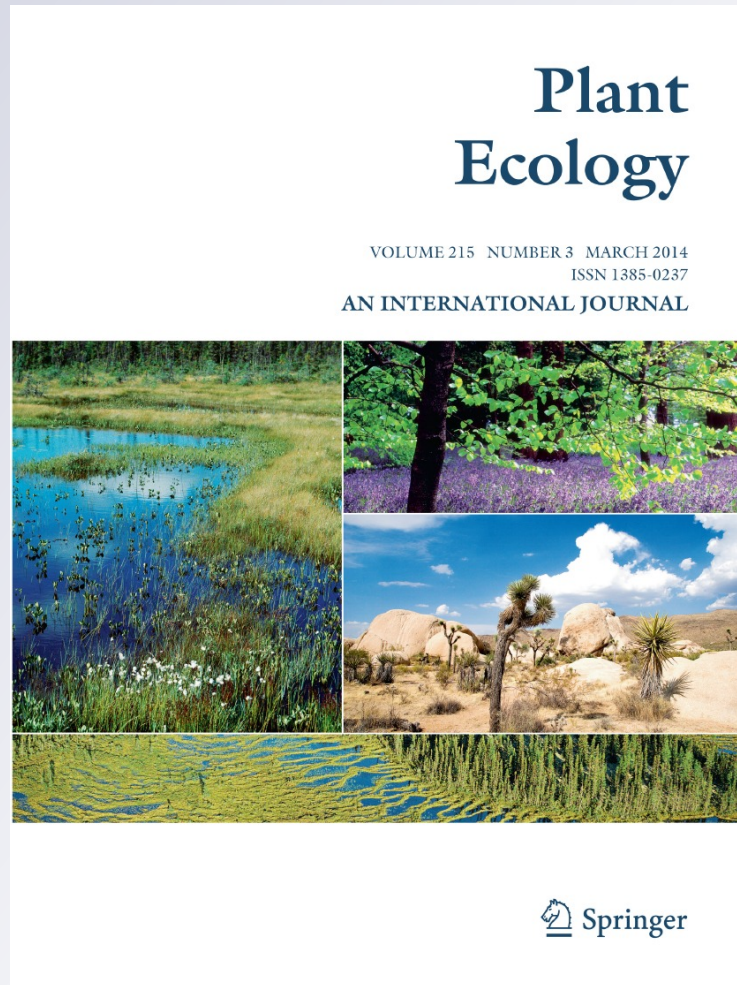# Long-term post-fire dynamics of co-occurring woody species in *Pinus brutia* forests: the role of regeneration mode

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Long-term post-fire dynamics of co-occurring woody species in *Pinus brutia* forests: the role of regeneration mode

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Abstract Regeneration mode is one of the key attributes determining population structure and dynamics of plant species. We investigated long-term patterns after fire in the cover of plant species in a 100-year chronosequence of burned *Pinus brutia* forests in a humid Mediterranean climate region in Turkey. Significant trends were present in the change of cover in major species through post-fire chronosequence, and species with similar trends were clustered in relation to their regeneration modes. Obligate resprouters increased their cover from the early post-fire years to the later stages, while cover of obligate seeders with a soil seed bank increased in the early years, but then decreased through time. Facultative resprouters were at an intermediate position, with an increase in cover until mid-successional stages and then a decrease through time. The cover of the only obligate seeder with a canopy seed bank (*P. brutia*) followed a linear increasing trend during the succession. When species with the same regeneration mode were grouped, the same trends were observed with more explained variances. A few life-history traits were enough to explain the observed trends. Our study shows that regeneration mode is an explanatory functional grouping system for describing long-term post-fire dynamics of Mediterranean Basin woody species. We suggest that regeneration mode must be a major component of any vegetation or forest stand dynamics model in the Mediterranean Basin. This result has important implications for the management of Mediterranean Basin ecosystems, and can potentially be extrapolated to other Mediterranean-type fire-prone ecosystems.

Keywords Post-fire succession · Obligate seeder · Obligate resprouter · Facultative resprouter · The Mediterranean Basin · Vegetation dynamics

