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Positive plant interactions in the Iberian Southeast: Mechanisms, environmental gradients, and ecosystem function

F.I. Pugnaire [a,*], C. Armas [a], F.T. Maestre [b]

[a] Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Carretera de Sacramento s/n, E-04120 La Cañada de San Urbano, Almería, Spain
[b] Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/ Tulipán s/n, Móstoles, 28933 Madrid, Spain

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ABSTRACT

Semi-arid ecosystems are privileged sites to address the effects of plant interactions on community structure and dynamics because environmental conditions are demanding and may change quickly, altering in significant ways the balance between positive and negative effects among neighboring plants. Plant interaction processes have been well documented in the semi-arid region of Southeast Spain over the last 15 years. In this article we review the growing body of research on plant–plant interactions available from this area, highlighting its importance in increasing our knowledge on this field of study. This review has been organized in five sections, i) facilitation mechanisms; ii) the nurse effect; iii) the balance of interactions and environmental, ontogenic, temporal, and spatial gradients; iv) the effects of facilitation on biodiversity; and, v) facilitation and ecosystem functioning. Mechanisms of facilitation in these systems are relatively well known, but not completely explored. In these environments competition, mainly for water, is intense between neighbors and switches in intensity from belowground to aboveground as productivity increases. By contrast, facilitation may decrease quickly with increasing productivity, although the balance between facilitation and competition is not fully understood, and is further complicated because shifts can also be driven by factors such as life history or physiology of interacting species. Positive interactions are critical for maintaining biodiversity in some ecosystems in SE Spain, but their role as a driver of ecosystem functioning is less clear. Research on plant–plant interactions in this region has been highly influential and has contributed to our overall understanding of plant community dynamics. Despite the important progress achieved during the last 15 years, there is still substantial scope for exploring the effects of plant interactions at the ecosystem level, and their role as modulators of disturbances such as the current global environmental change.

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1. Introduction

Arid and semi-arid ecosystems are characterized by scarce and highly variable resources (water and nutrients) in space and time, and by overall harsh climatic conditions. In these environments, dominant perennial plants cause changes in micro-climate and soil properties leading to the formation of so-called "fertile islands" under plant canopies. These particular microsites are spots of high biological activity that concentrate an important part of the local flora and fauna (Gutiérrez et al., 1993; Maestre and Cortina, 2005; Pugnaire et al., 1996b; Pugnaire and Lázaro, 2000; Vetaas, 1992). In fertile islands facilitation, or the net positive effect of one plant species on another, predominates but interactions between species are complex. Survival and growth of plants in such patches may be mediated by improved micro-climate (Moro et al., 1997a, 1997b; Valiente-Banuet and Ezcurra, 1991), higher water availability (Dawson, 1993) or soil nutrient content (Armas et al., 2008; Pugnaire et al., 1996a; Reynolds et al., 1999) caused by perennial species, while light deprivation and mechanical and chemical effects of litter (Holmgren et al., 1997; Moro et al., 1997a) may have negative effects. Overall, facilitation plays a prominent role in plant community dynamics in arid environments (Flores and Jurado, 2003; McAuliffe, 1988; Pugnaire et al., 1996a).

During the last two decades there has been an unprecedented surge in interest on facilitative interactions worldwide, which has prompted important advances in our knowledge of the factors shaping composition, structure, and functioning of plant communities (see Brooker et al., 2008 and Callaway, 2007 for recent reviews). In this review we address how plants facilitate growth of others in semi-arid environments of SE Spain, the mechanisms

* Corresponding author. Tel.: +34 950 281045; fax: +34 950 277110.
E-mail address: fip@eeza.csic.es (F.I. Pugnaire).

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underlying facilitation processes, the variability of these processes influenced by resource gradients, and their consequences at the community and ecosystem level, highlighting the contribution of positive interactions to the general ecological theory. We used evidence based on observational experiments as well as on field manipulations and glasshouse experiments, including spatial pattern analysis, physiological measurements, and isotopic determinations (Fig. 1). These topics are organized in five sections, which encompass the bulk of research carried out in the last 15 years on plant–plant interactions in SE Spain. We also discuss the contribution and implications of this research to our understanding of community ecology in arid and semi-arid Mediterranean ecosystems. Other topics, relevant to plant interactions, such as biological soil crusts, trophic interactions, or ecosystem restoration, are treated elsewhere in this issue (Cortina et al., 2011; González-Megías et al., 2011; Maestre et al., 2011), and thus will not be discussed here.

The south-eastern corner of Spain is characterized by a warm, dry Mediterranean climate. The proximity of the sea and the relative low elevation causes lack of frost and mean annual temperatures in the 16–19 °C range. Extreme summer temperatures are common and daytime maximum of 45 °C have been recorded in some years, while soil surface may reach 80 °C. Mean annual rainfall in this region is low, with higher precipitation in autumn (linked to heavy storms and torrential phenomena) and early spring. There is also marked inter-annual rainfall variability (Lázaro et al., 2001). Mean annual rainfall is below 350–400 mm but precipitations lower than 200 mm are registered locally in some coastal areas (e.g., Cabo de Gata). Conversely, precipitation in mountains is often above 400 mm. It is, however, important to note the existence of hidden precipitations (by fog condensation) and the fact that high air humidity in coastal areas may cause an important decrease of evapotranspiration (Domingo et al., 2011). The low rainfall in this area is a direct consequence of its geographical isolation, originated by a chain of mountains over 2000 m in elevation (the Betic Ranges) that surround the region to the west and north. These mountains prevent the arrival of Atlantic fronts that sweep the rest of Spain, and make this the driest zone in Europe. Such singular environmental conditions limit plant growth and the establishment of forests, which are restricted to the top of mountains, and microsites with high humidity and deep soil profiles. These forests are dominated by holm oak (*Quercus ilex*) and xeric coniferous species such as Aleppo pine (*Pinus halepensis* Mill.) and several species of juniper (*Juniperus oxycedrus* L. and *J. phoenicea* L.).

2. Main facilitation mechanisms

In arid and semi-arid environments in SE Spain facilitation involves mainly shade, increased water or nutrient availability, improvement of microclimatic conditions as well as protection from herbivores. These mechanisms are discussed below.

