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RESEARCH ARTICLE

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Fire season modifies the perennial plant community composition through a differential effect on obligate seeders in eastern Mediterranean woodlands

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Abstract

Aim: Plant species regenerate after fire either through vegetative growth (i.e., obligate resprouters) or seed germination (i.e., obligate seeders), with some species adopting both strategies (i.e., facultative seeders). Fire season can have important consequences for the relative abundance of plant species adopting these regeneration strategies. The present study aimed to test for differential effects of fire season on perennial plant community composition.

Location: Eastern Mediterranean woodland in the Judea Mountains, Israel.

Methods: We conducted, for the first time, a large-scale field experiment, involving prescribed spring and autumn burns in a typical eastern Mediterranean woodland. We sampled the perennial plant community before and after the burns, quantifying temporal changes in community composition caused by seasonal fires.

Results: Although fire intensity and severity were consistent between the two seasonal fires, plant community composition differed between areas subjected to spring or autumn burns. The abundances of all common species, *Pistacia lenticus* (obligate resprouter), *Cistus* spp. (obligate seeders) and *Teucrium divaricatum* (facultative seeder), were all reduced by both fires. Yet, their dominance in the post-fire perennial plant community was retained. Differential fire season effects were detected only among obligate seeders, which experienced a stronger reduction in abundance after spring than after autumn burns.

Conclusions: Differential fire season effects on the perennial plant community resulted from phenological rather than fire intensity/severity effects. Such changes in community composition may have important implications for plant community dynamics, because they affect the circle of "fire event–plant regeneration–fire reoccurrence", determining the probability and intensity of future fires. Furthermore, even though the eastern mediterranean ecosystem is considered highly resilient to disturbances, increased spatio-temporal variation in fire season, may result in a new vegetation mosaic, differing from the contemporary one, i.e., an alternative stable state.

KEYWORDS

community composition, facultative seeders, fire disturbance, obligate resprouters, obligate seeders, plant life form, plant regeneration strategy

1 | INTRODUCTION

Plant community dynamics is affected by the interplay between environmental disturbances, species traits and life-history trade-offs (Keeley & Fotheringham, 2000). Disturbances introduce a major source of variation in community dynamics (Sousa, 1984) due to alteration in the physical environment and essential resources (Pickett & White, 1985; Tilman, Kilham, & Kilham, 1982). Furthermore, disturbances including fire can cause plant communities to shift from one stable state to an alternative state (Beisner, Haydon, & Cuddington, 2003; Mutch, 1970; Odion, Moritz, & DellaSala, 2010; Pausas, Keeley, & Schwilk, 2017), while influencing the occurrence, intensity and behaviour of future fires (Cumming, 2001; Dantas, Hirota, Oliveira, & Pausas, 2016; Hargrove, Gardner, Turner, Romme, & Despain, 2000; Hoffmann et al., 2012; Ormeño et al., 2009; Pausas et al., 2017). Hence, the increase in fire frequency associated with anthropogenic effects, combined with increasing temperatures and aridity in some parts of the world, all highlight the need for extensive research exploring the effects of fire on vegetation dynamics (Marlon et al., 2009).

Perennial plant species can be classified by their post-fire regeneration strategy: (a) obligate resprouters, (b) obligate seeders and (c) facultative seeders (Herrera, 1992; Pausas & Keeley, 2014; Verdú, 2000). Perennial seeders and resprouters differ in their reproductive syndromes (Keeley, 1986a). Fire triggers seed germination in obligate seeders (Chamorro, Luna, & Moreno, 2013; Herrero, San Martin, & Bravo, 2007), while resprouters are capable of withstanding fires and regenerate vegetatively after fire events (Keeley, 2012; Paula, Naulin, Arce, Galaz, & Pausas, 2016). Facultative seeders can utilize both strategies, post-fire resprouting and seedling recruitment from the fire-cued dormant seed bank (Keeley & Bond, 1997; Keeley, Fotheringham, & Baer-Keeley, 2006). Recent studies have illustrated that flammability is often linked to the plant regeneration strategy (Bond & Midgley, 1995; Dantas et al., 2016; Pausas et al., 2017; Saura-Mas, Paula, Pausas, & Lloret, 2010), with seeders being more flammable than resprouters. Furthermore, traits which enhance or reduce flammability are selected for/against through the process of natural selection (Verdú, 2000; Schwilk & Ackerly, 2001; Moreira, Castellanos, & Pausas, 2014) .

The post-fire regeneration of perennial plants adopting these different strategies can be affected by fire timing, as it may largely influence fire behaviour (Knapp, Estes, & Skinner, 2009). Although in the eastern Mediterranean region, fires usually occur during the summer (Levin & Saaroni, 1999), the intensity and behaviour of fires can differ between spring and autumn. Spring fires are usually less severe than autumn fires (in total burned area) because they occur shortly after the wet season, when the water capacity of both the fuel (live and dead vegetation) and soil are relatively high (Neary, Klopatek, DeBano, & Ffolliott, 1999). Thus, autumn fires are expected to cause a stronger reduction in plant abundance/biomass, and a larger change in soil characteristics. Increased soil temperature, associated with autumn fires, may lead to decreased soil water content, along with an increase in the amount of nutrients available to the local biota (Certini, 2005; Neary et al., 1999).

