FIRE REDUCES MORPHOSPACE OCCUPATION IN PLANT COMMUNITIES

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Abstract. The two main assembly processes claimed to structure plant communities are habitat filtering and competitive interactions. The set of species growing in fire-prone communities has been filtered in such a way that species without fire-persistence traits have not successfully entered the community. Because plant traits are evolutionarily conserved and fire traits are correlated with other plant traits, communities under high fire frequency should not include all possible trait combinations, and thus the morphospace occupation by species in these communities should be lower than expected by chance (underoccupied). In contrast, communities under low fire frequency would lack the filtering factor, and thus their underoccupation of the morphospace is not expected. We test this prediction by comparing the morphospace occupation by species in communities located in the western Mediterranean Basin, five of them subject to high fire frequency (HiFi) and four to low fire frequency (LowFi). We first compile a set of morphological and functional traits for the species growing on the nine sites, then we compute the morphospace occupation of each site as a convex hull volume, and finally, to assert that our results are not a product of a random branching pattern of evolution, we simulate our traits under a null model of neutral evolution and compare the morphospace occupation of the simulated traits with the results from the empirical data. The results suggest that, as predicted, there is a clear differential morphospace occupation between communities under different fire regimes in such a way that the morphospace is underoccupied in HiFi communities only. The simulation of a neutral evolutionary model does not replicate the observed pattern of differential morphospace occupation, and thus it should be attributed to assembly processes. In conclusion, our results suggest that fire is a strong community assembling process, filtering the species that have fire-persistent traits and thus assembling phenotypically and phylogenetically clustered communities with vacant zones in the morphospace.

Key words: community structure; fire regime; habitat filtering; niche volume; phenotypic clustering; phylogenetic clustering; plant traits.

INTRODUCTION

The structure of communities depends on abiotic factors as well as on species interaction processes such as competition, predation, and mutualism (Paine 1966, Diamond 1975, van der Valk 1981). In recent years, plant ecology has focused on two community assembly processes (Webb et al. 2002): (1) the advantage a species gains by having a trait that allows it to occupy a given habitat (habitat filtering), and (2) the competitive interactions among species, which limit their long-term coexistence. If traits are evolutionarily conserved (i.e., closely related species share similar traits), species living in communities driven by habitat filtering should be more closely related than expected by chance, while species living in communities driven by competition should be less closely related. In fact, measures of phylogenetic distance among coexisting species have

been used as an indicator for detecting which of these two main processes are dominant in a given community (Webb et al. 2002, Anderson et al. 2004, Cavender-Bares et al. 2004, Slingsby and Verboom 2006, Helmus et al. 2007, Verdú and Pausas 2007).

In fire-prone plant communities (i.e., where fire is a strong evolutionary force), possessing traits that enable a quick and efficient postfire regeneration is fundamental for the success and persistence of populations (Keeley and Zedler 1978, Bond and Midgley 2001, Pausas et al. 2004). The sensitivity of these communities to such traits makes them an excellent framework to test community assembling theories. Indeed, recent work in Mediterranean ecosystems has suggested that communities under high fire frequency show lower phylogenetic distances, and those under low fire frequency show higher phylogenetic distances, than could be expected under a null model (Verdú and Pausas 2007). From these results, it is inferred that habitat filtering is the dominant ecological process assembling communities under high fire frequency, while competition governs communities under low fire frequency.

The morphospace of a community can be defined as the distribution of trait values within a community (Ricklefs and Travis 1980). Given that many plant traits are phylogenetically conserved (Lord et al. 1995, Prizing et al. 2001, Blomberg et al. 2003), the species in communities dominated by habitat filtering processes should not include all possible trait combinations. Under such conditions, the morphospace in the community should be underoccupied (less occupied than expected by chance) or, in other words, phenotypically clustered. This is because habitat filtering can be viewed as a reduction in the range of successful strategies among coexisting species (Keddy 1992, Weiher et al. 1998). At the other extreme, in the absence of a filtering factor, trait combinations should not be restricted and underoccupation of the morphospace is not expected. Thus, by quantifying the morphospace occupied by the species in a community, we can infer whether habitat filtering is a dominant community structuring process (Cornwell et al. 2006).

