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Early postfire vegetation recovery of *Pinus brutia* forests: effects of fire severity, prefire stand age, and aspect

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Abstract: Forests dominated by serotinous tree species are usually generalized to follow an autosuccessional model of postfire recovery. However, recent studies have suggested that prefire conditions, topography, and idiosyncrasies of the fire disturbance can have notable effects on how such forests respond to fire. We investigated the effects of fire severity, prefire stand age, and aspect (slope orientation) on the early postfire recovery of *Pinus brutia* forest. The study site was the area of 2008 Serik-Tasağıl Fire, one of the largest forest fires in Turkish recorded history. We sampled early postfire conditions at five sites having different conditions in terms of fire severity, prefire stand age, and aspect. Sampling was carried out for 5 years after fire. First year floristic composition was clearly different from the following years and floristic differentiation generally slowed by the fifth year. Plant species richness declined in young stands and mature stands experiencing crown fire, whereas it was more stable in mature stands experiencing surface and mixed fire. In mature stands, richness of annual and obligate seeders varied according to fire severity while stands of different prefire stand age showed differences in richness of annuals, Asteraceae and Poaceae. Young stands with different aspects were also significantly differentiated in terms of annuals, obligate seeders, and Asteraceae. Every site in the study was dominated by woody plants but no *P. brutia* regeneration was observed in stands that were still young when they burned, suggesting that in the absence of direct *P. brutia* planting such sites will remain under the dominance of other woody plants. Our results showed that differences in stand age, fire severity, and topography play an important role in defining the actual direction and velocity of forest recovery after fire. Regenerative traits of species play important roles as well. Our findings provide valuable information for managers and scientists interested in the postfire restoration of *P. brutia* forests. Managers should take into account prefire conditions, topography, and fire severity when developing restoration strategies for forests dominated by serotinous species.

Key words: Autosuccession, direct recovery, fire, Mediterranean, postfire restoration, vegetation

1. Introduction

Fire is a natural phenomenon in the Mediterranean climate regions (Moreno and Oechel, 1994; Moreira et al., 2012) and it is considered one of the most important ecological and evolutionary factors shaping Mediterranean ecosystems (Rodrigo et al., 2004; Keeley et al., 2012). In the Mediterranean Basin, thousands of fires occur each year, most of which are attributed to human causes (Bilgili and Goldammer, 2000; JRC, 2007; Moreira et al., 2012). Most Mediterranean plant species have some form of adaptive mechanism to survive fire, and most vegetation types in the Mediterranean Basin are resilient to some characteristic fire regime (Trabaud, 1994; Keeley

et al., 2012; Vallejo et al., 2012). Some of these adaptive mechanisms are serotinous cones, resprouting, heat-shock triggered germination, germination triggered by combustion chemicals, flammability, thick bark, and self-pruning of branches (Keeley et al., 2011).

Postfire vegetation dynamics in the Mediterranean Basin have been intensively studied (Gotzenberger et al., 2003; Kazanis and Arianoutsou, 2004; Arnan et al., 2007, 2013; Tavşanoğlu and Gürkan, 2014). According to the traditionally accepted approach, postfire succession in the Mediterranean Basin is primarily an autosuccessional process. In this model, the effects of fire on plant communities are more to induce a change in the

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abundances of component species than a change in species composition (Hanes, 1971; Trabaud and Lepart, 1980; Gotzenberger et al., 2003; Kazanis and Arianoutsou, 2004). On the other hand, recent studies showed that postfire responses can differ from the autosuccessional model in some cases, depending on fire frequency, intensity, and/or severity (Pausas et al., 2003; Lippitt et al., 2013; Meng et al., 2014, 2015; Tessler et al., 2016). It has also been shown that prefire plant community type and prefire management can have important effects on postfire vegetation dynamics (Broncano and Retana, 2004; De Luis et al., 2006; Arnan et al., 2007; Torres et al., 2016). Dominant trees and their regenerative traits play a major role in defining postfire floristic composition (Kavgacı et al., 2010; Tavşanoğlu and Gürkan, 2014). Where rapid tree regeneration does not take place—especially for serotinous species—major changes in environmental conditions can occur, which may open the door for major floristic changes as well (Arnan et al., 2007).

Despite the adaptive traits of plants in fire-prone ecosystems, plants are not adapted to fire per se but rather to a fire regime (Sugihara et al., 2006; Keeley et al., 2011). There is an interaction between fire regime and vegetation, since fire regimes depend on a vegetation fuel source and vegetation can tolerate a particular fire regime thanks to the adaptive traits of plants (Sugihara et al., 2006). Thus, if the fire regime changes, plants with adaptive traits to a particular fire regime can be at risk (Keeley et al., 2011).

As a disturbance, forest fires can be a function of both natural and anthropogenic conditions, and changes in these conditions—such as through climate change—will affect the fire regime (Dale et al., 2000, 2001). Climate affects fire regimes at both short- and long-term timescales, in the first instance because weather closely controls fire ignition and propagation; in the second because climate determines primary productivity and vegetation, all of which determine global fire patterns (Urbietta et al., 2015). According to climate change scenarios for the Mediterranean Basin, drought and heat wave extremes are projected to increase (Meehl and Tebaldi, 2004; Dequé, 2007; Beniston et al., 2007) and those will increasingly support the occurrence and propagation of fire (Moriondo et al., 2006). Thus, knowledge about postfire vegetation dynamics is not only useful for assessing current conditions and planning management response, but it is also useful to help predict how vegetation might change under continued climate warming (Sugihara et al., 2006).

Pinus brutia Ten. (Turkish red pine, Calabrian pine) inhabits an area of nearly 5 million hectares in Turkey (Orman Genel Müdürlüğü, 2014). *P. brutia* is an obligate seeder, which is thought to be an adaptation to recurrent and severe fires (Neyişçi, 1993; Keeley et al., 2011). *P. brutia* supports an aerial seed bank held in serotinous

cones (Thanos and Marcou, 1991; Turna and Bilgili, 2006). The species is relatively sensitive to fire and although larger trees can survive low intensity burning, the typical result of crown fire is 80%–100% mortality (Fernandes et al., 2008), which results in even-aged stands on most of the landscape. *P. brutia* is also a shade intolerant species and its seedlings cannot survive under shady conditions (Boydak, 2004). Because of this, clearcutting based on natural regeneration is the main regeneration technique for *P. brutia* forests in Turkey and regeneration of mature forests is generally realized by fires under natural conditions (Boydak et al., 2006). Postfire recovery of the vegetation in *P. brutia* forests is directly connected with the reestablishment of the trees, which typically quickly dominate the burned landscape within 5–10 years of fire (Spanos et al., 2000).

