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Temporal shifts from facilitation to competition occur between closely related taxa

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Summary

1. The relative contribution of positive and negative interactions to the organization of ecological communities is an important area, though poorly understood because of the complexity inherent to long-term interactions. For example, positive interactions like plant facilitation turn into negative interactions (competition) along the ontogeny of a plant or in response to temporal fluctuations in the environment. Furthermore, when many plants grow together indirect effects are usually positive and alleviate direct competitive effects.

2. The large number of direct and indirect interactions potentially occurring in natural communities and the temporal scale necessary to account for the ontogenetic shifts in the sign of the interaction makes a fully experimental approach prohibitive. Here, we propose that the phylogenetic distance among co-occurring species is a good proxy to detect competition as a long-term force assembling community composition. Our proposal is based on the observation that closely related species tend to be phenotypically similar and therefore compete for the same niche.

3. We test the relationship between phylogenetic relatedness and the persistence of pairwise (nurse-facilitated) interactions occurring between 102 woody species in three Mexican semi-arid communities in order to quantify the balance between competition and facilitation at the community level.

4. Our results indicate that facilitation turns into competition with increasing taxa relatedness. After validating the association between competition and phylogenetic relatedness, we estimate that 57% of the interactions remain with time while 43% become competitive. [Correction added after publication, 4 March 2008: in the preceding sentence, values corrected from 53% and 47%, respectively.] The preponderance of positive interactions may be explained if facilitation is considered as a mutualism in which both species benefit leading to vegetation clumps in communities.

5. *Synthesis*. We provide a new perspective on the balance between positive and negative interactions based on a phylogenetically structured network of interactions. This approach promises to contribute to our understanding of long standing issues in plant ecology and to reveal new areas of future research by testing the existence and the nature of the mutualisms as well as their complexity–stability properties on communities as a whole.

Key-words: community organization, competition, facilitation, mutualism, phylogenetic distance, Tehuacán-Cuicatlán Valley, vegetation clumps

Introduction

In the last two decades, research in plant ecology has been dealing with the assessment of the relative importance of positive and negative interactions in community organization (Hacker & Gaines 1997; Holmgren *et al*. 1997; Tielborger & Kadmon 2000). Both kinds of interactions seem to act simultaneously and the balance between them depends primarily on the harshness of the physical environment (Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998).

Empirical studies indicate that facilitative interactions increase in intensity and importance with abiotic stress, whereas negative interactions prevail under more benign conditions (Bertness & Callaway 1994; Greenlee & Callaway 1996; Hacker & Gaines 1997; Michalet *et al*. 2006, see discussion in Maestre *et al*. 2005, 2006; Lortie & Callaway 2006).

In addition to the effect of spatial variation on the balance between positive and negative interactions, temporal variation

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also modifies the balance, leading to interaction shifts throughout the ontogeny of a plant or in response to temporal fluctuations in the environment (Kitzberger *et al.* 2000; Tielborger & Kadmon 2000; Gasque & García-Fayos 2004; Miriti 2006). For example, most of the studies evaluating facilitation processes in long-lived plants (usually focused on pairs of species) provide evidence that facilitation turns gradually into competition as plants become adults (McAuliffe 1988; Valiente-Banuet *et al.* 1991; Flores-Martínez *et al.* 1994; Verdú *et al.* 2004; Miriti 2006). However, when all the species of a community are considered together the evidence indicates that there is a tendency towards the maintenance of positive interactions during the interaction ontogeny leading to multispecific vegetation clumps (Prentice & Werger 1985; Couteron & Kokou 1997; Eccles *et al.* 1999). Although provocative, this pattern has been overlooked and previous studies have claimed the occurrence of facultative mutualism to explain it (Eccles *et al.* 1999). Both direct and indirect effects among plant species commonly occur within a community and therefore studies on species pairs, or on a few species, cannot appropriately inform us about the balance between facilitation and competition. Consequently, only when we include all the species of the community will we be able to assess realistically the relative role of positive and negative interactions in community organization. This can be done by comparing the observed proportions of positive and negative interactions occurring in a community with a neutral model in which a proportion of 0.5 for both kinds of interactions is expected if one randomly selects pairs of species from a community (Dodds 1997). However, the large number of direct and indirect interactions potentially occurring in natural communities, as well as the shift of the sign of the interaction according to the change of biotic and abiotic conditions along the life of the interaction (Callaway 2007), prohibits a fully experimental approach.