It has also been suggested that differential morphospace occupation of communities by species may arise simply as a consequence of the dynamics of a branching random walk rather than as a product of an underlying adaptive process (Pie and Weitz 2005). For instance, underoccupation (phenotypic clustering) may be produced when extinction occurs everywhere in the morphospace but speciation occurs next to an extant lineage, which is a plausible scenario given the evolutionary history of Mediterranean Basin flora (Herrera 1992, Pausas and Verdú 2005). Thus, we also need to test whether our observed pattern of morphospace occupation departs from the one obtained under a neutral evolutionary model.

Within this framework, we test the hypothesis that fire regimes are associated with morphospace occupation. More specifically, we predict that high fire frequency communities should be underoccupied while low fire communities should not. Consequently, we test the relative occupancy of the morphospace in Mediterranean ecosystems under contrasted fire regimes by: (1) characterizing the species niches using a set of morphological and functional traits, (2) evaluating whether these niches are evolutionarily conserved (Blomberg et al. 2003), (3) estimating the morphospace occupation by species in each community (Cornwell et al. 2006) for the two different fire regimes considered, and finally (4) testing the association between fire and the morphospace occupation occurring under a neutral model of evolution (Revell et al. 2007).

Methods

We used the presence–absence species matrix from Verdú and Pausas (2007) in the eastern Iberian Peninsula. This data set includes the presence–absence of 89 woody species on nine sites, five occurring in warm and dry coastal Mediterranean climate (<800 m a.s.l. [above sea level]) subject to high fire frequency (HiFi),

and four occurring in a montane area (>800 m a.s.l.) subject to a subhumid climate where fires are rare (LowFi). In the study area, fire is strongly linked to climatic conditions, specifically to drought (Pausas 2004). Indeed, recent fire history information shows that >50% of the study area dominated by HiFi burned at least once during the 1978–2001 period, while for LowFi, this proportion was ~15% (Abdel Malak 2003). Previous analysis showed that the role of fire in the phylogenetic structure of these communities is not confounded by other factors such as climate and soil (Verdú and Pausas 2007).

We characterized the niche of all the species by compiling 11 traits (Table 1; also see Appendix); two were quantitative traits (plant height [m] and seed mass [mg]), and nine were binary traits (spinescence [yes/no], leaf type [sclerophyllous/non-sclerophyllous], leaf habit [evergreen/deciduous], flower size [perianth depth × width <25 mm/>25 mm], flower sexuality [unisexual/hermaphroditic], perianth color [colored/brownish or greenish], perianth reduction [complete/at least one verticil absent or much reduced], pollinator type [insect/wind], and seed dispersal mode [endozoochorous/non-endozoochorous]). Plant height was obtained from local floras (Bolòs et al. 1990); seed mass was obtained from a local Seed Bank (Banc de Llavors de la Generalitat Valenciana, Valencia, Spain) and from our own databases. Binary data were obtained from Herrera (1992) and from local floras. Note that none of the traits are explicitly related to fire response. We reduced the dimensionality of the niche by summarizing all of the trait information into three orthogonal ordination axes (Ricklefs and Travis 1980, Losos et al. 2003), using the principal components analysis for mixed data (Hill and Smith 1976) implemented in the ade4 software (Chessel et al. 2004).

Phylogenetic conservatism on the trait axes was evaluated by comparing the correlation value between the phylogenetic and the axes 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). We used the same phylogeny as Verdú and Pausas (2007).

The morphospace occupied by the species in each of the nine communities was computed as a convex hull volume from the three ordination axes using the TraitHull software (Cornwell et al. 2006). This software computes the hypervolume based on the algorithm described in Barber et al. (1996) and generates the null model on the basis of the species richness in each community, following the works by Lawlor (1980), Winemiller and Pianka (1990), and Gotelli and Graves (1996). We standardized the relative morphospace occupation by computing the occupation index as: $OI = (Vol - rndVol)/sd.rndVol$, where Vol is the observed convex hull volume, rndVol is the volume estimated by the null model, and sd.rndVol is the standard deviation

TABLE 1. Correlation between the 11 plant traits and the three ordination axes for 89 woody species in the eastern Iberian Peninsula.