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Introduction

Fire is a significant natural phenomenon in the parts of the world subjected to recurrent fires, i.e., fire-prone ecosystems. Among these areas, Mediterranean ecosystems are the characteristic example of an ecosystem that has evolved under the selective pressure of fire for many million years (Keeley et al. 2012). This long-term evolutionary history results in the current

fire-shaped plant community structure (Verdú and Pausas 2007) and fire-adapted traits of plant species (Paula et al. 2009) in these ecosystems. Plant life-history traits in relation to fire are the ones which allow plant species to recover their populations quickly after fire. In terms of post-fire recovery, two main syndromes are described: (1) resprouting, the ability of a species to recover in a vegetative manner from underground or above-ground buds protected from fire by soil cover or thick bark, respectively, and (2) seeding, the ability of a species to recover in a reproductive way by seed germination and seedling establishment after fire. The former has been seen as an exaptation since the resprouting predates the presence of fire in Mediterranean ecosystems (Lloret et al. 1999), although it is an effective way to cope with such a disturbance. Actually, recent evidence of early presence of fire on the Earth, and the wide distribution of resprouting ability among a variety of plant taxonomic groups, especially in old lineages, suggest that resprouting is "an adaptation selected for in response to fire" (Pausas and Keeley 2009). Seeding has been seen as a more prominent fire-adaptation; since most seeder species have newer lineages that appeared after the rise of Mediterranean climates and fires in these areas (Guzmán et al. 2009). In many seeder species found in Mediterranean ecosystems, the germination of seeds found in the soil seed bank is stimulated by fire temperatures or by the chemicals found in burned plant material (fire-stimulated germination) (Moreira et al. 2010), or the seeds that remain inside the cones in the canopy for many years (i.e., the canopy seed bank) are protected from fire temperatures, and then released after fire (fire-stimulated seed release) (Keeley 2012). There are also many species able to recover after fire by both their seeds and resprouts. These are described as facultative resprouters and are found between the extremes of "obligate" resprouters and "obligate" seeders within the window of resprouting (Keeley 1986).

These regeneration mechanisms allow Mediterranean vegetation to recover naturally after a fire and plant species to persist in these ecosystems (Paula et al. 2009). This recovery potential has been realized in most cases, however recent and predicted future fire regime changes in the Mediterranean Basin (Mouillot et al. 2002; Pausas and Fernández-Muñoz 2012) may restrict the establishment of some species, and fire results in a change in the species composition and

plant community structure in some cases (Pausas et al. 2008). These changes have important consequences on biodiversity, and on case-specific restoration plans in which the information of fire-related plant traits and post-fire regeneration potential of individual species may be crucial to give better post-fire management decisions.

Considerable attention has been paid to the post-fire succession in Mediterranean plant communities. Due to methodological constraints at the temporal scale, however, most of these studies focus only on early post-fire successional dynamics (e.g., Pérez and Moreno 1998; Calvo et al. 2002) using the diachronic method (i.e., monitoring the same site for many years). By using the synchronic method (i.e., constituting a chronosequence) as an alternative methodological approach, some studies intended to resolve the question of post-fire community restructuring and dynamics of species diversity through the succession process (Kazanis and Arianoutsou 1996, 2004; Tavşanoğlu and Gürkan 2009; Kavgacı et al. 2010), whereas others regarded long-term post-fire dynamics of individual Mediterranean Basin species (Schiller et al. 1997; Tavşanoğlu and Gürkan 2005; Capitiano and Carcaillet 2008; Baeza et al. 2011). Other attempts to explain long-term fire-related dynamics of Mediterranean vegetation are based on modeling studies considering the regeneration mode of species as the main functional group (Pausas 1999a, 2003, 2006). The outputs of these models are comparable with field observations (Lloret et al. 2003), and therefore fire-free scenarios of the models correspond to post-fire long-term dynamics of species or functional groups.

The importance of the functional group approach is acknowledged for describing post-fire Mediterranean vegetation dynamics (Pausas and Lavorel 2003; Arianoutsou 2004; Kazanis and Arianoutsou 2004). Long-term post-fire response of co-occurring Mediterranean Basin species was studied by Capitiano and Carcaillet (2008). However, the functional group approach based on growth form used in this study did not thoroughly explain the post-fire behavior of co-occurring species. Similarly, cover change of different growth forms through successional time did not clearly separate different modes of responses in Mediterranean Basin plant communities (Trabaud 1983). It is known that the most important groups that define Mediterranean Basin vegetation structure are the ones based on the regeneration mode of plants, at

least for woody species (Kazanis and Arianoutsou 2004). Similar conclusions have also been reached in other Mediterranean-type ecosystems (Pausas et al. 2004; Keith et al. 2007). On the other hand, although fire-related long-term dynamics of Mediterranean Basin vegetation has already been modeled (Pausas 1999a, 2003, 2006), there is no field-based research describing long-term post-fire dynamics of functional groups in relation to regeneration mode in the Mediterranean Basin.

In the present study, we investigated the long-term dynamics of coexisting woody species along a post-fire successional gradient in *Pinus brutia* Ten. (Turkish red pine) forests of southwestern Turkey. The aims of the study were (1) to determine the post-fire cover change dynamics of woody species co-occurring in a Mediterranean plant community, (2) to test if different regeneration modes (obligate resprouters, facultative resprouters, and obligate seeders) show different patterns along a successional gradient, and (3) to determine if Mediterranean Basin plant woody species follow the same post-fire successional pattern as the rest of the species categorized in the same regeneration mode. Our study also gives an opportunity to test if the predictions of fire-free scenarios of vegetation dynamics models developed for Mediterranean vegetation are supported by field data, and to understand if these models can be applied to a wide geography within the Mediterranean Basin.

