

Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities

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Summary

1. Many Mediterranean plant species persist after fire because their seeds are protected from the heat of the fire (e.g. hard-coated seeds, serotinous cones), thus permitting rapid post-fire recruitment. For simplicity, this trait will hereafter be called **P** and its two possible phenotypes **P+** (seeder) and **P–** (non-seeder).

2. Because **P+** appears in a narrow taxonomic spectrum and confers persistence under high fire frequencies, we test the extent to which communities with different fire histories have different phenotypic and phylogenetic structures. Specifically, we compare coastal vegetation growing in a warm and dry Mediterranean climate subject to high fire frequency (HiFi vegetation) with montane vegetation subject to a subhumid climate where fires are rare (LowFi) under the hypothesis that **P+** species will be over-represented in HiFi communities, thus producing phenotypic and phylogenetic clustering.

3. Trait conservatism on **P** is evaluated by testing the presence of a phylogenetic signal, phenotypic clustering is tested by correlating co-occurrence and phenotypic distance matrices, and the phylogenetic structure is evaluated by testing whether the phylogenetic distances between species in each community are different from those expected by chance.

4. The results suggest that: (a) **P** is a strongly conserved trait; (b) co-occurring species have similar **P** phenotypes (phenotypic clustering); and (c) the phylogenetic structure in HiFi vegetation is significantly clustered while LowFi vegetation tends to be overdispersed.

5. *Synthesis*: Fire is a strong driving force in assembling HiFi communities while other forces, such as competitive interactions, are the main assembly mechanisms in LowFi communities. This result supports the role of recurrent disturbances as filters driving phylogenetic community structure.

Key-words: evolutionary filtering, fire regime, phylogenetic structure, plant traits, post-fire recruitment, seeders

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Introduction

Plant populations of many Mediterranean species persist after the occurrence of fires due to their capacity to form a seed bank that resists fire, and thus allows post-fire recruitment (Keeley & Fotheringham 2000). This resistance to the heat of a fire can be conferred by different properties such as the hard-coating of many seeds (soil seed banks) or the protection of the seeds by

cones (canopy seed banks; Lamont *et al.* 1991). These species recruit quickly after a fire and, as such, they are often called seeders, recruiters or propagule (seed)-persisters (Naveh 1975; Keeley 1991, 1998; Pausas 1999; Pausas *et al.* 2004). In many cases, fire (i.e. fire-related effects such as heat or smoke) may trigger germination by breaking seed dormancy, or it may trigger seed release by opening cones (Keeley & Fotheringham 2000). For simplicity, we refer to this trait collectively as **P** and to the two possible phenotypes (states of the trait) as **P+** (seeder) and **P–** (non-seeder) (Pausas *et al.* 2004).

In the Mediterranean Basin the **P+** state appears in a narrow taxonomic spectrum (Pausas & Paula 2005;

Pausas *et al.* 2006a) that includes many Fabaceae and Cistaceae (Herranz *et al.* 1998; Herranz *et al.* 1999), and therefore we could expect P to be evolutionarily conserved (i.e. closely related species share the same P state because of common ancestry). Likewise, other physiological and morphological traits would also be shared through common ancestry, resulting in strong competitive interactions among these closely related species. If P+ is an important trait for persisting in fire-prone communities, then the fire-filtering process becomes strongly relevant as a force for community assembly. In fire-prone environments, based on the evidence that P+ species are favoured by fire, we expect fire to act as an environmental filter clustering the P+ phenotype. For instance, the proportion of P+ species increases with short fire intervals in Australian heathlands (Pausas *et al.* 2004), and with fire-prone conditions in the Mediterranean Basin (Lloret *et al.* 2005). Furthermore, there is a bulk of information (see review by Keeley & Fotheringham 2000) suggesting that many P+ species are favoured by fire because their germination is stimulated by fire-derived factors (e.g. heat, smoke, charred wood). On the other hand, in communities with low fire frequency, P+ may not be relevant for persistence, and competition may be the main force structuring communities. Following the framework proposed by Webb and collaborators (Webb *et al.* 2002; Cavender-Bares *et al.* 2004; see also Anderson *et al.* 2004), in communities where the fire filtering mechanism is the dominant assembly process, the phylogenetic structure of the community should be clustered; in other words, coexisting species with a conserved trait should be closely related. In contrast, in the absence of fire as a filter, low fire frequency communities should be shaped by other forces, such as competitive interaction (but see also neutralism and facilitation; Hubbell 2001; Valiente-Banuet & Verdú in press). Such

communities should therefore be characterized by phylogenetic overdispersion, i.e. coexisting species with a conserved trait should not be closely related so as to avoid niche overlap. Indeed, a strong relationship between niche and post-fire regeneration strategies has been shown, with seeders often recruiting in open microsites (Keeley 1998), such as those caused by recurrent fires, and resprouters being dependent upon nurse plants to establish (Pausas *et al.* 2006b; Valiente-Banuet *et al.* 2006). Furthermore, such niches are highly conserved through evolutionary time (Valiente-Banuet & Verdú in press).

