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SPECIAL FEATURE

FACILITATION IN PLANT COMMUNITIES

Phylogenetic signatures of facilitation and competition in successional communities

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Summary

1. The balance between facilitation and competition through time is at the core of models for successional dynamics. However, since the 1980s, the studies of facilitation have shifted away from successional processes. In a return to the traditional roots of the study of facilitation, we assessed the phylogenetic signatures of competition and facilitation in Mediterranean successional communities and compared them with those recently quantified in non-successional communities of the Mexican desert.

2. Based on previous work, we hypothesized that facilitation between distantly related lineages is an important driver of successional dynamics, as has been shown in non-successional systems. However, we also predicted that the balance between facilitation and competition will be different in successional systems because many species disappear from communities during the process of succession, which does not occur in non-successional systems.

3. We sampled plant species composition over a chronosequence of post-fire succession and predicted phylogenetic clustering in communities at the early stages caused by species that reproduce by seed ('seeders', belonging to a few specific families) being favoured by fire; overdispersion in intermediate stages driven by facilitation interactions among distantly related species; and randomness in the final stage caused by the competitive exclusion of pioneer species belonging to a few families and the survival of species in many other families.

4. In the pioneer stage, we found a random phylogenetic pattern because seeders and many resprouter species were present at this stage, indicating that autosuccession was also occurring. In intermediate phases, once pioneers had recruited into open spaces and facilitated late-successional species, most of which were ancient taxa originating during the Tertiary, phylogenetic overdispersion predominated. Finally, in the later stages competitive exclusion of pioneer species reduced phylogenetic diversity, leading to a random phylogenetic structure.

5. *Synthesis*. As previously found for non-successional communities, facilitation among distantly related lineages appeared to drive successional dynamics. However, subsequent competition reduced phylogenetic diversity during succession in this Mediterranean system, and some species disappeared from the community.

Key-words: community phylogenetics, competition, cyclical dynamics, facilitation, Mediterranean communities, phylogenetic overdispersion, succession

Introduction

Facilitation is a classic mechanism for succession (Connell & Slatyer 1977), but since the 1980s the overwhelming focus on

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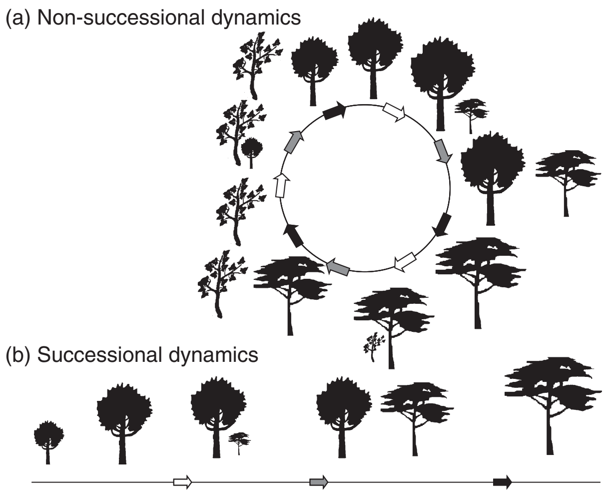

Fig. 1. Two different types of vegetation dynamics mediated by facilitation (white arrows), competition (grey arrows) and exclusion (black arrows).

facilitation has been on non-successional communities (Callaway 2007; Brooker *et al.* 2008; see Fig. 1, for a simple example of both types of processes). In this non-successional context, most efforts have been devoted to integrating facilitation into the mainstream of community ecology conceptual theory (Bertness & Callaway 1994; Callaway 1997, 2007; Bruno, Stachowicz & Bertness 2003). However, recently efforts have been made to link facilitation to historical perspectives on plant evolution (Valiente-Banuet *et al.* 2006; Valiente-Banuet & Verdú 2007; Valiente-Banuet & Verdú 2008). This bridge between facilitation and evolution has been constructed within the community phylogenetics framework developed by Webb *et al.* (2002) and has combined information on trait evolution (conserved versus convergent) and phylogenetic relatedness of the co-occurring species (with high relatedness indicating phylogenetic clustering and low relatedness indicating phylogenetic overdispersion). This combination has been used to identify mechanisms responsible for the assembling of ecological communities (mainly competition versus habitat filtering). When traits are evolutionarily conserved, then phylogenetic clustering is indicative of habitat filtering whereas phylogenetic overdispersion is indicative of competition (Webb *et al.* 2002; Cavender-Bares *et al.* 2004). As a caveat however, studies have shown that different processes (i.e. predation, pollination, herbivory, facilitation) may lead to the same phylogenetic pattern and that the same process may lead to different phylogenetic patterns (see examples in Vamosi *et al.* 2009; Cavender-Bares *et al.* 2009). Regardless, this approach is informative about basic patterns of phylogenetic diversity, a crucial component of biodiversity, that are captured by each community, with clustering indicating low values of phylogenetic diversity and overdispersion indicating high phylogenetic diversity values (Faith 1992; Proches, Wilson & Cowling 2006).