Although postfire recovery of serotinous forests has long been viewed as autosuccessional, recent studies have identified factors that can influence the rate and density of postfire regeneration (Broncano and Retana, 2004). The age of the prefire stand is one of these factors since species like *P. brutia* can require 20–30 years to mature and accumulate sufficient seed in their crown (Ürgenç, 1977; Spanos et al., 2000). The intensity of fire, which affects the crown seed bank, is another factor influencing postfire regeneration (Broncano, 2000; Pausas et al., 2003; Vacchiano et al., 2014; Meng et al., 2015). Physical site conditions like aspect (slope orientation) are also influential on postfire vegetation dynamics (Broncano and Retana, 2004; Rodrigo et al., 2004). Additionally, soil properties, water availability, and postfire climate are some of the other factors that can affect the postfire vegetation dynamics (Jain et al., 2012; Meng et al., 2015).

Postfire vegetation response is one of the primary indicators of fire's ecological impacts as well as what restoration practices might be undertaken to mitigate such impacts (Moreira and Vallejo, 2009; Vallejo et al., 2012). Given the importance of predictability in the postfire response of widespread conifers, the principle objective of the study was to better understand postfire dynamics of *P. brutia* forest in a landscape with variability in fire severity, prefire stand age, and aspect. Thus we hypothesized that fire severity/fire type, prefire stand age, or aspect may be important drivers of the postfire changes of *P. brutia* forests.

2. Materials and methods

2.1. Study area

The study was carried out within the perimeter of the Serik-Tasağıl Fire (Antalya, Turkey), which burned in 2008 and was one of the largest forest fires to date in the Republic of Turkey, with 15,795 hectares of forest burned (Figure 1). The fire started on 31 July 2008 and burned for

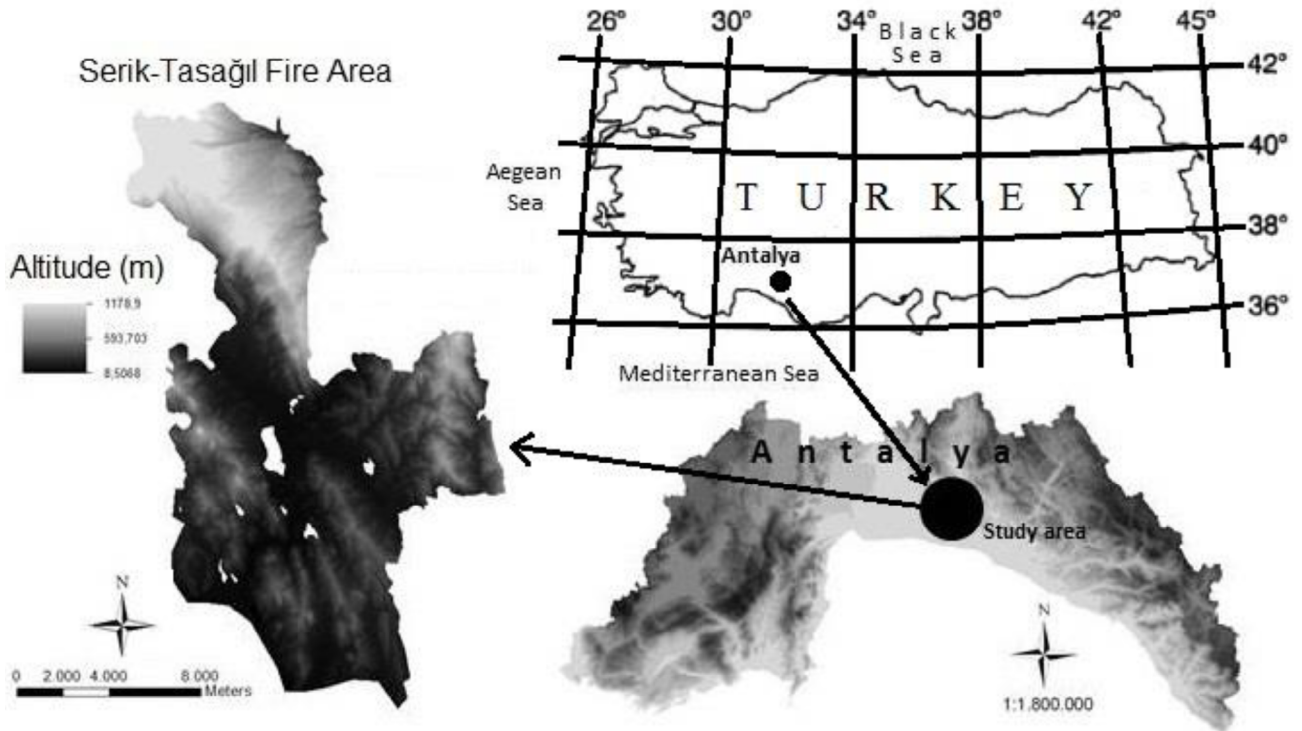


Figure 1. Location of the study area.

5 days. The Antalya region is one of the most fire prone areas in Turkey (Kavgacı et al., 2011). Climate in the study area is Mediterranean, with a hot, dry summer and wet, cool winter. Mean annual precipitation is approximately 1089 mm and mean annual temperature is 18 °C (Kavgacı et al., 2010). Mean minimum and mean maximum temperatures for January and July are 6.9 °C and 33.5 °C, respectively. The study area is underlain by limestone and soils generally consist of mullrendzinan, pararendzinan, and xerosols soils (Ayaşlıgil, 1987).

The vegetation of the study area is mainly dominated by *P. brutia* and maquis species like *Olea europea*, *Quercus coccifera*, *Styrax officinalis*, *Pistacia terebinthus*, *Arbutus andrachne*, *Myrtus communis*, *Cistus creticus*, and *C.*

salvifolius. Locations where *P. brutia* does not grow are dominated by maquis or garrigue.

2.2. Sampling technique

A diachronic approach was used in the study. After the Serik-Tasağil fire, five different sites in the same hydrologic basin were chosen to better understand postfire dynamics. Each of these sites had different characteristics in terms of prefire stand age, fire severity, and aspect (Table 1). Other factors like soil properties, water availability, and postfire climate following fires were not included in the study because they have less variation in the study area.

Each factor in the study was represented by two levels (Table 1). Fire severity included surface and crown fires.

Table 1. Field characteristics of the study sites in terms of fire severity, prefire stand age, and aspect. The abbreviation of the study sites represents the first letter of each factor. Coordinates represents one of the samplings in the study sites.