Traits (units or states)	Axis 1	Axis 2	Axis 3
Quantitative traits			
Plant height (m)	−0.618	0.554	−0.021
Seed mass (mg)	−0.457	0.369	−0.397
Binary traits (0/1)			
Spinescense (no/yes)	−0.219	−0.547	−0.558
Leaf type (sclerophyllous/others)	0.783	0.289	−0.405
Leaf habit (deciduous/evergreen)	−0.520	−0.365	0.541
Flower size (large/small†)	−0.819	−0.163	0.115
Flower sexuality (hermaphroditic/unisexual)	−0.787	0.018	−0.163
Perianth color (colored/brownish or greenish)	−0.803	−0.093	−0.049
Perianth reduction (complete/reduced)	−0.765	−0.040	0.173
Pollinator type (insect/wind)	−0.675	0.302	0.141
Seed dispersal mode (endozoochorous/otherwise)	0.454	0.766	−0.158

Note: Correlation coefficients used were Pearson for quantitative traits and Spearman for qualitative traits.

† Small, perianth depth × width < 25 mm; large, otherwise.

of the null model. Communities in which the observed volume is lower than the null volume (OI < 0) are considered to have underoccupied morphospaces.

To assert that phenotypic clustering is not the product of a neutral evolutionary process as described in Pie and Weitz (2005), we first validated that our phylogenetic tree is produced by one of the branching processes that could generate phenotypic clustering. To do this, we compared the fits of (1) pure birth, (2) rate-constant birth–death, and (3) rate-variable birth–death models by means of likelihood ratio tests using the LASER package for R (Rabosky 2006). Then, we simulated the evolution of the trait axes using the phylogeny and the observed independent contrasts between the trait axes (i.e., the evolutionary variance–covariance matrix; Revell et al. 2007) using the GEIGER software (Harmon et al. 2008). We simulated the three trait axes following a Brownian motion model and computed the convex hull volume as with the real data. This procedure was repeated 100 times. If the simulated data reproduced our observed pattern of differential morphospace occupation in low and high fire frequency communities, then we could not reject the possibility of our pattern being driven by random processes (Pie and Weitz 2005), otherwise our clustering pattern should be driven by a community assembly process (habitat filtering).

RESULTS

The principal component analysis of the 11 traits produced three axes that accounted for 29.4%, 20.4%, and 8.5% of the trait variability. It clearly segregated large evergreen sclerophyllous plants with small, wind-pollinated unisexual flowers that produce large seeds dispersed by animals (endozoochory), from plants with complementary traits (Table 1).

We found a strong phylogenetic signal ($P < 0.001$) for the trait axes in such a way that all simulated correlations between the phylogenetic and the axes distance matrices were lower (ranged between −0.15 and 0.20) than the observed correlation (0.46). That is, our trait axes are evolutionarily conserved, indicating that closely related species have similar phenotypes (Fig. 1).

LowFi and HiFi sites showed a contrasted pattern of morphospace occupation by species in the community (Fig. 2); LowFi communities showed OI > 0 while HiFi showed OI < 0. A significant association between fire regimes (HiFi and LowFi) and morphospace occupation was observed, with HiFi communities being under-occupied as opposed to LowFi ones ($\chi^2_1 = 5.4$; $P = 0.02$).

The branching pattern of our phylogeny fits a rate-variable birth–death model better than either a simple pure birth (2LR = 3.56, df = 3, $P < 0.002$) or a rate-constant birth–death model (2LR = 5.96, df = 2, $P < 0.002$). Most of the morphospaces computed from the 100 sets of simulated axes differed from the pattern found in the empirical data, and only 7% showed a significant ($P < 0.05$, χ^2 test) relation between fire regime (HiFi/LowFi) and niche occupancy in the same direction as the empirical data.

