvestris* forests at the south-western distribution

limit of the species has already been reported (Pausas et al., 2008; Beghin et al., 2010). *Pinus sylvestris* stands in dry sites will more likely be affected, with possible vegetation shifts towards shrublands or mixed resprouter forests (Rodrigo et al., 2004; Vilà-Cabrera et al., 2012). Post-fire rehabilitation and restoration treatments of these ecosystems should thus be implemented in the light of this scenario, acknowledging their potential to alter microsites variety and diversity, with possible implications on the species composition of restored forests.

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Table1. Environmental and regeneration variables included in the ordinations for site-scale analyses

Variable category	Code	Description	Unit	Data source
Environmental	Slope	Slope	°	DTM (LiDAR)
	HLI	Heat Load Index (McCune & Grace 2002)	-	DTM (LiDAR)
	Cover-div	Ground cover diversity (Shannon index applied to ground cover types)	-	Field
	Shrubs	Shrub cover	%	Field (visually estimated)
	Forbs	Forb cover	%	Field (visually estimated)
	Grasses	Grass cover	%	Field (visually estimated)
	Soil	Bare soil cover	%	Field (visually estimated)
	Gravel	Gravel cover	%	Field (visually estimated)
	Litter	Litter cover	%	Field (visually estimated)
	Ly.deadwood	Coarse woody debris cover	%	Field (visually estimated)
	St.deadwood	Snag density	# ha^{-1}	Field
	Salvage logging	Post fire logging treatment	-	Nominal variable
	No intervention	Absence of post fire treatment	-	Nominal variable
Regeneration structure	PT	*Populus tremula* regeneration density	# ha^{-1}	Field
	Other trees	Regeneration density of all tree species except *P. tremula*	# ha^{-1}	Field
	RCD-Mean	Mean root collar diameter	cm	Field
	RCD-ST.dev.	Standard deviation of root collar diameter	cm	Field
	Age-Max	Age of the oldest seedling	years	Field

Diversity	Tree species diversity (Shannon index applied to tree species)	-	Field

Table 2. Mean density (regeneration/ha) and standard error (in parentheses) of regeneration at site-scale, divided by species and management type.

Species	Passive management	Salvage logging
Pinus sylvestris	14.50 (±12.28)	---
Larix decidua	14.72 (±7.53)	5.06 (± 5.06)
Populus tremula	387.90 (±238.92)	504.61 (±325.02)
Quercus pubescens	7.65 (±5.64)	54.91 (± 30.36)
Fraxinus excelsior	10.02 (±7.82)	10.32 (± 7.11)
Betula pendula	7.21 (±4.06)	---
Salix caprea	66.27 (±14.10)	72.64 (± 48.28)
Sorbus aria	---	25.00 (± 16.15)
Sorbus aucuparia	17.63 (±8.05)	---
Juniperus communis	27.04 (±9.28)	9.77 (± 6.73)
Tot.	558 (± 242)	702 (± 355)

Table 3. Results of conditional logistic regression analysis for 360 matched pairs data (seedlings and controls) at microsite-scale. The significant explanatory variables used in the conditional logistic regression model are expressed in bold. Only variables having an odds ratio above 1 (i.e. indicating a higher occurrence of seedlings on a given microsite than what would be expected by chance) are reported.

Explanatory variable	*Beta*	S.E.	*P*-value	Odds Ratio	95% confidence interval for odds ratio
Proximity to					
Deadwood_W	1.281	0.279	0.000	3.600	2.084-6.221
Deadwood_S	0.957	0.260	0.000	2.605	1.566-4.334
Deadwood_E	0.937	0.236	0.000	2.553	1.607-4.057
Deadwood_N	0.612	0.254	0.016	1.844	1.122-3.033
Rocks_N	0.608	0.603	0.313	1.837	0.563-5.99
Rocks_W	0.390	0.846	0.645	1.477	0.281-7.753
Rocks_S	0.387	0.800	0.628	1.473	0.307-7.064

Table 4. Mean and standard error (in parentheses) of explanatory variables used in the conditional logistic regression model of plots with (cases) *vs.* without seedlings (controls) at microsite-scale.

