COMMUNITY ECOLOGY - ORIGINAL PAPER

Soil shapes community structure through fire

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Abstract Recurrent wildfires constitute a major selecting force in shaping the structure of plant communities. At the regional scale, fire favours phenotypic and phylogenetic clustering in Mediterranean woody plant communities. Nevertheless, the incidence of fire within a fire-prone region may present strong variations at the local, landscape scale. This study tests the prediction that woody communities on acid, nutrient-poor soils should exhibit more pronounced phenotypic and phylogenetic clustering patterns than woody communities on fertile soils, as a consequence of their higher flammability and, hence, presumably higher propensity to recurrent fire. Results confirm the predictions and show that habitat filtering driven by fire may be detected even in local communities from an already fire-filtered regional flora. They also provide a new perspective from which to consider a preponderant role of fire as a key evolutionary force in acid, infertile Mediterranean heathlands.

Keywords Community phylogenetics · Fire traits · Mediterranean heathlands · Nutrient-poor soils · Phenotypic clustering

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Introduction

The ecological advantage conferred by a trait (or set of traits) on individual members of a species under a given set of environmental conditions allows the species to occupy that particular habitat (i.e. environmental or habitat filtering). This habitat filtering is one of the key processes structuring community assemblages (van der Valk 1981; Keddy 1992; Webb et al. 2002).

In many ecosystems, recurrent wildfires constitute a major selecting force in shaping the structure and function of plant communities (Bond and van Wilgen 1996; Bond and Keeley 2005; Pausas and Keeley 2009). All Mediterranean-type climate regions, except the Chilean one, include fire-controlled plant communities (Cowling et al. 1996), which are characterized by species having traits that ensure the persistence of populations under recurrent fires (Keeley 1986). In woody plants, two basic fire-associated traits have been traditionally described: resprouting ability (resprouter/non-sprouter), and fire-induced germination [fire-induced (P+)/non-fire-induced germination (P−); Pausas et al. 2004; Pausas and Verdú 2005]. P+ is widely accepted as an adaptive trait state to the recurrent presence of fire (Bond and van Wilgen 1996; Keeley and Bond 1997; Pausas et al. 2006).

At the regional scale, frequent fires favour an over-representation of P+ species in woody plant communities of the Mediterranean basin (Verdú and Pausas 2007). This over-representation of a particular phenotype (i.e. phenotypic clustering) is a consequence of habitat filtering of those species having the focal trait state (P+). When the trait is evolutionarily conserved, phenotypic clustering subsequently determines phylogenetic clustering (Webb et al. 2002). Indeed, the fire-induced germination trait (P+/−) is strongly conserved in the woody flora of the Mediterranean

Basin and woody plant communities under high fire frequency show both phenotypic and phylogenetic clustering (Verdú and Pausas 2007; Pausas and Verdú 2008) Cavender-Bares et al. (2004) found strong phenotypic clustering among co-occurring *Quercus* species sharing fire-related traits in Floridian oak communities, thus evidencing habitat filtering.

Although this pattern of fire-driven phenotypic and phylogenetic clustering of Mediterranean plant communities has been reported at the regional scale, little is known at the local, landscape scale, where marked differences in the fire regime may also occur (e.g. van Wilgen et al. 1990; Clarke 2002). At this scale, soil features such as rockiness (Clarke and Knox 2002) or fertility (e.g. Kellman 1984) may cause heterogeneous burn patterns and thus determine divergent fire regimes in terms of frequency and severity. Indeed, soil fertility decreases the flammability of plant fuels and thus lessens fire propensity (e.g. frequency) of plant communities (Kellman 1984; Orians and Milewski 2007). In contrast, plants on acid, nutrient-poor soils accumulate large amounts of polyphenolic compounds (Northup et al. 1998; Kraus et al. 2003), most of which are flammable (Orians and Milewski 2007). They also hinder litter decomposition rates and may constitute a chemical defence against herbivory (Hättenschwiler and Vitousek 2000; Kraus et al. 2003), thus favouring the retention of dead branches in the canopy and hence the probability of ignition and spread of fire (Schwilk 2003).