2.1. Shade

Shade provided by the canopy of large plants may protect seedlings and other plants from temperature extremes, reducing thermal stress and water loss through transpiration, thereby protecting seedlings from photoinhibition (Moro et al., 1997a, b). Shading may impose a cost on photosynthesis, but most species from arid environments have photosynthetic optima under the prevailing radiation in such environments (Gómez-Aparicio et al., 2006; Valladares and Niinemets, 2008; Valladares and Pugnaire, 1999) and many benefit from the decrease in radiation provided by perennial plant canopies. With soil surface reaching over 70°C under full sunlight, any plant or object casting a shade has beneficial effects on other plants (Armas and Pugnaire, 2005; Moro et al., 1997b; Pugnaire et al., 1996a), and establishment of many species is mainly restricted to shady places. Shade benefits are at the core of

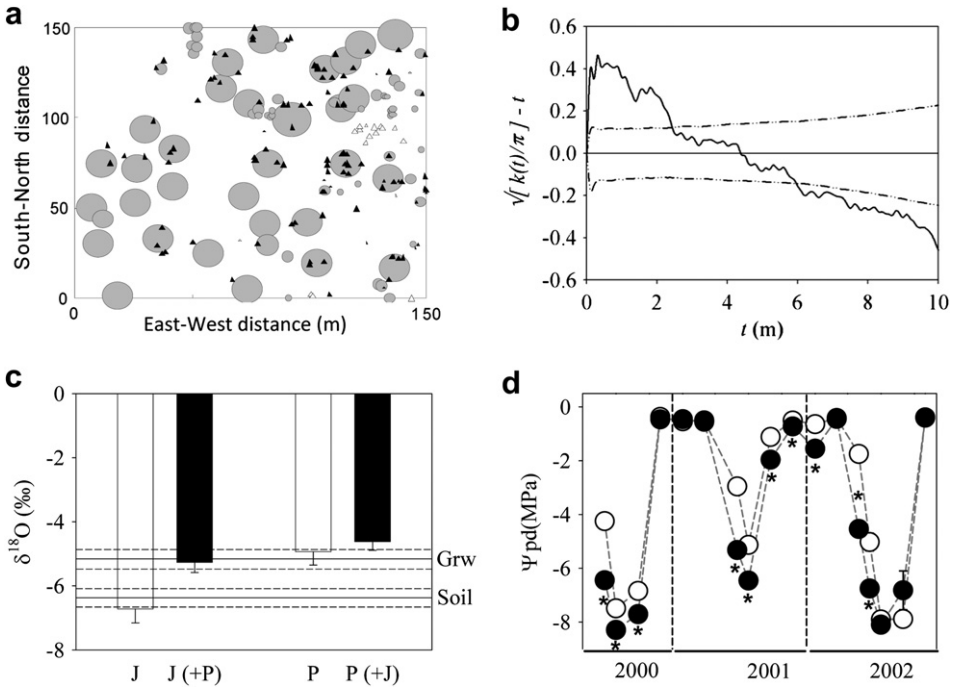

Fig. 1. Evidence on plant interactions in SE Spain was based on observational experiments as well as on field manipulations and glasshouse experiments, including spatial pattern analysis, physiological measurements, and isotopic determinations. Examples are the mapping of *Ziziphus lotus* and *Asparagus albus* in a coastal sand dune (a); spatial point pattern analysis of juvenile *Stipa* tussocks vs. *Cistus* shrubs (b); isotopic comparison of ^{18}O in sap of *J. phoenicea* (J) and *P. lentiscus* (P) living isolated (clear bars) or with the other species (solid bars) compared to soil and ground water (Grw) (c); and pre-dawn water potential of *J. phoenicea* growing with (solid dots) and without (clear dots) *P. lentiscus* (* significant differences at $P < 0.05$). Original data from a) Tirado and Pugnaire (2005); b and d) Armas and Pugnaire (2005, 2009); and c) Armas et al. (2010).

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positive spatial association between species in arid environments (see below), and such non-random spatial structure often relies on species whose establishment depends on conditions provided by other species (Tirado and Pugnaire, 2005).

Different gradients (radiation, temperature, nutrients) that can be found under plant canopies allow for different species to coexist in a heterogeneous environment. Moro et al. (1997b) showed how several herbaceous species positioned themselves differently under the canopy of *Retama sphaerocarpa* L., a leguminous shrub, in response to several gradients including irradiance and temperature. Radiation at the soil level in a central position under the canopy was 60% of that outside, and temperature differences reached up to 7°C. Sheltering from direct radiation has an effect on biomass production, although differences under different species do not always parallel the understorey light environment. Pugnaire et al. (1996b) found a non-linear, positive effect of canopy size on the diversity of understorey species in *Retama*, and Maestre and Cortina (2005) found a similar effect in *Stipa tenacissima* L. steppes, suggesting an increase in suitable niches promoted by increased plant size.

Finally, shade from perennial plants reduces thermal amplitudes and decreases soil water evaporation under the canopy (Domingo et al., 1999), which promotes an increase in soil moisture compared with bare ground and overall, a better water balance for the plant (Callaway, 2007; Maestre et al., 2003a; Pugnaire et al., 2004). Increases in soil moisture linked to reduced evapotranspiration have been identified as a key mechanism driving positive effects of *Stipa* on shrub seedlings in semi-arid ecosystems of SE Spain (Maestre et al., 2001, 2003a).

2.2. Soil moisture

The effects of plants on soil moisture are complex and may be positive or negative depending on factors like plant architecture, physiology, and the magnitude of rainfall events. In SE Spain higher values of soil moisture under the canopy compared to bare ground areas have been reported for key species such as *Stipa* (Maestre et al., 2003a; Maestre and Cortina, 2003), and *Retama* (Pugnaire and Luque, 2001; Pugnaire et al., 2004), but these effects are not general (Cuesta et al., 2010; Maestre et al., 2002).