Abbreviation	Prefire stand age	Fire severity	Aspect	Mean elevation	Bedrock	Longitude	Latitude
MCN	Mature stand	Crown fire	North	110 m	Limestone	335371	4093198
YCS	Young stand	Crown fire	South	49 m	Limestone	336171	4092428
YCN	Young stand	Crown fire	North	14 m	Limestone	335705	4091969
MSS	Mature stand	Surface fire	South	158 m	Limestone	336288	4094641
MSN	Mature stand	Surface fire	North	52 m	Limestone	336121	4093011

Surface fire = ground surface of the stand was completely burned, stems were charred, crowns were scorched by flames but not burned, and trees were dead; crown fire = all stems, crowns, and surface layers were consumed by fire and trees were dead. Prefire stand age was categorized as young and mature. Young stands were 13 years old while mature stands were nearly 60 years old. Since the crown base of young *P. brutia* stands is very close to the ground, they are generally subject to crown fires. Due to that, the young stand with surface fire could not be included as a variable in the study. The two aspect classes were north-facing (“north”) and south-facing (“south”).

All burned and unburned trees in the study areas and other surrounding stands were clear cut by the Turkish Regional Forest Service in the autumn after fire, which was after seed dispersal of *P. brutia* had occurred. Study sites were chosen immediately after fire and before harvesting to allow assignment of the different fire severity and prefire stand types. The exact age of the stands was defined by counting the annual rings of harvested trees. After harvesting, ten 0.01 ha permanent plots were established at each site (a total of 50 plots). During the first 5 years after fire, vegetation sampling was carried out to understand the effects of fire severity, prefire stand age, and aspect on vegetation dynamics of *P. brutia* forests. The first sampling was carried out in April 2009 (about 9 months after fire) and continued during the same time in the following years.

During sampling, vegetation was firstly divided into two layers depending on the height of plants: up to 0.5 m for the herb layer and higher than 0.5 for the shrub layer—see Westhoff and van der Maarel (1973). This was especially important to understand vegetation structural change and the dominance of woody species in the postfire vegetation. We recorded the presence and cover of all vascular plants in these two layers. For cover estimation, the Braun-Blanquet (1964) scale was used, and cover was visually estimated. For further analyses, the two layers were merged as a default option in the JUICE program (Tichý, 2002). Collected plants were identified with the *Flora of Turkey* (Davis 1965–1985; Davis et al., 1988).

In addition to the vegetation sampling, *P. brutia* seedling emergence and survival were sampled. We established four 1 × 1 m subplots at the corners of each permanent plot. Seedlings in these subplots were periodically counted and we averaged the results to get the mean number of seedlings for each 10 × 10 m plot. We counted seedlings in November of each year of the study. In our statistical analysis, the emergence and survival of *P. brutia* were submitted as the mean number of seedlings of each successional stage for each different site.

2.3. Data analysis

Vegetation cover data were stored in the TURBOVEG database management program (Hennekens and

Schaminée, 2001) after completing the identification of all plants. Floristic differentiation along time for each different site was explored with Nonmetric Multidimensional Scaling (NMDS) in the R software (R Core Development Team, 2014) by using the package VEGAN. Calculations of species richness (number of species) and species diversity (Shannon diversity index), as well as the diversity of taxonomic families, life forms and postfire regeneration strategies (seeders and resprouters), were carried out in the JUICE program (Tichý, 2002).

The effects of fire severity, prefire stand age, and aspect on species richness, species diversity, family distribution, life form, and postfire regeneration strategies (obligate resprouter and obligate seeders) were analyzed. To understand the effects of these variables, repeated measures ANOVA was used since the postfire vegetation was measured multiple times in each combination of different conditions (fire severity, prefire stand age, and aspect). We compared pairs of sites that differed with respect to fire severity (MSN vs. MCN), prefire stand age (MCN vs. YCN), and aspect (MSS vs. MSN, and YCS vs. YCN) (see Table 1 for the abbreviations). Prior to analysis, data were checked for normality and log- or square root-transformed to approach normality when necessary. Analyses were carried out in the R program (R Core Development Team, 2014).

3. Results

3.1. Floristic structure, species richness, and diversity

A total of 262 plant species belonging to 49 different families were collected in the 5 years after fire from our plots. NMDS analysis showed that the species composition of the first year after fire is highly differentiated from the following years. During the ensuing years, there was a gradual temporal change in floristics at each site. YCN showed a somewhat clearer floristic differentiation between years than the other sites. In all of the sites, floristic composition in year 5 “retreated” and was less different from year 3 than year 4 was (Figure 2).

Species richness (number of species) was higher in the crown fire sites than in the surface fire sites (Figure 3; Table 2). Richness also showed a general decline for the sites that experienced crown fire (MCN, YCS, and YCN) whereas it was more stable for surface fire sites MSS and MSN (Figure 3; Table 2), such that the difference in species richness between two fire severities diminished over time.

Prefire stand age also had a significant effect on species richness (Table 3). The young stand (YCN) contained more species than the mature stands (MCN) during the 5 years after fire (Figure 3; Table 2). Richness declined over time at both sites.

Aspect showed a significant effect on species richness for both mature and young stands (Table 3). The mature