Here, we test the prediction that, at the landscape level within a region characterized by the recurrent occurrence of fire, woody plant communities on acid, infertile soils should exhibit more pronounced phenotypic and phylogenetic clustering patterns than neighbouring communities on non-acid, fertile soils. This may be so because infertile plant communities should burn comparatively more often owing to their higher flammability. We focused on Mediterranean shrubland communities from two markedly different soil types frequent in Los Alcornocales Natural Park, at the northern side of the Strait of Gibraltar (southern Spain). These shrub communities occur in coastal and subcoastal mountains under mild Mediterranean conditions and the region is characterized by a high fire incidence (Ojeda et al. 1995, 2000). They are thus assembled from a fire-filtered flora at the regional scale (Verdú and Pausas 2007). This scenario provides an excellent opportunity to explore whether: (1) a presumably spatial variability in fire incidence at the landscape scale is reflected in differences in the phenotypic and phylogenetic structure of local communities; and, if so, whether (2) fire may still act as a filter in an already fire-filtered regional flora. By using detailed inventories and functional information of the woody flora and soil data in local community samples we compare the structure of shrubland communities in two edaphically contrasting

habitats under the hypothesis that acid, nutrient-poor soils shape the phenotypic and phylogenetic community structure through fire.

Materials and methods

Study area

The northern (European) side of the Strait of Gibraltar region, at the westernmost point of the Mediterranean Basin, stands out within the Mediterranean for the singularity of its plant biodiversity (Rodríguez et al. 2008). Most of this region lies within Los Alcornocales Natural Park (ca. 1,700 km^2) and has a rugged topography, albeit no high elevations (500–1,100 m asl). These mountain chains are mainly formed by folded siliceous Oligo-Miocene sandstone (González-Donoso et al. 1987). In mountain tops and ridges, this sandstone gives rise to very acid, weathered soils, characterized by a high content of soluble aluminium (Ojeda et al. 1995, 1996), an indicator of severe nutrient deficiency (Woolhouse 1981; Prasad and Power 1999; Schroth et al. 2003). These acid, infertile soil patches are abundant in the region, surrounded by non-acid and more fertile limestone and/or marl-derived soils (Ojeda et al. 1996). Acid and infertile sandstone soils harbour open heathlands, dominated by fine-leaved, low shrubs, whereas marl and limestone soils are mostly covered by broad-leaved, sclerophyllous shrublands and thickets (Ojeda et al. 1995, 2000).

Floristic, edaphic and functional data

We selected 16 plots, eight on acid, nutrient-poor, sandstone soils (LowFer) and eight on non-acid, fertile, limestone and marl soils (HiFer) from two previous studies (Ojeda et al. 1995; Garrido and Hidalgo 1998). Data on woody species composition in 100-m line transects were obtained for each plot from these two sources, as well as soil pH and soluble aluminium (Table 1), as surrogates for soil fertility (see above; see also Ojeda et al. 1995). LowFer plots were open heathlands while the HiFer plots were sclerophyllous shrublands and thickets. Each species was classified as P+/− depending on the ability of its seeds to resist the action of fire and present fire-cued recruitment on the basis of published information (Paula et al. 2009) and field observations (see Fig. 1). Based on flammability tests of Mediterranean woody species by Elvira-Martín and Hernando-Lara (1989) we were able to ascertain that flammability levels were higher in LowFer community samples (average 79% of high-flammable species) than in HiFer ones (average 53% of high-flammable species; t test $= -5.24$, P-value $= 0.0002$).