Facilitation structures communities by increasing the abundance of some species, creating conditions that permit the local existence of some species (Callaway 2007) and increasing phylogenetic diversity (Valiente-Banuet *et al.* 2006). The regeneration niche, approximately defined in this context as facilitated versus non-facilitated, is an evolutionarily conserved trait indicating that closely related species tend to have similar niches (Valiente-Banuet & Verdú 2007). Consequently, facilitative associations are mainly produced between distantly related species, ultimately leading to low relatedness between coexisting species (Valiente-Banuet & Verdú 2007).

Virtually all knowledge about the evolutionary importance of facilitation comes from non-successional systems. In these communities, facilitative interactions lead to phylogenetic overdispersion as explained above. Many of these facilitative interactions between benefactors (e.g. nurses) and beneficiary species (e.g. facilitated seedlings) shift to competition when beneficiaries mature and compete with the benefactors (see McAuliffe 1984; Miriti 2006; Callaway 2007). Because this temporal shift from facilitation to competition occurs more frequently between closely related taxa, competition tends to exaggerate overdispersion in the phylogenetic structure of the communities (Valiente-Banuet & Verdú 2008; Verdú *et al.*, unpubl. data). Understanding these connections between phylogenetic patterns in facilitation and evolution originated in studies from Mediterranean plant communities (Valiente-Banuet *et al.* 2006). By integrating palaeobotanical, ecological and phylogenetic analyses, it was shown that ancient Tertiary lineages in Mediterranean-climate ecosystems survived thanks to the facilitative or 'nurse' effects of modern Quaternary lineages. Modern lineages are able to recruit in the arid conditions imposed by the Mediterranean climate and in turn facilitate the recruitment of Tertiary species beneath their canopies (Valiente-Banuet *et al.* 2006).

Post-fire regeneration in Mediterranean plant communities includes both seeders and resprouters (Trabaud & Lepart 1980; Pausas *et al.* 2004), and these two post-fire regeneration strategies are linked to the evolutionary origins with resprouters predominantly belonging to the Tertiary group and seeders to the Quaternary group (Verdú 2000; Pausas & Verdú 2005). Differences in the predominance of seeders versus resprouters are dependent on disturbance regime and climate, and may ultimately lead to different successional trajectories after fire (autosuccession and succession). Autosuccession, *sensu* Hanes (1971), occurs when the same species composition is found shortly after disturbance, without successional stages, and can be achieved by either resprouting adults or by seeders recolonizing areas occupied by parents immediately after fire and inhibiting colonization by other species. In contrast, succession may be triggered when some species facilitate the entrance of new species in the community and later competition excludes some other species (Siles *et al.* 2008). Both autosuccession and succession may act simultaneously and leave different signatures in the phylogenetic structure of the community. Autosuccesssion would not lead to changes in the phylogenetic diversity of communities over time because the species composition of the community remains unchanged. However, succession driven by facilitation and subsequent competition would imply gains and losses of species and therefore changes in the phylogenetic diversity over time. Because Quaternary species in the Mediterranean region belong to just a few families, we predict that the first stage of successional dynamics should be characterized by the coexistence of closely related species (i.e. phylogenetic clustering) (Verdú & Pausas 2007). Intermediate successional stages, during which pioneers facilitate other species, should be characterized by phylogenetic overdispersion if facilitation occurs between distantly related species, as in non-successional dynamics. Finally, facilitation may turn into competition with time as facilitated plants grow large enough to significantly deplete the resources of nurse plants (Miriti 2006; Valiente-Banuet & Verdú 2008), resulting in a replacement of pioneer species by facilitated plants when the mature forest is established. The loss of pioneers may represent the extinction of entire clades from the community and consequently a loss of phylogenetic diversity. Because the surviving, facilitated, species belong to the Tertiary group and are from many different families, the loss of phylogenetic diversity after competitive exclusion of pioneer species would be far less drastic and lead to phylogenetic clustering.

In this article, we study the phylogenetic structure of the community in different post-fire successional stages to test whether facilitation interactions occur between distantly related species, and then if such interactions lead to a concomitant increment in phylogenetic diversity along the succession. We subsequently test whether competitive exclusion of pioneers, occurring when the mature communities are established, leads to a reduction of phylogenetic diversity. Finally, we compare these results with those from non-successional communities to identify the underlying mechanisms that drive different types of vegetation dynamics.

Materials and methods

STUDY SITES AND SUCCESSIONAL STAGES

The study was conducted during 2003 and 2004 in two sites (Puerto de Las Palomas (PP) and Torre del Vinagre (TV)) affected by wildfires in the Natural Park of Sierra de Cazorla, Segura y Las Villas (Jaen province, south-eastern Spain). The fire at PP site (37°57′12″ N, 2°56′06″ W) occurred in 2001 and affected 836 ha, while TV burned in 1986 (38°00′43″ N, 2°52′48″ W) and affected 1000 ha. This last site underwent largely unsuccessful pine reforestation (1988–89; *Pinus pinaster* and *Pinus halepensis*), which included removal of naturally regenerated species and mechanical soil preparation, but no reforestation had been conducted at PP by the time of this study. The sites are *c.* 7.5 km apart, have the same soil type (calcareous limestone) and aspect, and are exposed to the same climatic conditions (see below). Environmental heterogeneity in the whole study area arises from variation in altitude (ranging from 900 to 1300 m a.s.l.), slope and soil depth (with zones of rocky outcrops at higher altitudes and deeper soils in middle and basal zones). Despite the environmental heterogeneity, potential late successional native vegetation is the same in both areas: mixed forest of *Pinus nigra*, *Quercus ilex* and *Quercus faginea* (Siles *et al.* 2008). Overall, fire recurrence in the same site is low and intervals between fires can be many decades, allowing regeneration of mature vegetation in the intervals between fires.