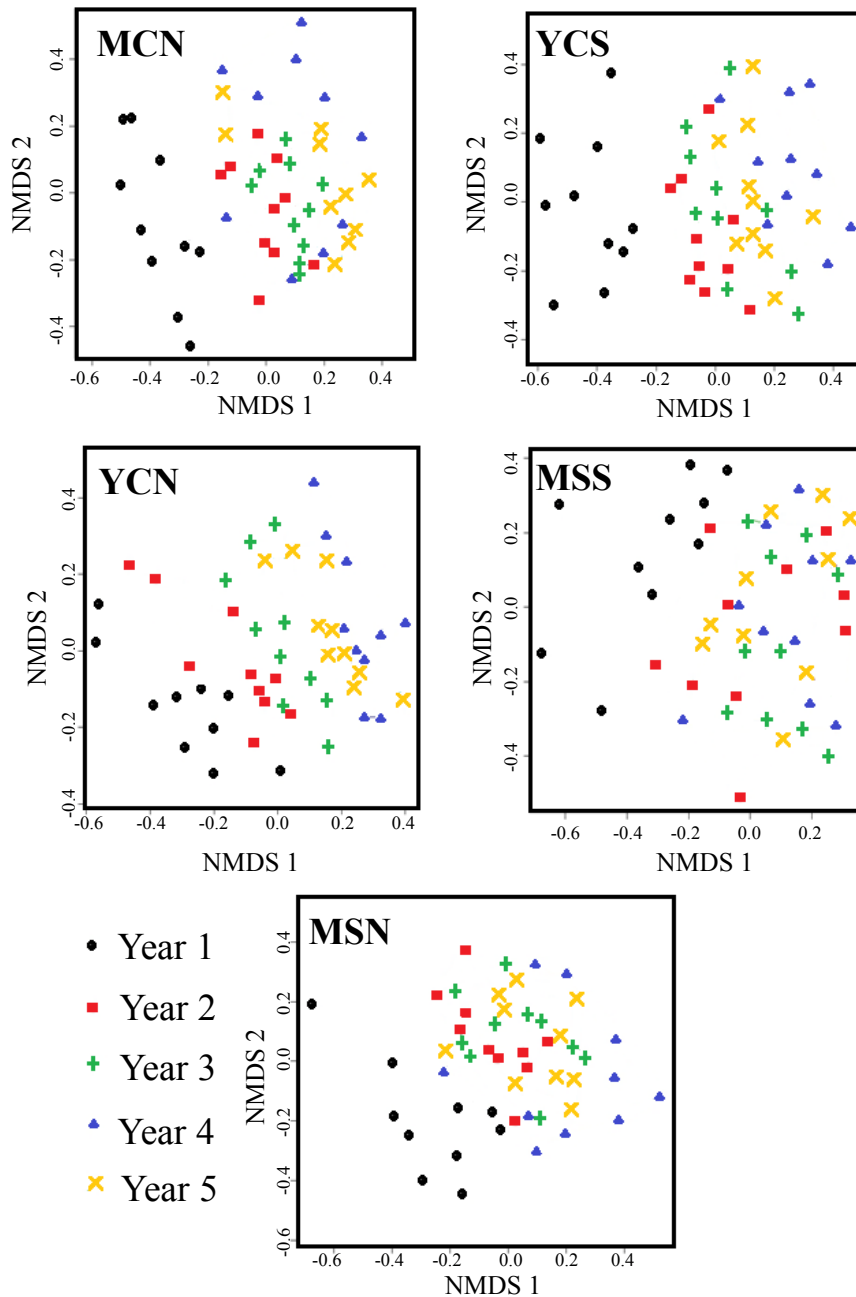


Figure 2. Floristic differentiation of the vegetation over time after fire (Nonmetric Multidimensional Scaling). The symbols within each polygon are the 10 plots found at each site/stand condition in a given year after fire. MCN: Mature stand, Crown fire, North aspect; YCS: Young stand, Crown fire, South aspect; YCN: Young stand, Crown fire, North aspect; MSS: Mature stand, Surface fire, South aspect; MSN: Mature stand, Surface fire, North aspect.

and young stands with northern aspects (MSN and YCN) were more species-rich than the mature and young stands with southern aspects (MSS and YCS), respectively (Figure 3; Table 2).

The mature stand with crown fire (MCN) showed significantly higher diversity than the mature surface fire site (MSN) (Table 3). Similarly, species diversity was

significantly different between the sites with different prefire stand ages (MCN and YCN) (Figure 3; Table 2).

Species richness of Fabaceae increased until the third year after fire and later decreased in MSS. At the rest of the sites species richness of Fabaceae generally tended to decrease until the fourth year after fire and then increased in the fifth year (Figure 3; Table 2). Asteraceae decreased

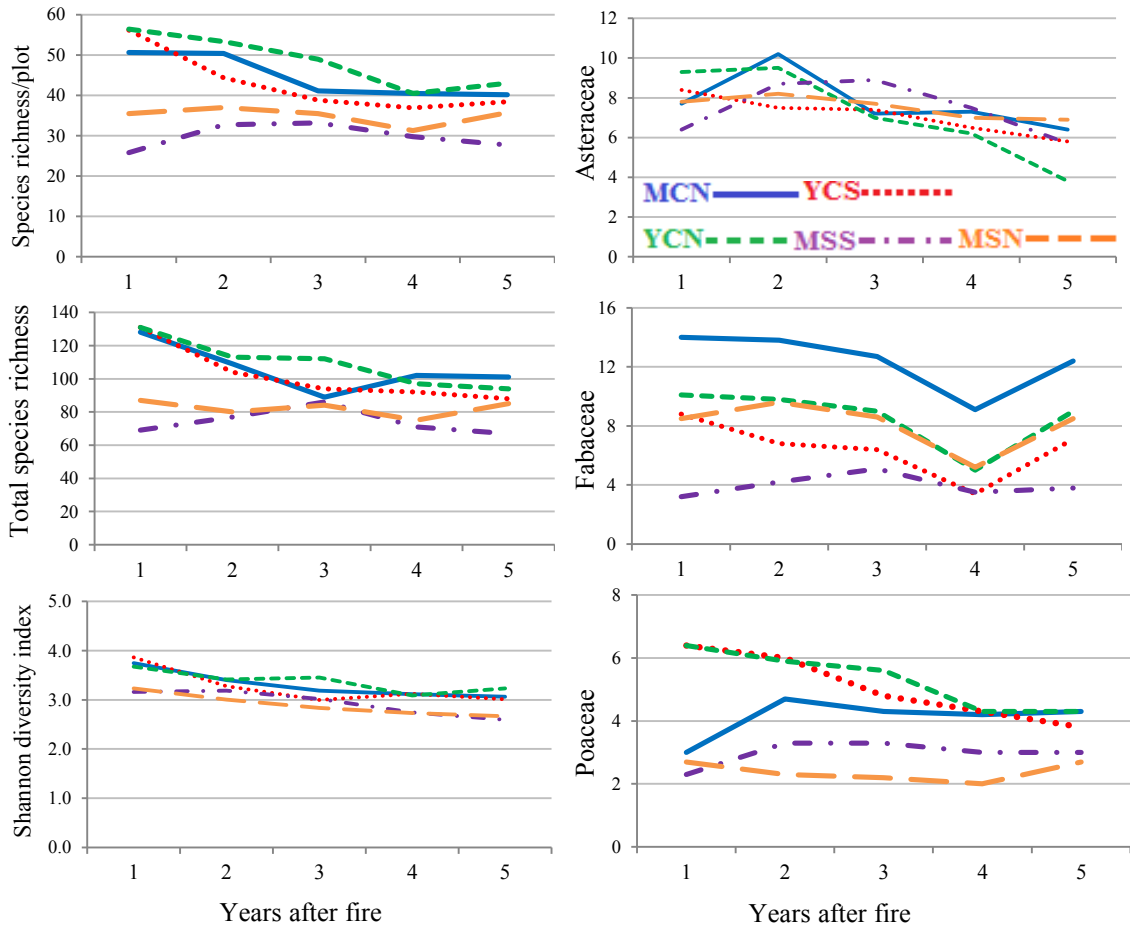


Figure 3. Temporal changes in species richness, diversity, and the richness of species of Asteraceae, Fabaceae, and Poaceae after fire. MCN: Mature stand, Crown fire, North aspect; YCS: Young stand, Crown fire, South aspect; YCN: Young stand, Crown fire, North aspect; MSS: Mature stand, Surface fire, South aspect; MSN: Mature stand, Surface fire, North aspect.

in richness at all sites except for MSS (Figure 3; Table 3). For Asteraceae, prefire stand age and aspect in young stands showed an interaction with time (Table 3). Poaceae decreased with time after fire in the young stands (Figure 3; Table 2) and this decrease was significant (Table 3). Only the prefire stand age–time correlation was significant for Poaceae (MCN–YCN) (Table 3).