Here we propose that a good proxy to assess the net effects of the combination of positive and negative interactions throughout the lifetime of all the interactions at the community level can be obtained from the developing field of phylogenetic community ecology (Webb *et al.* 2002). A similar approach has proven useful in previous studies; for example, the mean phylogenetic distance (MPD) among co-occurring species is a good proxy for competition as a long-term force assembling the community composition. The logic of the association between MPD and competition is based on the fact that the outcome of interspecific interactions is not random with respect to the phenotypes of both partners. Instead, phenotypically similar species will tend to compete for the same niche while dissimilar species may coexist by exploiting different niches. On the other hand, we know that phenotypically similar species are also phylogenetically closely related species because the phenotypes associated with both the regeneration and adult niches are evolutionary conserved traits (Valiente-Banuet & Verdú 2007; Verdú & Pausas 2007; Pausas & Verdú 2008). Following this rationale, we expect competition to be stronger between closely related taxa.

In a previous study, Valiente-Banuet & Verdú (2007) found that in semi-arid communities driven by facilitation the MPD between the nurse and facilitated plant species was longer than expected under a null model, indicating that facilitation occurs among distantly related species. Likewise, by comparing that MPD obtained from facilitation with that found in the adult community they found an increase in the MPD, suggesting that some facilitative interactions may turn into competition when beneficiary species grow up. In this paper we identify, within the same communities, the number of pairwise interactions between nurses and seedlings of facilitated plants that are no longer maintained between adults of both partners. If such interactions are lost due to competition, we would expect them to occur between the pairs involving closely related partners. In contrast, pairwise associations maintained over time would indicate that facilitation is still acting, or even that facilitation can switch to facultative mutualism. Consequently, in this study we verify the relationship between phylogenetic relatedness and the persistence of pairwise interactions, in order to quantify the balance between interspecific interactions at the community level. Likewise, by considering the neutral model for interaction type proposed by Dodds (1997) we assess the relative role of positive and negative interactions in our study communities by simulating two possible scenarios in which either commensalism or mutualism is the main interaction maintaining the interspecific associations with time.

Methods

The spatial association between nurses and facilitated species was measured, as explained in Valiente-Banuet & Verdú (2007), by sampling a total of 4000 m^2 community^{-1} in the following 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, a local basin of the Tehuacán-Cuicatlán Valley, Puebla, Mexico. The first two communities are located within the boundaries of the Botanical Garden 'Helia Bravo' (latitude 18°20′N, longitude 97°28′W) and have not been affected by grazing for more than 20 years. The third community is located near the San Juan Raya town (latitude 18°19′N, longitude 97°38′W) and has been affected by moderate grazing. However, despite the difference in herbivory pressure, all the communities presented a similar pattern of interspecific plant associations (Valiente-Banuet & Verdú 2007) suggesting that such associations are not caused by herbivory. These communities are physiognomically dominated by columnar cacti and maintain high species richness. Most of the shrubs are deciduous, 40–200 cm high, and most of the species (97%) recruit under nurses (see Appendix S1 in Supplementary Material). A detailed description of these communities can be found in Valiente-Banuet *et al.* (2000).

We counted the number of seedlings and saplings (< 30 cm height) growing beneath canopies and in open spaces along four transects of 1000 m^2 area per community. With this information, we could determine whether two species were spatially associated early on time (i.e. association between seedlings of facilitated plants and adult nurses). We registered 102 woody species behaving as nurses (51 spp) and/or facilitated plants (95 spp) and, based on spatial association, we identified 761 pairs of nurses and seedlings of facilitated species. Subsequently, we tested whether these facilitative interactions between nurses and seedlings of facilitated species persisted later in time (i.e. when seedlings of the facilitated plants become adults). This test was done by recording in four transects of 1000 m^2 area per community whether nurses and adults of facilitated species remained spatially associated. We considered that the presence of at least one facilitated adult under a nurse was enough to classify a facilitated relationship as maintained; otherwise, the association was considered to be lost.

