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IDEA AND PERSPECTIVE

Facilitation can increase the phylogenetic diversity of plant communities

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Abstract

With the advent of molecular phylogenies the assessment of community assembly processes has become a central topic in community ecology. These processes have focused almost exclusively on habitat filtering and competitive exclusion. Recent evidence, however, indicates that facilitation has been important in preserving biodiversity over evolutionary time, with recent lineages conserving the regeneration niches of older, distant lineages. Here we test whether, if facilitation among distant-related species has preserved the regeneration niche of plant lineages, this has increased the phylogenetic diversity of communities. By analyzing a large worldwide database of species, we showed that the regeneration niches were strongly conserved across evolutionary history. Likewise, a phylogenetic supertree of all species of three communities driven by facilitation showed that nurse species facilitated distantly related species and increased phylogenetic diversity.

Keywords

Community assembly rules, facilitation, phylogenetic community structure, phylogenetic diversity, regeneration niche conservatism, sustenance of global biodiversity, Tehuacán–Cuicatlán Valley.

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INTRODUCTION

The correspondence between the characteristics of the environment where particular taxa evolved and the contemporary regeneration niche of species strongly suggests that regeneration niches are highly conserved. For example, Valiente-Banuet *et al.* (2006) found that most extant woody taxa in Mediterranean-type ecosystems with ancient Tertiary origins and evolved in woodlands under a mesic climate [65–2 million years (Myr) B.P.] currently recruit beneath the canopies of perennial species that evolved more recently under a harsher climate. Thus, the shaded conditions below canopies of drought-tolerant species that evolved in the Quaternary provide ancient-lineage species with microclimates similar to their ancestral regeneration niches. This 'nursing' effect has tended to retain traits allowing old lineages to regenerate, and preserved global biodiversity over evolutionary time.

Facilitative interactions appear to have been particularly critical during the shift from mesic Tertiary to the unprecedented dry Quaternary (Valiente-Banuet *et al.* 2006) when most deserts developed (Axelrod 1979). Thus, the importance of facilitation increased when climate became more stressful, consistent with current literature demonstrating that facilitative interactions: (i) commonly increase in intensity and importance as with abiotic stress (Hacker & Gaines 1997; Lortie & Callaway 2006; Michalet *et al.* 2006), (ii) increase biological diversity by ameliorating harsh environments (Callaway 1995; Gómez-Aparicio *et al.* 2004), and (iii) can expand the realized niches of less stress tolerant species (Bruno *et al.* 2003; Baumeister & Callaway 2006).

There is often conservatism of traits in evolutionary lineages (Blomberg *et al.* 2003), and positive relationships between species' phylogenetic relatedness, overall life history and ecological similarity (Webb 2000; Cavender-Bares *et al.* 2004; Webb *et al.* 2006a,b). Thus, we propose that the phylogenetic structure of a community provides insight into how facilitation affects evolutionary relationships between extant species and community organization.

If facilitation among plants affects the evolutionary relationships of species within communities this would challenge the current models of phylogenetic community organization. For example, if habitat filtering is the assembly community process and plants exhibit evolutionary niche conservatism, then closely related species with similar traits should coexist more commonly than expected by chance within a community (i.e. phylogenetic clustering) (Webb *et al.* 2002, 2006a,b; Cavender-Bares *et al.* 2004). In contrast, if competitive exclusion is a primary driver of community composition over evolutionary time, this should limit coexistence of closely related species with similar niches. Therefore, distantly related species should co-exist more commonly than expected by chance (i.e. phylogenetic overdispersion or evenness; Webb *et al.* 2002; Cavender-Bares *et al.* 2004; Kraft *et al.* 2007). However, we propose that, if the regeneration niche is evolutionarily conserved and positive interactions tend to occur between phylogenetically distant species (e.g. Quaternary vs. Tertiary; Valiente-Banuet *et al.* 2006), then facilitation should favour phylogenetic overdispersion of the community (Fig. 1).