DISCUSSION

Fire changes the structure of plant communities by increasing the representation of species with high ability to germinate after fire (Keeley 1986, Trabaud 1987, Lamont et al. 1991, Pausas et al. 2004). The blooming of molecular data and the parallel development of phylogenetic and comparative methods allows us to accurately test the evolutionary role of fire in the structuring of plant communities (Verdú and Pausas 2007). Indeed this new approach has demonstrated that species occurring in communities under high fire frequency are more closely related than expected and share the ability to recruit after fire. This is consistent with fire acting as a filter and assembling the communities (Webb 2000). In the present work we demonstrate that this filtering limits the combination of morphological and functional traits that can occupy a given community (van der Valk 1981). More specifically, we show that the morphospace in
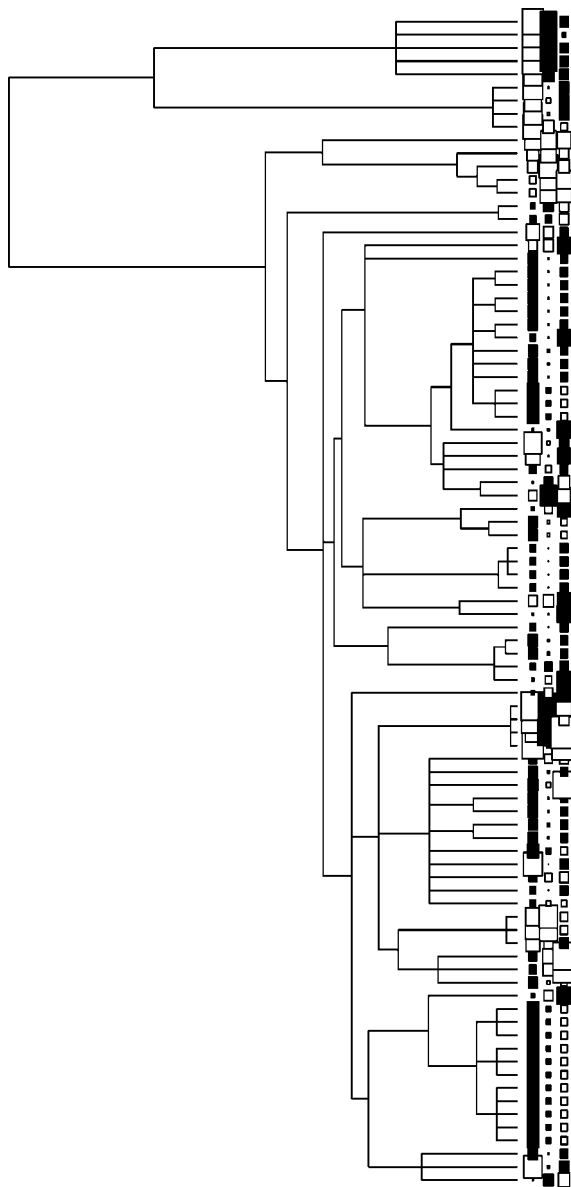
Fig. 1. Graphical representation of the relationship between the phylogeny and the three trait axes (the three columns of symbols) for 89 woody species in the eastern Iberian Peninsula. For each axis, the size of the symbols is proportional to the magnitude of the principal component, with positive values in black and negative values in white. Species are, from bottom to top: *Acer granatense, Pistacia lentiscus, Ruta angustifolia, Cistus albidus, C. clusii, C. crispus, C. monspeliensis, C. salviifolius, F. ericoides, F. laevipes, F. thymifolia, Helianthemum apenninum, H. hirtum, H. syriacum, Daphne gnidium, Amelanchier ovalis, Crataegus monogyna, Prunus spinosa, Rhamnus alaternus, R. lycioides, R. oleoides, Anthyllis cytisoides, Argyrolobium zanonii, Calicotome spinosa, Ceratonia siliqua, Colutea arborescens, Coronilla juncea, C. minima, Dorycnium hirsutum, D. pentaphyllum, Genista scorpius, Spartium junceum, Ulex parviflorus, Quercus coccifera, Q. faginea, Q. rotundifolia, Q. suber, Myrtus communis, Arbutus unedo, Calluna vulgaris, Erica arborea, E. multiflora, Coris monspeliensis, Bupleurum fruticosum, Hedera helix, Helichrysum stoechas, Phagnalon rupestre, P. saxatile, P. sordidum, Lonicera*
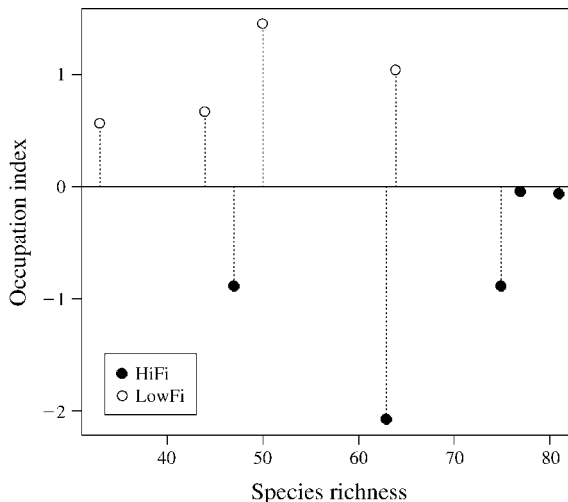