Methods

Study area, climate, and study sites

The study was conducted in the Marmaris region of southwestern Turkey in the eastern Mediterranean Basin (36°49′–36°59′N, 28°07′–28°20′E). The climate is a Mediterranean one with distinct wet and dry periods. The mean annual temperature is 18.7 °C, the total annual precipitation (P) is 1211.7 mm, with only 57 mm falling during the 5-month-long dry period. The annual potential evapotranspiration (PET) is 962.2 mm, annual actual evapotranspiration is 397.1 mm, and aridity index (P/PET) is 1.26, corresponding to a humid climate. Therefore, the area has higher productivity than similar sites around the eastern Mediterranean Basin region. This allows for the development of dense fire-prone vegetation, and as a consequence, the area has

been one of the most burned regions in Turkey over the last 30 years. The original vegetation cover is Turkish red pine (*P. brutia*) forest including sclerophyllous shrubs underneath the canopy, but currently the study area is characterized by a fire created habitat mosaic consisting of sites at different stages of the post-fire succession. There are also remaining unburned patches of pine forests within the region, sometimes more than 100 years old.

Among many sites representing different post-fire successional stages in the area, we selected seven recently burned areas (burned in years 2002, 1999, 1997, 1996, 1995, 1989, and 1979) and two long-unburned (for at least 50 and 100 years) pine stands to create a post-fire chronosequence. The sites were selected by the type of geological material which was found, the proximity to each other, and their pre-fire vegetation structure. Thus, all the selected sites were located on the ophiolitic rocks producing serpentine soils, were located relatively close to each other (found within 400 km^2 area), and had the same original vegetation (pine forest) before the latest fire occurred. Physical and chemical properties of the soils of study sites were similar (Tavşanoğlu and Gürkan 2010). The mean altitude of the study sites was 101 m (min: 2 m, max: 290 m) a.s.l. The chronosequence obtained by the study sites included 3, 6, 8, 9, 10, 16, 26, 50, and 100 years of the post-fire succession.

The space-for-time substitution (i.e., chronosequence) approach has frequently been used in succession studies (e.g., Bonet and Pausas 2004; Kavgacı et al. 2010; Porto et al. 2013), but there are critical drawbacks of this methodology (Johnson and Miyanishi 2008). First, the study sites at different ages in a chronosequence may differ in their history (e.g., initial community structure before disturbance, management past, and stochastic events). Second, local topographic (e.g., slope, aspect) and environmental conditions (e.g., soil, geology, and climate) might have shaped the plant communities in the study sites in chronosequence differently. These limitations make chronosequence-based studies weaker than permanent-plot-based ones; especially in the case that characteristics of the study sites in the chronosequence are not similar. However, space-for-time substitution approach is well suited to our study, since the deterministic rather than stochastic structure of the successional process in question, the similar pre-fire characteristics of the study sites we selected, and the association between

the studied time interval and the life spans of the considered species rule out many of the limitations of using chronosequence in successional studies (Walker et al. 2010).

Sampling design

Within each study site representing different post-fire successional ages, we selected five plots 1 ha in size that had been established for natural regeneration by forest management directorates. Within each plot, an additional five quadrats 100 m^2 in size (10 × 10 m) were indiscriminately established using random table numbers. Thus, a total of 25 quadrats was used for each study site. A plot in the 100-year age site was excluded from the data set before the analysis, because we later realized that the soil moisture characteristics of this plot was wetter than the other four replicates within the same study site. In total, our study includes nine study sites, 44 plots nested in the study sites, and 220 quadrats nested in the plots.

Cover of each woody species in each quadrat was estimated by the point intercept sampling procedure. The presence of a species every 1 m along the four sides of the quadrat and in a diagonal transect between two corners was recorded. Thus, 54 points in total were used to estimate cover of a species in each quadrat. The data from these quadrats were used to estimate the mean cover of each woody species in each plot.

Sampling was performed during the dry period of 2005 (from June to September). The plant specimens that could not be identified at the species level in the field were brought to the herbarium for further inspection on their taxonomic status. Nomenclature follows Davis (1965–1985), but also Greuter and Raus (1989) for a new combination of a taxon, and Stevens (2001 onwards) for the current family names.

