

Post-fire effects and short-term regeneration dynamics following high-severity crown fires in a Mediterranean forest

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Resilience against fire disturbance of Mediterranean vegetation has been frequently described. However, due to climatic change and abandonment of local land use practices, the fire regime is changing, probably leading to higher intensities and frequencies of disturbance events. The forthcoming scenario calls for a full understanding of post-disturbance tree recruitment processes, structural resilience and possible consequences on the overall forest biodiversity. In particular, knowledge on severe crown fires' effects on forest stand structural attributes needs to be further explored. In this work, we describe and quantify fire impact and short-term response of a Mediterranean forest affected by high severity crown fires, focusing on the compositional and structural diversity of living and dead trees, spatial pattern of fire-induced mortality, recovery dynamics of tree species. The analysis, based on a synchronic approach, was carried out within four burned and two not burned fully stem-mapped research plots located in NW Italy, belonging to two forest categories differing for their main tree restoration strategies. Distance-dependent and distance-independent indices were applied to assess structural diversity dynamics over time since fire occurrence. Within the analyzed forests fire was found to affect mostly forest structure rather than its composition. Number of snags largely increases immediately after the fire, but it levels off due to their fall dynamics. Regeneration strategies and fire severity influenced species abundance and consequently diversity patterns. Stem diameter and height diversity were modified as well, with a strong increase in the first post-fire year and a sharp reduction six years after the disturbance. Fire determined also a higher heterogeneity in crown cover and vertical structure. Spatial patterns of surviving trees and snags were greatly affected by fire, producing an increase in aggregation and segregation mechanisms. Autosuccessional processes are supposed to preserve current forest structure and composition, but the ecosystem self-restoring capability should be analyzed in the light of the possible changes in fire regime.

Keywords: Structural diversity, Snag dynamics, *Pinus pinaster*, Regeneration strategies, Fire severity

Introduction

Fire is recognized as the most important natural disturbance in Mediterranean ecosystems (Trabaud 1994, Whelan 1995). In the Mediterranean basin, given the long historical human impact on ecosystems, the incidence of fire has always been particularly high (Le Houérou 1987, Trabaud 1987a). In addition to natural causes of ignition, burning was one of the management tools commonly used by man (Naveh 1975, Lloret & Mari 2001). Fire thus acted as a fundamental factor on ecosystem functioning and as a major ecological driver of vegetation changes (Attiwill 1994, Moreno & Oechel 1994, Lavorel et al. 1998), by modeling landscapes (Gillson 2009) and contributing to maintain habitat heterogeneity and biological diversity

(Moreira et al. 2001, Blondel et al. 2010).

Even though fires have been a major factor in Mediterranean ecosystems for millennia, the general trend in number of fires and area burned in European Mediterranean areas has dramatically increased during the last decades, principally due to land-use and climatic changes (Piñol et al. 1998, Lloret & Mari 2001, Mouillot et al. 2002, González & Pukkala 2007, Pausas & Fernández-Muñoz 2012). According to the predicted climate change scenarios for the Mediterranean region, further increases in wildfire frequency and burned areas are expected (Carvalho et al. 2008, Good et al. 2008).

Although Mediterranean vegetation is able to cope with fire (Trabaud 1987a, Pausas 1999a), alterations in the fire regime (in

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terms for instance of higher fire recurrence or incidence of large events) can generate important consequences for Mediterranean ecosystems (Zedler et al. 1983, Vázquez & Moreno 2001, Lloret et al. 2003) and their plant diversity. Given the very strong effect of fire on vegetation, plant distribution and ecosystem function could likely be more heavily affected by the ongoing modifications in fire regime consequent to global changes than by the direct effect of climate changes (Pausas & Fernández-Muñoz 2012). Moreover, the combined impact of these fire regime changes and enlarged environmental limitations for post-fire tree recruitment could deeply affect the species composition of Mediterranean forests (Peñuelas & Filella 2001, Peñuelas et al. 2002, Lloret et al. 2004, 2009).