Fire timing can also have important implications for the regeneration of perennial plants owing to phenological effects (Knapp et al., 2009; Ooi, 2010). Obligate resprouters have swollen structures at the stem base (e.g., lignotubers or burls; Canadell & Zedler, 1995; James, 1984; Paula et al., 2016; Vesk & Westoby, 2004). These organs function as carbohydrate and nutrient storage sites, supporting plant regrowth after disturbance (Moreira, Tormo, & Pausas, 2012). Cruz, Perez, and Moreno (2003) illustrated that the concentration of carbohydrates in the storage organ of *Erica australis*, a common resprouter in the western Mediterranean Basin, was lowest in early summer, remaining relatively low until early autumn. Therefore, the post-fire regeneration of obligate resprouters should be faster during spring than during autumn, when levels of stored carbohydrates are higher. Most perennial seeders in the Mediterranean Basin are characterized by hard-coated seeds (i.e., physical dormancy; Brown & Van Staden, 1997; Moreira & Pausas, 2012; Chamorro et al., 2013). Hence, in areas subjected to spring fires the physical dormancy of these seeds is broken prior to the summer, and they are forced to survive the long dry summer period unprotected before having a chance to germinate (Chamorro et al., 2017). All of the above suggests that the regeneration of obligate seeders should be slower after spring than after autumn fires.

Field studies examining the consequences of fire season on plant community composition have been conducted mostly in North America (Knapp et al., 2009). In recent years, controlled fire experiments were also carried out in the western Mediterranean Basin (Céspedes, Luna, Pérez, Urbieta, & Moreno, 2014; Céspedes, Torres, Luna, Perez, & Moreno, 2012). Unlike the western Mediterranean region, the summer in the eastern Mediterranean Basin is completely dry (Goldreich, 2012). Moreover, this region has experienced increased fire occurrences during the last two decades (Wittenberg & Malkinson, 2009). Although plant communities characterizing the Mediterranean Basin are considered largely resilient to fires (Peterson, Allen, & Holling, 1998), severe disturbances, including stand replacing fires, that are common in Mediterranean woodlands and mixed pine–oak forests, often bring about long-term landscape changes, potentially leading to a shift in the dominant vegetation type (Keeley, 2012; Pausas et al., 2017; Pickett & McDonnell, 1989). The present study tested, for the first time, the effect of fire season on the perennial plant community in typical eastern Mediterranean woodlands.

We hypothesized that autumn fires, occurring after the long dry Mediterranean summer, should be more severe than spring fires. We also hypothesized that fire season should differentially influence the perennial plant community composition. Specifically, we posited that fire in general and autumn fires in particular should reduce the relative abundance of dominant plant species while increasing the relative abundance of less common species. The below-ground carbohydrate storage of obligate resprouters is lower during autumn than during spring (Cruz & Moreno, 2001; Delillis & Fontanella, 1992). We thus posited that the relative abundance of obligate resprouters would be lower after autumn than after spring fires (Malanson & Trabaud, 1988; Paula & Ojeda, 2009; Paula et al., 2016; Rosas, Galiano, Ogaya, Peñuelas, & Martínez-Vilalta, 2013). In addition, seed whose

physical dormancy is broken during a spring fire would have to survive the long dry summer without protection, and hence would have reduce chances to germinate during the following rainy season (Chamorro et al., 2017). We thus posited that the relative abundance of obligate seeders should be lower after spring than after autumn fires. Since facultative seeders can both reseed and resprout post-fire (Bradbury et al., 2016), we predicted that fire season would have minimal to no effect on their relative abundances.

2 | METHODS

2.1 | Study area

The study was done in Har Yaaran (Figure 1) located in the Judean Mountains, Israel (600 m a.s.l.; 31°42′25N, 35°2′17E). This region is characterized by an east mediterranean climate with short, mild and wet winters and contrasting long, dry and hot summers (average temperature: winter = 8.7°C, summer = 23.5°C; Goldreich, 2012). The dominant soil type is Terra Rosa, distributed between large limestone plates (Singer, 2007). The average annual precipitation is 464 ± 32 mm (2007–2016, Jerusalem, IMS). The vegetation formation is typical Mediterranean woodland (Garrigue), composed of phanerophyte shrubs (e.g., *Pistacia lentiscus*, *Rhamnus lycioides*, *Calicotome villosa* and *Quercus coccifera*), chamaeophytes (e.g., *Cistus salviifolius*, *Cistus creticus*, *Teucrium divaricatum*, *Fumana arabica* and *Hyparrhenia hirta*) and climbers (e.g., *Rubia tenuifolia*, *Smilax aspera*, *Prasium majus* and *Ephedra foeminea*). The obligate resprouter *P. lentiscus* is a dominant shrub up to 1.5 m in height with a wide branching architecture. The facultative seeder *T. divaricatum* is commonly found under the *P. lentiscus* canopy, together with other climbers such as *R. tenuifolia* and *P. majus*. Other chamaeophytes such as the obligate seeders *C. salviifolius* and *C. creticus* grow adjacent to the