We expand on community assembly rules by quantitatively analyzing the patterns of regeneration niche conservatism in a large database of species in different communities worldwide, for which facilitation vs. non-facilitation interactions have been documented. For a broader analysis of phylogenetic community structure, we measured the regeneration niches of all woody species in three highly diverse Mexican semi-arid communities, previously shown to be shaped by facilitation (Valiente-Banuet *et al.* 2002). We intended to determine whether facilitation expands community assembly principles by adding phylogenetically distant species and therefore increasing phylogenetic diversity.

METHODS

Conservation of the regeneration niche

We qualitatively defined regeneration niches as 'non-facilitated' and 'facilitated'. Facilitated species were those recruiting under vegetation (nurses) more often than expected by chance. Non-facilitated species were those recruiting on open ground more often. This simple definition does not capture all important characteristics of a species' regeneration, but it does encapsulate considerable ecological and evolutionary information (Valiente-Banuet *et al.* 2006). An exhaustive literature review identified the current regeneration niches of species at the community level in North and South America, the Mediterranean Basin, South Africa and Australia. In addition, we conducted field sampling in seven communities in central Mexico and Baja California, providing measurements of 429 species from 225 genera and 74 families. Sampled communities were arid, semiarid and humid systems including desert, Mediterranean climate vegetation and Mexical shrubland (Valiente-Banuet *et al.* 2006), and tropical savannas. A phylogenetic supertree for these taxa was assembled using the program Phylomatic as implemented in Phylocom 3.40 (Webb *et al.* 2005). All families used matched the family names of the angiosperm megatree in Phylomatic (R20050610.new), based on work of the Angiosperm Phylogeny Group (Stevens 2005). The branch lengths of the working phylogenetic tree were adjusted with the Bladj algorithm using age estimates for major nodes from Wikstrom *et al.* (2001) and distributing undated nodes evenly between dated nodes (Webb *et al.* 2005).

Conservation of the regeneration niche was determined in the working phylogeny by calculating the existence of a significant phylogenetic signal (Maddison & Slatkin 1991).

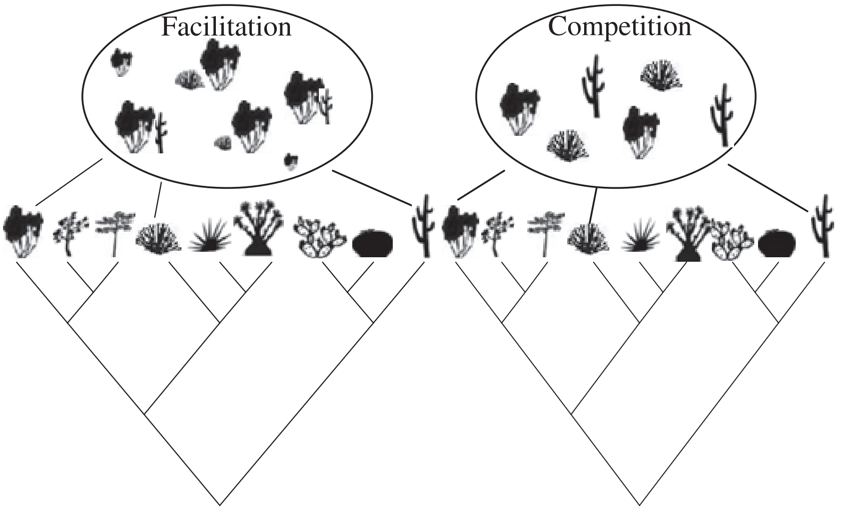

Figure 1 Two different ways how phylogenetic overdispersion in communities can be produced. In the case of competition, overdispersion is achieved by the exclusion of close-related species producing a checkerboard spatial pattern. In the case of facilitation, overdispersion is achieved because nurses add distant-related species to the community producing a clumped association pattern among species.