Table 1 Soil pH values and concentration of soluble aluminium (in p.p.m.) and percentage of fire-induced-germination (%P+) species in the eight acid, nutrient-poor, sandstone soils (*LowFer*) and eight non-acid, fertile, limestone and marl soils (*HiFer*) plots

Plot	Soil pH[a]	Aluminium[a]	%P+
LowFer			
L1	4.9	239	76.2
L2	4.7	486	100.0
L3	4.7	49	81.3
L4	4.7	263	88.9
L5	4.9	48	92.3
L6	4.8	69	85.7
L7	5.4	82	60.0
L8	4.3	310	87.5
HiFer			
H1	6.0	0	31.6
H2	6.0	0	18.8
H3	6.4	0	14.3
H4	6.6	0	11.5
H5	6.5	0	30.8
H6	6.5	0	27.3
H7	6.6	0	17.4
H8	7.0	0	20.0

[a] Soil data have been obtained from Ojeda et al. (1995) and Garrido and Hidalgo (1998)

Phenotypic and phylogenetic structure

The phenotypic structure of each community was evaluated by testing whether species with similar P phenotypes co-occurred more often than expected by chance (i.e. phenotypic clustering). The co-occurrence matrix was calculated as the pairwise binary distances between species occurrence in the 16 samples; the phenotypic distance matrix was computed as the pairwise binary distances between P states of the species. A Mantel test correlating co-occurrence and phenotypic distance matrices was run and significance obtained after 1,000 iterations (Legendre et al. 1994; Cavender-Bares et al. 2004) in the ADE4 software for R (Thioulouse et al. 1996; R Development Core Team 2007).

The phylogenetic relationships between the 133 species of the woody flora of Los Alcornocales Natural Park (Coca-Pérez 2001) were established with the help of the Phylomatic2 components (http://www.phylodiversity.net/phylomatic/). These components consist of a database of phylogenetic trees which can be assembled into a megatree by means of a GAWK script named makemega. We used all the trees stored in the phylomatic2 repository plus other trees resolving the relationship within Cistaceae (Guzmán and Vargas 2005), Asteraceae (Bayer et al. 2000), Oleaceae (Wallander
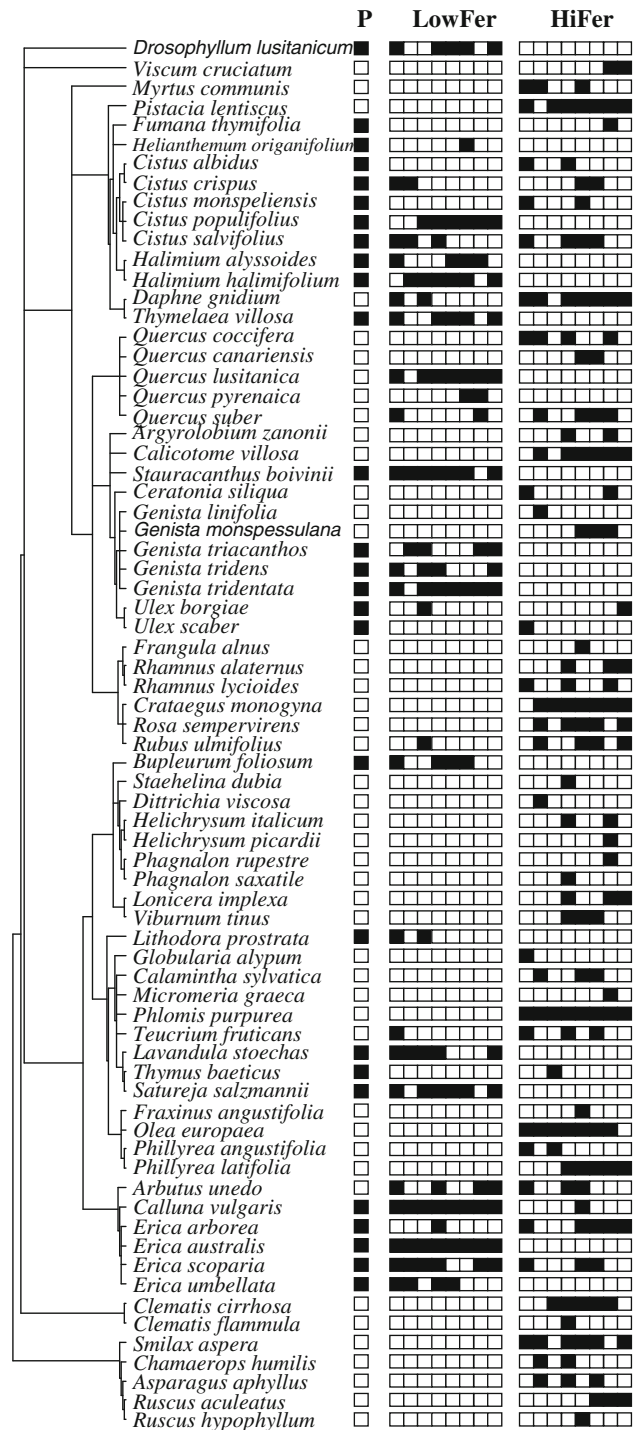