Functional groups

We used two different functional grouping systems. The first one is based on the regeneration traits of plant species in crown-fire ecosystems (Pausas et al. 2004) and is used to group species to their regeneration mode: obligate resprouters (R+P−), facultative resprouters (R+P+), obligate seeders (R−P+), and the species without any specific regeneration mechanism (R−P−). Here, R+ and R− indicate that species are

able to resprout after fire, or not, respectively; and P+ and P− refer to the presence or absence of propagule (seed or fruit) persistence after fire, respectively (Pausas et al. 2004). Moreover, we separated obligate seeder species into two more groups according to the seed bank type: obligate seeders with a soil seed bank and with a canopy seed bank (as used in Pausas 1999a). The second functional grouping system is based on Raunkiaer's life forms. Since we only considered woody species in this study, only phanerophyte and chamaephyte groups could be included as life forms. The classification of species in functional groups was based on BROT database, a comprehensive plant trait database for Mediterranean Basin species (Paula et al. 2009), Flora of Turkey (Davis 1965–1985), and field observations.

Data analysis

Since point intercept sampling may not sufficiently capture the less abundant species, we performed a rarefaction analysis to test the accuracy of the sampling. Species–plot number curve based on randomly selected plot-based data was asymptotic (Fig. S1 in Supplementary), and the expected number of species richness was 53.9 according to the Jackknife estimate of species richness (Krebs 1989). The estimates were satisfactory to conduct further analysis using plot data.

To obtain cover values for each functional group, we summed the cover of individual species that were included in the corresponding functional group for each sample quadrat, and we obtained the mean cover values for each plot by averaging quadrat values for each functional group. Since we estimated the cover of functional groups as species totals, the cover of any functional group may exceed 100 %.

We used linear or polynomial regressions to fit a regression line or curve, respectively, to the cover data of individual species and functional groups through the post-fire succession. Mean cover of 1-ha plots estimated as average of five quadrats 100 m^2 in size was used as the dependent variable in the analyses. We used model I regressions considering the cover and post-fire age as random and fixed variables, respectively. We followed the model selection process described in Sokal and Rohlf (1995); we first fit a linear regression to the data, and then quadratic (2nd order) and cubic (3rd order) functions were tested

against each other using a stepwise procedure. If a statistically significant improvement was achieved for any step against the previous (and the simple) model, then we used the more complex model to describe the dynamics in the change in the cover of species and/or functional groups. By this procedure, we were able to identify the order of regression equation that significantly contributes to predicting cover change of a species or functional group through successional time. All the regression analyses were performed on log-transformed data. Only the species found in at least four study sites were included to the analysis. All the analyses were performed by R statistical software (version 2.15, http://www.R-project.org).

Since we performed 35 regression tests in total (for 27 taxa, 6 regeneration modes, and 2 life forms), we considered the significance level as $P < 0.01$ to decrease the possibility of making a type-I error rather than using the Bonferroni correction which is a very conservative measure (Moran 2003) for not decreasing the power.

Results

A total of 48 woody taxa were recorded in the study sites (Table S1 in Supplementary). Most of the taxa were included in the obligate resprouter (23) and the facultative resprouter (16) functional groups, while there were only five obligate seeder species with a soil seed bank. The least representative functional groups in our data were the obligate seeder species with a canopy seed bank (only *P. brutia*) and the species without any specific regeneration mode (3). Among all the species recorded, 18 have short- or long-term persistent soil seed banks, but those all belonged to the obligate seeder or facultative resprouter functional groups (Table S1 in Supplementary).

The cover of individual species varied among the study sites (Table S2 in Supplementary). Most of the species had lower cover values in the early post-fire years, but their cover was higher in the older sites or vice versa, while some of them achieved their highest cover values in the mid-successional stages. Moreover, we found significant trends in the change of cover through post-fire chronosequence, especially in the dominant species such as *P. brutia*, *Cistus* spp., *Phillyrea latifolia*, *Erica manipuliflora*, *Genista acanthoclada*, *Myrtus communis*, *Calicotome villosa*,

and *Smilax aspera* (Fig. 1). Among the species that showed significant cover change trends over time, the species with similar trends were clustered according to their regeneration modes, but this was not the case when only life forms were considered. Specifically, the obligate resprouter species (*Arbutus andrachne*, *S. aspera*, *M. communis*, *P. latifolia*, and *Styrax officinalis*) increased their cover starting from the early post-fire years to the later stages, while cover of obligate seeders with a soil seed bank increased in early years, but then decreased through time. Facultative resprouters (*Ptilostemon chamaepeuce*, *C. villosa*, *E. manipuliflora*, and *G. acanthoclada*) were at an intermediate position, with a cover increase until the mid-successional stages and then a decrease with time. The cover of obligate seeder species with a canopy seed bank, i.e., *P. brutia*, followed a linear increasing trend through post-fire succession. However, obligate seeders species with a soil seed bank (*Cistus salviifolius* and *Cistus creticus*) increased their cover during the first post-fire years, but then a significant decline in cover was observed down to the succession (Fig. 1).