This tests the resemblance of related species (i.e. to have similar niches) more than expected by chance, and is based on the number of parsimony steps reconstructed in the tree. The minimum number of evolutionary steps was compared among taxa within the facilitated or non-facilitated groups. Whether the steps occurred less than expected by chance was determined under a null model in which data were reshuffled 1000 times across the tips of the phylogeny. To account for the topological uncertainty derived from the polytomies in the tree, the test was repeated in 100 trees in which polytomies were randomly resolved. All tests used the Mesquite 1.12 program (Maddison & Maddison 2006).

Facilitation and the phylogenetic structure of communities

To verify that current community composition was governed by facilitation, we selected three communities: Tetechera *Nt*, Tetechera of *Neobuxbaumia tetetzo*; Cardonal *Cc-t*, Cardonal of *Cephalocereus columna-trajani*, and Tetechera *Nm*, Tetechera of *Neobuxbaumia mezcalaensis* in the Zapotitlán Valley, (lat 18°20′ N, long 97°28′ W), a basin of the Tehuacán–Cuicatlán Valley, Puebla, México. A detailed description of these communities can be found in Valiente-Banuet *et al.* (2000). For each community the total cover of perennial plants and open space were measured in four 1000-m^2 transects. For each species, we counted the number of seedlings and saplings (< 30 cm height) growing beneath canopies and in open spaces, a total of 4984 seedlings (Table 1). We then conducted a contingency analysis for all species together with the number of young individuals growing beneath plant canopies vs. open areas, compared with the expected number of individuals derived from the proportions of area of plant-cover vs. open space.

To verify that nurse species facilitate distantly related species, we identified all interactions (761) between each pair of nurse-facilitated species in the three communities. To do this, we transformed the 4984 seedling matrix into a qualitative matrix with nurses in columns and facilitated plants in rows. Each cell of this matrix was filled with one if the facilitated species recruited beneath the canopy of the nurse species or 0 otherwise. The mean phylogenetic distance between species in each pair was obtained using the 'phydist' command in Phylocom. Observed mean distances were compared against a null distribution generated by calculating 9999 times the mean phylogenetic distance between 761 random (without replacement) pairs of species drawn from the matrix of phylogenetic distances between all the nurses and the facilitated species of the three communities. By pooling, the three communities the same regional species pool was analyzed as used later in the analysis of phylogenetic community structure. If nurses facilitate distant-related species, we would expect observed mean distance to be > 95% of the mean distances of the null model. The phylogenetic structure of such communities was tested by comparing the mean phylogenetic distance (MPD) of species coexisting in a community against the MPD of a null model. MPDs were calculated from the phylogenetic tree of the regional species pool, as previously explained. The null model (rndMPD) was constructed by reshuffling 9999 times the species labels across the phylogenetic tree of the regional species pool. The regional pool was composed of 104 species while the study plots averaged 37 species (range 27–50; Table 2). Consequently, the percentages of the local to the regional species pool were intermediate (mean 37%, range 26–48%), representing the situation with the greatest statistical power to detect community structure (Kraft *et al.* 2007; see also Swenson *et al.* 2006 for the problems of scale dependency in community phylogenetics).

Table 1. Regeneration niche of species in three semi-arid communities in the Tehuacán-Cuicatlán Valley, Mexico: Tetechera *Nt*, Tetechera of *Neobuxbaumia tetetzo*; Cardonal *Cc-t*, Cardonal of *Cephalocereus columna-trajani* and Tetechera *Nm*, Tetechera of *Neobuxbaumia mezcalaensis*

Community	No. species	No. nurse species	% species facilitated*	Total no. individuals beneath nurse plants	Total no. individuals in open space	Total plant cover (%)	Open ground cover (%)	χ^2-value	*P*-value
Tetechera *Nt*	58	21	96	1237	92	71.1	28.9	367.5	< 0.00001
Cardonal *Cc-t*	57	26	95	1076	33	66.6	33.4	510.4	< 0.00001
Tetechera *Nm*	77	26	100	2231	15	73.7	26.3	890.9	< 0.00001

A detailed description of these communities can be found in Valiente-Banuet *et al.* (2000). The χ^2-test is significant if the observed number of individuals (all species pooled) recruiting under nurses vs. open areas compared with the expected number of individuals derived from the proportions of area occupied by plant-cover vs. open space.