To test the role of fire as a filtering mechanism for trait P, we studied the evolutionary conservatism of P as well as the phenotypic and phylogenetic structure on nine sites belonging to two Mediterranean vegetation types with different fire histories. Specifically, we compared coastal vegetation growing in a warm and dry Mediterranean climate subject to high fire frequency (hereafter HiFi communities) with montane vegetation subject to a subhumid climate where fires are rare (hereafter LowFi communities). Trait conservatism on P is evaluated by testing the presence of a phylogenetic signal (Blomberg *et al.* 2003), phenotypic clustering is assessed by testing whether similarity of P was related to species co-occurrence within communities (Legendre *et al.* 1994; Cavender-Bares *et al.* 2004), and the phylogenetic structure is evaluated by testing whether the phylogenetic distances between species in each community are different from those expected by chance (Webb 2000).

Methods

STUDY AREA AND DATA

We selected nine sites located in the eastern Iberian Peninsula (Spain, west Mediterranean Basin; Fig. 1),

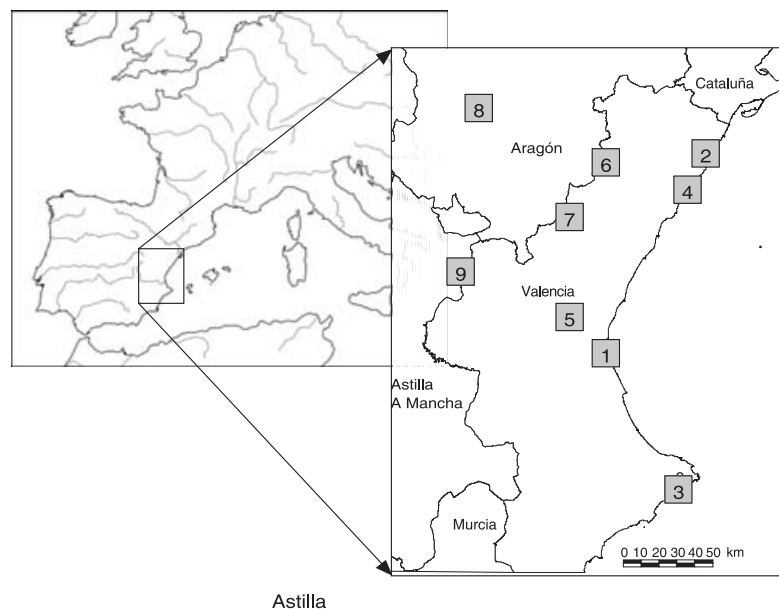


Fig. 1. Location of the nine sites within the study area.

Table 1. Location, characteristics and source of the species information for the nine sites studied. T, mean annual temperature (°C); P, annual precipitation (mm); carbonated, proportion of carbonated bedrocks expressed as 1 (100%), 2 (85–95%), 3 (50–60%); size, size of the study site (ha)

Community	Site	Locality	T	P	Carbonated	Size	Source
HiFi	1	El Saler	17.5	464	1	900	Vizcaino & Mateo (1990)
HiFi	2	Baix Maestrat	18.8	577	1	48 500	Villaescusa (2000)
HiFi	3	Montgó	17.3	674	1	2 500	Stübing & Estévez (1990)
HiFi	4	Plana Alta	15.7	641	2	36 600	Tirado (1998)
HiFi	5	Calderona	15.9	566	2	1 800	Crespo (1989)
LowFi	6	Palomita y Bovalar	11.0	631	1	1 800	Pitarch (1995)
LowFi	7	Penyagolosa	5.3	843	2	1 100	Vigo (1968)
LowFi	8	Albarracin	8.7	789	3	70 000	Barrera (1983)
LowFi	9	Mira y Talayuela	13.2	538	3	67 000	Mateo (1983)

corresponding to five replicates of HiFi and four of LowFi treatments (Table 1). Independence of the sites was ensured because sites were sufficiently separated so that single fires do not burn two sites. HiFi areas correspond to coastal vegetation from sea level up to about 800 m a.s.l., with a warm and dry Mediterranean climate (fire-prone ecosystems), in which fuel loads are high enough to maintain a high frequency of crown fires. LowFi areas correspond to montane Mediterranean vegetation with a subhumid climate occurring at higher altitudes and farther inland; the climate is colder and moister and fires are rare. In the study area, fire is strongly linked to climatic conditions, specifically to drought (Piñol *et al.* 1998; Pausas 2004); furthermore, recent fire history information shows that more than 50% of the study area dominated by HiFi burned at least once during the 1978–2001 period, while for LowFi, this proportion was about 15% (Abdel Malak 2003). General climatic and fire characteristics of the study area can be found in Pausas (2004).