At the study sites, vegetation differed substantially in cover and composition as a consequence of the length of time since fire. We took advantage of these circumstances to determine a successional chronosequence. At a simple scale, the vegetation we chose is classified into three types of regeneration states: (i) 2-year, early successional shrub-dominated community, on non-rocky substrates and relatively deep soils in PP; (ii) 18-year, native late successional scrubland, established in basal zones with deep soils in TV (hereafter, building state or BUI); and (iii) 18-year, spontaneous-regeneration pine stands, in rocky soil at the medium to high elevation of TV (hereafter, pine regeneration state or PINE). The early successional shrub state represents a pioneer stage (hereafter, PIO) whereas both BUI and PINE represent distinct forms of intermediate stages in succession (Siles *et al.* 2008). We sampled the vegetation in all these three states (see below). To complete the successional chronosequence, we further sampled the intact mature native vegetation in the surroundings of the burned area (avoiding previously reforested areas and/or logged vegetation) as representative of the mature community state (MAT hereafter). Patches of mature vegetation are comparable to the potential late successional native vegetation of the study area as they have remained unburned over many decades (Siles *et al.* 2008). The definition of the three discrete successional stages is subjective; however, the species- and life-form composition and structure of these stages are consistent with post-fire successional phases described for the Mediterranean region of Spain through combination of long time series of Landsat data and field observations of post-fire succession (Röder *et al.* 2008). Furthermore, the use of a discrete series in this case may be a better criterion than in other studies (e.g. years since disturbance), because vegetation dynamics in the area may be arrested for long periods of time (see Siles *et al.* 2008) due to ungulate grazing, seed limitation, and soil and nutrient loss. All these processes vary in the area at small spatial scales and may lead to different successional pathways within the area affected by the same fire event (Siles *et al.* 2008). The community composition of each successional stage is shown in Table S1 in Supporting Information. Climate in the whole study area is Mediterranean subhumid. Mean annual rainfall in two weather stations close to the study area is 770.7 and 1155.6 mm (concentrated in autumn and spring), and mean annual temperature is 11.6 and 14.2 °C.

SURVEY OF NATURAL VEGETATION

We randomly delimited 100-m linear transects in areas of each regeneration state and of the mature state, and sampled several plots that were evenly distributed along each transect. The plot size was larger at PIO (100 m^2) than at the rest of the stages (25 m^2) to account for the low cover in the 2-year pioneer stage. Overall, we sampled 40 plots in PIO, 44 in BUI, 35 in PINE and 30 in MAT. In each plot, we recorded the presence of all woody species and estimated total woody cover using as reference a metric tape bordering the perimeter of the plot.

Facilitation interactions were recorded at BUI and PINE in the same 25-m^2 plots used for estimates of species presence. We considered association of juveniles with larger plants as evidence of a facilitative interaction. Although the spatial patterns we measured do not provide experimental evidence of recruitment niches, there is a great deal of experimental evidence on the regeneration niches of many of the species in our system that indicates that the spatial associations between species recorded in the field result from facilitation and not from mere spatial coincidence (Gómez-Aparicio *et al.* 2004; Rey, Siles & Alcántara 2009). Moreover, experimental evidence in our study system (Siles 2008; Siles *et al.*, unpubl. data) and other Mediterranean mountains (Gómez-Aparicio *et al.* 2004) shows that facilitation interactions between nurses and facilitated species are not randomly produced but follow a high level of life-form specificity, giving rise to plant facilitation-mediated assemblage rules during succession. We looked for juvenile recruitment (seedling or saplings < 0.5 m height, non-reproductive plants) and identified the adult plants acting as nurses for such juveniles. Juveniles recruiting in open ground within these plots were also identified and counted. The regeneration niche of each species (facilitated versus non-facilitated) was calculated as the proportion of plots in which each species recruited under nurses. This proportion was compared against the random expectation by means of binomial tests. The random expectation was calculated as the woody cover measured in the plots.

Finally, we tested whether the regeneration niche was different between seeders and resprouters and between lineages originated in the Tertiary and Quaternary. The information to assign lineage age and post-fire regeneration strategy for each species was obtained from Herrera (1992), Verdú (2000) and Paula *et al.* (2009).

PHYLOGENETIC ANALYSES

The phylogenetic distances between all the species sampled in our study area were calculated from a phylogenetic supertree (Fig. 2) assembled after matching our genus and family names with those contained in the Angiosperm Phylogeny Group (Stevens 2005) megatree of the Phylomatic package as implemented in Phylocom 4.0 (Webb, Ackerly & Kembel 2008). Branch lengths of this tree are calibrated with the age estimates for major nodes in the tree from Wikström, Savolainen & Chase (2001) and the help of BLADJ algorithm implemented in Phylocom 4.0.