*A species was considered to be facilitated when the percentage of individuals recruiting under nurses was greater than expected by the percentage of the nurse cover in the community with respect to open space. Individual χ^2-tests were conducted for the dominant species (Tables S1–S3 are available as Supplementary Material).

Table 2. Phylogenetic structure of the three Mexican semi-arid communities showing the species richness (*N*), the observed (MPD) and randomized (rndMPD) Mean Phylogenetic Distances, the standard deviation of the rndMPD, the Net Relatedness Index (NRI) and the *P*-value calculated as the proportion of simulated runs whose MPD does not exceed the observed MPD

Community	Plot	*N*	MPD (Myr)	rndMPD (Myr)	sdrndMPD (Myr)	NRI	*P*-value
Tetechera *Nt*	1	31	257.20	230.11	8.07	−3.36	< 0.0001
Tetechera *Nt*	2	35	244.27	230.12	7.60	−1.86	0.0232
Tetechera *Nt*	3	29	267.20	229.99	8.78	−4.23	< 0.0001
Tetechera *Nt*	4	27	257.74	230.20	9.21	−2.99	0.0002
Tetechera *Nm*	5	49	252.95	230.16	5.67	−4.00	< 0.0001
Tetechera *Nm*	6	39	250.87	230.13	6.89	−3.00	< 0.0001
Tetechera *Nm*	7	50	265.66	230.08	5.50	−6.47	< 0.0001
Tetechera *Nm*	8	47	251.38	230.08	5.87	−3.63	< 0.0001
Cardonal *Cct*	9	39	260.76	230.20	6.87	−4.45	< 0.0001
Cardonal *Cct*	10	34	251.10	230.17	7.67	−2.72	0.0003
Cardonal *Cct*	11	28	267.43	230.25	8.93	−4.16	< 0.0001
Cardonal *Cct*	12	35	269.12	230.27	7.42	−5.23	< 0.0001

Distances are measured in millions of years (Myr). See the legend of Table 1 for the names of the communities.

Other null models randomizing patterns of species co-occurrences between plots were tested but results did not change (data not shown). Finally, we standardized the measures of phylogenetic relatedness for each community by calculating the Net Relatedness Index (NRI) as follows (Webb *et al.* 2002):

$$\mathrm{NRI} = -1 \times \frac{\mathrm{MPD} - \mathrm{rndMPD}}{\mathrm{sdrndMPD}},$$

where sdrndMPD is the standard deviation of rndMPD values. NRI < 0 indicates higher MPD than from the null model, indicating overdispersion (Webb *et al.* 2002). The analyses of the community phylogenetic structure were run with the comstruct algorithm in Phylocom 3.40 (Webb *et al.* 2005).

RESULTS

Conservation of the regeneration niche

The regeneration niche of species is strongly conserved across the evolution of lineages because closely related species have similar niches (Fig. 2). Accordingly, there were 51 evolutionary transitions between facilitated and non-facilitated regeneration niches, a value significantly lower than from the null model (mean 120, range 111–128; $P < 0.001$). This result was robust to topological uncertainty because all trees with randomly resolved polytomies had fewer transitions (42–50) than expected by chance.

Facilitation and the phylogenetic structure of the community

In study communities, 97% of species recruited under nurses, clearly indicating that facilitation is a primary driver of community dynamics. There were 21–26 nurse species, representing 36, 46, and 34% of the species composition for Tetechera *Nt.*, Cardonal *C.c-t.*, and Tetechera *Nm*, respectively, indicating that less species are facilitators (Table 1). Most of the species are deciduous shrubs 40–200 cm high. The taxonomy of the three most important nurse species varied; Fabaceae for Tetechera *Nt*; Simarubaceae, Verbenaceae and Malpighiaceae for Cardonal *C.c-t*; and Verbenaceae, Cactaceae and Anacardiaceae for Tetechera *Nm*.