It is well documented that Mediterranean ecosystems recover readily after fire through an autosuccessional process (Hanes 1971, Trabaud 1994) based on efficient regeneration strategies. Post-fire recovery is usually realized by direct regeneration, *i.e.*, the fast recovery of a plant community made up by the same species pool that existed before the disturbance (Rodrigo et al. 2004). Two main plant regeneration strategies conferring resilience to Mediterranean ecosystems are the capacity to resprout after fire (resprouter species), and the stimulation of the recruitment by fire (seeder species - Bond & van Wilgen 1996, Verdú et al. 2007). In several fire-prone communities varying proportions of woody sprouters and seeders are included (Hodgkinson 1998, Lloret & Vilà 2003). Fire regime may influence the relative abundance of sprouters and seeders (Lloret et al. 2005). Since significant changes in disturbance regimes are predicted by global change scenarios, more attention must be paid to the ecosystems' ability to recover

(Dury et al. 2011). Among the main research needs for Mediterranean forests, key topics are resilience to disturbance in general (Lavorel 1999, Scarascia-Mugnozza et al. 2000) and post-fire recruitment processes in particular (Vega et al. 2010).

The main aim of this work was to describe and quantify short-term vegetation response after high-severity crown fires in a Mediterranean forest with stands featuring a different composition of seeder and resprouter woody species in the tree layer. Recovery processes were investigated to disclose differences in resilience mechanisms among species with different restoration strategies. Specific research goals were the assessment of: (a) compositional and structural diversity of living and dead trees; (b) spatial pattern of fire-induced mortality; (c) recovery dynamics of tree species.

Materials and methods

Study site

The study was carried out in the province of Savona, Central Liguria, NW Italy (lat 44° 12' - 44° 19' N, long 8° 22' - 8° 28' E). The geologic bedrock is quite heterogeneous and is mainly represented by Cenozoic and Mesozoic igneous and metamorphic rocks. The climate is typical Mediterranean, with mild and moderately moist winters and warm and dry summers, characterized by a significant summer drought. Along with a few remaining monospecific *Pinus pinaster* Aiton stands, the majority of forests are mixed stands, with both conifer (mainly *P. pinaster*) and broadleaved species (including mainly oaks - *Quercus pubescens* Willd., *Quercus ilex* L., as well as *Castanea sativa* Miller, *Fraxinus ornus* L., and other woody species like *Erica arborea* L., *Arbutus unedo* L.) or with a predominance of broadleaves. The fire regime, as throughout Liguria Region, is characterized by frequent and severe wildfires, spread all over the year, but mostly concentrated during summer (Mar-

zano 2006).

Two high severity crown fire events, located in close proximity (< 10 km), were selected for a case study. The first wildfire occurred in August 1998 and burned 146 ha, while the second occurred in August 2003 and burned 235 ha. Burned areas within the fire perimeters were differentiated according to the percentage of seeder and sprouter species in the overstory, identifying two main forest categories: the mixed-broadleaved forest category (henceforth: MB) characterized by the predominance of sprouters, and the broadleaved-coniferous forest category (BC) made up by both sprouters and obligate seeders.

Sampling

We established one intensive sampling plot for each forest category inside the fire perimeters (BC_03; BC_98; MB_03; MB_98) and another one for each forest category in the surrounding unburned area as control plot (BC_nb; MB_nb). The latter were not burned by high intensity fires since 20 years at least.

Each plot (50 x 50 m) has one side parallel to the maximum slope. Within each plot all living trees and shrubs (stems with dbh \geq 3 cm), snags (standing dead trees with dbh \geq 3 cm and height > 1 m), logs (downed dead trees or part of, with the biggest size diameter \geq 10 cm), and stumps (surface diameter \geq 10 cm and height \leq 1 m) were identified, labeled with numbered plastic tags and mapped with a total survey station (Geotronics - Geodimeter 400). Sampling activities were carried out in summer 2004.

For every living stem, we recorded species, diameter at breast height (dbh), total height, height of lowest living branches (upslope and downslope), four radii of the crown projection on the ground. For each snag, log or stump inside the plot, the species based on distinguishing traits not modified by fire, the diameter (dbh for snags, diameter on both ends for logs, diameter at the root collar for

stumps) and the total height (snags, stumps) or length (logs) were recorded. The number of post-fire resprouts of tree and shrub species was also recorded. Tree seedlings and saplings were recorded within sixteen square subplots (6.25 m²) randomly established inside each 50 x 50 m plot.

Structural diversity

Structural diversity within plots was assessed applying both distance-independent and distance-dependent measures. For more details on the diversity indices used, see Appendix 1.