Mechanisms other than shade can also account for an increase in soil moisture under plant canopies. Deep-rooted species are common in dry environments (Schenk and Jackson, 2002), and some of them are engaged in *hydraulic lift* (HL; Richards and Caldwell, 1987). This mechanism accounts for the passive movement of water between deep, moist soils and dry surface soils via plant roots, driven by water potential gradients. Prieto et al. (2010) assessed the occurrence of HL in *Retama* shrubs, which have a root system reaching at least 30 m deep (Haase et al., 1996b), and established the relationship between HL and transpiration processes. HL was linked to previous-day water depletion and related to soil water potential that, in turn, influenced seasonal variations in HL. This lifting of water is at the base of the positive effects of *Retama*, as understory plants may use hydraulically lifted water (Prieto, 2010) to have better water relations and growth rates than those that do not have access to this source of water (Zou et al., 2005). But HL is not always beneficial for neighboring species. In a semi-arid coastal sand dune system in SE Spain, Armas et al. (2010) analyzed the interaction between two shrub species, *Juniperus phoenicea* Guss. and *Pistacia lentiscus* L. During drought, *Pistacia* relied primarily on the permanent salty water table, while isolated *Juniperus* plants took up fresh water stored in upper soil layers. As drought progressed, soil layers dried out and the physiological activity of *Juniperus* nearly stopped while *Pistacia* was barely affected. However, *Juniperus* individuals growing with *Pistacia* had a xylem sap isotopic signature matching that of *Pistacia*, and differed greatly from isolated *Juniperus* individuals (Fig. 1c). It turned out that the water supplied by *Pistacia* via HL depressed the physiological performance of *Juniperus* because *Pistacia*, which withstands high salinity levels, was pumping salty water to salt-sensitive *Juniperus* causing its demise in the long-term.

Understory plants may also enhance water conditions for the overstory plants. Pugnaire et al. (1996a) found that *Retama* shrubs in Almería had higher water potentials when a perennial forb, *Marrubium vulgare* L., occupied the understory than when it did not. This effect was observed in spring but not in summer, suggesting that the presence of a dense understory helped retain water in the soil mound that accumulated under the shrub. Water catched by the canopy increases water infiltration close to the trunk (Martinez-Meza and Whitford, 1996) after small-to-medium rainfall events. During heavy rainfall events stem-flow is unlikely to make substantial differences in water availability under shrubs and surrounding soil (Pugnaire and Luque, 2001; Tewksbury and Lloyd, 2001).

Plants can also reduce soil moisture through direct water uptake and rainfall interception. In semi-arid afforestations of SE Spain, *P. halepensis* has been found to intercept a substantial amount of rainfall (Maestre et al., 2003b), and to reduce soil moisture (Bellot et al., 2004), an effect that was exacerbated as plant density increased and after spring and late-summer rainfalls. This reduction in soil moisture had a negative effect on the performance of understory shrub species (*Quercus coccifera* L., *Erica multiflora* L., and *Rhamnus lycioides* L.), who had more negative pre-dawn water potentials and lower (up to 56%) values of mean net photosynthesis and stomatal conductance under the canopy of *Pinus* (Bellot et al., 2004). These negative effects increased with increasing *Pinus* density, suggesting the presence of a strong competition for water between this species and their understory shrubs.

The conspicuous herbaceous community under many shrubs has complex effects on soil moisture. Negative effects of the herbaceous understory on soil moisture have been found under *Pinus* (Maestre et al., 2004) and under *Retama* (Cuesta et al., 2010) which in turn negatively affected survival of *P. lentiscus* and *Quercus ilex* L. seedlings, respectively. In very dry environments, the understory community usually depends on the permanence of water supply, which differs among shrub species (Pugnaire et al., 2004).

Shrubs with a large community in the understory, counter-intuitively, may not show lower moisture levels than shrubs with a smaller community, even though transpiration would be higher in the latter; lowering soil temperature by a dense understory seems to reduce evaporation above transpiration losses, providing overall better water balance for the shrub (Domingo et al., 1999; Pugnaire et al., 2004).

2.3. Soil nutrients

Soils beneath the canopy of perennial species are often richer in nutrients than soils in surrounding open spaces without perennial cover (Cortina and Maestre, 2005). Subcanopy soil enrichment may occur from “nutrient pumping” (*sensu* Richards and Caldwell, 1987), as deep-rooted perennials take up nutrients unavailable to shallow-rooted species and deposit them on the soil surface via litterfall and throughfall. In addition, the canopy of perennial species may trap airborne particles, which eventually are deposited at the base of the plant (Pugnaire et al., 1996b; Whitford et al., 1997). Soil nutrient enrichment may also occur via nitrogen fixation.

Increased soil nutrients have been reported under perennial species in many systems throughout the world, but these effects

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have been described most often in savannas and other semi-arid regions with clearly demarked understory and open microhabitat (Armas and Pugnaire, 2009, 2008; Goberna et al., 2007; Maestre et al., 2001; Moro et al., 1997a, b; Pugnaire et al., 2004, 1996a, 1996b; Tirado and Pugnaire, 2003).

Pugnaire et al. (1996a) reported a "mutual facilitation" between the shrub *Retama sphaerocarpa* and the herb *M. vulgare* based on improvements in soil nutrients and water. *Marrubium* plants under *Retama* had greater leaf specific area, leaf mass, shoot mass, leaf area, flowers, higher leaf nitrogen content, and more N per plant than those that were not under *Retama* (Fig. 2). Conversely, *Retama* shrubs with *Marrubium* underneath had larger cladodes, greater total biomass, nitrogen content, and higher shoot water potential than shrubs without *Marrubium* in the understory, suggesting that facilitation could be bi- rather than uni-directional.

Moro et al. (1997b) showed that the interaction between *Retama* and its understory vegetation was strongly affected by gradients of litter accumulation and decomposition, both of which influenced species composition. The abundance of annual herbs produced a more favorable habitat for soil micro-organisms, which increased mineralization rate, enhanced litter decomposition and increased nutrient dynamics under *Retama* shrubs. However, litter may have both positive and negative effects on plant growth, as has been shown elsewhere (Facelli, 1994; Hoffman, 1996).