We selected the most representative woody species (chamaephytes and phanerophytes) of the shrublands and woodlands of the study area (regional species pool). Each species was assigned a qualitative state to the trait P that indicates whether or not its seeds persist after fire on the basis of field (post-fire germination) evidences and experimental germination treatments (heat and smoke treatments). This information was obtained from an ongoing data base compilation on plant traits for Mediterranean ecosystems (Pausas & Paula 2005). Thus species with evidence of post-fire seed persistence were classified as P+ (seeder or propagule-persister species) while species with evidence of no post-fire persistence were classified as P-. In this way, we identified 46 species with post-fire seed persistence (P+) and 43 species without this attribute (P-). We assigned the presence or absence of each species on each of the nine sites based on local floras (Table 1, Fig. 2). Species ranked as very rare or naturalized were not considered.

Climatic and soil characteristics have been claimed to be associated with the differential representation of post-fire strategies, with seeder species being more abundant in dry and infertile sites (Knox & Clarke

2005; Lloret *et al.* 2005; Pausas & Bradstock 2007). As an increase of the seeder proportion is expected to increase the phenotypic and phylogenetic clustering within communities, then climatic and soil characteristics may also explain the phylogenetic structure of the communities. To explore these alternatives we compiled climatic data (mean annual temperature and annual precipitation) from the nearest climatic stations to each site (Table 1). As the presence of carbonates in the soil may limit soil fertility (Marschner 1995), we use the proportion of carbonated bedrock types estimated from local bedrock maps. Three different ranges were found: 100%, 85–95% and 50–60% (Table 1).

PHENOTYPIC ANALYSIS

We evaluate whether co-occurring species have similar P phenotypes (phenotypic clustering) by correlating co-occurrence and phenotypic distance matrices using a Mantel test (1000 iterations; Legendre *et al.* 1994; Cavender-Bares *et al.* 2004). Pairwise values of species co-occurrence in the nine sites were calculated using a binary distance index. Similarly, the phenotypic distance matrix was computed by calculating the pairwise binary distances between P states of the species. These analyses were run using the ADE4 software, as implemented in R (Thioulouse *et al.* 1996; R Development Core Team 2007).

PHYLOGENETIC ANALYSIS

A phylogenetic tree was assembled for the 89 species in our data set (Fig. 2) with the help of the Phylomatic package as implemented in Phylocom 3.41 (Webb *et al.* 2005). Thus, we obtained a working phylogenetic tree after matching the genus and family names of our study species to those contained in the angiosperm megatree (version R20050610.new). This megatree follows the work of the Angiosperm Phylogeny Group, which is constantly changing (Stevens 2001) and includes adjusted branch lengths. The adjustment method takes the age estimates for major nodes in the tree from Wikström *et al.* (2001) and distributes undated nodes evenly between nodes of known ages.



Fig. 2. Phylogenetic tree of the species considered, including the state of P in the tips (P+ and P– in black and white squares, respectively) and the presence-absence matrix (black and white squares, respectively) for the five HiFi and the four LowFi sites studied (see Table 1 for details of the sites).

Evolutionary conservatism in the P trait was analysed by evaluating the existence of a phylogenetic signal in our tree. To ensure that the conservatism of P is not a reflection of the local filtering processes we further evaluate the phylogenetic signal in a worldwide data set (from Pausas *et al.* 2004) that includes 1039 species. There is evidence of little correspondence between the different methods for testing trait conservatism (Webb *et al.* 2002); thus we used two different methods. The first method compares the correlation value between the phylogenetic and the trait distance matrices against the distribution generated by a null model in which the tips of the phylogeny were randomly

reshuffled 1000 times (Legendre *et al.* 1994; Cavender-Bares *et al.* 2004). The second method (Maddison & Slatkin 1991) investigates whether the minimum number of evolutionary steps between P+ and P–, based on parsimony reconstruction, occurred fewer times than expected by chance under a null model in which the data were reshuffled 1000 times across the tips of the phylogeny. Parsimony reconstruction and the null model were run in the Mesquite 1.12 program (Maddison & Maddison 2006).