Although many of the phanerophyte species (all the species mentioned above and in Fig. 1) showed a significant cover change trend over successional time, none of the chamaephytes followed a trend except *Asparagus aphyllus* (a R+P− species) in which a significant linear increase in cover throughout the succession was demonstrated ($y = 0.55x − 1.92$, $r^2 = 0.20$, $p = 0.002$, not shown in the figure). Accordingly, in functional group level, the cover of phanerophytes increased through time while that of chamaephytes lacked any significant trend (Fig. 2).

On the contrary, when the species with the same regeneration mode were grouped together, the same trends of those observed in individual species still existed (Fig. 3). The cover of the obligate resprouter group (R+P−) exhibited an increasing trend over time, while that of facultative resprouter group (R+P+) increased at first, but showed a decline in later successional stages. Cover of the group consisting of the species without any specific regeneration mechanism (R−P−) increased in mid-successional stages, but then decreased over time. Although there was a statistically significant increase in the cover of obligate seeder group (R−P+) over time, more explanatory models were obtained when obligate seeders were separated into two more groups according to the location of their seed bank (soil vs. canopy).
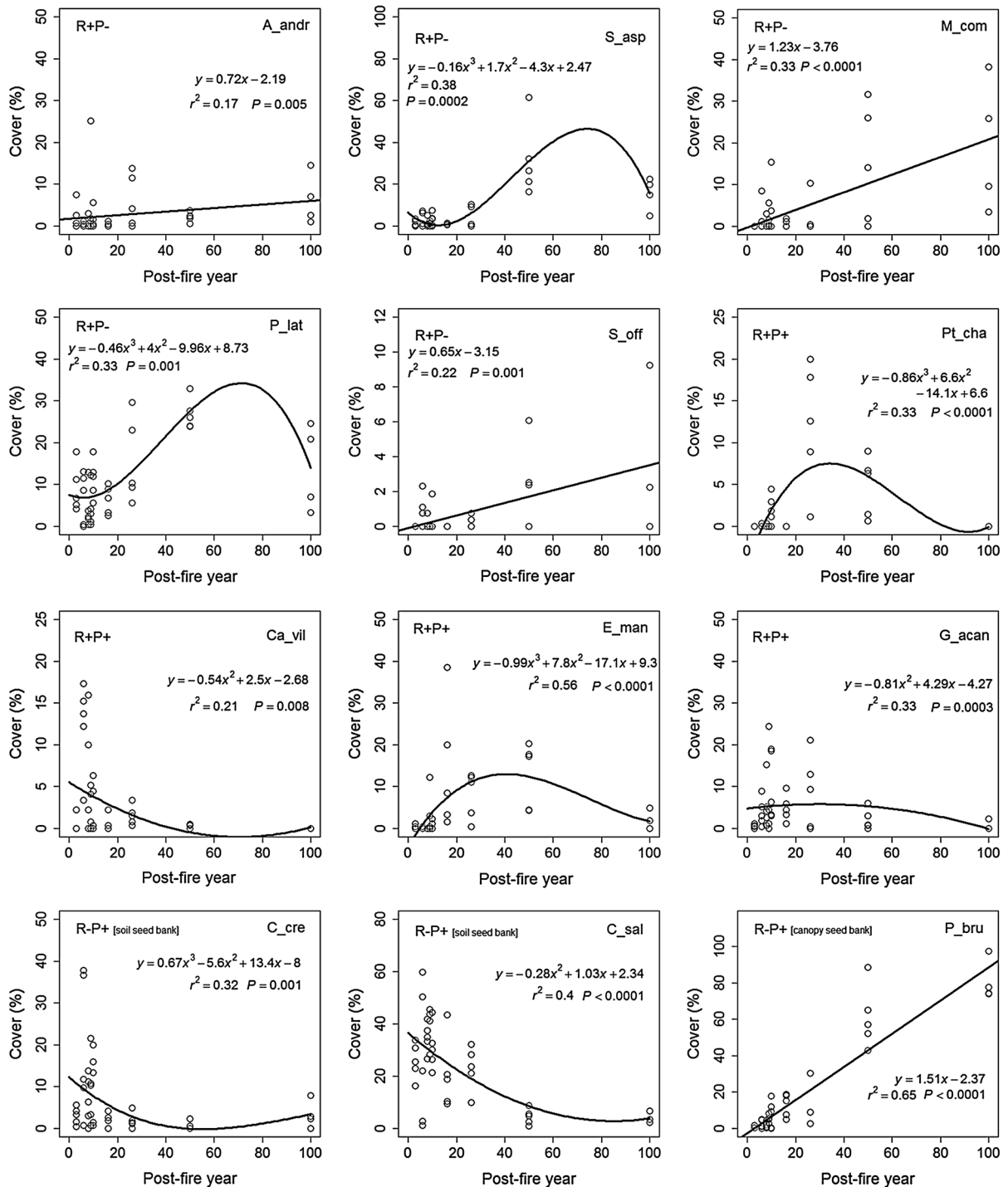
Fig. 1 Cover change dynamics of plant species through post-fire succession. Each point represents the cover of 1-ha plot, estimated as average of five quadrats 100 m² in size. Species codes were given in Table S1 in Supplementary. For each species, the presence (+) or absence (−) of resprouting ability (R) and propagule persistence (P) is given. Information on the presence of a soil or canopy seed bank was given for "R−P+" species for further separation within this regeneration mode (see "Methods" section for details). Fitted lines or curves are significant ($p < 0.01$) linear or nonlinear regressions, and non-significant regressions are not shown. Regression equations and analysis are based on log-transformed data
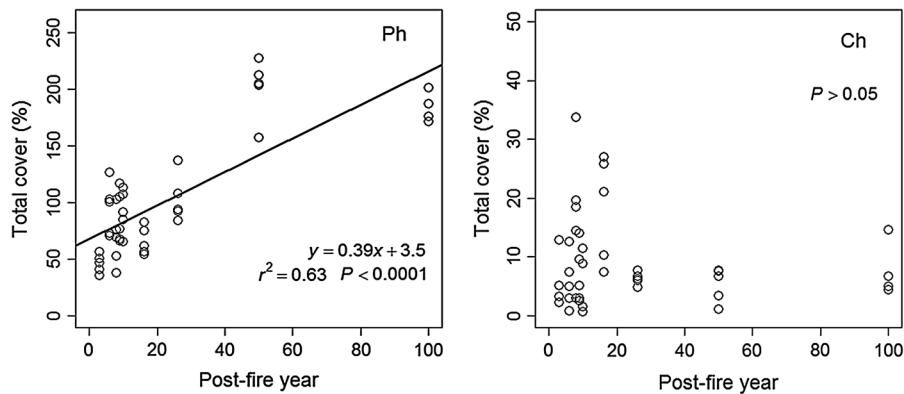
Fig. 2 Cover change dynamics of life form groups through post-fire succession. Each point represents the cover of 1-ha plot, estimated as average of five quadrats 100 m² in size. *Ph* is phanerophytes and *Ch* is chamaephytes. Fitted line in *Ph* is significant ($p < 0.01$) linear regression, and non-significant regression line in *Ch* is not shown. Regression equation and analysis are based on log-transformed data