Two different patterns were detected in these communities, considering the number of species that recruit in open spaces and if they facilitate the establishment of other species (Tables S1–S3 are available as Supplementary Material). The first pattern is that of Tetechera *Nt* where the most important nurse plant was *Mimosa luisana* (Fabaceae), able to recruit in open space and facilitate most other species. There was a similar pattern in the Cardonal *C.c-t.* in which some species recruiting in the open were also important nurse plants. In contrast, in the Tetechera *Nm*, there were no species recruiting in the open and facilitation was conducted by many species, opening the question of which was the first nurse.

In the present study, nurse species facilitated distantly related species, as the mean phylogenetic distance between nurse species and their currently spatially associated species (240 Myr) was significantly greater than expected by the null model (mean 226 Myr, range 216–236; $P < 0.0001$). The long phylogenetic distances between nurses and facilitated plants combined with the overwhelming importance of facilitation leads to strong phylogenetic overdispersion in the community (Table 2).

DISCUSSION

Conservation of the regeneration niche

We found that the regeneration niche of species was strongly conserved during evolution of the lineages because

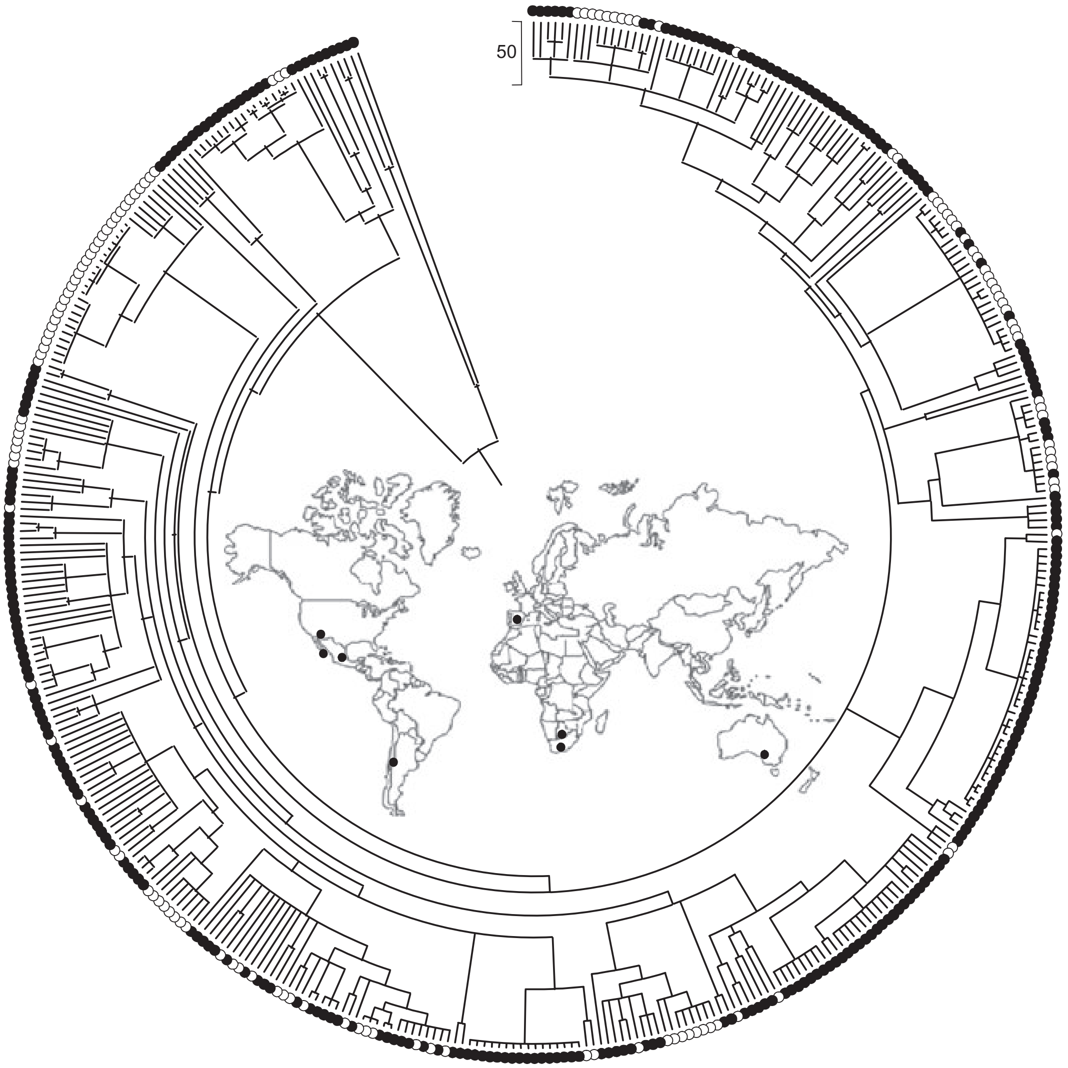

Figure 2 Phylogenetic tree showing the evolutionary relationships between the study species and the regeneration niche mapped onto the tips. Filled dots represent facilitated niche while unfilled dots represent non-facilitated niches. Species labels have been omitted for clarity. The world map shows the sites where data were obtained. (Database S4, including the phylogenetic tree, taxa labels, character scoring (facilitated vs. non-facilitated), parsimony reconstruction and null model for niche conservatism test). The file was created with the free software Mesquite (http://mesquiteproject.org/mesquite/mesquite.html).

closely related species had similar niches. From an adaptive viewpoint, natural selection may be stabilizing the regeneration niches at different optima, as demonstrated for Tertiary (facilitated) and Quaternary (non-facilitated) taxa in the Mexical shrubland (Valiente-Banuet *et al.