The phylogenetic distances between the paired partners early in time (i.e. between adult nurses and seedlings of facilitated plant species) and later in time (i.e. between adults of both nurses and facilitated plant species) were estimated by assembling a phylogenetic supertree with the help of the program Phylomatic as implemented in Phylocom 3.40 (Webb *et al.* 2007). All the families in our data base matched the family names of the angiosperm megatree used in Phylomatic (R20050610.new), which is based on the work of the Angiosperm Phylogeny Group (Stevens 2001). The branch lengths of our working phylogenetic tree were adjusted with the Bladj algorithm by taking the age estimates for major nodes in our tree from Wikstrom *et al.* (2001) and distributing undated nodes evenly between nodes of known ages (Webb *et al.* 2007). We calculated the MPD between the species involved in each pairwise interaction early in time (adult nurses vs. seedlings of facilitated plants) with the help of the phydist command as implemented in the PHYLOCOM 3.40 package. Using the same procedure, we calculated the MPD of the interactions between adult nurses and adults of facilitated plants both remaining and disappearing later in time. The MPD of the lost and remaining interactions were compared against a null distribution generated by calculating 9999 times the expected MPD between *n* randomly sampled pairs of species drawn from the MPD matrix of the early interactions, being '*n*' the number of lost or remaining interactions.

We expect competition to be stronger between closely-related species and therefore to act particularly on the interactions in which the phylogenetic distance between the nurse and the facilitated plant is shorter. Thus, we would expect the MPD of the lost interactions to be significantly < 95% of the MPDs obtained by the null model.

We applied Dodd's neutral model to test his prediction on similar proportion of positive (P+) and negative (P–) interactions. Dodds (1997) identifies facilitation as an exploitation (+ –) interaction in which one species causes a benefit to another and receive a reciprocal negative effect. Similarly, Callaway (2007) suggests that most of the facilitative interactions probably occur as +–interactions, although commensalism (+0) may be common and mutualism (++) also exist. We assigned the lost interactions to exploitation (+ –) and the remaining interactions to commensalism (+0) or mutualism (++). As we cannot distinguish commensalism from mutualism, we simulated the two possible scenarios: (i) commensalism vs. exploitation and (ii) mutualism vs. exploitation. To estimate P+ and P–, we counted and calculated the percentage of the unidirectional positive and negative interactions resulting from each pairwise interaction (i.e. exploitation (+ –) leads to one positive and one negative interaction; mutualism (++) leads to two positive and zero negative interactions and commensalism (+0) leads to one positive and zero negative interactions). Significant differences between P+ and P– were tested by means of a Wilcoxon Signed-Rank test.

Results

The MPD between the 761 pairs of adult nurses and seedlings of facilitated plant species observed early in time was 240.4 million years (Myr). Once facilitated plants grew under the nurses, the partners of 57% of these pairs remained associated in the field while such association disappeared in 43% of the pairs. [Correction added after publication, 4 March 2008: in the preceding sentence, values corrected from 53% and 47%, respectively.] The probability of a facilitative interaction disappearing with time was not determined by chance but inversely determined by the phylogenetic distance between the nurse and its facilitated plant. MPD of the lost interactions was 235.31 Myr, which is significantly lower than expected by chance (Fig. 1). Similarly, the MPD of the remaining interactions was 244.05 Myr, significantly higher than expected by chance (Fig. 1). [Correction added after publication, 4 March 2008: in the preceding two sentence, values corrected from 235.65 Myr and 244.13 Myr, respectively.]