The phylogenetic structure (phylogenetic clustering vs. overdispersion) of the HiFi and LowFi communities was tested by comparing the mean phylogenetic

distance (MPD) of the species inhabiting each of the nine sites against the MPD values obtained under a null model. The null model was constructed by reshuffling the species labels across the phylogenetic tree assembled as explained above. For $\alpha = 0.05$, a P -value < 0.025 indicates a significant clustering while a P -value > 0.975 indicates a significant overdispersion (Webb *et al.* 2005). These analyses were run with the help of the *comstruct* algorithm implemented in Phylocom 3.41 (Webb *et al.* 2005). Other, more complex, null models, as implemented in this software, were also tested and the results did not differ from the simplest model. To account for the possible different species richness due to different sizes of the study sites, we calculated the net relatedness index (NRI, Webb *et al.* 2005), which is a standard measure of the phylogenetic structure of the communities, as follows: $NRI = -(\text{MPD} - \text{rndMPD})/\text{sd.rndMPD}$, where sd.rndMPD is the standard deviation of the 999 random MPD (rndMPD) values. Thus, NRI standardizes the differences between the average phylogenetic distances in the observed and null communities by the standard deviation of phylogenetic distances in the null communities (Webb *et al.* 2005). NRI increases with increasing clustering and becomes negative with overdispersion (Webb *et al.* 2002). Furthermore, we tested the extent to which NRI values covaried with both fire regime (HiFi vs. LowFi), climatic (mean annual temperature and precipitation) and soil fertility (percentage of carbonated bedrock) variables. We also tested if NRI was dependent on the size of the study sites.

Results

P+ species are represented on all sites and in both HiFi and LowFi communities. The percentage of P+ species was significantly higher on HiFi sites than on LowFi ones (mean and SD, $56 \pm 2\%$ vs. $44 \pm 4\%$, respectively; ANOVA, $F_{1,7} = 46.7$; $P = 0.0002$). Thus, there is a tendency for P+ to be more common in HiFi than in LowFi. Furthermore, the similarity of P was related to species co-occurrence within communities as proved with the

significant correlation between co-occurrence and phenotypic distance matrices (P -value, 0.012; Mantel test). All these results indicate the phenotypic clustering of P.

We found a strong phylogenetic signal for P when using either the data from our sites or the compiled data worldwide. The results were the same using either the method based on the correlation between distance matrices (all simulated correlations were lower than the observed correlation for both our study sites and for the worldwide data base; $P < 0.001$) or the method based on the parsimony steps between P+ and P- (12 and 77 steps for our sites and the worldwide data base, respectively; both values were significantly lower than expected from their respective null models, 33 (range = 24–42) and 135 (range = 128–136) expected parsimony number of steps; both $P < 0.001$). Thus, P is a strongly conserved trait.

The mean phylogenetic distances and the net relatedness index are strongly contrasted in HiFi and LowFi communities, with high NRI values (1.47 to 3.85) on HiFi sites and low values (–1.29 to –2.00) on LowFi sites (Table 2). The mean phylogenetic distances were significantly shorter or marginally significantly shorter than expected by chance in the HiFi communities, suggesting that the species there are phylogenetically clustered (Table 2). In contrast, there is no evidence of clustering in the LowFi communities. In fact, mean phylogenetic distances of LowFi communities tend to be longer than expected by chance, which suggests a phylogenetic overdispersion, as indicated by the negative net relatedness index and the P -values close to significance (Table 2). This pattern is driven by the over-representation of closely related seeders in HiFi sites as it is shown in the high and positive correlation between NRI and proportion of the seeders ($r = 0.84$, $P = 0.004$).

Among the alternative explanations for fire that could explain the phylogenetic structure of the communities, only temperature ($F_{1,7} = 9.4$, $P = 0.01$) is related to NRI; however, the fire regime (HiFi vs. LowFi) remains significant when both fire and temperature are

Table 2. Number of taxa (N), observed (MPD) and randomized (rndMPD) mean phylogenetic distances, standard deviation of the rndMPD (sd.rndMPD), and the net relatedness index (NRI, Webb 2000). The P -value and the suggested pattern of the phylogenetic structure for each study site reflects the departure of the observed MPD value from the null model