To test whether facilitation interactions occur between phylogenetically distant species, we compared the mean phylogenetic distance (MPD) between nurses and their facilitated plants against a null model in which species labels were randomly reshuffled (see Valiente-Banuet & Verdú 2007, for a similar procedure). The phylogenetic structure of the communities across the successional stages was assessed by testing whether the MPD of the species living in each plot departed from the MPD expected under a null model in which species were reshuffled across the phylogenetic tree. Phylogenetic clustering (overdispersion) occurs when the observed MPD is significantly lower (higher) than the null expectation (Webb *et al.* 2002). Net Relatedness Index (NRI), a standardized measure of MPDs, was used to allow comparison among plots (Webb *et al.* 2002). NRI was calculated as

$$\mathrm{NRI} = -(\mathrm{MPD} - \mathrm{rndMPD})/\mathrm{sd.rndMPD},$$

where sd.rndMPD is the standard deviation of the 999 random MPD (rndMPD) values.

Positive (negative) values of NRI indicate that coexisting species are phylogenetically more (less) related than expected by chance, leading thus to a community pattern of phylogenetic clustering (overdispersion). NRI is an inverse measure of phylogenetic diversity independent of species richness, because the higher the relatedness of coexisting species, the lower the phylogenetic diversity of the community. All these analyses were run with the help of the construct algorithm implemented in Phylocom 4.0 (Webb, Ackerly & Kembel 2008). Following a similar rationale, the phylogenetic structure of the communities can be measured by calculating the Nearest Taxon Index (NTI), which focuses on the relatedness between the phylogenetically nearest neighbours. As the results obtained with NTI were the same as those obtained with NRI, we will only show the latter.

We also computed the phylogenetic species variability (PSV) to study the phylogenetic structure of the community. This metric measures the variance, among species of a community, in the value of a hypothetical neutral trait evolving under a Brownian motion model and ranges from 0 (phylogenetic clustering) to 1 (overdispersion) (Helmus *et al.* 2007). The null model was generated by randomizing the presence–absence data within plots. These analyses were run with

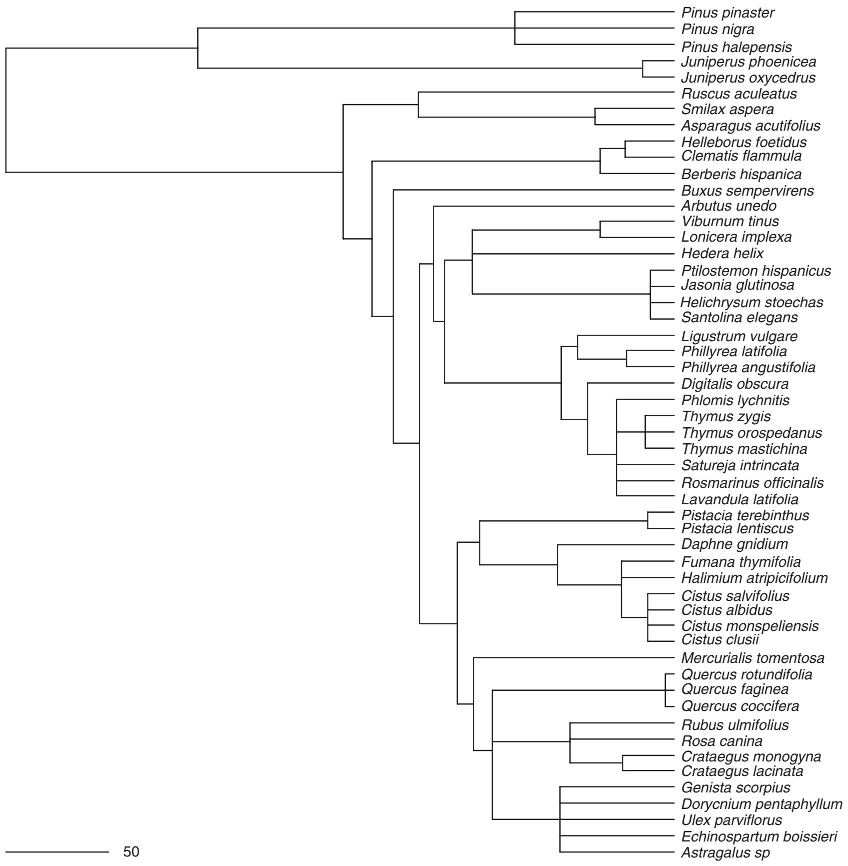

Fig. 2. Phylogenetic tree of the species present in the post-fire communities. The scale bar indicates million years.

the help of the Picante package implemented in R (Kembel *et al.* 2009). To check the sensitivity of our results to the topological uncertainty of the phylogenetic tree (Fig. 2), we randomly resolved the polytomies of the tree and re-ran the analyses 25 times. In all the analyses the conclusions were the same and therefore they will not be shown here.