The Brillouin index (*HB*) and the Evenness (*E*) for the Brillouin index (Brillouin 1956, Magurran 2004) were computed to describe the variability in woody species abundance.

Following Kuuluvainen et al. (1998), we used the distribution of tree heights to represent the vertical structure of the forest. The tree height diversity (THD) index was computed for living stems and snags (Kuuluvainen et al. 1996), adopting 2.5-m-deep horizontal layers. We also applied the tree diameter diversity (TDD) index (Rouvinen & Kuuluvainen 2005) to 5 cm dbh classes of living and dead stems.

The vertical distribution of canopy cover within the plots was assessed through the Vertical Evenness (VE) index by Neumann & Starlinger (2001).

To describe the tree spatial pattern within the plots, Point Pattern Analysis (PPA) techniques were applied by means of Ripley's *K* (Ripley 1977) using the software SPPA 2.0 (Haase 2001). Since the cumulative *K*-function confounds effects at larger distances with effects at shorter distances (Getis & Franklin 1987), the *O*-ring functions (Wiegand et al. 1998) were adopted as complementary analyses using the PROGRAMITA software (Wiegand & Moloney 2004).

To determine the distributions of trees or tree-classes as random, regular or clumped, univariate Ripley's *K(t)* and *O(r)* functions were applied. To assess the relationships between classes (*i.e.*, living vs. dead), we examined bivariate spatial interactions using Ripley's *K*₁₂(*t*) (Lotwick & Silverman 1982) and *O*₁₂(*r*) functions (Wiegand et al. 1998).

We considered as living the individual stools showing at least one shoot (dbh \geq 3 cm) alive. All the analyses were carried out only for classes having more than 20 elements, and starting from 1 m up to 25 m applying a 1 m lag distance, thus not exceeding half of the study area in order to limit the influence of the margin effects (Haase 1995).

Null models were chosen for the different analyses to avoid misinterpretation of the results (Goreaud & Pélissier 2003). Complete spatial randomness (CSR) was adopted as null model for the univariate analyses. For the living vs. dead stems analysis, we chose the null hypothesis of random mortality ap-

Tab. 1 - Stand characteristics of the six investigated plots. (BC_nb): not burned broadleaved-coniferous forest stand; (BC_03): broadleaved-coniferous forest stand burned in 2003; (BC_98): broadleaved-coniferous forest stand burned in 1998; (MB_nb): not burned mixed-broadleaved forest stand; (MB_03): mixed-broadleaved forest stand burned in 2003; (MB_98): mixed-broadleaved forest stand burned in 1998.

Plots	BC_nb	BC_03	BC_98	MB_nb	MB_03	MB_98
Mean elevation (m a.s.l.)	277	231	277	236	225	170
Aspect	N-E	N-E	N-E	S-E	S-W	N-W
Slope (degrees)	22	28	22	29	19	17
Living stem density (stems ha ⁻¹)	2310	182	929	3787	394	994
Living stem basal area (m ² ha ⁻¹)	15.8	5.8	2.9	16.8	7.9	4.9
Snag density (stems ha ⁻¹)	345	2716	1421	425	2643	348
Snag basal area (m ² ha ⁻¹)	4.3	23.8	10.1	2.1	19.9	1.1
Regeneration density (n ha ⁻¹)	9800	11100	21900	7300	11900	1600
Regeneration richness (n taxa)	5	6	10	7	10	7