Fig. 1 Phylogenetic tree of the woody species considered, including their fire-induced germination trait states [fire-induced germination (P+; *solid squares*)/non-fire-induced germination (P−; *open squares*)] and the presence (*solid squares*)-absence (*open squares*) matrix for the plots on acid, nutrient-poor soils (*LowFer*) and non-acid, fertile soils (*HiFer*; *n* = 8 each)

and Albert 2000), Ericaceae (Kron and Chase 1993) and Rosaceae (Dickinson's Lab homepage at http://www.botany.utoronto.ca/faculty/dickinson/DickinsonLab.html).

The ordinal level trees were based on the Angiosperm Phylogeny Group data (Stevens 2001). Once we had assembled the megatree, we adjusted its branch lengths with the help of the phylocom BLADJ algorithm, which 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. Finally, our working phylogenetic tree was obtained after matching the genus and family names of our study species to those contained in the angiosperm megatree. All these analyses were run with the Phylocom 4.0 package (Webb et al. 2005).

The phylogenetic community structure was assessed by testing whether the mean phylogenetic distance (MPD) of the species living in each site was significantly different from the MPD values obtained under a null model (i.e. reshuffling the species labels across the phylogenetic tree). An observed MPD significantly lower than the null expectation indicates phylogenetic clustering, while an observed MPD significantly higher than the null expectation indicates phylogenetic overdispersion (Webb et al. 2005). MPDs were standardized to allow comparison among plots by calculating the net relatedness index (NRI; Webb et al. 2005), as NRI = −(MPD − rndMPD)/sd.rndMPD, where sd.rndMPD is the SD of the 999 random MPD (rndMPD) values. NRI increases with increasing phylogenetic clustering (Webb et al. 2002). We also used the mean nearest neighbour distance (MNND), and its standardized form, the nearest taxon index [NTI = −(MNND − rndMNND/sd.rndMNND)] as another metric to test for the phylogenetic structure of the community. All these analyses were run with the help of the comstruct algorithm implemented in Phylocom 4.0.1b (Webb et al. 2005). To ensure the robustness of our results against the topological uncertainty contained in the phylogenetic tree, we randomly resolved the polytomies and re-run the analyses 100 times. We also accounted for the uncertainty in the branch length estimation by adding random noise to the branch lengths; the noise was normally distributed, with variance proportional to current branch length. A variance multiplier of 0.1 was entered to add to branch lengths.

We explored which taxa were responsible for clustering in each community by testing which nodes in the phylogenetic tree had more species than expected by chance. This test was run with the help of phylocom NODESIG algorithm.

Results

The number of woody species in the plots ranged from seven to 27 (Table 2) with an overall of 72 species occurring in the 16 plots (Fig. 1). The percentage of P+ species in LowFer community samples (83.98 ± 12.0%, mean ± SD)

Table 2 Number of taxa (*n*), observed mean phylogenetic distances (*MPD*), mean nearest neighbour distances (*MNND*), and the corresponding standardized indices, i.e. the net relatedness index (*NRI*) and nearest taxon index (*NTI*), for the eight LowFer and eight HiFer plots