The improvement of soil fertility by shrubs, and particularly the accruement of organic matter (OM), is apparently a primary source of facilitation under the canopy of shrubs like *Retama*, as OM build-up changes soil physical properties and improves soil water relations (Pugnaire et al., 2004; Puigdefábregas et al., 1999). Although sheltering from direct sunlight did affect understory growth, the biomass under the canopy of different shrub species did not correlate with the incident radiation reaching the soil (Pugnaire et al., 2004). This does not agree well with the interpretation of experimental manipulations in other arid ecosystems, where shade is suspected the most important facilitation factor (Flores and Jurado, 2003; Valiente-Banuet and Ezcurra, 1991). Transpiration and leaf temperature, however, may remain high in the understory because of the heated air and energy advected from the surroundings (Scholes and Archer, 1997). The attributed shade effects may result, thus, from a combination of factors including several of those mentioned above. A positive balance of the interaction among plants, essentially mediated by changes in soil properties, may be one of the predominant outcomes of plant interactions in semi-arid communities of SE Spain.

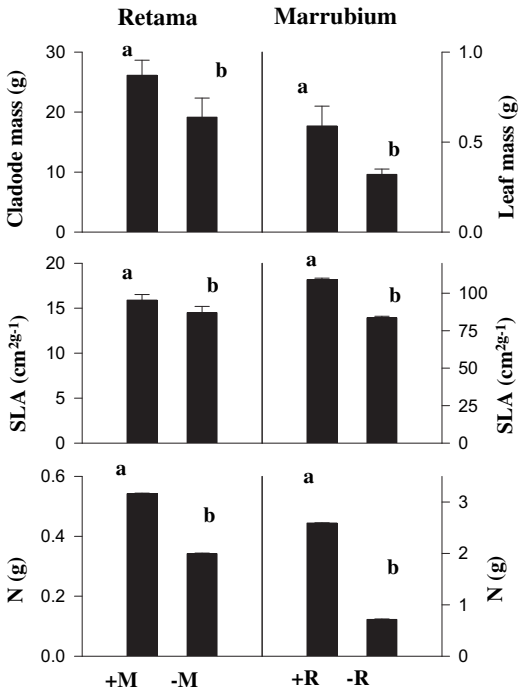

Fig. 2. Dry mass of cladodes or leaves per branch, specific leaf area (SLA), and nitrogen content in 3-yr old branches of *Retama sphaerocarpa* (*R*) and whole plants of *M. vulgare* (*M*) growing in association (+*R*, +*M*) or alone (-*R*, -*M*) in Almería, Spain (From Pugnaire et al., 1996a).

2.4. Protection from herbivores

Positive interactions may be indirectly mediated through herbivores. For instance, *Whitania frutescens* (L.) Pauquy, a native shrub from the Iberian SE, is a preferred fodder and suffers high impact from grazers when not associated with the less palatable, heavily defended shrub *Maytenus senegalensis* (Lam.) Exell (Tirado, 2003). When associated to spiny *Maytenus*, *Whitania* looses less mass, having four-times more twigs and 2.5 times more leaf mass than those unprotected from herbivory. Similar examples of associational defences have been reported elsewhere (Baraza et al., 2006; Smit et al., 2006). In SE Spain, unpalatable *Artemisia barrelieri* Bresser shrubs facilitate seed germination and seedling establishment of more palatable *Anthyllis cytisoides* L. in addition to providing shelter from herbivory during early stages of growth, and before being competitively displaced by *Artemisia* (Haase et al., 1997). *Stipa* tussocks have also been found to reduce browsing by rabbits in planted seedlings of species like *Retama* (Soliveres et al., 2010) and *Medicago arborea* (Maestre et al., 2001). Alados et al. (2006a) also observed a positive association among palatable species such as *Ballota hirsuta* Benth., *Thymus hyemalis* Lange, *Teucrium lusitanicum* Schreb. or *Sideritis osteoxylla* Pau. and co-occurring unpalatable species. This association was more evident in the most palatable species (*Ballota*), whose association with unpalatable species increased with grazing pressure. In most cases, benefactor species appear to physically shelter or hide beneficiary species from herbivores (Baraza et al., 2006, 2007).

3. The nurse effect

Of particular importance in water-limited systems is the so-called 'nurse plant syndrome' (*sensu* Niering et al., 1963), where establishment of seedling of one species is facilitated under the canopy of adult plants of the same or other species. This phenomenon, also called 'nurse effect', has been documented in different ecosystems, but it seems to be critical in dry habitats. More than half the studies reporting this phenomenon come from arid and semi-arid communities (Flores and Jurado, 2003). Seedlings often grow beneath nurses because they trap seeds of other species, and because they benefit from higher water and nutrient availability, ameliorated micro-climate or because of protection from herbivores (Flores and Jurado, 2003).

Puigdefábregas and Sánchez (1996) showed that, in SE Spain, *Stipa* traps water and sediments when growing in steep slopes, forming small terraces upslope. García-Fayos and Gasque (2002) showed that these terraces were sites of increased plant survival compared to bare soil, particularly during severe drought periods. Maestre et al. (2001, 2003a) experimentally showed the potential of *Stipa* as a nurse species, as soils under tussocks have higher organic matter content and water availability than soils in the open, and the micro-climate is improved in the surroundings of *Stipa* canopies.

But the effects of nurses are not always equal for all species. Padilla and Pugnaire (2009) showed that the effect of *Retama* on survival of planted seedlings was dependent on the species identity

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and environmental conditions, ranging from positive for *Olea europaea* L. to neutral for *Pistacia* to negative for *Ziziphus lotus* L. Similar results have been found for *Stipa*, which had positive, neutral or negative effects on survival of species like *Pistacia* (Maestre et al., 2001, 2003a), *Q. coccifera* (Maestre et al., 2002) or *Retama* (Soliveres et al., unpublished data), respectively. Such effects vary depending on the spatio-temporal changes of rainfall conditions (see Discussion below). In cold semi-arid mountains of eastern Spain, Montesinos et al. (2007) showed that *Juniperus thurifera* L. trees acted as nurses for seedlings of the same species by ameliorating conditions beneath canopies. However, most seedlings were found under female trees because of bird perching on reproductive females, concluding that in dioecious species the gender of nurse plants can determine the spatial structure of recruitment. The joint effects of facilitation and this perch effect were also explored by Pausas et al. (2006), who tested whether the carob tree (*Ceratonia siliqua* L.) generated nucleation patterns in old-fields in SE Spain. They found that woody species colonizing abandoned fields in this area were not randomly distributed, but rather followed a nucleation pattern with higher plant densities under tree canopies. However, the nucleation pattern was only significant for fleshy-fruited species, suggesting that the perch effect played an important role in pattern generation. Total plant density and density of non-fleshy-fruited species did not increase with time after abandonment, while the perch effect (density of fleshy-fruited species) did increase significantly. Thus, the authors concluded that the nucleation pattern found in this old-field succession was best explained by the perch effect, while facilitation had a secondary importance.