3.2. Life form richness

Forty of the collected plant species in the study were woody, while 54 were perennial herbs and 168 were annual herbs. Woody plants showed similar successional trends among sites (Table 3). Perennial herbs showed a more or less stable trend during succession (Figure 4; Table 2). The sites with different fire severity (MCN and MSN), prefire stand age (MCN and YCN), and young stands with different aspect (YCS and YCN) showed different temporal trends after fire in terms of the richness of annual plants (Table 3). Number of annual plants in young stands and the mature stand with crown fire

decreased until the fourth year after fire and increased in the fifth year (Figure 4; Table 2).

The shrub layer, which is completely composed of woody species, appeared in the second and third years after fire in the young stands and mature stands, respectively, and quickly dominated the vegetation (see the appendix in detail for woody species and their shrub layer frequency and coverage). In the young stands, shrub cover developed more rapidly on the north-facing slope than on the south-facing slope, and averaged 80% by the fifth year after fire, versus about 60% on the south-facing slope.

3.3. Postfire regeneration

The number of obligate resprouters showed a more or less stable trend during early succession after fire for all sites (Figure 5; Table 2). The higher number of resprouters at the young stand with northern aspect (YCN) was very clear. The number of resprouters showed differences according to fire severity, prefire stand age, and aspect of young stands (Table 3).

Table 2. Species richness of the study sites during the 5 years after fire (mean with standard deviation from 10 replicates) and richness of various species groups (families, life form, regeneration category). Shaded numbers represent the highest value in a single row. s.d., standard deviation. MCN: Mature stand, Crown fire, North aspect; YCS: Young stand, Crown fire, South aspect; YCN: Young stand, Crown fire, North aspect; MSS: Mature stand, Surface fire, South aspect; MSN: Mature stand, Surface fire, North aspect.

Study site	Years after fire	1		2		3		4		5	
		Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd	Mean	Sd
MCN	Number of species	50.60	6.29	50.40	7.49	41.10	9.12	40.50	8.87	40.20	9.66
MCN	Shannon index	3.75	0.17	3.40	0.26	3.19	0.36	3.11	0.49	3.06	0.44
MCN	Number of Asteraceae species	7.70	1.49	10.20	1.93	7.20	2.04	7.30	1.70	6.40	2.07
MCN	Number of Fabaceae species	14.00	2.16	13.80	1.81	12.70	2.95	9.10	2.47	12.40	2.50
MCN	Number of Poaceae species	3.00	1.56	4.70	1.95	4.30	1.34	4.20	1.23	4.30	1.16
MCN	Number of resprouter species	17.60	4.95	17.50	2.76	14.50	3.66	17.50	4.45	15.90	3.87
MCN	Number of seeder species	30.70	5.19	30.30	5.93	24.40	6.69	20.50	4.84	21.80	5.79
MCN	Number of annual species	29.10	6.19	28.70	5.98	23.80	7.13	19.80	5.63	21.50	6.87
MCN	Number of perennial species	14.40	3.31	14.10	1.66	12.20	2.39	15.70	2.91	13.70	2.63
MCN	Number of woody species	4.80	2.44	4.70	1.64	4.50	2.01	4.50	2.22	4.60	1.90
YCS	Number of species	56.20	6.36	44.40	4.09	38.80	4.52	36.90	4.15	38.40	5.13
YCS	Shannon index	3.86	0.16	3.30	0.35	3.09	0.42	3.09	0.21	3.05	0.24
YCS	Number of Asteraceae species	8.40	1.90	7.50	2.46	7.40	2.22	6.50	1.65	5.80	1.62
YCS	Number of Fabaceae species	8.80	2.57	6.80	1.99	6.40	1.90	3.40	1.58	7.10	1.37
YCS	Number of Poaceae species	6.40	1.43	6.00	1.89	4.80	1.75	4.30	1.77	3.80	1.23
YCS	Number of resprouter species	21.80	2.15	21.20	2.78	19.40	2.72	21.30	3.20	21.00	2.98
YCS	Number of seeder species	32.60	5.78	21.30	2.54	17.60	3.72	14.60	2.32	16.30	3.83
YCS	Number of annual species	31.00	5.62	20.60	2.67	17.30	3.50	13.20	2.35	15.60	3.78
YCS	Number of perennial species	18.20	1.32	16.90	1.66	15.60	2.55	18.00	2.36	16.60	2.01
YCS	Number of woody species	5.20	1.75	5.20	1.62	5.30	1.16	5.40	1.65	6.10	2.02
YCN	Number of species	57.50	8.18	53.30	10.34	49.00	8.14	40.50	5.78	43.00	7.13
YCN	Shannon index	3.69	0.32	3.49	0.31	3.45	0.33	3.09	0.19	3.23	0.30
YCN	Number of Asteraceae species	9.30	1.49	9.50	1.90	7.00	1.83	6.20	1.48	3.80	1.40
YCN	Number of Fabaceae species	10.10	2.85	9.80	2.39	9.00	1.56	5.00	0.47	9.00	1.25
YCN	Number of Poaceae species	6.40	1.90	5.90	2.08	5.60	2.72	4.30	1.77	4.30	2.31
YCN	Number of resprouter species	24.30	4.45	24.20	3.52	24.70	4.90	26.30	4.45	24.40	3.84
YCN	Number of seeder species	31.00	5.56	26.40	7.46	21.70	4.40	12.70	2.54	16.70	4.16
YCN	Number of annual species	29.90	5.72	24.90	7.87	21.40	4.77	10.80	2.86	15.30	4.83
YCN	Number of perennial species	15.70	3.27	17.10	1.85	16.40	2.95	18.30	2.45	15.80	2.25
YCN	Number of woody species	9.80	2.25	9.30	1.64	10.00	1.76	10.50	2.01	11.20	1.99
MSS	Number of species	25.80	5.57	32.70	4.57	33.20	3.12	29.80	4.44	27.70	4.64
MSS	Shannon index	3.16	0.18	3.19	0.32	3.02	0.18	2.74	0.39	2.59	0.25
MSS	Number of Asteraceae species	6.40	1.90	8.70	1.83	8.90	1.91	7.50	1.90	5.70	1.49
MSS	Number of Fabaceae species	3.20	1.81	4.20	1.87	5.10	2.13	3.50	1.43	3.80	1.55
MSS	Number of Poaceae species	2.30	0.82	3.30	0.82	3.30	0.95	3.00	1.05	3.00	0.82
MSS	Number of resprouter species	14.10	2.92	15.40	3.03	15.90	2.88	17.10	1.73	15.30	2.31
MSS	Number of seeder species	11.30	2.67	16.50	3.41	16.20	2.74	11.50	3.84	11.30	3.20
MSS	Number of annual species	9.80	2.82	14.40	3.37	14.70	2.79	11.20	4.10	10.70	3.23
MSS	Number of perennial species	10.80	2.57	10.50	2.17	12.00	2.40	12.50	1.51	10.90	2.33
MSS	Number of woody species	4.50	1.18	5.40	1.17	5.10	1.66	5.20	1.23	5.70	1.42
MSN	Number of species	35.50	5.84	37.00	3.77	35.50	4.81	31.30	5.19	35.70	5.12
MSN	Shannon index	3.24	0.25	3.01	0.22	2.84	0.27	2.73	0.29	2.76	0.29
MSN	Number of Asteraceae species	7.80	2.30	8.20	1.23	7.70	2.11	7.00	1.89	6.90	2.08
MSN	Number of Fabaceae species	8.50	1.65	9.60	1.58	8.60	2.17	5.20	1.62	8.50	1.90
MSN	Number of Poaceae species	2.70	0.67	2.30	0.95	2.20	1.48	2.00	0.82	2.70	0.67
MSN	Number of resprouter species	16.30	3.13	16.00	2.67	15.20	2.25	16.30	3.37	15.40	2.41
MSN	Number of seeder species	18.00	4.00	19.90	2.64	19.30	4.47	13.70	3.59	18.30	4.00
MSN	Number of annual species	15.70	4.00	17.70	2.54	17.70	4.16	12.50	3.44	17.70	4.30
MSN	Number of perennial species	13.00	2.62	11.30	2.26	11.40	1.17	13.20	3.05	12.60	2.17
MSN	Number of woody species	4.60	1.78	5.40	1.35	5.10	1.10	5.00	1.33	5.20	1.03