Plot	*n*	MPD	NRI	*P*	MNND	NTI	*P*
LowFer							
L1	21	219.42	1.18	0.08	95.02	1.89	0.02
L2	10	198.58	1.25	0.02	81.66	2.38	0.01
L3	16	209.84	1.33	0.02	86.00	2.42	0.00
L4	18	212.14	1.37	0.03	85.82	2.36	0.01
L5	13	219.08	1.02	0.11	121.15	1.38	0.08
L6	14	215.83	1.17	0.06	119.01	1.46	0.07
L7	11	198.28	1.35	0.01	54.46	3.24	0.00
L8	16	217.75	1.14	0.07	95.61	2.05	0.01
HiFer							
H1	19	232.29	0.6	0.37	135.90	0.25	0.41
H2	17	249.16	0.14	0.52	161.96	−0.47	0.69
H3	7	231.79	0.38	0.49	164.17	0.47	0.33
H4	26	252.83	0.02	0.50	120.18	0.61	0.28
H5	27	240.09	0.6	0.31	133.17	−0.08	0.54
H6	23	250.52	0.14	0.47	125.70	0.55	0.31
H7	23	238.37	0.59	0.36	142.79	−0.21	0.59
H8	15	250.63	0.14	0.57	199.16	−1.45	0.91

For other abbreviations, see Table 1

P-values reflect the departure of the observed MPD and MNND values from the null model

was 4 times higher than in HiFer ones (21.45 ± 7.5%; change in deviance = 110, *df* = 1, *P*-value = 0.0001, binomial test; Table 1; Fig. 2a). The species with the same P trait state tended to co-occur more often than expected by chance, as indicated by the significant positive correlation between the phenotypic and co-occurrence distance matrices (*r* = 0.253, *P* = 0.0009; Mantel test).

Regarding the phylogenetic structure of the community, species co-occurring in LowFer samples were more phylogenetically related (lower MPD and MNND; Table 2) than expected under the null model, while this was not true for HiFer samples. Indeed, NRI and NTI values were significantly higher in LowFer than in HiFer communities (*t* = −7.58, *P* < 0.0001 for NRI and *t* = −6.24, *P* < 0.0001 for NTI; Fig. 2b). Differences between HiFer and LowFer in both NRI and NTI remained significant in all the 100 runs accommodating topological and branch length uncertainty.

Clades responsible for the clustering in LowFer plots were families dominated by P+ taxa, such as Ericaceae (five out of eight plots), Cistaceae (three out of eight plots), and Fabaceae (two out of eight plots). Only one LowFer plot showed a clade of P− species (Fagaceae) contributing significantly to phylogenetic clustering.
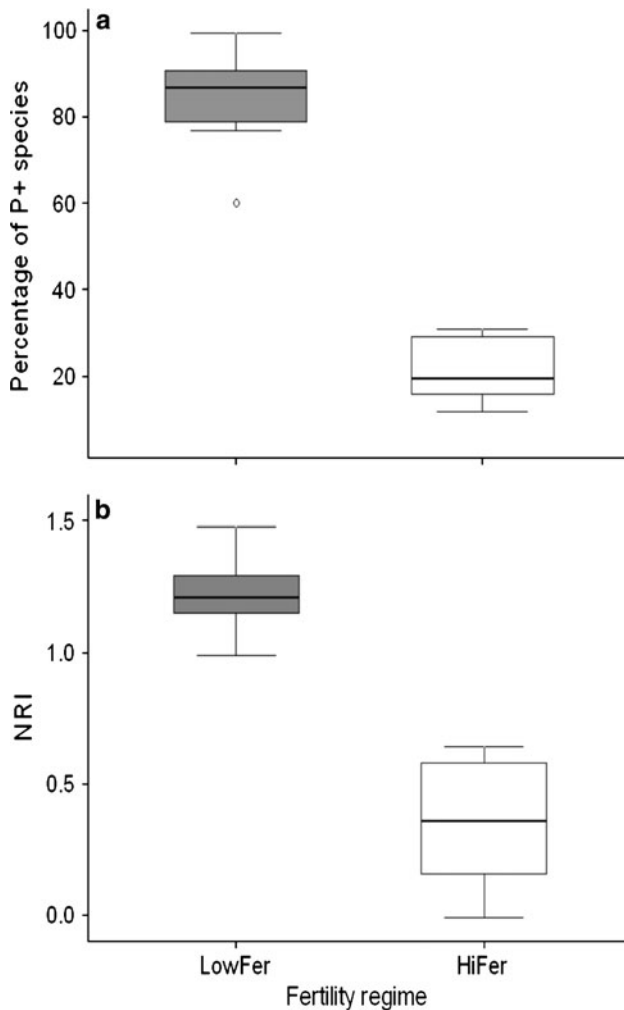
Fig. 2 Box plots of **a** percentage of P+ species and **b** net relatedness index (*NRI*) of the eight plots on LowFer and HiFer (*n* = 8). For other abbreviations, see Fig. 1