Finally, de la Cruz et al. (2008) showed that survival of *Helianthemum squamatum* (L.) Dum. -Cours. seedlings under nurse shrubs was spatially structured, and that spatial patterns shifted through time. Of major importance was the time of seedling emergence. Seedlings emerging late in the season under the canopy of adult plants died from drought stress more often than expected, whereas those emerging earlier in the same microsite survived better than expected. The identity of neighbors also affected the spatio-temporal dynamics of seedling mortality. Overall, these results suggested that the time of seedling emergence, its age and the identity of its neighbors determined the sign and the spatial scale of plant–plant interactions.

Beyond the nurse effect, some species modify their environment in such a way that become ecosystem engineers. Species such as *Retama sphaerocarpa* or *Ziziphus lotus* have effects with important consequences at the local scale, not only affecting community structure (i.e., species composition and spatial patterns) and productivity, but essentially changing ecosystem function (Crain and Bertness, 2006). These effects are mediated by indirect interactions and modulated by climate.

4. Interaction balance over gradients

4.1. The balance of plant–plant interactions along resource and environmental gradients

Complex combinations of competition and facilitation operating simultaneously among different species of plants seem to be widespread in nature (Aguiar and Sala, 1994; Callaway and Walker, 1997; Holmgren et al., 1997; Holzapfel and Mahall, 1999). Both competition and facilitation intensities change along gradients of resource availability (Bertness and Callaway, 1994; Brooker and Callaghan, 1998; Grime, 1979; Tilman, 1988), so that plant interactions are best viewed as dynamic relationships in which the outcome, in terms of productivity or fitness of the interacting species, depends on abiotic conditions. For instance, Maestre et al. (2003a) conducted a manipulative field experiment in SE Spain to disentangle the positive and negative effects involved in the interaction between *Stipa* and *Pistacia* seedlings. They found that both competition (mostly for water) and facilitation (mostly by micro-climate amelioration) where acting at the same time, and that the intensity of facilitation was higher than that of competition, resulting in a net facilitative effect of *Stipa* on *Pistacia*. These positive and negative effects changed in a non-proportional manner along short-term temporal abiotic stress gradients. Similarly, changes in the interaction balance between different plant species along a gradient of environmental stress were documented in the dry Tabernas basin (Pugnaire and Luque, 2001) using *Retama* and its well documented facilitative effects on understory species as a model. The contrast between the environment under shrub canopies and gaps between shrubs were expected to change with elevation, so that differences at high elevation –with relatively less stressful conditions- could be smaller than at low elevation –with relatively more severe conditions. Pugnaire and Luque (2001) found that in both upper and lower elevations understory soils were more fertile than gap soils and that in the lower valley site plants growing in the understory were larger than plants growing outside, pointing to a change in the balance of the interaction caused more by a decline in facilitation than by a change in competition. Facilitation proved to be more important in more stressful environments, while aboveground competition strength decreased with increasing stress, although there was a simultaneous increase in belowground competition.

Although the dynamic nature of plant–plant interactions is being increasingly considered (Brooker et al., 2008; Maestre et al., 2009b), there is some disagreement on the patterns observed in the field. For example, while competition for light increases toward the more productive end in a gradient of environmental resource availability (Grime, 1977; Tilman, 1988), competition for belowground resources may or may not change (Reynolds and Rajaniemi, 2007). Experimental evidence supporting shifts in total competition intensity along productivity gradients seems to depend on whether above- and belowground competition are negatively correlated (Armas et al., 2009), on changes in species composition or diversity (Peltzer et al., 1998), or on the consistency of resource supply vs. demand (Taylor and Aarsen, 1990). On the other hand, positive interactions are expected to be more important in plant communities under increased abiotic stress or consumer pressure, because neighbors buffer one another from extremes of the abiotic environment and herbivory, and competitive interactions, in turn, dominate when physical stress and consumer pressure are both relatively low (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). In this regard, the stress-gradient hypothesis (SGH) of Bertness and Callaway (1994) predicted a positive monotonic pattern in the relationship between the severity of abiotic conditions and plant–plant interactions. This severity-interaction relationship pattern has been widely supported by empirical evidence (Callaway, 2007). However, and based on recent empirical data, other authors proposed that positive interactions may increase with environmental severity until they reach a plateau, which is also a monotonic pattern (see reviews in Kawai and Tokeshi, 2007; le Roux and McGeoch, 2010), take a hump-shaped pattern – i.e., negative interactions at both low and high levels of environmental severity and positive interactions at intermediate levels (Kawai and Tokeshi, 2007; Maestre and Cortina, 2004a,b; Michalet et al., 2006), or follow a combination of the above patterns.

There are some studies that analyzed this severity-interaction relationship pattern in SE Spain. Armas et al. (unpublished) tested whether the net interaction balance changed along an aridity gradient at three points comprising the whole distribution range of *Retama* in Europe. Their results showed that the intensity,

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importance, and frequency of facilitation on the herbaceous understory by *Retama* shrubs increased monotonically with increasing environmental severity, lending support to the SGH. Maestre and Cortina (2004a,b) evaluated how the net effect of *Stipa* on *Pistacia* varied across a gradient of abiotic stress in ten semi-arid Mediterranean steppes from SE Spain. They found that the outcome of this interaction followed a hump-shaped pattern, with competitive interactions dominating at both extremes of the gradient. These results do not support predictions of the SGH, and suggest that a shift from facilitation to competition under high stress conditions is likely to occur when levels of the most limiting resource are so low that the facilitator species cannot meet its own needs. A synthesis of different planting experiments carried out in *Stipa* steppes and *P. halepensis* afforestations in SE Spain is presented in Fig. 3. Most these studies were not designed with the idea of testing the SGH, but as they were conducted using a standardized methodology and were carried out under different rainfall conditions, they provide some insights on how abiotic stress may affect the outcome of plant–plant interactions. The main feature of this figure is the high scatter found in the data at the highest abiotic stress level, as measured using the performance of the planted seedlings (Lortie and Callaway, 2006). The effects of *Stipa* and *Pinus* on survival of woody seedlings ranged from highly negative to highly positive under such conditions, a result that does not support predictions from the SGH. Furthermore, there is no clear relationship between abiotic stress and the intensity of the interaction, regardless whether all data are taking together or only a subset is considered. These results illustrate the difficulties associated to predicting the outcome of plant–plant interactions along abiotic stress gradients, even when studying the same or a limited set of nurse species, and when comparing studies carried out using the same methodology in a given region.