Fig. 2. Morphospace occupation index (OI) for each site, in relation to fire regime (HiFi, high fire frequency; LowFi, low fire frequency) and species richness (number of species). Negative values indicate underoccupation.

communities with high fire frequency (HiFi) is less occupied than would be expected by chance (underoccupied).

One may ask why morphospaces defined by traits not directly related to fire are different under different fire regimes. This is because, in Mediterranean Basin flora, traits that confer population persistence in fire-prone ecosystems (postfire recruitment) are strongly linked to other morphological and functional traits (Pausas et al. 2004, Pausas and Verdú 2005). Indeed, our ordination analysis reproduces Herrera's (1992) syndromes for Mediterranean species, segregating vertebrate-dispersed wind-pollinated evergreen sclerophyllous plants from plants with complementary traits. These syndromes, which are defined by morphological (leaf and flower) and functional (pollination and dispersal) traits, are strongly related to postfire regeneration strategies (Verdú 2000, Pausas and Verdú 2005). Thus, the explanation for our trait clustering may lie in the fact that the most important trait conferring persistence in fire-prone Mediterranean ecosystems, i.e., having a fire-persistent seed bank that allows germination and recruitment after fire, is a derived (non-ancestral) trait

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etrusca, L. implexa, Viburnum tinus, Fraxinus angustifolia, F. ornus, Jasminum fruticans, Olea europaea, Phillyrea latifolia, Globularia alypum, Lavandula dentata, L. latifolia, Lavandula stoechas, Phlomis lychnitis, Rosmarinus officinalis, Salvia officinalis, Sideritis hirsuta, S. tragoriganum, Teucrium chamadrys, T. pseudochamaepitys, Thymus piperella, T. vulgaris, Lithodora fruticosa, Rubia peregrina, Osyris alba, Clematis flammula, C. vitalba, Asparagus acutifolius, A. horridus, Ruscus aculeatus, Smilax aspera, Chamaerops humilis, Juniperus oxycedrus, J. phoenicia, J. sabina, J. thurifera, Pinus halepensis, P. nigra, P. pinaster, P. pinea, and *P. sylvestris.*

(Pausas and Verdú 2005), and only a few, recent, lineages occupy the areas of trait space favored by a derived optimum (Kraft et al. 2007).