Table 3. Results of the repeated measures ANOVA for pairs of the sites having different fire severity, prefire stand age, and aspect. Results for aspect are shown for mature and young stands separately. Values are P-values from ANOVA test. MCN: Mature stand, Crown fire, North aspect; YCS: Young stand, Crown fire, South aspect; YCN: Young stand, Crown fire, North aspect; MSS: Mature stand, Surface fire, South aspect; MSN: Mature stand, Surface fire, North aspect. ***: P < 0.001, **: P < 0.01, *: P < 0.05.

	MCN-MSN			MCN-YCN			MSS-MSN			YCS-YCN		
	Fire severity	Time	Fire severity/ Time	Prefire stand age	Time	Prefire stand age/Time	Aspect (mature stand)	Time	Aspect/ Time	Aspect (young stand)	Time	Aspect/ Time
Species richness	0.0167 *	0.0002 ***	0.0509 .	0.0025 **	4.44e-08 ***	0.5322	3.12e-07 ***	0.532	0.379	0.0003 ***	1.03e-13 ***	0.1804
Shannon diversity	0.0405 *	1.56e-09 ***	0.3088	0.0104 *	4.12e-09 ***	0.4591	0.0882	4.59e-11 ***	0.3495	0.1982	8.17e-10 ***	0.0582 .
Richness of annuals	0.0222 *	2.51e-05 ***	0.0374 *	0.839	1.72e-11 ***	0.032 *	4.09e-08 ***	0.624	0.97	0.2246	<2e-16 ***	0.0369 *
Richness of perennials	0.0354 *	0.0232 *	0.5115	1.18e-08 ***	0.647	0.731	0.0021 **	0.3092	0.7340	0.498	0.84	0.313
Richness of woody plants	0.613	0.934	0.562	1.17e-06 ***	0.2196	0.0978	0.288	0.113	0.457	1.65e-09 ***	0.169	0.970
Richness of Asteraceae	0.0075 **	0.0024 **	0.3621	0.4059	5.63e-11 ***	0.0014 **	0.0028 **	0.0423 *	0.8834	0.0428 *	1.62e-12 ***	0.0018 **
Richness of Fabaceae	0.9125	0.0006 ***	0.3192	0.0862	9.66e-05 ***	0.8063	1.02e-09 ***	0.1748	0.0891	0.0001 ***	8.34e-05 ***	0.9526
Richness of Poaceae	0.776	0.319	0.185	0.0669 .	0.3503	0.0126 *	0.716	0.553	0.3	0.9503	0.0002 ***	0.9571
Richness of obligate resprouters	0.0164 *	0.2036	0.7731	8.32e-10 ***	0.839	0.295	0.105	0.494	0.143	0.0010 **	0.60404	0.6477
Richness of obligate seeders	0.0137 *	1.41e-07 ***	0.0373 *	0.8076	1.13e-13 ***	0.0713	1.03e-07 ***	0.0557	0.9129	0.0204 *	<2e-16 ***	0.0357 *

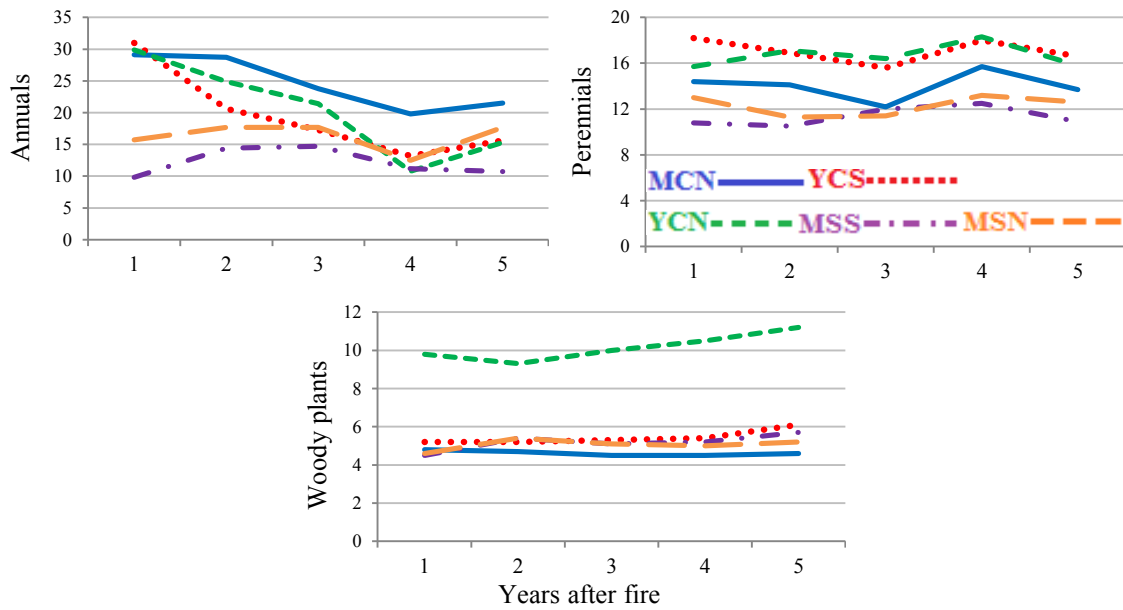


Figure 4. Temporal changes of mean number of three plant life forms after fire (annuals, perennials, and woody plants). MCN: Mature stand, Crown fire, North aspect; YCS: Young stand, Crown fire, South aspect; YCN: Young stand, Crown fire, North aspect; MSS: Mature stand, Surface fire, South aspect; MSN: Mature stand, Surface fire, North aspect.