Community	Site	N	MPD	rndMPD	sd.rndMPD	NRI	P	Pattern
HiFi	1	47	272.5	306.2	21.29	1.58	0.057	Clustered
HiFi	2	77	293.3	307.0	9.35	1.47	0.095	Clustered
HiFi	3	64	282.3	306.9	14.99	1.60	0.073	Clustered
HiFi	4	80	281.2	307.4	7.68	3.41	0.004	Clustered
HiFi	5	75	275.5	307.2	10.20	3.11	0.004	Clustered
Overall		85	286.5	307.1	5.37	3.85	0.005	Clustered
LowFi	6	33	364.6	306.3	29.21	–2.00	0.987	Overdispersed
LowFi	7	50	335.9	307.4	20.00	–1.43	0.926	Overdispersed
LowFi	8	44	340.2	308.2	23.38	–1.37	0.919	Overdispersed
LowFi	9	64	325.4	306.6	14.49	–1.29	0.904	Overdispersed
Overall		71	325.0	306.8	12.17	–1.49	0.934	Overdispersed

included in the model ($F_{1,6} = 33.8$, $F_{1,6} = 19.1$, $P < 0.003$). Neither soil ($F_{2,6} = 1.4$, $P = 0.3$) nor rainfall ($F_{1,7} = 1.5$, $P = 0.2$) are significantly related to NRI. Finally, the NRI values are not related to the size of the study sites ($F_{1,7} = 0.3$, $P = 0.6$).

Discussion

The post-fire persistent seed bank (P) is a conserved trait, and communities under different fire regimes showed different phylogenetic structures. That is, we found significant phylogenetic clustering in communities with high fire frequency and overdispersion in those with low fire frequency. Thus, HiFi communities 'sample' closely related species that share the same state of P due to common ancestry (phenotypic clustering or attraction). This is consistent with the habitat-filtering scenario proposed by Webb *et al.* (2002; see also Cavender-Bares *et al.* 2004). In situations where fires are uncommon and P+ is not relevant for persistence (LowFi), the species are less related than expected by chance (phylogenetic overdispersion), reflecting a scenario where other factors like competitive exclusions have shaped the community assembly (Webb *et al.* 2002; Anderson *et al.* 2004). That is, because communities are not constrained to 'sample' P+ species, this trait is not phenotypically clustered among coexisting species.

P is an evolutionary conserved trait across a phylogenetic megatree including species from different continents and taxonomic orders. Such trait conservatism is especially evident in the Mediterranean flora given the narrow taxonomic distribution of P+ species (Pausas *et al.* 2006a). It is well known that P+ species are concentrated in a few families, mainly the Fabaceae (Arianoutsou & Thanos 1996; Herranz *et al.* 1998), Cistaceae (Thanos *et al.* 1992; Herranz *et al.* 1999), and some Lamiaceae. This taxonomic pattern is somewhat different from other Mediterranean climate areas, probably reflecting different historical processes (Pausas *et al.* 2004). For example, there is evidence of P+ species predating the appearance of Mediterranean fire-prone conditions in the Californian flora but not the Mediterranean Basin flora (Pausas *et al.* 2006a).

In the Mediterranean Basin, the P+ state is very rare in old lineages; it appeared concomitantly with fire during the Quaternary (Pausas & Verdú 2005). Herrera (1992) suggested a high diversification of Quaternary Mediterranean flora, and most P+ species correspond to this flora (Verdú 2000). It is tempting to conceive of fire as a force that triggers diversification (Wells 1969; Cowling 1987; Ojeda 1998; but see Verdú *et al.* in press). If fire is indeed a diversification trigger for P+ species, then an over-representation of P+ lineages (e.g. *Cistaceae*, *Fabaceae*) would occur in HiFi and the phylogenetic clustering would increase. This would mean that the phylogenetic structure of communities reflects not only the filtering processes but also the force driving the diversification of P+ species. Accordingly,

community assembly processes represent a historical legacy and thus our results need to be interpreted not only in terms of fire filtering but also as an adaptive evolution to fire.

Soil fertility has also been invoked as a factor controlling the relative abundance of different post-fire strategies, with seeders being less abundant in high fertility soils (Knox & Clarke 2005). With our crude estimation of soil fertility we cannot support this prediction, and more accurate data on soil fertility are needed to unambiguously test this hypothesis. Other characteristics related to Mediterranean conditions, such as droughts, have been considered as a selective factor shaping plant communities. In arid conditions, P+ may also be selected (Jurado & Westoby 1992; Auld 1995); however, in such conditions fire is limited by fuel loads and continuity (Pausas & Bradstock 2007). In our HiFi, where P+ is selected, community fuels are high enough to sustain frequent crown fires, and thus arid conditions are not expected to be an important driving force for P+ species. Furthermore, we found that fire regime significantly explained a proportion of the NRI variability even after statistically controlling for the climatic variables.

In conclusion, our results strongly support the role of fire in shaping the phylogenetic structure of communities. It would be interesting to study to what extent this pattern also occurs in other fire-prone ecosystems with different evolutionary histories.

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