The strong phylogenetic signal shown by the trait axes indicates that plant phenotypes have been conserved through evolution and, thus, that closely related species share similar phenotypes. Consequently, our results are consistent with a habitat-level filter that limits the multivariate range of trait space that species can occupy at a given site (van der Valk 1981, Keddy 1992). Indeed, our results are in agreement with a previous analysis of the same sites where filtering and competition exclusion processes were inferred for HiFi and LowFi communities based on phylogenetic relatedness of taxa (Verdú and Pausas 2007). Cavender-Bares et al. (2004) also found evidence of habitat filtering for traits related to persistence and regeneration after fire in Floridian oaks. Given that closely related species share similar phenotypes, then short mean phylogenetic distances between taxa are indicative of communities assembled by habitat filtering. The use of both a phylogenetic distance measure such as NRI (Net Relatedness Index) and the morphospace occupation index (OI) clearly segregates the communities under the two fire regimes, with HiFi communities showing high NRI (low mean phylogenetic distance or phylogenetic clustering) and low trait occupation (phenotypic clustering) and LowFi communities showing high trait occupation and low NRI (Fig. 3). The empty areas in the phylogenetic and phenotypic clustering space (Fig. 3) may be reserved for cases where traits are not evolutionarily conserved (e.g., Losos et al. 2003, Cavender-Bares et al. 2004). That is, phylogenetic overdispersion and phenotypic clustering (under-occupation; bottom-left space in Fig. 3) may arise from filtering processes acting on nonconserved traits (Webb et al. 2002), while for other assembly processes (e.g., competition), a random phylogenetic pattern with phenotypic overdispersion (top-right space in Fig. 3) is expected (Webb et al. 2002, Kraft et al. 2007). Although these empty spaces have the potential to become occupied, the conserved nature of most of the morphological and functional traits (Blomberg et al. 2003) may preclude their occupation.

The phylogeny used reflects the rate-variable birth–death model in which both speciation and extinction have occurred at different times during the evolutionary process. This is congruent with the differential extinction and diversification for different lineages (those that trace back to the Tertiary vs. more recent Quaternary lineages) proposed by Herrera (1992). This evolutionary scenario is subject to produce morphospace clustering under a neutral evolutionary model (Pie and Weitz 2005). However, the simulated traits evolving under this model do not reproduce the differential morphospace occupation in different fire regimes observed in the empirical data set, and thus habitat filtering can be claimed as the process behind the pattern. To what extent previous reports of trait phenotypic clustering
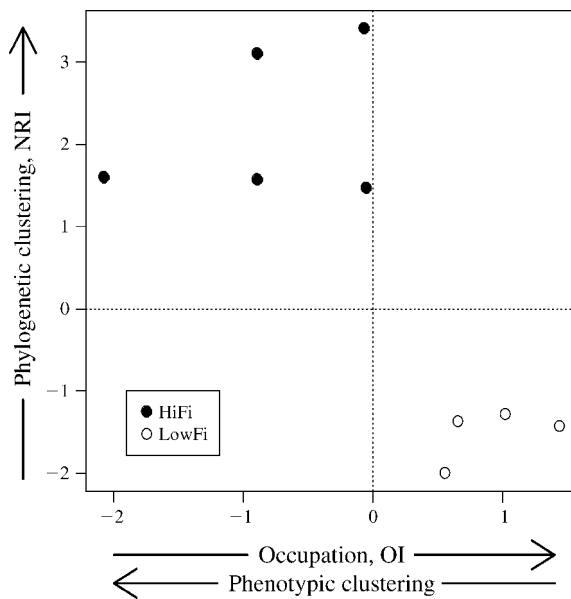

Fig. 3. Relationship between phenotypic clustering (measured by the morphospace occupation index) and phylogenetic clustering (measured by the net relatedness index) for the nine sites in the two fire regimes (HiFi, solid symbols; LowFi, open symbols).

(e.g., Cavender-Bares et al. 2004, Bruzgul and Hadly 2007) are a consequence of neutral trait evolution remains to be tested.

Our results unambiguously support the hypothesis that fire is a strong community-assembling process in the Mediterranean Basin by filtering the species that have fire-persistent traits and thus assembling phenotypically and phylogenetically clustered communities with vacant zones in the morphospace. In this way, our work highlights the role of disturbance in the structuring of communities and provides a basis to predict changes in both phylogenetic and morphofunctional diversity.

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APPENDIX

Species-trait matrix together with the three principal component axes (*Ecological Archives* E089-124-A1).