* 2006). It is clear that natural selection favours taxa with appropriate characteristics for each of the regeneration niches (Wiens & Graham 2005). The main character associated with regeneration niches is fruit type. Seeds from fleshy-fruited species can be preferentially dispersed by animals beneath covered, nurse microhabitats while dry-fruits cannot (Verdú & García-Fayos 1996). The evolution of fleshy fruits is phylogenetically conserved and the origin seems restricted to the Tertiary period or earlier (Herrera 1989; Jordano 1995; Tiffney 2004; Bolmgren & Eriksson 2005). Thus, it is not surprising that fruit type and consequently regeneration niche are highly conserved. Niche conservatism is the rule rather than the exception (Prinzing *et al.* 2001).

Facilitation and the phylogenetic structure of the community

There is previous evidence of facilitation playing a dominant role in structuring communities, by species establishment beneath canopies of others (McAuliffe 1988; Tirado & Pugnaire 2005; Valiente-Banuet *et al.* 2006). For example, in the Sonoran Desert *Ambrosia deltoidea* establishes preferentially on open ground, but 86% of other perennial species along a bajada gradient preferentially establish under *A. deltoidea* or other established perennial canopies (McAuliffe 1988). This pattern was found in two communities (Tetechera *Nt* and Cardonal *C. c-t*) in which a species such as *M. luisana* established in open space and then enhanced establishment of many other species. In the other community (Tetechera *Nm*) the pattern was diffuse because no species recruited in the open ground and most species contributed to establishment of other species. This last pattern might explain why strong disturbances that remove the nurse species (i.e. agricultural tillage) lead to no apparent recovery in vegetation succession after abandonment (A. Valiente-Banuet, personal observation). Although speculative, this pattern suggests that this community has relied on facilitation by maintaining nurse species since ancient times.

The mechanisms allowing recruitment beneath other plants are related to physical differences between shrub canopies and open areas. These include accumulation of fine, windblown material beneath canopies that enhance seed germination (Wallace & Romney 1980), reduction of solar radiation and temperature beneath canopies (McAuliffe 1988; Valiente-Banuet & Ezcurra 1991), and higher soil nutrient levels beneath canopies by accumulation of organic debris or nitrogen fixation (Tiedemann & Klemmedson 1973; Lajtha & Schlesinger 1986), which together may enhance seedling survival under nurse plants.