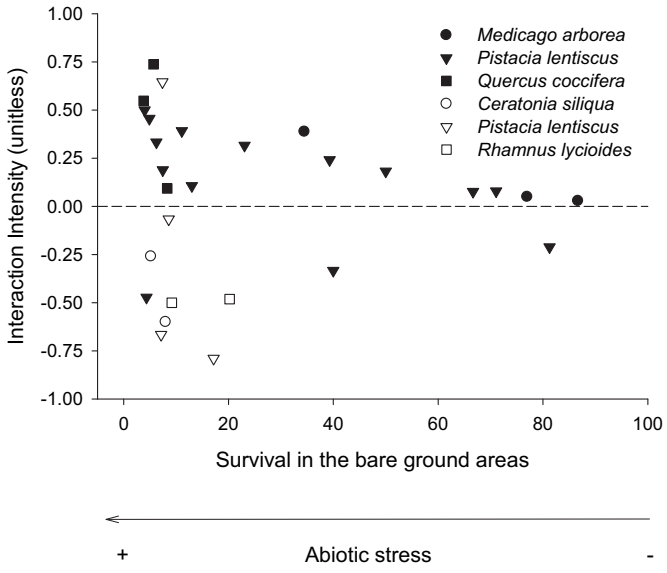

Fig. 3. Results of the intensity of the interaction, as measured with the RII index, between *P. halepensis* (white symbols) or *S. tenacissima* (black symbols) and seedlings of multiple Mediterranean shrub and tree species. RII was calculated as $(SU_N\text{-}SU_O)/(SU_N + SU_O)$, where SU_N and SU_O are the survival of seedlings planted under the canopy of either *Pinus* or *Stipa* and in open areas devoid of vascular plants, respectively (Armas et al., 2004). Positive and negative RII values indicate net facilitative and competitive interactions, respectively. We used SU_O as an overall indicator of abiotic stress (Lortie and Callaway, 2006). All data come from experiments conducted with the same methodological (one-year old seedlings planted using manually-dig holes) and carried out in semi-arid *S. tenacissima* steppes and *P. halepensis* plantations from Alicante (SE Spain). In all cases data are obtained from post-summer survival (between eight and ten months after planting). Original data from Maestre et al. (2001, 2003a, 2003b, 2004) and Maestre and Cortina (2004a,b).

Contrasting results such as discussed in the preceding paragraph are not fully surprising, as many of them were carried out at the dry end of an aridity gradient (Lortie and Callaway, 2006; Maestre et al., 2005b), where negative interactions could prevail (Maestre and Cortina, 2004a,b; Tielbörger and Kadmon, 2000; but see Holzapfel et al., 2006). In dry and hot environments, plant communities are limited by water, and the effects of drought are exacerbated by high temperatures. This could impair performance of one in a pair of interacting species through competition for water (Tielbörger and Kadmon, 2000). Facilitation would then occur only if benefits from enhanced nutrient availability or shade exceed competition for water (Holmgren et al., 1997) or if the benefactor species can increase the availability of water (Maestre et al., 2009b). Predicting how plant–plant interactions vary along stress gradients is further complicated because shifts in the net balance of an interaction (i.e., from competition to facilitation or vice-versa) have also been observed in several systems driven by factors such as life-history stage or the physiology of interacting species (Armas and Pugnaire, 2009, 2005; Haase et al., 1996a; Pugnaire et al., 1996b for examples from SE Spain). Field experiments and substantive indirect evidence have also shown a strong relationship between the degree of abiotic stress and such changes (Brooker et al., 2008; Callaway, 2007). Other non-experimental studies also indicate that competitive effects are stronger in wet and cool years and facilitative in dry, hot years (Callaway, 2007; Pugnaire and Lázaro, 2000).

4.2. Temporal and physical gradients

Interactions between different species may change with the ontogeny of the interacting individuals as plant development affects the demand for resources, but also vary in response to environmental fluctuations. In arid ecosystems it is frequent that nurse species compete or even get competitively displaced by beneficiary species (Callaway and Walker, 1997; Flores and Jurado, 2003; Valiente-Banuet and Verdú, 2008). In a coastal sand dune in SE Spain, colonization processes are triggered by facilitation and shaped by physiological traits of the different species. Plant–plant interactions, strongly affected by environmental gradients, drive the dynamics of this community. Here, Armas and Pugnaire (2009) found a strong bi-directional interaction between *P. lentiscus* and *J. phoenicea* with a net balance that changed in sign with plant development. While mature individuals facilitated the establishment of seedlings of both species, adult mortality patterns suggested asymmetric competition at later life stages. The interaction with *Pistacia* negatively affected *Juniperus* growth and physiology (Fig. 1d) and contributed to high mortality rates, while *Juniperus* had almost no effect on mature *Pistacia* plants. As explained before, Armas et al. (2010) showed that hydraulic lift of salty water was the mechanism by which *Pistacia* demised *Juniperus*.

In another plant community Armas and Pugnaire (2005) analyzed the balance of interactions between the shrub *Cistus clusii* Dunal and the perennial grass *S. tenacissima* at two different life stages. *Cistus* acted as nurse for juvenile *Stipa* improving water status, nutrient content, carbon assimilation rate, and growth. The underlying mechanisms were improvement of microclimatic conditions and soil physiochemical properties under shrub canopies. Juvenile *Stipa* plants had an overall neutral effect on *Cistus* shrubs, although they suffered some competitive effects during water shortage periods. For both species, the short-term outcome of the interaction was dependent on resource availability. In adult plants, close spatial association had no negative effects for the interacting species, suggesting that positive effects most likely counter-balanced negative ones. The long-term outcome of the

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interaction was reflected in the spatial distribution of both species (Fig. 1b), and determined population dynamics in this community.