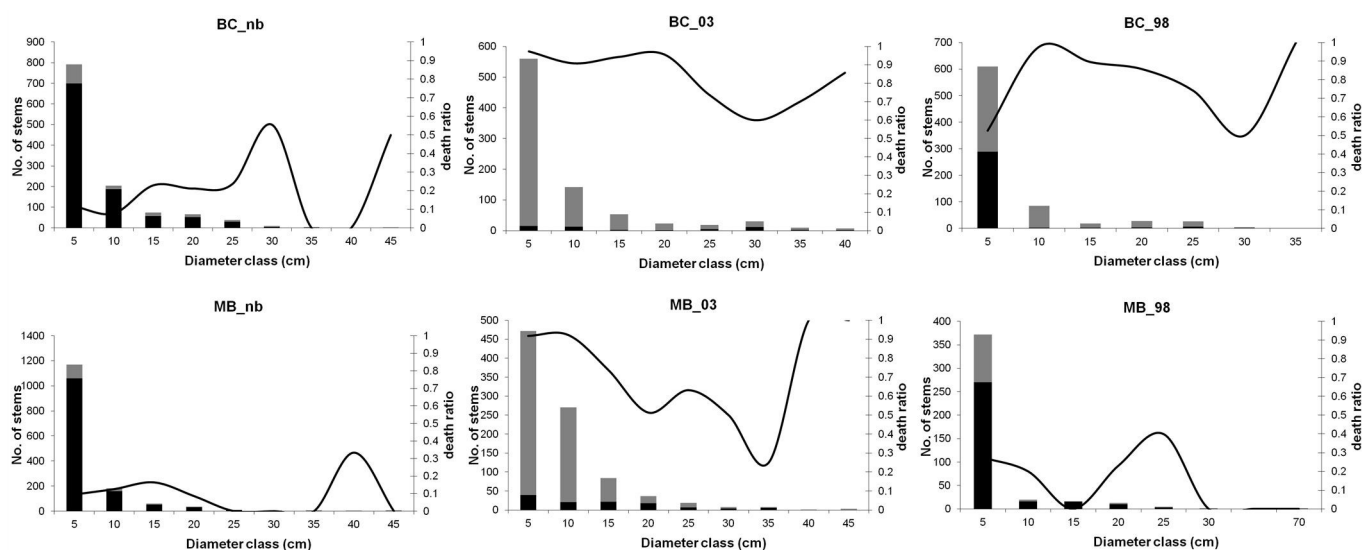


Fig. 1 - Diameter distribution of living stems and snags. Living stems are represented in black, snags in grey. Solid lines correspond to the death ratio, *i.e.*, the proportion between dead and total stems in a given diameter class.

plying the random labeling (Kenkel 1988), since the mortality agents (*i.e.*, wildfires) can only work within the limits set by the distribution of living trees prior to the disturbance events themselves (Aakala et al. 2007).

Results

A total of 6482 living stems, snags, logs and stumps were recorded, mapped and measured in the tree layer of the 6 investigated plots. Living stem density (Tab. 1) ranged from 182 stems ha⁻¹ (BC_03) to 3787 stems ha⁻¹ (MB_nb). Snag density ranged from 345 stems ha⁻¹ (BC_nb) to 2716 stems ha⁻¹ (BC_03). Basal area of living stems (Tab. 1) ranged from 2.9 m² ha⁻¹ (BC_98) to 16.8 m² ha⁻¹ (MB_nb). Concerning snags, the lowest basal area (1.1 m² ha⁻¹) was also recorded in MB_98, while the maximum value (23.8 m² ha⁻¹) was found in BC_03.

Comparable values in density of seed germinated individuals were found for unburned plots and those burned in 2003 (Mann-Whitney test; *p*>0.05), whereas a highly significant difference occurred in 1998-burned plots (Mann-Whitney test; *p*<0.001).

The size-class distribution of living stems and snags was reverse *J*-shaped for all the six plots (Fig. 1). Larger stems were mostly maritime pine trees, secondarily oaks and chestnut. The major difference between plots is the different contribution of snags and living stems to size classes. Along the post-fire chronosequence, the most represented size class was the 5-cm one. In the unburned plots almost 90% of stems belonging to this size class was made up by living stems, while immediately following the fire events, it included almost exclusively dead stems.

Among the most abundant species in the overstory, *Arbutus unedo* and *Fraxinus*

ornus showed a high resprouting percentage in both 2003 plots (Tab. 2), while as expected in the two 1998-burned plots the percentage is reduced, with no significant differences in BC and MB (χ^2 test; *p*>0.05). *Erica arborea* had a different behavior in the

two plots burned in 2003, with a higher resprouting percentage in BC_03 (χ^2 test; *p*<0.001). In the two 1998-burned plots the resprouting percentages are still high, with no significant differences. Similarly, *Castanea sativa* showed a higher resprouting per-

Tab. 2 - Number of top-killed stools and resprouting percentage [Re. (%)] in the four burned plots, for the main resprouting species. (BC_03): broadleaved-coniferous forest stand burned in 2003; (BC_98): broadleaved-coniferous forest stand burned in 1998; (MB_03): mixed-broadleaved forest stand burned in 2003; (MB_98): mixed-broadleaved forest stand burned in 1998.