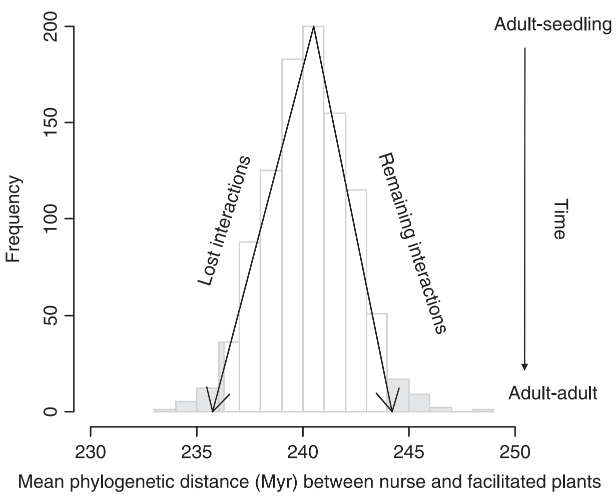

Fig. 1. The facilitative interactions between close-related species disappear with time. The histogram shows the frequency distribution of expected mean phylogenetic distance (MPD) in millions of years (Myr) under a null model. The shadowed portion in both tails of the histogram represents 5% of the distribution (i.e. rejection) area. The arrows indicate the changes in MPD occurring for the facilitative interactions that disappear (or remain) when the seedlings of facilitated plants grow up, in three semi-arid communities.

The two possible scenarios of the balance between facilitation and competition showed that positive interactions are much more frequent than expected by Dodd's neutral model (Table 1). The first scenario depicting commensalism as the main interaction maintaining the facilitative associations with time shows a twofold frequency of positive relative to negative interactions. If the maintenance of facilitative associations with time occurs through facultative mutualism between nurses and facilitated plants, the relative frequency of positive to negative interactions yields a threefold increase. In other words, under the two scenarios there is evidence for general positive interactions.

Discussion

The probability of a facilitative association disappearing with time is significantly correlated with a proxy of interspecific competition, that is, the phylogenetic relatedness between the nurse and beneficiary species. The relationship between competition and relatedness was already anticipated by Darwin (1859) who noted that competition between congeneric species would be more severe than between species of distinct genera. The underlying rationale of this relationship is that

Table 1. Quantification of the number of positive and negative interactions for different scenarios of species interactions. [Correction added after publication, 4 March 2008: in Table 1, columns 3 to 11 changed from: first data row: 406, –, 355, 406, 761, 355, 0.27, 0.50, 0.23; and V of column 12 from 425018; second data row: –, 406, 355, –, 1167, 355, –, 0.77, 0.23, and V of column 12 from 888670. Corrected values are presented in the table, as below.]

Remaining interactions	Lost interactions	+0	++	+ –	Σ0	Σ+	Σ–	P0	P+	P–	Dodds null model supported?
Commensalism (+0)	Exploitation (+ –)	431	–	330	431	761	330	0.28	0.50	0.22	NO; $V = 415506$, $P < 2.2\text{e-}16$
Mutualism (++)	Exploitation (+ –)	–	431	330	–	1192	330	–	0.78	0.22	NO; $V = 907708$, $P < 2.2\text{e-}16$

The number of spatial associations between nurses and facilitated plants remaining in time (431) were assigned to commensalism or mutualism, while those associations disappearing with time (330) were assigned to exploitation (Dodds 1997; Callaway 2007). The sum and percentage of the unidirectional neutral (Σ0, P0), positive (Σ+, P+) and negative (Σ–, P–) interactions resulting from all the pairwise interactions are shown along with the statistical test of similar percentages of P+ and P– predicted by Dodd's neutral model.

closely related species are more likely to share similar niche requirements and therefore will compete more strongly for the same resources. Thanks to the increasing availability of molecular phylogenies, a number of studies are starting to use phylogenetic relatedness as a proxy of competition. For example, Webb *et al*. (2006) found that the phylogenetic distance among competing species is a strong predictor of seedling mortality rates even after controlling for the effects of density. At the community level, M. Cadotte *et al*. (unpubl. data) also found that phylogenetic distance is a proxy for niche differences and therefore community productivity (i.e. community biomass increased with increasing MPD between co-occurring species). Interestingly, when the competition-relatedness hypothesis is tested by considering selected pairs of species, the tendency for plant species to compete more intensively with their close relatives vanishes (Cahill *et al*. 2007). These apparently contradictory results highlight the fact that the outcome of competition between pairs of species is not informing us appropriately about what is happening at the community level. In other words, communities have emerging properties that cannot be explained by the sum of their parts (M. Verdú & A. Valiente-Banuet, unpubl. data). Furthermore, these authors show that the network of facilitative interactions have the same emerging properties than other mutualistic networks.