In a semi-arid steppe in central Spain, Soliveres et al. (2010) explored the interaction between *Stipa* and the shrub *Lepidium subulatum* L. throughout the life cycle of the shrub, analyzing the spatio-temporal variability in abiotic stress as a modulator of the outcome of the interaction. *Stipa* acted as a nurse for *Lepidium*, being particularly important during germination, but shifted to competition after establishment.

A particular case of changes in the interaction balance with plant age was analyzed by Verdú et al. (2004), who accounted for differences in gender in two dioecious *Juniperus* shrub species in eastern Spain due to differences in reproductive effort. *Juniperus sabina* L. acted as a nurse for *Juniperus communis* L., and the authors tested whether this association represented a more stressful condition for females than for males of both species because of the greater reproductive effort of females. The authors observed that the association with the nurse plant reduced growth and reproductive capacity of both genders in *J. communis*. In contrast, the association with *J. communis* did not affect the fitness of the nurse plant, *J. sabina*, although a gender effect was found on several physiological parameters; *J. sabina*-associated females had a more negative water potential and carbon isotope discrimination than the associated males, but there were no differences between genders when growing in isolation.

Overall, these data show that the short-term balance of plant interactions may easily shift in response to environmental variability, which in turn may have important consequences for plant community structure. Therefore, measuring interaction intensity at only one point in time, one life stage, or one response variable is not enough for drawing conclusions about the long-term effects of plant–plant interactions on population dynamics (Armas and Pugnaire, 2005, 2009; Schiffers and Tielbörger, 2006), nor their responses under changing environmental conditions (Brooker, 2006; Brooker et al., 2008; Tielbörger and Kadmon, 2000).

4.3. Spatial patterns

Plant interactions control population dynamics and spatial patterns, and ultimately have consequences at the ecosystem level. In SE Spain, Tirado and Pugnaire (2003) analyzed the distribution of two shrub species (one large and dominant, *Ziziphus lotus*, the other smaller and subordinate, *Asparagus albus* L.) and estimated the reproductive consequences of their distribution for the smaller species. Spatial distribution patterns showed that the two species were significantly aggregated and their association affected *Asparagus albus* fitness (Fig. 1a). *Asparagus* seedlings had higher survival rates under *Ziziphus* than in the open. Plants produced more flowers, fruits, and showed a higher mass of seeds when living in aggregates with *Ziziphus* than when isolated. The mechanisms responsible for this facilitative effect seemed to be related to soil enrichment in patches. Thus, these results suggested that the spatial aggregation of species can be indicative of a positive interaction among them, directly affecting the fitness of at least one of the species.

In another study, Tirado and Pugnaire (2005) quantified species co-occurrence and interaction in seven environmentally contrasted communities, including four different semi-arid habitats in SE Spain. They combined indirect evidence from community structure with direct data on species interactions to identify processes that shape plant communities. The four semi-arid sites in Spain showed a high degree of positive species association. Direct experimental measurement of neighbors' effect showed that positive interactions prevailed in communities where positive species association dominated, thus providing a link between spatial patterns and species interactions. Aggregation points to positive interactions and segregation to competitive or interference effects (Fig. 4). In all cases, the appearance of a benefactor species increased species richness compared with the surrounding inter-shrub spaces, suggesting that facilitation was a relevant process shaping communities under environmental constraints. Other studies in SE Spain found similar results (Alados et al., 2006b; Armas and Pugnaire, 2005; Gasque and Garcia-Fayos, 2004; Haase et al., 1996a, 1997; Maestre et al., 2005a) overall suggesting that plant community structure bears information linking spatial patterns and ecological processes.

5. Effects of facilitation on biodiversity

Several studies showed significant transient (climatic) and permanent (soil-related) micro-environmental differences under the canopy of different shrub species that affect biodiversity. In an observational study in SE Spain, Pugnaire et al. (2004) showed that the influence of shrubs on the herbaceous community ranged from negative (e.g., under *Thymus*) to very positive (e.g., under *Retama*), although facilitation predominated as biomass of annuals under most shrubs in this community was larger than in gaps. Mean species richness was similar under individual shrubs and in gaps, but 40% of all species – excluding Poaceae – were found only under shrubs and overall species under shrubs outnumbered species in gaps; shrubs with the most intense facilitation effect were the ones that differed most from gaps. The influence of shrubs on understory communities was often caused by changes in soil physical and chemical characteristics, the most important factor seemed to be organic matter accruement. Organic matter has an effect on soil thermal characteristics and water relations, decoupling soil temperature and moisture.

Isolated shrub patches are a key element for ecosystem structure, functioning and dynamics in semi-arid steppes of SE Spain (Maestre and Cortina, 2004b; Maestre et al., 2009a). They have been found to increase the richness and diversity of vascular plants of these ecosystems (Maestre et al., 2009a). Maestre and Cortina (2005) found that understorey species richness was significantly related to the size of individual shrubs according to a simple power relationship. Site characteristics (climatic feature, elevation, geographical coordinates and slope), shrub patch characteristics (size and number), and shrub species identity significantly explained the occurrence of understory species on shrub patches. However, the relative importance of site characteristics was higher than that of patch characteristics and species identity in explaining patterns of understory occurrence. In other two studies from SE Spain, Pugnaire et al. (1996b) and Pugnaire and Lázaro (2000) analyzed whether the facilitative effect of *Retama* was dependent on the shrub life history. Pugnaire et al. (1996b) found that plant diversity in the understory increased with shrub age, with a parallel increase in soil nutrients, water-holding capacity, and ameliorated soil texture. Larger and older canopies increased environmental heterogeneity underneath, which favored the establishment of a larger number of species. Although soil seed bank was rather uniform across shrub ages and dispersal was not limiting, canopy size was a major sorting factor for species richness (Pugnaire and Lázaro, 2000). Drought-resistant species, typical of open areas between shrubs were displaced from the understory center by taller, more mesic species over the age gradient (Pugnaire et al., 1996b). Overall, understory community composition depended on multiple interspecific interactions, such as facilitation by the shrub and competition from neighbors, as well as on dispersal processes, highlighting that facilitation was a key feature determining the structure of these plant communities.