Species	BC_03		BC_98		MB_03		MB_98	
	# stools	Re. (%)	# stools	Re. (%)	# stools	Re. (%)	# stools	Re. (%)
<i>Arbutus unedo</i>	41	92.7	18	44.4	31	77.5	35	25.7
<i>Castanea sativa</i>	100	49	72	9.7	13	27.7	-	-
<i>Erica arborea</i>	82	72	114	77.2	13	34.2	12	58.3
<i>Fraxinus ornus</i>	74	68.9	1	0	87	55.4	7	0
<i>Quercus ilex</i>	-	-	3	100	33	75	6	0
<i>Quercus pubescens</i>	-	-	5	60	17	65.4	14	7.1

Tab. 3 - Structural diversity in the tree layer through distance-independent variables. Measures were computed for living trees with Brillouin and Vertical Evenness (VE) indices, while tree height diversity (THD) index and tree diameter diversity (TDD) index were calculated for both living stems and snags. (BC_nb): not burned broadleaved-coniferous forest stand; (BC_03): broadleaved-coniferous forest stand burned in 2003; (BC_98): broadleaved-coniferous forest stand burned in 1998; (MB_nb): not burned mixed-broadleaved forest stand; (MB_03): mixed-broadleaved forest stand burned in 2003; (MB_98): mixed-broadleaved forest stand burned in 1998.

Structural diversity	BC_nb	BC_03	BC_98	MB_nb	MB_03	MB_98
Richness (n taxa)	10	5	9	7	8	8
Brillouin diversity (HB)	1.617	1.077	1.273	1.55	1.489	1.402
Brillouin evenness (E)	0.717	0.749	0.616	0.81	0.781	0.707
THD living stems	1.469	1.838	0.795	1.28	1.887	1.026
THD snags	1.516	1.487	1.122	0.966	1.716	0.668
TDD living stems	1.02	1.736	0.296	0.731	1.713	0.628
TDD snags	1.314	1.063	1.009	0.8	1.119	0.367
VE	0.86	0.82	0.97	0.81	0.8	0.88

Tab. 4 - Ripley's $K(t)$ for living stems, snags and total stems in the six plots. Clumped distribution is indicated by "o", while "-" indicates no statistically significant difference from the CSR (Complete Spatial Randomness) hypothesis ($p < 0.01$). Dark symbols ("•") stands for the $K(t)$ statistics being consistent with the $O(r)$. (BC_nb): not burned broadleaved-coniferous forest stand; (BC_03): broadleaved-coniferous forest stand burned in 2003; BC_98: broadleaved-coniferous forest stand burned in 1998; (MB_nb): not burned mixed-broadleaved forest stand; (MB_03): mixed-broadleaved forest stand burned in 2003; MB_98: mixed-broadleaved forest stand burned in 1998.

Plot	Classes	Distance (m)																									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
BC_nb	Living stems	•	•	•	•	•	•	•	•	•	•	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
	Snags	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	o	•	•	•	o	•
	Total Stems	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	o	o	o	•	o	o
BC_03	Living stems	-	-	-	-	•	o	o	o	o	o	o	-	-	-	-	o	-	-	-	-	•	o	o	•	o	
	Snags	-	-	•	•	•	•	•	•	•	•	o	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o
	Total Stems	-	-	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	o	•	o	•	•	•	•
BC_98	Living stems	-	•	o	•	•	•	•	o	•	o	•	o	o	o	o	o	•	o	o	o	o	o	o	o	o	o
	Snags	-	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	o	o
	Total Stems	-	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	o
MB_nb	Living stems	-	•	•	•	•	•	•	o	o	•	o	•	•	o	o	o	o	o	o	o	o	o	o	-	-	-
	Snags	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Total Stems	-	•	•	•	•	•	•	•	•	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	o	-
MB_03	Living stems	•	•	•	•	•	•	•	•	•	•	•	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o
	Snags	-	•	•	•	•	•	o	•	o	•	o	o	•	o	•	•	o	o	o	o	o	o	o	o	o	-
	Total Stems	-	•	•	•	•	•	•	•	•	•	•	o	o	o	o	o	o	o	o	o	o	o	-	-	-	-
MB_98	Living stems	•	•	•	•	•	•	•	•	•	•	•	•	o	o	o	o	o	o	o	o	o	•	o	o	•	o
	Snags	-	-	-	-	-	-	-	-	o	o	o	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Total Stems	•	•	•	•	•	•	•	•	o	•	o	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o