After validating the correlation between competition and phylogenetic relatedness in our study communities, we can attribute the disappearance of early facilitative interactions to competition and thus quantify the net balance between facilitation and competition. Our estimates indicate that 57% of facilitation remains with time while 43% shift to competition at our study communities. [Correction added after publication, 4 March 2008: in the preceding sentence, values corrected from 53% and 47%, respectively.] Previous attempts to provide such estimates only considered small subsets of species within communities (Callaway 2007) and therefore indirect interactions and taxon sampling bias probably distorted the results.

Despite the old and widespread belief that competitive interactions are the prevalent forces assembling communities, the neutral model developed by Dodds (1997) predicted similar proportions of positive and negative interactions occurring in communities. Our quantification of positive interactions significantly departs from Dodds' expectation irrespective of the fact that facilitation is considered a mutualism in which both species benefit (++) or a commensalism in which just one species (usually the facilitated plant) benefits without affecting the other (+0). Our results indicate that positive interactions are from two- to threefold more frequent than negative interactions. A similar picture of the relative importance of positive and negative interactions structuring plant communities was given by Eccles *et al*. (1999), who estimated that positive interactions were from two- to fourfold more frequent than negative interactions. In communities assembled by positive interactions, a common and overlooked feature is a spatial pattern characterized by multispecific vegetation clumps (Eccles *et al*. 1999; Kéfi *et al*. 2007; Scanlon *et al*. 2007, this study).

The overwhelming frequency of positive interactions in communities shaped by facilitation is currently challenging not only the classical view of competition as the main force structuring communities, but also the opinion that communities driven by mutualisms should be considered as unstable (May 1974).

Indeed, empirical evidence of mutualistic interactions between neighbouring plants exists (Pugnaire *et al*. 1996) and probably mutualism is more common than currently expected (Brooker *et al*. 2008). At the community level, mutualism has also been invoked as the main force explaining the coexistence of species in clumps of vegetation found in semi-arid areas (Eccles *et al*. 1999). Furthermore, new theoretical models indicate that mutualistic communities stabilize diversity (Wilson & Nisbet 1997), and show largely positive complexity-stability relationships (Okuyama & Holland 2007), which is consistent with the role of facilitation in maintaining biodiversity (Valiente-Banuet *et al*. 2006; Valiente-Banuet & Verdú 2007).

Recent studies suggest that species coexistence might possibly be mediated through fungi-mediated resource sharing between different plant species (Bever 2003; Hart *et al*. 2003; Klironomos 2003; van der Heijden *et al*. 2003), and/or functional trait complementarity among co-occurring fungal species at each vegetation clump as a consequence of host specificity (Bever 2002; Maherali & Klironomos 2007). A further step in our analyses would be to check whether the phylogenetic relationships between taxa of below-ground communities are mirroring the phylogenetic relationships of the above-ground communities (i.e. distant-related plants may bring distant-related fungal taxa to the mycorrhizal network). If this is the case, our results showing that facilitative interactions between distantly related plant species are maintained with time may be explained by the increase in plant productivity produced by the functional complementarity of distantly-related microorganisms. Similarly, the disappearance of facilitative interactions in closely related plants may be the result of the low productivity of the below-ground, closely related microorganisms.

Empirical tests on the mutualistic nature of facilitation are needed, but the new perspective of the balance between positive and negative interactions under a network of phylogenetically structured interactions promises to contribute to our understanding of long standing issues in plant ecology, and to reveal new areas of future research. These necessarily should test the existence and the nature of the mutualisms as well as the complexity–stability properties of communities as a whole.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Spatial associations occurring between nurses and facilitated plant species.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2008.01357.x
(This link will take you to the article abstract).