Results

The regeneration niche was significantly different for species belonging to lineages that originated in different evolutionary ages. Tertiary taxa recruited preferentially under nurses and Quaternary taxa recruited preferentially on open ground (Table 1; Wilcoxon test $W = 49.5$, $P = 2.7 \times 10^{-10}$ for building stage and $W = 461.5$, $P = 1.18 \times 10^{-7}$ for pine forest). Similarly, regeneration niche differed between species with different post-fire regeneration strategies with seeders recruiting more in the open ground and resprouters more under nurses (Table 1; $W = 100$, $P = 3.1 \times 10^{-8}$ for building stage and $W = 454$, $P = 2.7 \times 10^{-7}$ for pine forest).

The phylogenetic structure of the community at the pioneer stage did not depart from that expected by chance because the number of plots showing lower and higher MPD values than the null expectation was 20 in both cases (Binomial test $P = 1$; Fig. 3). In agreement with this test, the PSV value did not depart from randomness ($\text{PSV}_{\text{obs}} = 0.48$, PSV_{null} 95% CI (0.42, 0.52)).

When succession entered into intermediate phases, through the building or pine stages, the structure of the community became phylogenetically overdispersed. In the building phase, 38 of 44 plots showed higher MPD than expected by chance (Binomial test $P = 9.4 \times 10^{-7}$; Fig. 3) and, accordingly, the PSV metric indicated phylogenetic overdispersion ($\text{PSV}_{\text{obs}} = 0.55$; PSV_{null} 95% CI (0.48, 0.52)). Similarly, in the pine phase, all 35 plots showed higher MPD than the null

Table 1. Evolutionary (lineage age) and functional (regeneration strategy and regeneration niche) information of each species present in the two intermediate successional stages (building and pine stages)

			Building		Pine	
Species	Lineage age	Regeneration strategy	Regeneration niche	P	Regeneration niche	P
Cistus albidus	Q	S	0.00	NA	0.20	0.20
Halimium atriplicifolium	Q	S	0.09	0.03	0.24	0.03
Rosmarinus officinalis	Q	S	0.13	0.00	0.08	0.00
Cistus monspeliensis	Q	S	0.20	0.00	0.29	0.01
Cistus clussi	Q	S	0.25	NA	0.50	NA
Ulex parviflorum	Q	S	0.25	NA	0.05	0.00
Lavandula latifolia	Q	S	0.29	0.08	–	NA
Thymus mastichina	Q	S	–	NA	0.00	NA
Cistus salvifolius	Q	S	0.33	0.41	0.32	0.05
Daphne gnidum	T	R	0.33	0.41	0.43	0.60
Dorycnium pentaphyllum	Q	S	0.50	NA	0.17	0.11
Pinus halepensis	T	S	0.50	0.50	0.91	0.01
Rubus ulmifolius	T	R	0.57	0.48	0.83	0.22
Juniperus oxycedrus	T	R	0.63	0.31	0.60	NA
Crataegus monogyna	T	R	0.67	0.58	–	NA
Phillyrea latifolia	T	R	0.67	0.58	0.67	NA
Phillyrea angustifolia	T	R	0.75	NA	1.00	NA
Quercus faginea	T	R	0.82	0.44	1.00	0.06
Rosa sp.	T	R	0.91	0.00	0.50	NA
Pistacia terebinthus	T	R	0.92	0.00	1.00	NA
Quercus coccifera	T	R	0.92	0.00	0.89	0.00
Acer monspessulanum	T	R	1.00	NA	–	NA
Berberis hispanica	T	R	1.00	NA	–	NA
Jasminum fruticans	T	R	1.00	NA	–	NA
Juniperus phoenicea	T	–	1.00	NA	–	NA
Pistacia lentiscus	T	R	1.00	0.00	1.00	0.00
Prunus spinosa	T	R	1.00	NA	–	NA
Quercus rotundifolia	T	R	1.00	0.00	0.92	0.00
Rhamnus alaternus	T	R	1.00	NA	1.00	NA
Rhamnus saxatilis	T	R	1.00	NA	–	NA
Sorbus torminalis	T	R	1.00	NA	–	NA
Ulmus minor	T	R	1.00	NA	–	NA

Lineage age: Q, Quaternary; T, Tertiary. Regeneration strategy after fire: S, seeder; R, resprouter. Regeneration niche is the proportion of plots in which each species recruited under nurses; *P* is the *P*-value of the binomial test comparing this proportion against the random expectation calculated as the woody cover measured in the plots (0.435 for BUI and 0.522 for PINE). NA indicates that the statistical test was not performed because sample size was too small ($n < 5$). Note that the binomial test is two-tailed and that $P < 0.05$ indicates that the regeneration niche is either significantly facilitated, when higher than woody cover, or non-facilitated, when lower than woody cover.