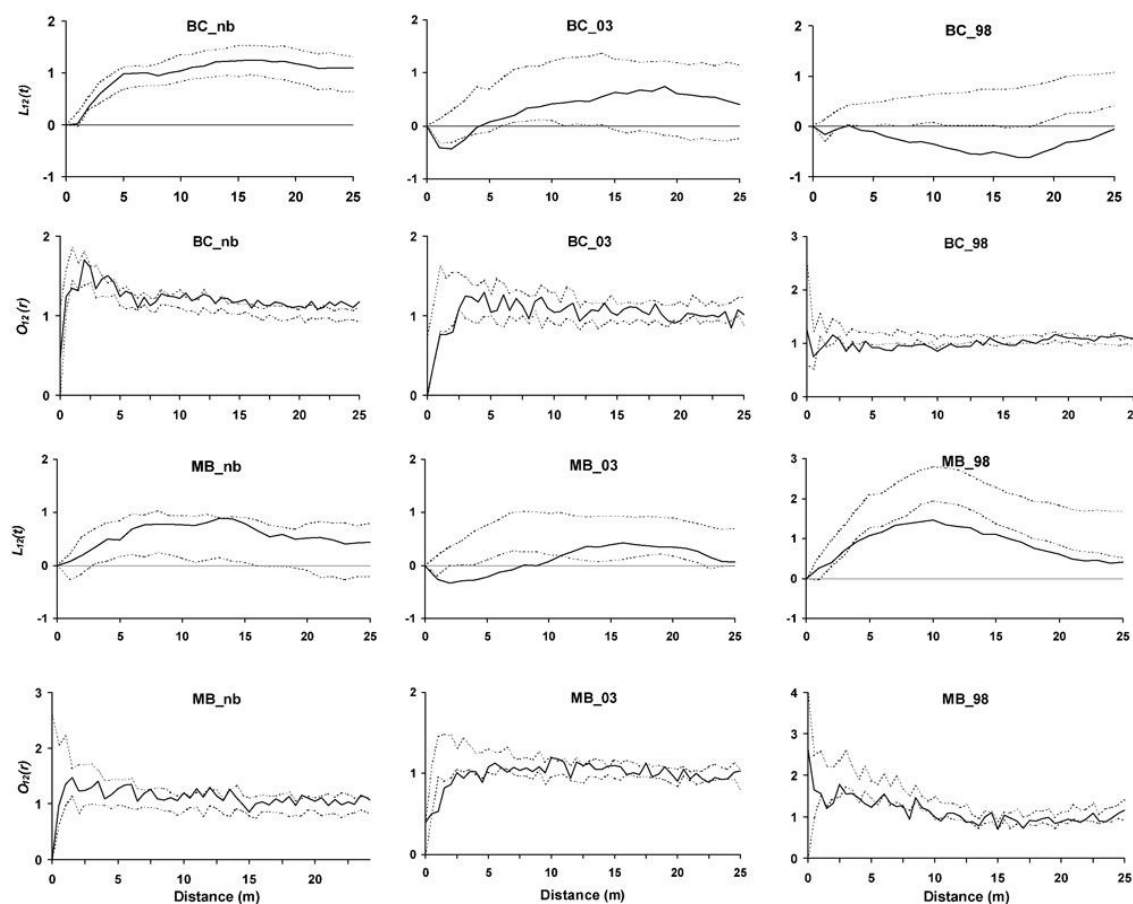


Fig. 2 - Second order bivariate Ripley's $L_{12}(t)$ and O-ring $O_{12}(r)$ analyses for living vs. dead stems inside the plots. Solid line is respectively $L_{12}(t)$ and $O_{12}(r)$, while dashed lines represent the 99% confidence envelopes under the random labelling null model. Points over the confidence envelope show positive spatial interactions (attraction), points below the confidence envelope show negative spatial interaction (repulsion), while points located inside the envelope show no significant spatial interaction.

centage in BC_03 (χ^2 test; $p < 0.05$).