This suggests that combining all the obligate seeders masked some biologically meaningful dynamics within this group. In summary, functional grouping according to the regeneration mode of species resulted in more explained variances and more significant statistical outputs than those achieved in regression models considering the individual species (Figs. 1, 3).

Discussion

Our study shows that significant trends are present in the change of cover in woody species through post-fire succession in *P. brutia* forests, and the species with similar trends were clustered in relation to their regeneration modes. This supports the idea that regeneration mode is an explanatory functional grouping system for describing long-term post-fire dynamics in Mediterranean Basin woody species. This is not the first conclusion ever reached on this matter; it is suggested that regeneration mode of Mediterranean Basin woody plants is important to define the vegetation structure (Kazanis and Arianoutsou 2004), and to construct vegetation dynamics models (Pausas 1999b) in Mediterranean Basin environments. Indeed, the simulation models based on regeneration mode predict the long-term fire response of Mediterranean Basin species well (Pausas 1999a; Lloret et al. 2003). However, our study is the first one that proves the idea of the importance of regeneration mode in long-term dynamics of Mediterranean Basin species with data from the field. Our results also support the predictions of the fire-free

scenarios of the vegetation dynamics models developed for Mediterranean Basin vegetation.

The intermediate fire-productivity model suggests that fire activity has a humped relationship with productivity/aridity gradient in a global basis (Pausas and Ribeiro 2013). More specifically, in Mediterranean ecosystems, more humid and more productive conditions result in more fire activity (Pausas and Paula 2012). It is known that resprouters are favored by high fire frequencies (Keeley and Zedler 1978; Bond and Midgley 2003), and recent studies revealed that in fire-prone ecosystems resprouters tend to dominate the plant community more in humid areas with high productivity than in drier ones with low productivity (Clarke et al. 2005; Pausas and Bradstock 2007; Russell-Smith et al. 2012). This can be attributed to the disturbance regime-productivity relationships, as higher fuel accumulation occurs in areas with higher productivity, fire regimes with more frequency and intensity occur. Distinctively, our study area is characterized by a humid Mediterranean climate with higher productivity than similar areas of the eastern Mediterranean region. Therefore, we suggest that relatively higher disturbance frequency derived by high productivity might have acted as a filter for the functional types of plant communities and resulted in the current resprouter-dominated vegetation structure of our study area.