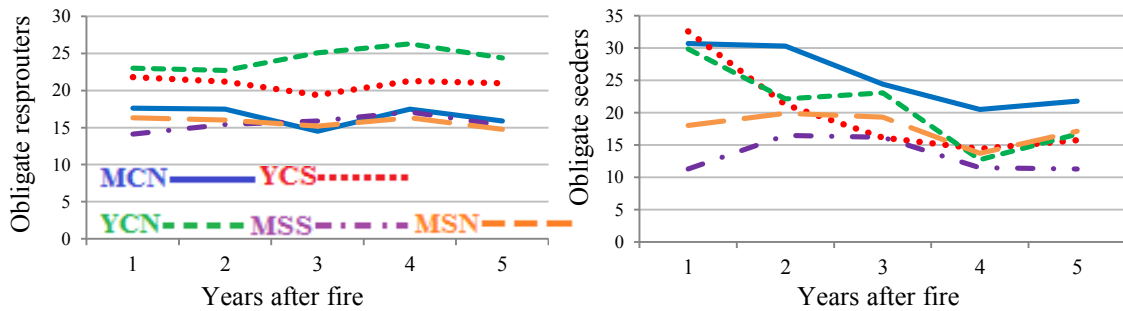


Figure 5. Temporal changes of mean number of plants having different postfire regeneration strategies after fire (obligate resprouters and obligate seeders). MCN: Mature stand, Crown fire, North aspect; YCS: Young stand, Crown fire, South aspect; YCN: Young stand, Crown fire, North aspect; MSS: Mature stand, Surface fire, South aspect; MSN: Mature stand, Surface fire, North aspect.

Obligate seeders generally decreased in richness during the 5 years after fire in the young stands and in the mature stands with surface fire (Figure 5; Table 2). The mature stands with different fire severity and young stands with different aspect had different trends in terms of the number of obligate seeders (Table 3).

3.4. Seedling emergence and survival of *P. brutia*

Seedling emergence did not occur in the young forest stands (YCN and YCS). On the other hand, high regeneration of *P. brutia* was observed in the mature stands, with notable differences across sites (Figure 6). MSN (surface fire, north aspect) showed much higher seedling densities than the other sites, and the mature crown fire site (MCN) consistently showed the lowest seedling densities. During

the first year after fire 0.925 (se ± 0.15), 1.7 (se ± 0.32), and 13.625 (se ± 2.87) seedlings per square meter were sampled at MCN, MSS, and MSN respectively. During the following years seedling densities quickly decreased and at the end of the fifth year after fire the numbers of seedlings for MCN, MSS, and MSN were measured at 0.225 (se ± 0.06), 0.725 (se ± 0.021), and 2.74 (se ± 0.72), respectively.

4. Discussion

Emergence of the obligate seeding *P. brutia* was not noted in our young stands and woody species quickly dominated the vegetation. It seems that this caused the conversion of young *P. brutia* forests to shrublands or forests dominated by resprouting tree species. This probable conversion is

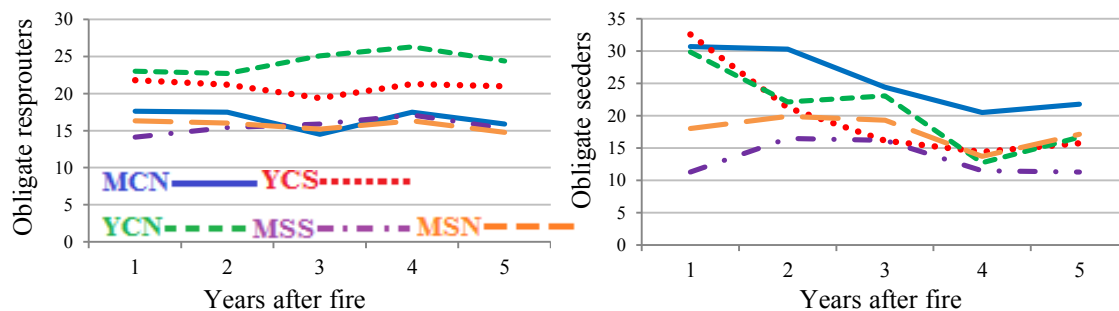


Figure 6. Temporal changes of mean number of *P. brutia* seedlings for each area after fire. MCN: Mature stand, Crown fire, North aspect; MSS: Mature stand, Surface fire, Southern aspect; MSN: Mature stand, Surface fire, Northern aspect (No seedling regeneration was observed in the young stands YCN and YCS). Error bars omitted to enhance clarity.

from the fact that most *P. brutia* individuals in the stand had not yet reached reproductive age due to the earlier fire occurrence (Tessler et al., 2014). Recruitment of *P. brutia* into these stands over the long term may be possible from neighboring seed sources when they mature. Thus, our results are similar to the results reported by Spanos et al. (2000), and they support the idea that postfire recovery of *P. brutia* forests does not always follow direct recovery (i.e. it is not always autosuccessional). This is important at scales much broader than our study area, as increased fire frequencies in some parts of the Mediterranean Basin are making it more likely that younger stands will burn (Pausas et al., 2004; De Luis et al., 2006; Arnan et al., 2007). As such young stands burn, sites may be converted to persistent shrublands or resprouter dominated forests (especially if frequent burning continues), or they may require investment in planting. Such a conversion due to frequent fire has also been documented in *P. halepensis* forests converted to *Arbutus unedo* woodlands, which is a resprouter species in NE Spain (Arnan et al., 2013). Short interval fire occurrence can also cause vegetation type conversion in shrublands, especially those dominated by obligate seeders, for example in California (Lippitt et al., 2013; Meng et al., 2014).