Higher species diversity values (*HB*) in the tree layer were found in both unburned plots (Tab. 3). The lowest diversity value was recorded in BC_03, while the index showed a higher value in BC_98. Within the MB plots the Brillouin index shows a decrease along the chronosequence. Lower evenness values (*E*) were obtained within both plots burned in 1998. BC_03 showed instead an *E* value higher than BC_nb. The opposite situation was found between MB_03 and MB_nb.

Living stems of both categories had similar THD and TDD patterns: early after fire occurrence higher values of the indices were encountered (Tab. 3). A sharp decrease was evident in the plots burned in 1998, which on the contrary showed the highest VE values. Snag THD and TDD values highlight a different behavior in BC and MB plots.

Ripley's *K(t)* for living trees revealed a clumped distribution in all the plots (Tab. 4). The tendency toward aggregation was confirmed at short distances by the *O-ring* analysis. Only BC_03 showed a slightly reduced aggregation. Standing dead trees were clumped in BC plots, while in MB plots there was a gradient from a random distribution in MB_nb to aggregation in MB_03, with MB_98 showing an intermediate situation. The living vs. dead trees analysis revealed similar tendencies among plots burned in the same wildfire, and differences within the same forest category (Fig. 2). Repulsion was found from 3 m on in MB_98 and BC_98, while in the more recently burned plots the negative interaction was evident up to 4 m (BC_03) and 11 m (MB_03). No significant spatial interactions were found in unburned plots. All the results are consistent with the *O-ring* analyses (Fig. 2).

Discussion

Fire caused a change in the population structure of both forest categories. The two communities were similar in terms of number and size of fire-killed and surviving tree stems. Fire affected mostly the smaller diameters, greatly reducing their number. At the same time, the majority of largest individuals, mainly maritime pines, were killed.

Following disturbance, the density of living stems and snags showed an opposite behaviour as a consequence of self-restoration strategies and fall dynamics. The processes of tree mortality and snag recruitment are balanced by snag decay and fall (Everett et al. 1999). Snag fall rates vary according to snag size, tree species, the microenvironment, cause and season of mortality. Snag longevity is a site-specific process that needs to be determined for each area of interest (Keen 1929, Everett et al. 1999). Smaller trees are more vulnerable to fire-induced death and usually tend to fall faster than larger diameter snags (Everett et al. 1999,

Chambers & Mast 2005). In the 1998 plots all snags belonged to the greatest size-classes.

The passage of a high intensity fire front induced a modification in the proportion of sprouters and seeders, due to the concurrent presence of species with varying degrees of resistance and resilience to fire. Regeneration strategies can directly influence species abundance and consequently both dominance and evenness values. Consistently with Lloret et al. (2005), the higher presence of sprouters in the mixed-broadleaved forest category determined stability in species richness, even in early successional stages. Highly resilient sprouters can assure species persistence thanks to their ability to produce new shoots immediately after the disturbance event (Keeley 1986, Trabaud 1987b).

Both forest categories showed a generalized increase in structural complexity of living stems immediately following the fire, while in the early post-fire years a decline was registered, reaching values lower than those found for unburned plots. By affecting mostly smaller size stems, fire reduced their pre-disturbance structural dominance. As a consequence, there were more even diameter and height distributions, leading to an increase in structural diversity. This was however a short-lived modification: six years after the perturbation, the high proportional abundance of sprout-origin individuals determined a renewed simplification in structural diversity.

Dissimilar patterns of mortality before the disturbance generated a different behavior in the structural diversity of dead stems. In the BC category, characterized by a high presence of chestnut and maritime pine affected respectively by *Chryphonectria parasitica* (Murr.) Barr. and *Matsucoccus feytaudi* Ducasse, stem mortality was rather high and distributed among the different diameter classes also in the unburned plot. On the contrary, in the MB category, no particular factor seems to have a role in determining tree mortality, except the usual competition dynamics.

Fire determined a larger heterogeneity of the vertical structure in the earlier burned plots, enhancing the evenness of cover distribution between the different layers through the recovery dynamics. The fire event induced an increase in aggregation within the stands. Disturbance by fire has actually been found to increase the degree of clumping (Rebertus et al. 1989, Davis et al. 2005). Fire frequency or intensities may differently affect patterns of aggregation (Davis et al. 2005). Tree mortality was clumped in all the burned sites, but mortality was also spatially aggregated in BC_nb, confirming that some allogenic mortality agents were acting in the stand.