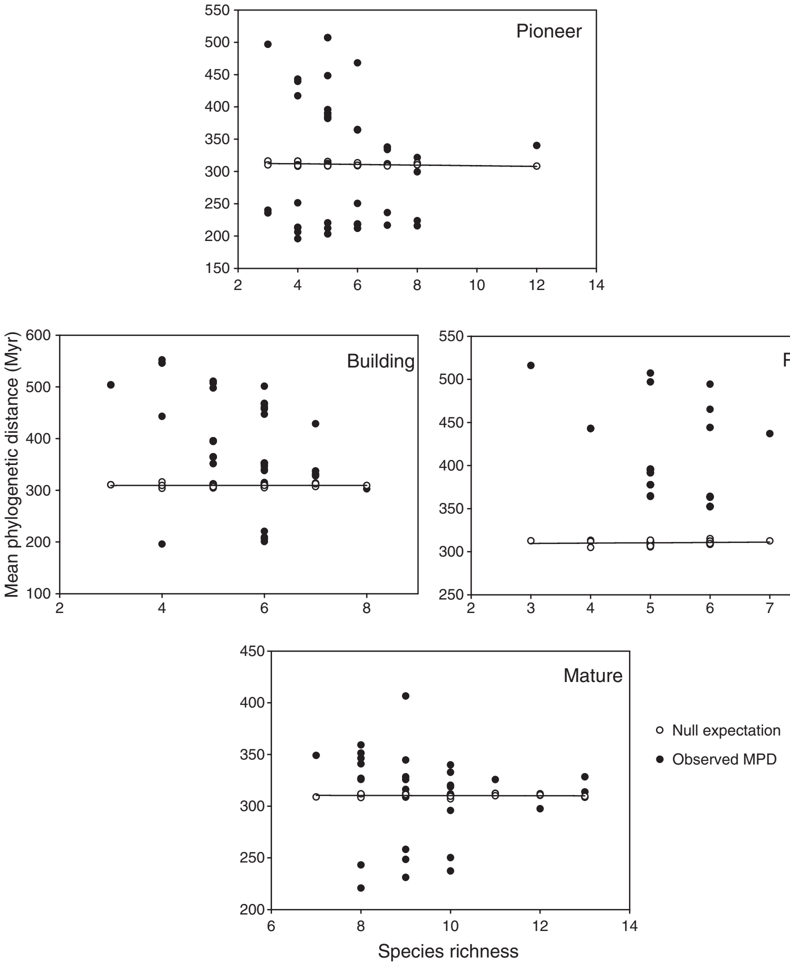

Fig. 3. Mean phylogenetic distance of the species inhabiting each plot from different successional stages. Solid dots show the observed MPD values and open dots show the mean of 999 null model trials at each of the corresponding levels of species richness. Plots with higher phylogenetic diversity than expected by chance are those above the line fitted through the null expectation points.

expectation (Binomial test $P = 5.8 \times 10^{-11}$; Fig. 3) and overdispersion was detected by PSV ($PSV_{obs} = 0.62$; PSV_{null} 95% CI (0.44, 0.53)). Such phylogenetic overdispersion can be explained because in these intermediate building stages, where pioneers facilitate other species, facilitative interactions (Table S2) occurred more frequently between distantly related species, as indicated by a MPD between nurses and facilitated plants, 314.3 million years (Myr), higher than expected by chance (mean 279.3 Myr, 95% CI (253.6, 300.3)) (Fig. 4 top). The same pattern was found in the pine regeneration stage, where the observed MPD between nurses and facilitated plants, 342.9 Myr, was higher than expected by chance (mean 265.5 Myr, 95% CI (240.3, 291.7)) (Fig. 4 bottom).

Finally, when succession reached the point of mature forest, the phylogenetic community structure turned again towards randomness: the number of plots with higher (20) and lower (10) MPD than the null model did not depart from the random expectation (Binomial test $P = 0.10$; Fig 3) and, accordingly, PSV was not significant ($PSV_{obs} = 0.48$; PSV_{null} 95% CI (0.45, 0.51)).

The NRI, an inverse measure of phylogenetic diversity, followed a clear pattern across the different successional stages, with intermediate (pine and building) phases containing more phylogenetically diverse species than pioneer and mature phases (Fig. 5).

Discussion

The main finding of this study is that facilitation is a process that assembles successional communities in ways that increase broad phylogenetic diversity. This process is identical to that occurring in non-successional communities (Valiente-Banuet *et al.* 2006; Valiente-Banuet & Verdú 2007) and allows us to generalize the importance of facilitation as a broadly based mechanism for community assembly. Another important finding is that the competition that occurs after facilitation decreases phylogenetic diversity in late successional communities, but not in mature non-successional communities.

We predicted that the phylogenetic structure of the community would change across the stages of the succession in the following directions: (i) clustering in the early stages caused by fire, favouring 'seeding' species that only occur in a few families, (ii) overdispersion in intermediate stages driven by facilitation occurring between distantly related species, and (iii) randomness in the final stage caused by the loss of pioneer species and the survival of species that belong to many other families.

PHYLOGENETIC CLUSTERING AT EARLY STAGES

Phylogenetic clustering is an expected outcome when evolutionarily conserved traits determine environmental filtering in