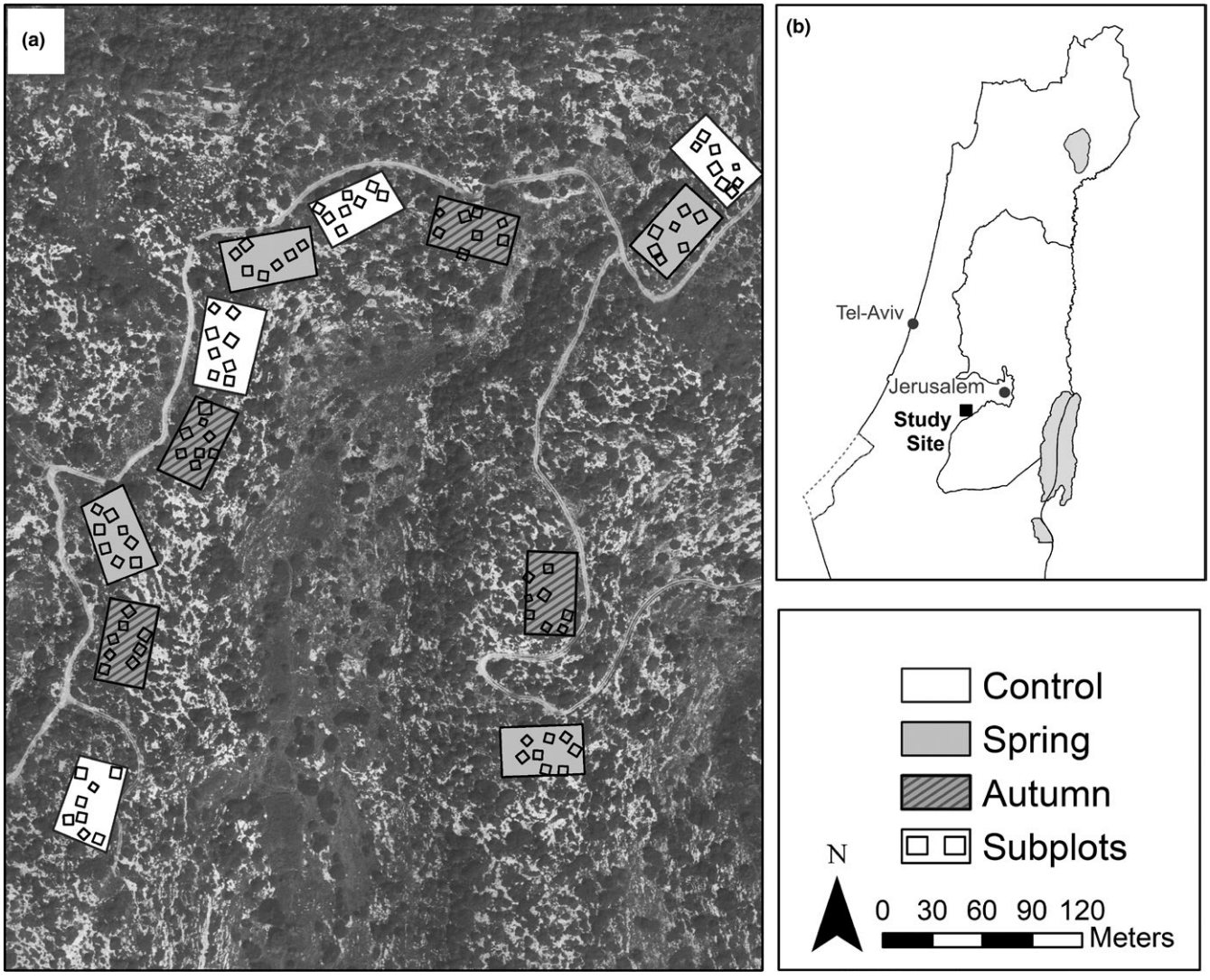

FIGURE 1 The study area in Har Yarran (a) located at the Judea Mountains, Israel (b). Each of the twelve experimental plots was randomly assigned to one of the following fire treatments: spring burn, autumn burn and unburned control. Each plot consists of eight 5 × 5 m subplots.

P. lentiscus shrubs, up to an average height of 0.4–0.6 m. Hence, the woodland in Har-Yaaran is mainly covered in patches of *P. lentiscus* (cover: ~20%) and *Cistus* spp. (*C. salviifolius* and *C. creticus*, both species combined cover: ~20%) with inter-shrub gaps occupied by annual herbs from winter to spring.

Fire history analysis revealed that more than 3,800 fires occurred in the Judean Mountains region between 1987 and 2009 – an average rate of 170 fires/year (Tessler, 2012). A more recent analysis based on data provided by the JNF (Jewish National Fund) indicated that at least 48 fire events occurred in the Judean Mountains during 2013 (i.e., 1 year prior to our seasonal fires), burning a total area of ~0.9 ha. Over half (54%) of the fires occurred during summer, 8% during autumn, 5% during winter and 33% during spring (Tsafrir A. and Ovadia O. unpubl data).

2.2 | Experimental design and data collection

The experiment consisted of 12 50 × 30 m plots (Figure 1), each included eight 5 × 5 m sampling subplots. Experimental plots were randomly assigned to one of the following three fire treatments: (a) spring burn (i.e., early Jun), (b) autumn burn (i.e., early Sept) and (c) unburned control, i.e., four replicates (plots) for each fire regime. All plots were located on south-facing slopes close to the ridge. Professional crews of the Israeli Forest Service (JNF) executed the burns using drip torches. The following measurements were taken from each subplot, every 5 min during the burns, using mobile weather stations: wind speed, relative humidity and air temperature. Flame heights (i.e., proxy of fire intensity) were estimated repeatedly by an observer walking behind the fire line. The fire was allowed to die out naturally. Plant water content was determined during each of the two fire seasons by weighing four trimmed twigs of five highly abundant plant species (*P. lentiscus*, *R. lycioides*, *Cistus* spp., *Q. coccifera* and *C. villosa*) from each plot, before and after oven drying (60°C, 48 hr). Soil moisture was determined by collecting soil samples (7-cm depth) from each of the 96 subplots during each of the two burning seasons. Soil moisture was estimated by weighing these soil samples before and after oven drying (105°C, 24 hr).