In communities without complete vegetation cover, such as in the present study, facilitation should concentrate spatial association of species to form vegetation clumps (Fig. 1 McAuliffe 1988; Eccles *et al.* 1999). Clumps contrast with the checkerboard pattern predicted from competition. Tirado & Pugnaire (2005) experimentally demonstrated such a link between the clumped pattern and facilitation (the 'neighbour's effect'). The vegetation, in the present study, showed a clumped spatial pattern, reinforcing that facilitation shaped community structure. Although we are assuming that both seedling–adult association and clumping vegetation are evidence of facilitation, an experimental approach would test our predictions. Similarly, it has been shown experimentally that facilitation in these habitats ameliorates the physical environment produced by nurse plants, rather than directing seed dispersal (Valiente-Banuet & Ezcurra 1991). Future community level experiments will help to quantify the importance of directed seed dispersal vs. microhabitat enhancement (Callaway 1995).

Interspecific differences in the regeneration niche are at the core of the classical explanation of maintenance of species-richness in plant communities (Grubb 1977). Facilitation provides important heterogeneity in the regeneration niches necessary to maintain species richness in semiarid communities (Valiente-Banuet *et al.* 2006). We have demonstrated that nurse species facilitate distantly related species, suggesting that facilitation organizes communities while increasing phylogenetic diversity. This result is explained by the phylogenetic conservatism of the regeneration niche. As facilitation occurs between species differing in the regeneration niche (nurses and facilitated species), both species will be more distantly related than expected by chance. An interesting analogy exists between the pattern described here and that in a cactus yeast community (Anderson *et al.* 2004). In restrictive habitats, like columnar cactus stem tissues, yeasts enhance one another's growth primarily of distantly related species, resulting in a phylogenetically overdispersed community. This indicates the importance of including positive interactions as assembly rules in models of community assembly, which should also include the myriad of interactions acting in community organization. For example, it is well known that facilitation may become competition as species mature (Valiente-Banuet *et al.* 1991; Verdú *et al.* 2004), what should be translated into higher overdispersion. The contributions of facilitation and competition to phylogenetic overdispersion can be estimated mathematically by comparing MPD in recruitment and adult stages. Facilitation increases the MPD from 226 Myr (expected by null model) to 240 Myr (observed between nurses and facilitated plants) and finally competition increases it to 258 Myr; (average from Table 2, third column). Other important interactions are those among neighbour seedlings beneath a nurse, as density and phylogenetic relatedness may explain such coexistence (Webb *et al.* 2006a,b). More realistic models including these and other interactions are clearly necessary to explain the complexity of community assembly.

Community assembly rules implications

Most theories explaining how competition affects community diversity have been based on interactions between pairs of species, most likely to simplify experimentation. However, more complicated approaches may have been affected also by inertia after the development of Lotka-Volterra models in which interactions (i.e. competition or predation) among pairs of species are mathematically isolated from other processes. Regardless, community ecologists have focused on competition and its avoidance, to understand species coexistence. The origin of this competitive paradigm is based on Malthusian population theory and attributed to Darwin, who thought competition was logically connected to the assumed universal density-dependent mechanisms of natural selection (Den Boer 1986). Thus competition was given pre-eminence as the driver of numerical processes in both populations and communities. More recent research has found the role of facilitation is ubiquitous in community structure, and often as important as competition (Callaway 1995; Bruno *et al.* 2003). The present results add to evidence from extant communities, by showing that facilitation can maintain diverse groups of distantly related species in communities and therefore increase phylogenetic diversity.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Regeneration patterns of species beneath perennial nurse plants and in open space in the Tetechera *Nt* community in the Tehuacán Valley, Mexico.

Table S2. Regeneration patterns of species beneath perennial nurse plants and in open space in the Cardonal *C.C-t.* community in the Tehuacán Valley, Mexico.

Table S3 Regeneration patterns of species beneath perennial nurse plants and in open space in the Tetechera *Nm* community in the Tehuacan Valley, Mexico.

S4. Database

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-248.2007.01100.x.

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