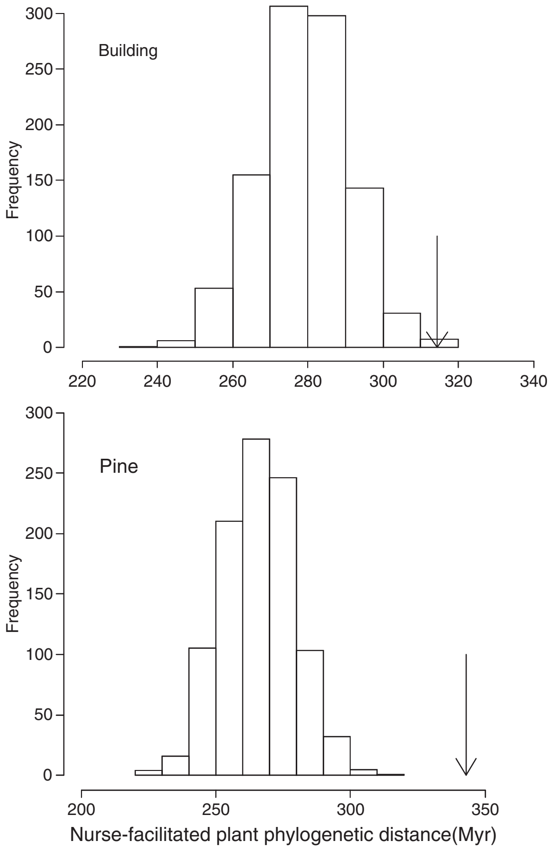

Fig. 4. Facilitative interactions between nurses and facilitated plants occur between distantly related species. The histogram shows the frequency distribution of expected mean phylogenetic distances (in million years, Myr) between nurses and facilitated plants under a null model. The arrows indicate the observed mean phylogenetic distance between nurses and facilitated plants in the two intermediate successional stages (building and pine phases).

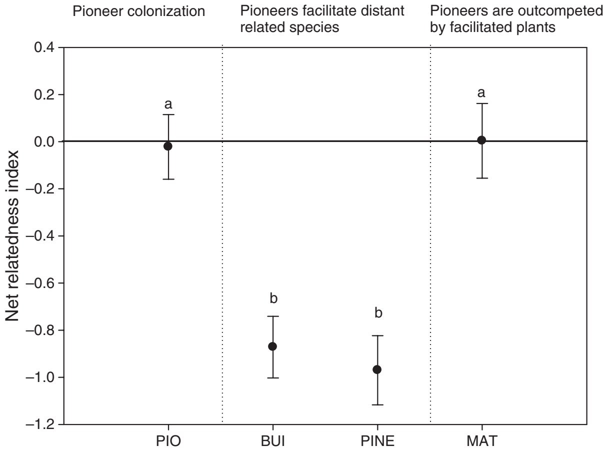

Fig. 5. Net Relatedness Index (NRI) changes with the post-fire successional stages. Mean ± 1 SE of the plots for each stage is shown. Different letters indicate significant differences at $\alpha = 0.05$. Positive NRI values indicate phylogenetic clustering and negative values indicate overdispersion.

such a way that only species possessing particular traits are able to persist within a community on the basis of their tolerance to the abiotic environment (Webb *et al.* 2002). In Mediterranean plant communities, fire is an environmental filter favouring seeder species that belong to only a few families and therefore clustering the phylogenetic structure of the community (Verdú & Pausas 2007). Despite this evidence, we failed to find significant phylogenetic clustering in the initial stages of succession. As expected, pioneer species from a few families (Cistaceae, Fabaceae and Lamiaceae) initiated succession. However, phylogenetic clustering did not occur because at the same time species associated with late successional stages were present due to resprouting. In another data set not shown here, we also found a random phylogenetic structure for a pioneer community, 10 km from our study area, 2 and 6 years after a wildfire.

Other studies have shown seeders triggering succession and resprouters self-perpetuating conspecific dominance (Keeley & Keeley 1981; Buhk *et al.* 2006). However, the relative abundance of seeders and resprouters after fire, and consequently the phylogenetic structure of communities at the initial stages of succession, should ultimately be determined by the frequency of the recurrence of fire. In general, short fire-return intervals may exhaust buds and the reserves of resprouters, and thus eliminate them, whereas low fire frequency may cause seeder populations to decline over time (Lloret, Pausas & Vilà 2003; Pausas *et al.* 2004). The result of these differential responses to fire frequency between seeders and resprouters is that Mediterranean plant communities that are subject to high frequency of fires are phylogenetically clustered (Verdú & Pausas 2007). Under less severe fire regimes, like those present in our study area, both seeders and resprouters may perform well and this is probably the reason why our pioneer community was not phylogenetically clustered.

Our results highlight the importance of integrating phylogenetic history into successional trajectories followed by different functional groups of species (Keeley, Fotheringham & Baer-Keeley 2006). The phylogenetic structure of a community depends on the distribution of relevant traits among the clades it contains, thus our phylogenetic approach can be improved by identifying specific individual traits that confer to particular species groups the ability to survive in certain environments (Mayfield, Boni & Ackerly 2009). Only when such information is accounted for can we fully explain the phylogenetic structure of these communities, which is crucial to understanding the subsequent stages of succession.

PHYLOGENETIC OVERDISPERSION AT INTERMEDIATE STAGES

In the intermediate stages of the succession, the patterns caused by facilitation become especially prominent (Siles *et al.* 2008). Similar to the processes occurring in non-successional scenarios (Valiente-Banuet & Verdú 2007), communities in intermediate successional stages are phylogenetically overdispersed as a consequence of facilitation. Phylogenetic overdispersion is produced because nurses and facilitated plants tend to be distantly related in phylogenies. Closely related plants have similar regeneration niches and thus are more likely to compete, whereas distantly related plants have dissimilar niches and are more likely to coexist.