Vegetation surveys were held before (Apr 2014) and two consecutive years after the burns (May–Jun 2015 and 2016). A uniform distribution of 25 points was established in each of the 96 subplots (12 plots × 8 subplots = 96 subplots). Perennial species (herbaceous and woody species) detected within the 20-cm radius around each sampling point were recorded. Species abundances were calculated as the number of points (out of 25 per subplot) at which each species was present. Fire severity was assessed 10 days after the burns using the same grid of sample points. At each point, we determined whether the vegetation was burned by the fire (black), died from the heat (dried out, but not burned – heat shock) or was not affected by the fire (i.e., remained green). Species regeneration traits taken from BROT (Paula et al., 2009), TRY databases (Kattge et al., 2011) and Naveh (1975) are summarized in Supporting Information Appendix S1.

2.3 | Statistical analysis

Conditions before the burns (i.e., soil moisture and plant water content), during the burns (i.e., wind speed, relative humidity and ambient temperature), and fire intensity (i.e., flame height) and severity (i.e., proportion of burned area and proportion of heat shock area) (Keeley, 2009) were analysed using one-way nested ANOVAs with fire season as an explanatory variable (Keeley, 2009).

The effects of fire season on perennial plant species (herbaceous and woody) community composition were first explored using NMDS (Clarke, 1993). Species abundances at the subplot level were summed to the plot level. Plant abundances were square root-transformed prior to calculating the Bray–Curtis similarity matrix. Using a PERMANOVA (Anderson, 2001), we tested for differences in species composition between fire treatments. SIMPER (similarity percentages) analysis was used to identify the species that contributed 90% in total to the dissimilarly between different pair-wise treatment combinations (e.g., unburned control vs autumn burn, unburned control vs spring burn) and to quantify the relative contribution of each species to the overall dissimilarity. A canonical analysis of principal coordinates (CAP) was applied in order to find the axes that best discriminate between a priori groups (i.e., unburned control, spring burn and autumn burn) and species (vectors) best correlating with the different groups. Species vectors projected were only those having Pearson correlation of $r > 0.55$. All these multivariate analyses were performed using PRIMER v.6 (Clarke & Warwick, 1994).

There was slight variation in plant abundances among experimental plots prior to the fire. To test for differential fire treatment effects on the abundances of perennial plants adopting different regeneration strategies (i.e., obligate resprouters, obligate seeders and facultative seeders), we calculated the proportional change in their total abundances in the first post-fire year relative to the pre-fire year. To test for differential recovery patterns, we calculated the proportional change in their total abundances in the second post-fire year relative to the first post-fire year. These data were analysed using one-way ANOVAs, with fire treatment (i.e., unburned control, spring burn and autumn burn) as the between subject factor, followed by Newman-Keuls post-hoc test designed to have more statistical power than the Tukey's post-hoc test (Abdi & Williams, 2010). All ANOVAs were done in STATISTICA v 12 (Dell, Tulsa, OK, USA).

3 | RESULTS

Ambient temperature was lower and relative humidity was higher during spring than during autumn burns (temperatures: $p = 0.037$; relative humidity: $p = 0.042$; Table 1). Wind speed was faster during spring than during autumn burns ($p = 0.001$; Table 1). Soil and plant water content were higher during spring than during autumn burns (soil moisture spring: $p = 0.003$; plant water content: $p = 0.008$; Table 1). Flame height (i.e., proxy of fire intensity) was slightly higher

TABLE 1 Environmental conditions prior (i.e., soil moisture and plant water content) and during (i.e., wind speed, relative humidity and ambient temperature) the burns

Variable	Spring	Autumn	$F_{(1,52)}$	p
Soil moisture (%)	7.60 ± 0.37	3.30 ± 0.22	22.457	0.003
Plant water content (%)	47.63 ± 0.45	37.36 ± 0.23	15.426	0.008
Wind speed (km/hr)	10.48 ± 0.67	3.35 ± 0.24	35.732	0.001
Relative humidity (%)	51.60 ± 1.36	41.05 ± 0.54	6.622	0.042
Ambient temperature (°C)	25.68 ± 0.48	29.50 ± 0.187	7.109	0.037
Flame height (m)	1.18 ± 0.16	2.21 ± 1.80	1.162	0.322
Burned area (%)	45.98 ± 4.16	37.11 ± 4.01	1.801	0.228
Heat shock area (%)	17.45 ± 2.25	21.00 ± 2.26	0.610	0.465

Notes. Flame height (i.e., proxy of fire intensity) and proportion of burned and heat shock areas (i.e., proxies of fire severity).