The functional grouping based on growth form (or life form) can be meaningful to describe the trends in vegetation through the succession in Mediterranean old fields (Bonet and Pausas 2004) and in grazed or

Fig. 3 Cover change dynamics of different regeneration modes through post-fire succession. Each point represents the cover of 1-ha plot, estimated as average of five quadrats 100 m^2 in size. Functional groups were shaped according to the presence (+) or absence (−) of resprouting ability (R) and propagule persistence (P) in species. The "R−P+" group was further separated based on the presence of a soil or canopy seed bank in species (see "Methods" section for details). Fitted lines or curves are significant ($p < 0.01$) linear or nonlinear regressions. Regression equations and analysis are based on log-transformed data
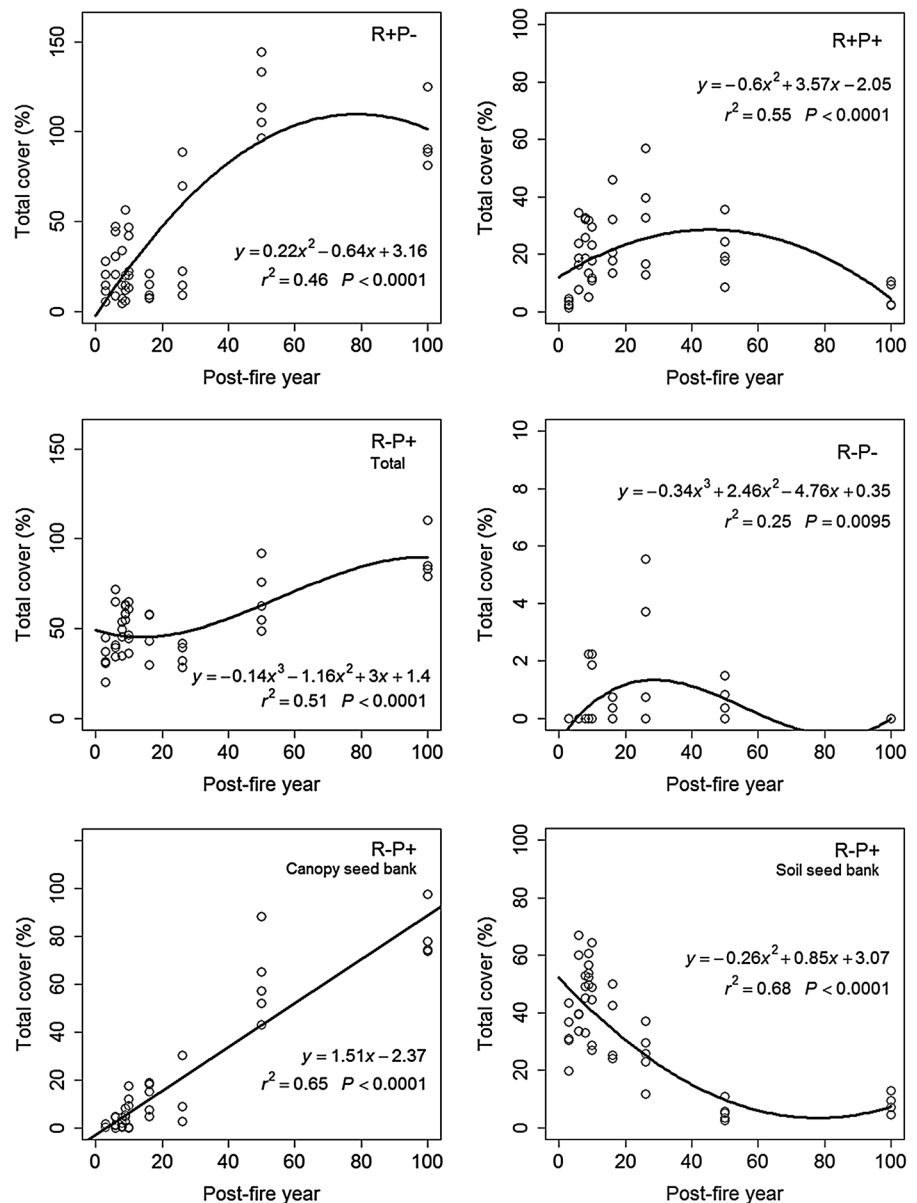
harvested shrublands (Carmel et al. 2001; Koniak and Noy-Meir 2009). In the case of post-fire successions, however, it is hard to use growth/life form effectively to reveal significant general trends in vegetation (e.g., Chapman and Crow 1981; Trabaud 1983; Capitiano and Carcaillet 2008). This is due to the fact that fire response of Mediterranean woody species is determined by regeneration traits, especially the ability of resprouting and post-fire establishment (Paula and Pausas 2008). Our results suggest that life form alone is not an explanatory functional grouping system for post-fire dynamics of Mediterranean woody plant communities. The use of growth/life form grouping may be advantageous to distinguish the dynamics of both woody and herbaceous species (Trabaud 1983; Keeley et al. 2006). Even in that case, however, regeneration mode must be used with growth form to understand the actual dynamics proceeding Mediterranean Basin fire-prone ecosystems.