Discussion

In this study, we have detected a differential occurrence of P+ species in woody plant communities from contrasting soil fertility conditions in such a way that these species are over-represented in communities on acid, infertile soils. This phenotypic clustering of a fire-related trait allows us to suggest that fire may be acting as an ecological filter by limiting P− and favouring P+ species to enter the LowFer community under high fire frequency. Other independent evidence that soil fertility shapes communities through fire is the differential flammability of woody communities found under different soil fertilities in our study area (see above; see also Ojeda 2001). Indeed, the existence of differences in fire incidence at the landscape scale tightly associated with soil fertility levels has been reported in other regions (e.g. Kellman 1984; van Wilgen et al. 1990; Orians

and Milewski 2007). According to this scenario, our results show clearly that the occurrence of recurrent fires not only acts as a strong habitat filtering force structuring plant communities but, more importantly, that this process may also operate at the local, landscape scale. Similar phenotypes (e.g. P+) co-occur more often than expected by chance in local communities from low-fertility soils in a landscape where high- and low-fertility soils are intermixed. As P is an evolutionarily conserved trait (Verdú and Pausas 2007), such strong phenotypic filtering is reflected in the phylogenetic structure of local communities, in such a way that shrub communities on acid, nutrient-poor soils are phylogenetically clustered, whereas those on non-acid, fertile soils are not.

Finally, we should emphasize that the habitat filtering by fire reported in this study has been detected in local communities from an already fire-filtered regional flora (e.g. see Verdú and Pausas 2007). To our knowledge, this is the first evidence showing that the same environmental factor drives community assembly at two different spatial scales. Previous attempts to separate the determinants of community structure have demonstrated the importance of scale but without considering the environmental factors or traits driving the pattern (Swenson et al. 2006; Helmus et al. 2007).

The extent to which fire may structure plant communities at the local scale depends on the variability of fire-persistence traits in the regional flora from which species are assembled into communities. Regional floras may have low variability in fire traits due to either a strong culling effect of fire-sensitive phenotypes or rapid diversification. For instance, there is an overwhelming dominance of the P+ trait state in Mediterranean-type floras of South Africa and Australia (Pausas et al. 2004; Pausas and Bradstock 2007) as a likely consequence of a high incidence of fire in these regions, at least since the Late Tertiary (Cowling et al. 1996). By contrast, an overall lower incidence of fire in the Mediterranean Basin (Cowling et al. 1996) provides its flora with a higher variability in fire persistence traits from which local communities can sample. Thus, fire may act simultaneously at different spatial scales (i.e. within-regional and between-regional floras) as a major habitat filtering process shaping the phenotypic—and phylogenetic—structure of plant communities.

The incidence of fire in the south-western Iberian Peninsula, dominated by nutrient-poor, acid substrates seems to have been high at least since the Late Pleistocene and not related to human activity (Daniau et al. 2007). Although the phenotypic and phylogenetic structure of local communities has been traditionally treated as the outcome of the ecological sorting of species traits by the environment (Webb et al. 2002), the role of evolutionary diversification and trait divergence is starting to be considered

in community-assembly theory (Prinzing et al. 2008). Hence, the results presented in this study, plus the fact that many P+ species from these poor-soil communities are narrow endemics (Rodríguez et al. 2008), invite consideration of a preponderant role of fire as a key evolutionary force for species living in nutrient-poor Mediterranean heathlands.

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