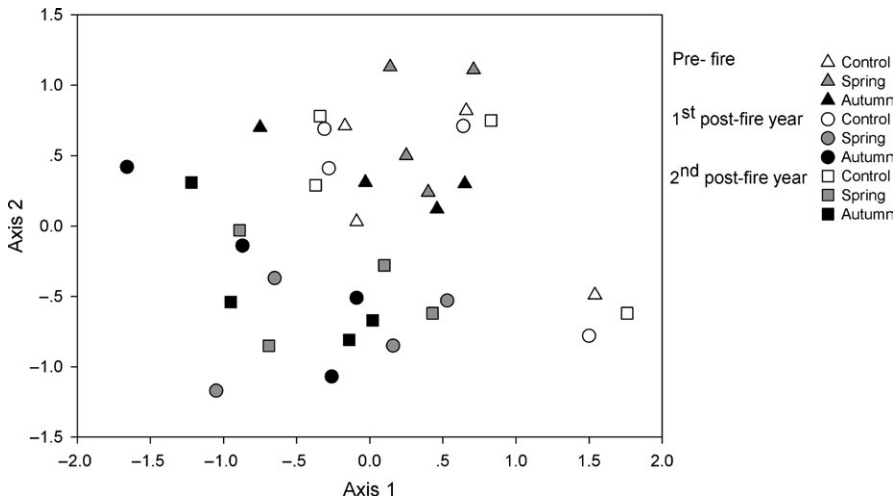

FIGURE 2 Non-metric multidimensional scaling (nMDS) ordination (stress = 0.18), based on Bray-Curtis similarity matrix, exploring differences in the perennial plant community composition between experimental plots prior to and after the prescribed spring and autumn burns

during autumn than during spring burns, but these differences were not significant (p = 0.322; Table 1). No significant differences in the proportions of burned or heat shock areas were detected between the two burning seasons (proportion of burned area: p = 0.228; proportion of heat shock area: p = 0.465; Table 1). These results imply that fire intensity and severity were largely consistent between spring and autumn burns (Table 1).

A species ordination (NMDS) illustrated that the unburned control plots were clustered together (Figure 2), and that they were separated from plots subjected to both spring and autumn fires (see species list in Supporting Information Appendix S2). Indeed, fire caused a significant shift in the perennial plant community composition (see PERMANOVA and pair-wise comparisons in Supporting Information Appendices S3 and S4). Prior to the burns, there were no significant differences in the composition of perennial plant species between plots. A year after the fires, species composition in plots subjected to spring and autumn burns varied significantly from that observed in the unburned control plots. Furthermore, marginally significant differences in species composition were detected between plots subjected to spring and autumn burns. Two years after the fires, the differences in species composition between unburned control and autumn burned plots became non-significant, while differences between unburned control and spring burned plots, and between autumn and spring burned plots remained significant (Figure 2, Supporting Information Appendix S4). The recovery trajectories of the perennial vegetation in four out of eight burned plots (two autumn and two spring burned plots) pointed towards the pre-fire state (Figure 2). In two other plots (one autumn and one spring burned plot) there were no signs of such a recovery, while in the remaining two plots perennial plant community composition tended to drift away from its pre-fire state (Figure 2).

Nine of the 40 perennial plant species that were found in the pre- and first post-fire vegetation surveys contributed about 50% (in total) to the dissimilarity between unburned control and spring burned plots, and between unburned control and autumn burned plots (Figure 3). In both pair-wise comparisons, the dominant perennial species were *P. lentiscus*, *Cistus* spp., *F. arabica* and *T. divaricatum*, contributing ~30% (in total) to the dissimilarities in community composition. Even though the dominant perennial plant species experienced the highest reductions in their abundances, they remained dominant in the perennial plant community in all burned plots. CAP analysis (Figure 4) illustrated that most of the perennial

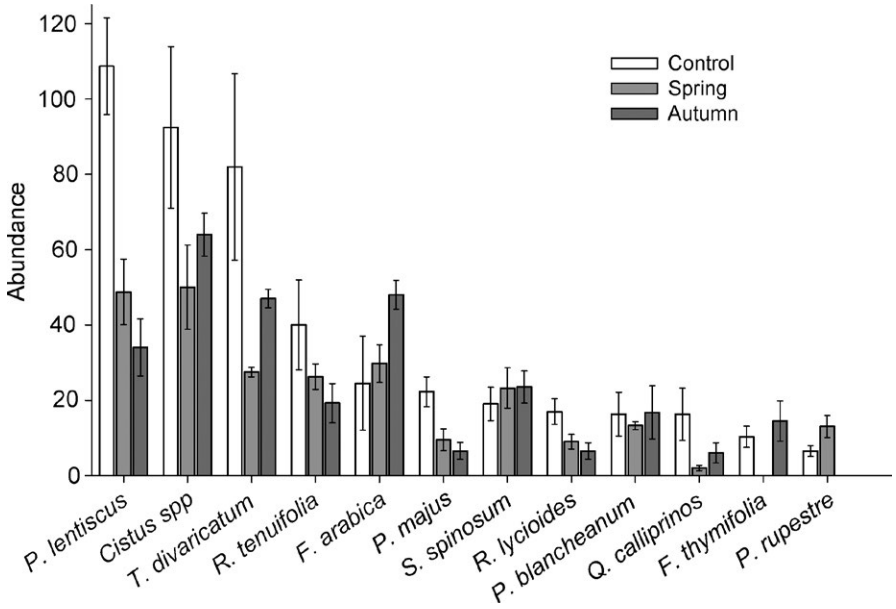

FIGURE 3 Total per plot abundances (±*SE*) of perennial species detected using SIMER (similarity percentages) analysis. The species are listed according to their contribution to the dissimilarity between unburned control and autumn burned plots, and between unburned control and spring burned plots, during the first post-fire year

species which were positively correlated with spring and autumn burns were less common in the study area prior to the fires, except for *F. arabica*. This species was dominant prior to the fires and exhibited increased abundance after the burns in general, and after autumn burns in particular (Supporting Information Appendix S2). Only one species, *Piptatherum miliaceum* (facultative seeder), was positively correlated with spring burned plots (Figure 4). This species was more abundant in plots subjected to spring burns than in the unburned control plots, while being completely absent from plots subjected to autumn burns. Seven species were positively correlated with autumn burned plots, six of which were obligate seeders (*Stipa bromoides*, *Micromeria nervosa*, *Phagnalon rupestre*, *F. arabica* and *Atractylis comosa*), and one a facultative seeder (*H. hirta*). In contrast, five obligate resprouters (*P. lentiscus*, *Q. coccifera*, *P. majus*, *R. tenuifolia* and *S. aspera*), two obligate seeders (*Cistus* sp. and *E. foeminea*) and one facultative seeder (*T. divaricatum*) were positively correlated with the unburned control plots (Figure 4, Supporting Information Appendix S2).