The similarity of long-term dynamics of the species belonging to the same regeneration mode is principally due to the life-history traits they shared (Table 1). For instance, obligate resprouter species have a long life span (in most cases more than

Table 1 Key life-history traits of the functional groups based on regeneration mode considered in the present study (sensu Pausas 1999a; Pausas et al. 2004). P is propagule persistence (+ is propagule-persister, − is propagule-non-persister), R is resprouting ability (+ is resprouter, − is non-resprouter), *sb.* seed bank, *fire-dep.* fire dependent, *mid.* intermediate

Life-history traits	Regeneration mode				
	P−R+	P+R+	P+R− soil sb.	P+R− canopy sb.	P−R−
Resprouting capacity	High	Mid.	No	No	No
Seed germination	Fire-free	Fire-dep.	Fire-dep.	Fire-dep.	Fire-free
Seed bank formation	No	Yes/no	Yes	Yes	No
Recruitment of seedlings	Fire-free	Fire-dep.	Fire-dep.	Fire-dep.	Fire-free
Early post-fire years	Low	Mid.	High	High	High
Later	Mid.	Low	Low	Low	Low
Longevity	Long	Mid.	Short	Long	Short
Growth rate	Low	Mid.	High	Low	High
Shade tolerance	High	Low	Low	Low	Low

200 years), they can tolerate shade for germination or growth, and their seed germination and seedling recruitment are independent from fire, besides their high resprouting ability (Bond and Midgley 2001; Pausas et al. 2004; Paula and Pausas 2008. These traits clearly explain the increase of the cover (our study), density (Capitiano and Carcaillet 2008) or phytomass (Trabaud 1991) of obligate resprouters as the succession proceeds. On the other hand, obligate seeders with a soil seed bank have no resprouting capacity and are fire dependent in seed germination and seedling establishment (Moreira et al. 2010). However, their seedling establishment is restricted to early post-fire years, and their longevity is short. Along with their intolerance to shade and the increase of vegetation cover by obligate resprouters and obligate seeders with a canopy seed bank in the burned areas through time, the long-term dynamics of obligate seeders with a soil seed bank are shaped, with a stand decline 15–20 years after fire (Roy and Sonié 1992), and with a decrease in cover through the succession (Schiller et al. 1997; Tavşanoğlu and Gürkan 2005; Baeza et al. 2011). Obligate seeders with a canopy seed bank (represented only by *P. brutia* in our case) show a different trend even though they share many traits with obligate seeders with a soil seed bank. The points that the two groups differentiated are the seed bank location (soil vs. canopy), longevity, and growth rate (Table 1). Although there is a reduction in tree density with successional time (Tsitsoni et al. 2004), the relatively longer life span of *Pinus* (ca. 150 years) allows the individuals of this species to persist more

than 100 years until the next fire occurs and to dominate the plant community in later periods of the succession. Facultative resprouters are found at an intermediate position between obligate seeders and obligate resprouters for many life-history traits. Although post-fire resprouting and seedling recruitment can both be observed in facultative resprouters, the lack of tolerance to shade and medium-length longevity shapes their post-fire dynamics. For instance, individuals of *E. manipuliflora* and *Sarcopoterium spinosum* can survive up to 40 (Lloret et al. 2003) and 15 years (Seligman and Henkin 2002), respectively, and this difference determines their peak and decreased time of cover during the succession. The importance of life-history traits has long been known to differentiate between the resprouting and seeding syndromes in Mediterranean ecosystems (Keeley and Zedler 1978). The need for using several life-history traits simultaneously to predict the success of these two syndromes in Mediterranean environments was also pronounced (Pausas 2001). Indeed, there is an obvious trade-off in regeneration traits between resprouters and non-resprouters in the Mediterranean Basin (Paula and Pausas 2008). Our results support these conclusions, and suggest that a few life-history traits can be effectively used to explain the long-term dynamics of Mediterranean Basin woody species with different regeneration modes.

The most appropriate modeling approach to predict Mediterranean Basin vegetation dynamics seems to be the ones based on life histories (Pausas 1999b; Mouillot et al. 2001). The results of our study are in

accordance with the simulation models based on regeneration mode and life-history traits of Mediterranean Basin species (Pausas 1999a; Lloret et al. 2003), as we found cover change trends similar to those suggested for long-term fire-free periods. In conclusion, we suggest that regeneration mode must be a major component of any vegetation or forest stand dynamics model in the Mediterranean Basin. This result has important implications for the management of Mediterranean Basin ecosystems, and can potentially be extrapolated to other Mediterranean-type fire-prone ecosystems.

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