This is what we expected, and found, based on information from Herrera (1992), who described marked differences in the niche occupied by two groups of Mediterranean plants by combining information on morpho-functional syndromes, successional strategies and evolutionary ages: Tertiary lineages are mainly vertebrate-dispersed species associated with late successional stages, and Quaternary lineages are mainly wind-dispersed species associated with early steps in succession. Interestingly, these groups also correspond to different post-fire strategies, with most Tertiary lineages being resprouters and most Quaternary lineages being seeders (Herrera 1987; Verdú 2000). All of these differences led us to infer that Quaternary lineages behave as nurses enhancing the microhabitat and facilitating the regeneration of Tertiary lineages (Valiente-Banuet *et al.* 2006). Here, we show that these facilitative interactions between nurses and beneficiary plants are produced between distantly related species, mainly between species with Quaternary and Tertiary origins.

These results support the importance of successional pathways driven by facilitation despite the recognized role of auto-succession in post-fire vegetation dynamics (Zavala 2000, 2003; Siles *et al.* 2008). The importance of facilitation in successional pathways is being increasingly recognized in the Mediterranean region (Zavala 2000, 2003; Siles *et al.* 2008). Insights on this are also emerging from restoration ecology in which the identification of assembly rules mediated by facilitation, mainly at intermediate stages (Gómez-Aparicio *et al.* 2004; Siles 2008; Gómez-Aparicio 2009, this issue; G. Siles *et al.*, unpubl. data), appear crucial for achieving the desired aim of promoting direct succession. Here, we have provided evidence that such an assembly rule leaves a phylogenetic signature throughout succession.

PHYLOGENETIC RANDOMNESS AT FINAL STAGES

The final, late, successional stage was characterized by a random phylogenetic structure of the community. Randomness was reached after a loss of phylogenetic diversity from the intermediate, overdispersed stage. Loss of phylogenetic diversity in the step from intermediate to final stage could be explained if facilitated plants grow up and out-compete their nurses.

Two possible scenarios may produce the competitive exclusion of pioneer species, which acted as nurses for late-successional species. First, a passive replacement of the nurse by the facilitated plant may occur if nurse taxa are shorter-lived on average. The mean longevity of Mediterranean nurse species like those in the Cistaceae, Fabaceae and Lamiaceae may range between 15 and 25 years, whereas facilitated plants like *Quercus* species may live for > 200 years (Lloret, Pausas & Vilà 2003; Pausas & Lloret 2007; Luis, Verdú & Raventos 2008). The second scenario of competitive exclusion is produced when the canopy of facilitated plants is extended, closing all the gaps available for pioneer recruitment (Gallego Fernandez, Rosario Garcia Mora & García Novo 2004) and imposing a shaded environment where nurses rarely achieve successful seedling establishment (Keeley 1992).

The loss of phylogenetic diversity produced by competitive exclusion appears to be the primary difference between successional and non-successional dynamics. This is a clear example in which the same process (competition) leads to different phylogenetic community structures (Cavender-Bares *et al.* 2009). In successional scenarios some species disappear from the community, whereas in non-successional dynamics species replace each other without disappearing from the community. For example, in non-successional communities from Mexican deserts, species X acts as nurse for the recruitment of Y, species Y acts as nurse for Z and Z acts as nurse for X (Fig. 1). This network of interactions makes these types of communities very robust to the extinction of some nurses (Verdú & Valiente-Banuet 2008). However, in extreme situations where most of the species in the community need nurses to recruit (McAuliffe 1988), the complete removal of nurses is likely to collapse the regeneration of the system because there are no species able to recruit on the open ground and reassembly the community through facilitation. The situation is very different when community dynamics are not driven by this cyclical replacement sequence but by a unidirectional successional replacement sequence, as it occurs after a disturbance like wildfire or field abandonment in Mediterranean ecosystems. In Mediterranean ecosystems, many species can recruit in the open ground created by a disturbance. These pioneer species enhance the microhabitat and act as nurses for other species (Valiente-Banuet *et al.* 2006). However, when these latecomers grow up, they occupy the habitat and exclude pioneers from the mature forest. In this mature stage, facilitation occurs (Valiente-Banuet *et al.* 2006), but is proportionally less predominant (Siles *et al.* 2008). Unlike communities with cyclic dynamics, those with successional dynamics are resilient to disturbance because pioneers can re-assemble the community through facilitation.

CONCLUDING REMARKS

We have shown that the phylogenetic signature left by facilitation in plant communities is similar in both successional and non-successional vegetation dynamics, but the final balance between facilitation and competition depends on the type of dynamics. The generality of facilitation as a mechanism for increasing phylogenetic diversity comes from the strong conservatism in the regeneration niche shown by many, if not all, plant lineages. In contrast, the differences in the balance between facilitation and competition that occurs in the vegetation dynamics of different systems might be better understood by accounting for historical effects (*sensu* Herrera 1992) that explain specific traits, especially those related to the regeneration niches.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Species presence in each of the study plots from different successional stages.

Table S2. Facilitation interactions occuring between nurses and facilitated plants in the two intermediate successional stages (Building and Pine phases).