The proportional change in total abundance of plants adopting different regeneration strategies between pre-fire year and the first post-fire year was negative (Figure 5a). This reduction was significant among obligate seeders (Figure 5a; $F_{2,\,9} = 6.987$, $p = 0.014$) and obligate resprouters (Figure 5a; $F_{2,\,9} = 36.441$, $p = 0.000$), but not among facultative seeders (Figure 5a; $F_{2,\,9} = 2.118$, $p = 0.176$). Pair-wise comparisons indicated that the proportional reduction in total abundance of obligate seeders was larger after spring than after autumn burns (Newman–Keuls post-hoc test: $p_{\text{control vs. spring}} = 0.001$, $p_{\text{control vs. autumn}} = 0.157$, $p_{\text{spring vs. autumn}} = 0.058$). No such differential fire season effect was detected among obligate resprouters (Newman–Keuls post-hoc test: $p_{\text{control vs. spring}} < 0.001$, $p_{\text{control vs. autumn}} < 0.001$, $p_{\text{spring vs. autumn}} = 0.843$). Similar patterns were detected for the most common species in a set of analyses at the species level (Supporting Information Appendix S5).

A significant increase in the abundance of facultative seeders was evident when contrasting the first and second post-fire years (Figure 5b; $F_{2,\,9} = 7.678$, $p = 0.011$), however, no such pattern was detected among obligate resprouters (Figure 5b; $F_{2,\,9} = 3.478$, $p = 0.078$) or obligate seeders (Figure 5b; $F_{2,\,9} = 1.57$, $p = 0.260$). Pair-wise comparisons indicated that the proportional recovery of facultative seeders was consistent between the two fire seasons (Newman–Keuls post-hoc test: $p_{\text{control vs. spring}} = 0.016$, $p_{\text{control vs. autumn}} = 0.0124$, $p_{\text{spring vs. autumn}} = 0.487$). Again, species level analyses revealed similar patterns (Supporting Information Appendix S5).

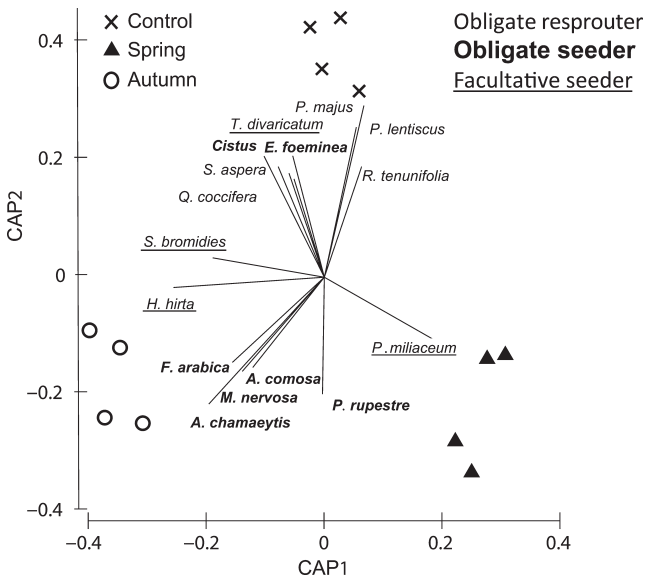

FIGURE 4 Canonical analysis of principal coordinates (CAP), based on Bray-Curtis similarity matrix, aiming to discriminate between experimental plots by the different fire treatment groups. Among the eight species positively correlating with the unburned control plots, five are obligate resprouters, two are obligate seeders, and one is a facultative seeder. Except for *H. hirta* (a facultative seeder), all other species, positively correlating with autumn burned plots, are obligate seeders