The presence or absence of seedlings in the postfire environment is of obvious importance to forest recuperation, but where seedlings are present their density is a further factor driving postfire succession. Our mature stands showed widely differing seedling responses to fire, with more than a 10-fold difference in seedling densities between sites, apparently driven mostly by differences in fire severity. Seedling density is important because it influences intraspecific competition and ultimately plays a major role in defining the spatial patterning of individual plants through the life span of the stand (Antonovics and Levin, 1980; Comita et al., 2010). Seedling densities of trees are especially influential on vegetation dynamics since they are the dominant life form (Gray and He, 2009). The strong differences in postfire seedling densities

in our mature stands of *P. brutia* indicate that levels of intraspecific competition will likely differ over time across our study landscape, which will have impacts on the actual progression of vegetation succession.

Mature stands showed different successional trends in terms of species richness of annuals and obligate seeders that were also best explained by differences in fire severity (crown fire vs. surface fire). Prefire stand age was an important factor in explaining differences between stands with respect to richness of annuals, and species from Asteraceae and Poaceae. Aspect also appeared as a driving factor for young stands in terms of the richness of annuals, obligate seeders, and number of Asteraceae species. Overall, the variation in successional patterns related to fire severity, stand age, and aspect indicates that “autosuccession” does not follow similar patterns even in mature stands. This may indicate that postfire succession may be better explained by other approaches like a vital attributes model (Noble and Slatyer, 1980) or other disturbance theories (Sugihara and van Wagtenonk, 2006).

In *P. brutia* and similar serotinous forest types (as well as in most Mediterranean shrublands) first year floristic composition is mainly determined by the prefire vegetation (Hanes, 1971). This is due to the dominance of fire-adapted sprouting and fire-cued seeding (Vallejo et al., 2012). After year one, colonizing species reach the site and floristic differentiation begins (Arianoutsou and Neëman, 2000; Kazanis and Arianoutsou, 2004). If the fire occurs early in the year, some colonizers may also be present in the first year, which can have important implications for longer-term succession. In our sites, we noted a clear “retrogression” in floristic differentiation in the fifth year after fire. This is connected to the increasing dominance of woody plants (reflected in the decrease in our measures of both richness and diversity), and perhaps decreases in site productivity. As is seen in most other studies of Mediterranean postfire succession (Kazanis and Arianoutsou, 2004; Kavgacı et al., 2010), annual species richness was high in the early postfire years but gradually

decreased, while the woody species were more or less stable or gradually increased.

Earlier studies have shown that species richness in *P. brutia* and *P. halepensis* forests tends to be highest in the first year after fire and over time it declines, and then increases gradually again as the forest matures (Schiller et al., 1997; Arianoutsou and Neeman, 2000; Tavşanoğlu and Gürkan, 2009; Kavgacı et al., 2010). Some of our sites also showed a first year postfire peak in richness, but others peaked in years two or three. Clearly, fire leads to an increase in species richness (and diversity) in *P. brutia* forests, and subsequent years see a reduction in both measures, but variability in various factors can modulate the exact nature of the temporal trend. Still, our results broadly support the generalization of Kutiel (1997), who stated that postfire vegetation in the Mediterranean Basin tends to reach the highest richness between the years 2 and 4 after fire.

In our study, the mature stand with crown fire (MCN) exhibited higher species richness than the mature stand with surface fire (MSN) during the early stage of postfire succession. Probably a number of different factors help to explain this pattern. First of all, the high severity stand (MCN) had fewer *P. brutia* seedlings and so competition for resources was much reduced for other species. Second, higher severity fire correlates with higher fire intensities (Keeley, 2009), which would have removed much more of the litter on the soil surface, leading to easier emergence for seedlings of other species, more access to light, and better access to mineral soil for seeds of other species arriving on site. Finally, it could be that the more complete combustion of litter and organics in the severely burned stand led to more nutrient availability in the upper soil layers (Kutiel and Naveh, 1987), although some of the nutrients might have volatilized. However, it can be expected that the remaining surface fuels after fire can be higher in the surface fire area, which would prevent the germination of the species by covering the soil and this could be effective on the lower species richness of this stand.

Despite the differences, species richness and diversity showed similar successional trends in two different aspects of both young and mature stands, which differs from the findings reported by Kutiel (1997), but aspect was an important driver of both richness and diversity. Southern aspects in the Mediterranean Basin experience much higher water stress than north aspects (Nadal-Romero et al., 2014), and this is likely the principal factor leading to higher species richness on north aspect sites than south aspects in our study.

Fabaceae has a specific role in postfire vegetation dynamics in the eastern Mediterranean Basin because it supplies organic material to the site and enriches it with nutrients (Doussi and Thanos, 1994; Arianoutsou

and Thanos, 1996; Arianoutsou and Neeman, 2000). In our work, the number of Fabaceae species was generally higher in the first year after fire and decreased thereafter until the fourth year, when there was an increase again; the sole exception was the mature stand with surface fire and southern aspect, where Fabaceae dominance was highest in the third postfire year. Kavgacı et al. (2010) generalized that Fabaceae tended to reach their highest species richness in *P. brutia* forests in the eastern Mediterranean at about 3 years after fire. Many studies have documented this pattern in early postfire succession in the eastern Mediterranean (Kazanis and Arianoutsou, 1996; Arianoutsou, 1998; Arianoutsou and Neeman, 2000; Türkmen and Duzenli, 2005). Overall our results support this generalization. The presence of high numbers of Fabaceae species (and their biomass as well) during early postfire years is due to the breaking of seed dormancy by fire (Moreira et al., 2010).

Although seedling emergence and survival were noted in all of the mature stands, seedling densities showed large differences between sites. In comparison with other mature stands, the mature stand with crown fire supported the lowest number of seedlings, which may be related to the high fire intensity, which could severely damage the crown seed bank of *P. brutia* at this stand. On the other hand, *P. brutia* stands with north aspect supported the highest number of seedlings, which probably also relates to the more favorable moisture balance on these slopes (Nadal-Romero et al., 2014). Seedling densities showed a decline during the 5 years at all sites after fire (most likely due to inter- and intraspecific competition) as observed in previous studies (Thanos et al., 1989; Thanos and Marcou, 1991; Spanos et al., 2000). Similar results for *P. halepensis* forests were obtained by Pausas et al. (2003).

From the standpoint of postfire restoration and forest management, prefire stand age and fire severity can have major effects on the postfire succession of *P. brutia* forests. Stands that burn at a young age (with trees <20–30 years old) are likely to convert to shrublands or forests dominated by resprouting tree species and will probably require artificial seeding or planting if a *P. brutia* forest is desired at the site. Seedling densities in mature stands are generally enough to naturally restore productive forests even where crown fire occurs: general reforestation guidelines in Turkey call for planting densities of about 1600 seedlings per hectare, and even our MCN stand would have met these standards. The more open stand that results from crown fire supports higher species richness. Therefore, variations in fire severity are important to landscape heterogeneity and species diversity. Our work demonstrates that prefire conditions, topography, and fire severity should all be taken into account when managers develop restoration strategies and projects in burned *Pinus brutia* forests.

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