Explanatory variable	With seedling (n = 360)	Without seedling (n = 360)
Seedbed (%)		
Grasses	29.25 (±1.49)	26.99 (±1.51)
Bare soil	24.95 (±1.21)	21.55 (±1.32)
Rotten wood	14.98 (±0.86)	15.99 (±1.16)
Forbs	14.38 (±0.80)	18.09 (±1.06)
Shrubs	14.37 (±1.13)	15.81 (±1.22)
Proximity to (n)		
Deadwood_S	0.27 (±0.03)	0.15 (±0.02)
Deadwood _N	0.25 (±0.03)	0.16 (±0.03)
Deadwood_E	0.19 (±0.03)	0.11 (±0.02)
Deadwood_W	0.19 (±0.03)	0.14 (±0.02)
Rocks_N	0.04 (±0.01)	0.02 (±0.01)
Rocks_E	0.04 (±0.01)	0.01 (±0.01)
Rocks_S	0.02 (±0.01)	0.02 (±0.01)
Rocks_W	0.02 (±0.01)	0.02 (±0.01)

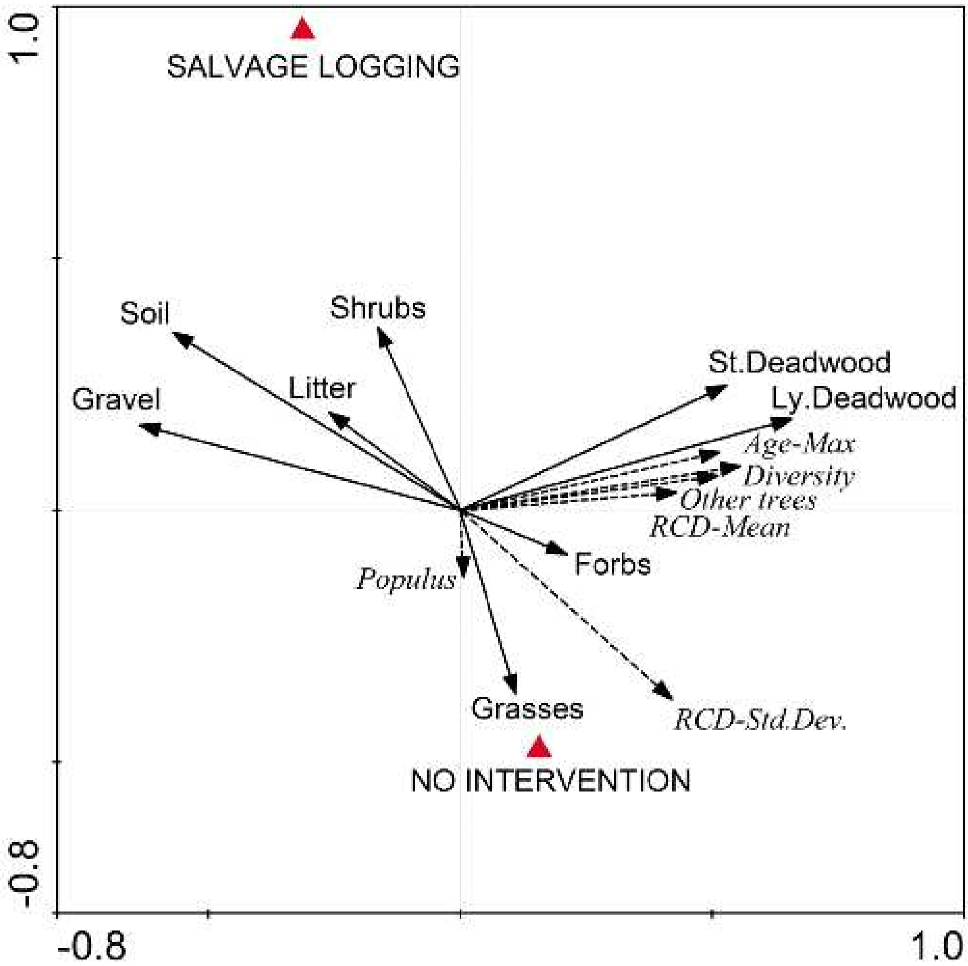

Figure 1. Redundancy analysis (RDA of 60 plots) of regeneration structure in relation to environmental characteristics and management options at site-scale.

Dashed arrows are the regeneration structure variables (RCD-Mean = average Root Collar Diameter; RCD-Std.Dev. = standard deviation of Root Collar Diameter; Diversity = Shannon diversity index; Populus = density of *Populus tremula*; Other trees = density of all tree species except *P. tremula*; Age-Max = maximum seedling age). Full line arrows represent the "biplot scores of environmental variables" (St.Deadwood = standing deadwood or snags; Ly.Deadwood = lying deadwood; Shrubs = shrubs cover; Litter = litter cover; Soil = bare soil cover; Gravel = gravel cover; Grasses = graminoids cover; Forbs = non-graminoid herb cover). Triangular dots are management options (No intervention = absence of post-fire treatment; Salvage logging = post-fire logging treatment) categorical variables. The species-environment correlation for the first RDA axis was 63.0.