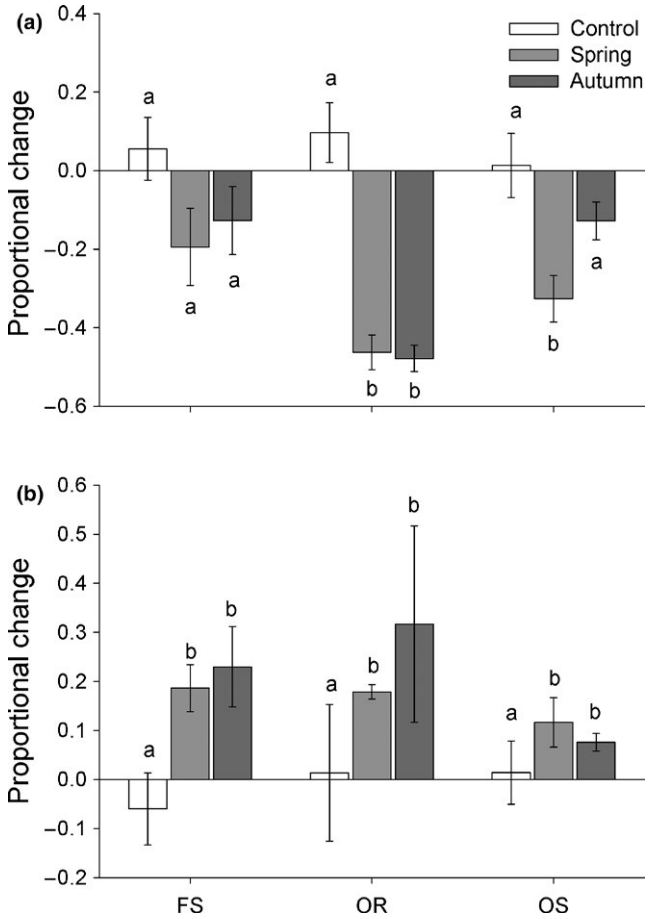

FIGURE 5 Proportional changes of the total abundances of facultative seeders (FS), obligate resprouters (OR), and obligate seeders (OS) in (a) the first post-fire year relative to the pre-fire year, and (b) in the second post-fire year relative to the first post-fire year

4 | DISCUSSION

Fire disturbance plays an important role in dictating plant community dynamics in a variety of ecosystems (Keeley, 1991; Naveh, 1975; Pausas & Keeley, 2009). We report here the results of a large-scale field experiment, examining the consequences of fire season on the community composition of perennial plants in a typical eastern Mediterranean woodland. We illustrate that fire in general and fire season, in particular, cause significant changes in the perennial plant community composition. Specifically, although fire intensity and severity were largely consistent between the two burning seasons, the overall negative effect of fire on the abundance of obligate seeders was stronger after spring burns, resulting in two distinct perennial plant communities (herbaceous and woody) that differed in their species composition.

Relative humidity was higher and wind speed was faster during spring than during autumn burns. The high relative humidity mitigated the positive effect of wind velocity on fire intensity and severity. Consequently, we could not detect significant differences in flame height (i.e., proxy of fire intensity) and proportion of burned area (i.e., proxy of fire severity) between the two burning seasons. We interpreted this to mean that the observed differential effect of fire season on the abundance of obligate seeders should be attributed to phenological effects. A similar result was reported in a previous study, in the western Mediterranean Basin, examining the effect of fire season on germination density from the soil seed bank (Céspedes et al., 2012). A vegetation survey in this same experimental system revealed no significant differences in the abundances of resprouters and seeders between burning seasons (Céspedes, Torres, Perez, Luna, & Moreno, 2014). Other studies asserted that germination of obligate seeders is affected by time between the physical dormancy break of seeds by fire heat and the onset of the rainy season (Daskalakou & Thanos, 2004; Ooi, Auld, & Whelan, 2004; Pausas, Ribeiro, & Vallejo, 2004; Prevosto, Gavinet, Ripert, & Fernandez, 2015). In the eastern Mediterranean woodlands the rainy season begins during autumn, and this may also explain why the abundance of obligate seeders was higher in areas subjected to autumn than to spring burns.

Pistacia lentiscus, the most dominant obligate resprouter in our system, exhibited a substantial decrease in its abundance irrespective of fire season. In contrast to obligate and facultative seeders, *P. lentiscus* abundance was low also during the second post-fire year, implying low recovery rate. The removal of the *P. lentiscus* canopy probably resulted in increased light and nutrient availability (Kutiel & Naveh, 1987; Ne'eman, 1997; Ne'eman, Henig-Sever, & Eshel, 1999; Ne'eman & Izhaki, 1999), allowing both obligate and facultative seeders to take over the open canopy gaps. Fire season had no differential effect on obligate resprouters in general and on *P. lentiscus* in particular. Our results are consistent with those of Céspedes, Luna et al. (2014), who also could not detect a significant effect of fire season on the abundance of obligate resprouters. Several studies have illustrated that resprouter species store reserves in excess of their needs for a single resprouting episode (Canadell & Lopez-Soria, 1998; Cruz et al., 2003; Wright & Clarke, 2007), and that these reserves are renewed between fire events (Paula & Ojeda, 2009). Cruz, Pérez, Quintana, and Moreno (2002) and Cruz et al. (2003) suggested that other factors, such as soil nutrients, water availability and/or plant size, can limit the post-disturbance regrowth of *Erica australis* more than its carbohydrate storage. Konstantinidis, Tsiourlis, and Xofis (2006) showed that the recovery rate of the common obligate resprouter, *Arbutus unedo*, tended to be higher after spring than after autumn burns in Greece; however, this pattern was evident only in the north and east aspects. The authors concluded that the relative importance of local environmental conditions (e.g., water availability) in determining plant regeneration patterns can be higher than that associated with fire season.

In the Mediterranean region, shoot growth of facultative seeders occurs during the spring and autumn seasons (e.g., *T. divaricatum C. villosa* and *S. spinosum*), while their physiological activity is restricted to the summer and winter (Delillis & Fontanella, 1992; Keeley & Bond, 1997; Keeley et al., 2006; Naveh, 1975; Yiotis, Psaras, & Manetas, 2008). In accordance with our hypothesis, the decrease in total abundance of facultative seeders was consistent

between the two fire seasons. In addition, the proportional change in total abundance of facultative seeders was lower than that of obligate resprouters, and higher than that of obligate seeders. One possible explanation is that facultative seeders may have compensated for the germination reduction caused by spring burns via vegetative growth. After autumn burns, the proportional change in total abundance of facultative seeders was similar to that of obligate seeders, and lower than that of obligate resprouters. The latter result suggests that facultative seeders may have compensated for their poor ability to resprout during autumn through seed germination (Marais, Pratt, Jacobs, Jacobsen, & Esler, 2014; Pratt et al., 2012).