Segregation mechanisms were generated by the fire, inducing a spatial repulsion between surviving and killed stems. Six years after the fire event, natural restoration dynamics and snag fall processes altered living and dead stems spatial relationships. Close to snags, positive afterlife effects (Kane et al. 2011) such as regeneration establishment and broadleaves resprouting mitigate repulsion.

Fire frequently creates a high degree of spatial variability in plant survival, which partially depends on the size of individuals (Johnson 1992, Huston 1994), fire-resistance mechanisms and flammability of species (McKenzie et al. 1996). Maritime pines were severely damaged by fire, influencing the spatial distribution of both dead and living stems. *P. pinaster* is actually a highly pyrophytic species (Velez 2000), with a high resin content, possibly favoring ignition (Van Wagner 1977) and increasing the amount of energy released when the foliage burns.

Fire severity influences the number and the type of plants dying in a fire and their consequent spatial patterns. Fires of low or medium severity produce a highly selective mortality, depending on the species and size of each individual, while fires of high severity usually kill all individuals, regardless of species or size (Turner et al. 1994). In the latter situation, plant survival is often confined in scattered safe sites (cool spots), resulting in clumps of surviving stems.

Fire severity also influences post-fire regeneration in the burned area (Agee 1993), which is also strongly dependent on the regenerative strategies of species (Pausas 1999b).

Seedling recruitment was similar in richness and abundance within both forest categories immediately after fire. In early successional stages after fire, an abundant establishment of saplings and sprouts has been documented by several authors (e.g., Fulé & Covington 1994), mostly as a consequence of the reduced competition for resources. However, in sprouter-dominated communities, seeders are often unfavoured (Naveh 1975, Trabaud 1987a). The dense shrub layer originated by the strong resprouting six years after the fire event in MB_98 probably hampered seedling survival, as confirmed by the very scarce seedling number. BC_98 has instead a very high seedling density, the majority of them being *P. pinaster* individuals. As found in other studies (e.g., Moravec 1990), five years after fire there is usually a high rate of pine establishment. Mortality of maritime pine seedlings is essentially affected by interspecific competition (Fernandes & Rigolot 2007), particularly with shrub species, whose detrimental effects on genus *Pinus* have been often described (De las Heras et al. 2002, Quevedo et al. 2007). Moreover, seeder species persistence could

be endangered by the alteration of fire regimes, leading to differences according to their range of tolerance (Verdú et al. 2007). Severe crown fires can negatively affect post-disturbance regeneration, causing higher damages, and reducing seed dispersal, viability and emergence rate (Fernandes & Rigolot 2007).

Fire effects were found to affect more tree dimensions and spatial patterns rather than composition. Snag dynamics, in particular, were a key element of the observed changes in forest structure, mainly as a consequence of their short-term evolution.

The sprouter-dominated forest stands reveal a major difficulty in restoring the pre-fire conditions. Since the majority of adult conifers in the whole area were killed by the fire, the low number of pine seedlings can cause a partial failure of direct regeneration (Rodrigo et al. 2004) and affect future forest composition.

The scarce number of tree seedlings six years after fire occurrence, along with the high resprouting rates and ground cover of shrub species, may suggest a shift towards a community dominated by a low structured, shrub vegetation. A similar scenario has been proposed for the Mediterranean basin with higher disturbance frequency (Naveh 1974, Trabaud 1991). An increase in the recurrence of high-intensity fires may alter recovery dynamics of usually resilient pine species as a consequence of shrub invasion, delaying succession processes and inducing a regression in the forest structure (Buscardo et al. 2011).

Forthcoming changes in fire regimes, yet largely unknown (Fulé & Covington 1998), and the need to study the response of fire-prone Mediterranean vegetation over several decades (Capitania & Carcaillet 2008), make it necessary to further investigate post-disturbance structural dynamics, also through a long-term monitoring approach (Beghin et al. 2010).

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Supplementary Material

Appendix 1 - Diversity indices and the corresponding equations.

Link: [Marzano_612@suppl001.pdf](#)