Community shifts between alternative stable states can occur when the disturbance is large enough to push the community out of the current stable state into an alternative one (Beisner et al., 2003; Odion et al., 2010). Mediterranean type regions and specifically the Mediterranean Basin are fire-prone ecosystems, where plant species evolved alongside recurring fire disturbances (Keeley, 2012; Ne'eman, Izhaki, & Keeley, 2012; Pausas & Keeley, 2014). Consequently, it is widely accepted that in these ecosystems an occasional fire event will not result in a community state transition (Keeley, 1986b; Lavorel, 1999; Malanson & Trabaud, 1987). For instance, following the 1988 wildfire that occurred in Mt. Carmel, Israel, woody perennial species (e.g., trees and shrubs) regenerated in the same locations where they existed prior the fire, while annual herbaceous species utilized the temporally unoccupied spaces (Kutiel, 1994). As the woody vegetation matured, the abundance of annual species returned to its limited pre-fire state, leaving a large seed bank in the soil (Kutiel, 1994; Ne'eman & Izhaki, 1999). This response pattern was also evident in other areas in Mt. Carmel subjected to repetitive fire incidents (Wittenberg, Malkinson, Beeri, Halutzy, & Tesler, 2007). Similarly, a large-scale field experiment conducted in Portugal, which included prescribed spring and autumn burns (Céspedes, Luna et al., 2014), illustrated that 4 years after spring and autumn burns, plant community composition returned to its pre-fire state. Nevertheless, we suggest that even if the plant community will most likely return to its pre-fire stable state, such short-term temporal changes can further affect the circle of "fire event–plant regeneration–fire reoccurrence", eventually determining the probability and intensity of future fires. For instance, recently studies have illustrated that flammability traits are often linked to plant regeneration strategy (Bond & Midgley, 1995; Pausas et al., 2017; Saura-Mas et al., 2010), suggesting that seeders are more flammable than resprouters. Hence, the differential fire season effect on obligate seeders can translate into differences in fuel accumulation rates, creating different conditions that influence the fire-free interval, next fire behavior and plant regeneration (Bond & Midgley, 2001; Clarke, Knox, Bradstock, Munoz-Robles, & Kumar, 2014; Cochrane et al., 1999; Keeley, Brennan, & Pfaff, 2008; Ormeño et al., 2009; Pausas, 2015; Pausas et al., 2016). Furthermore, at the landscape scale, fire events taking place at different locations and in different seasons can result in a landscape mosaic comprised of patches differing in their perennial plant composition (Turner, Gardner, & O'neill, 2001; Turner, 2005) and flammability (Dantas et al., 2016; Pausas et al., 2017). We thus suggest that increased spatio-temporal heterogeneity in fire season may result in a new landscape mosaic, differing from the contemporary one to the extent that it can be considered as an alternative stable state.

Forest managers have long recognized that pyrodiversity (i.e., variability in the spatiotemporal distribution of fires) can promote and maintain biodiversity in fire-prone ecosystems (Bradstock, Bedward, Gill, & Cohn, 2005; Martin & Sapsis, 1992; Parr & Andersen, 2006). This idea has served as the basis for development of the variable mosaic concept, implying that managers should aim to promote variability in both the visible fire mosaic (i.e., time since fire, fire size, fire severity, fire patchiness) and the underlying invisible mosaic (i.e., lengths of past inter-fire intervals, fire frequencies; Bradstock et al., 2005; Ponisio et al., 2016; Tingley, Ruiz-Gutierrez, Wilkerson, Howell, & Siegel, 2016). More recent work has shown that translating this concept into a system-specific management plan may be challenging (Driscoll et al., 2010; Foster, Barton, MacGregor, Robinson, & Lindenmayer, 2017; Kelly, Brotons, & McCarthy, 2017; Parr & Andersen, 2006). Nevertheless, our findings may have important implications for conservation and management of the eastern Mediterranean ecosystem. We show that irrespective of fire intensity and severity, seasonal fires differentially influence the perennial seeders. We interpret this to mean that fire season is an important component of the visible fire mosaic, and that promoting spatio-temporal variability in fire season can play a key role in maintaining biodiversity in this unique ecosystem.

An effective way to prevent the spread of wildfires is to reduce the amount of flammable substances (i.e., live and dead vegetation) and to break their contiguity using fire breaks and buffer zones (Fischer, 1984). We illustrate that spring burns have a stronger negative effect on the abundance of perennial seeders compared to autumn burns, and that no such differential effect exists among resprouters. Since perennial seeders are more flammable than resprouters (Pausas et al., 2017; Saura-Mas et al., 2010), conducting spring burns can be an effective way to reduce the flammability of the live vegetation in fire breaks and buffer zones.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1. Species growth form and regeneration strategy.

APPENDIX S2. List of detected species and their respective abundances.

APPENDIX S3. Repeated measures PERMANOVA, testing for differences in species composition between fire treatments.

APPENDIX S4. PERMANOVA – Pair-wise comparisons between the different fire treatments before and after the prescribed burns.

APPENDIX S5. ANOVAs testing for the effect of fire treatment on the proportional change in the abundance of each plant species.

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