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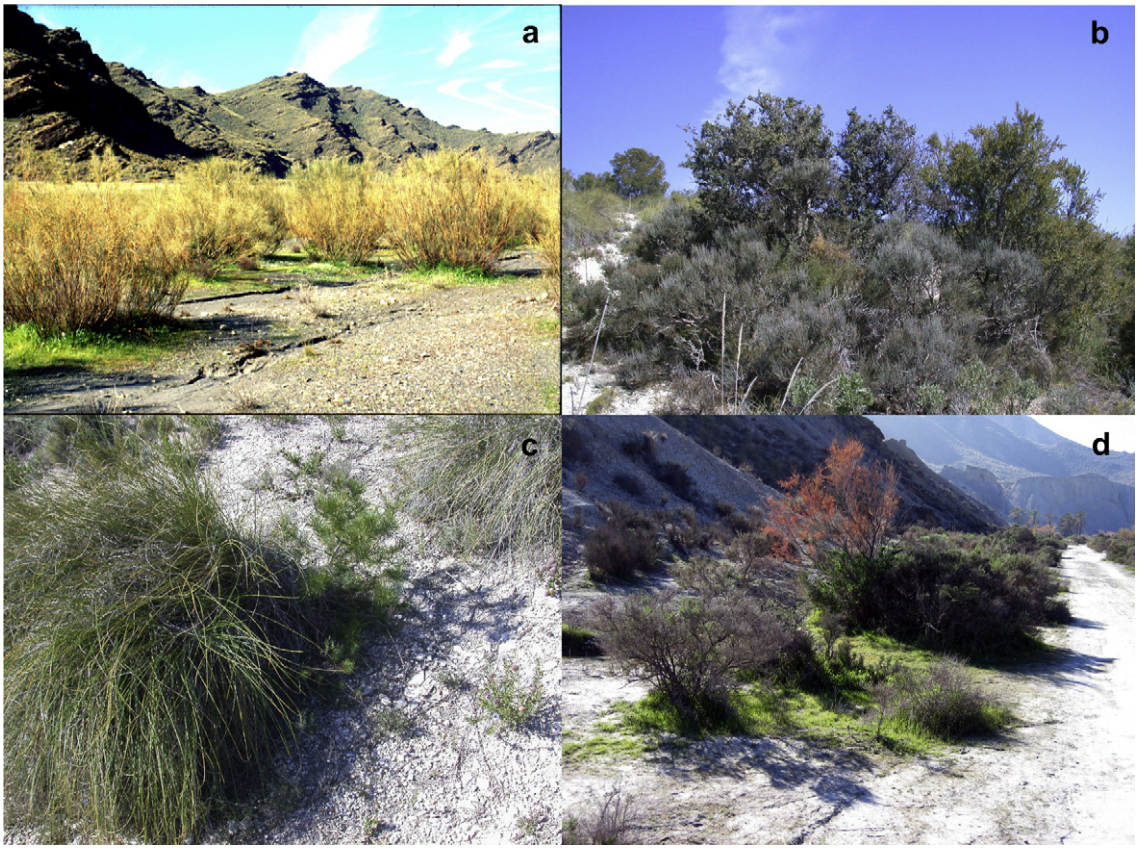

Fig. 4. Shrubs in semi-arid environments often show a conspicuous community in the understory which contrasts with surrounding bare ground, like in *Retama sphaerocarpa* (a) and several species (d) in a river bed in Almería, Spain; vegetation patches are occupied by several tree and shrub species where often facilitation prevails (b); the nurse plant syndrome is common in semi-arid environments, as in this case where *S. tenacissima* facilitates a sapling of *P. halepensis*. Photos F. I. Pugnaire (a and d), Fernando T. Maestre (b and c).

6. Facilitation and ecosystem functioning

Because of the important role plant interactions play in determining community composition and structure, facilitation and competition can largely control ecosystem functioning (Hooper et al., 2005; Michalet et al., 2006; Yachi and Loreau, 2007). Yet, despite its potential importance, few studies have evaluated empirically the role of positive interactions on ecosystem functioning (Kikvidze et al., 2005; Mulder et al., 2001). Therefore the importance of facilitation as a driver of ecosystem functioning remains largely unknown (Callaway, 2007). In a recent study, Maestre et al. (2010) tested the relative importance of facilitative–competitive interactions at the community level along with other community attributes (cover, species richness and species evenness) as drivers of ecosystem functioning in *Stipa* steppes along a wide environmental gradient from central to SE Spain. Biotic interactions, measured as co-occurrence patterns, shifted from facilitation to competition along stress gradients driven by water availability and temperature. These authors found little evidence to suggest that biotic interactions are a major direct influence upon indicators of ecosystem functioning (soil respiration, organic carbon, water-holding capacity, compaction and the activity of enzymes related to the carbon, nitrogen and phosphorus cycles) along environmental gradients. However, attributes such as total community cover showed a direct positive effect on ecosystem functioning. These results indicate that the role of biotic interactions may be of secondary importance for ecosystem functioning compared to biotic attributes such as cover.

7. Concluding remarks and future directions

Research carried out in the Iberian SE has substantially contributed to our overall understanding of plant–plant interactions and their role in community dynamics, shedding light into the mechanisms involved in these interactions, their role as determinants of ecosystem structure and functioning, and their temporal and spatial variability. Despite the important advances in knowledge, there is substantial scope for further research exploring these and other key topics. As highlighted by Brooker et al. (2008), indirect facilitative effects, which have been barely addressed in SE Spain, their impacts on diversity and evolution, the degree of non-transitivity in plant competitive networks, and the contribution of facilitation to species coexistence at spatial scales beyond discrete plant patches are venues for exciting new research. Of particular interest are the elucidation of the effects of plant interactions as drivers of ecosystem structure and functioning under the ongoing global environmental change, and the development of better conceptual and mathematical models to improve our ability to predict the interplay between facilitation and competition along resource and environmental gradients. While we are still far from a fully understanding of the relationship between plant–plant interactions and abiotic stress, recent conceptual advances, numerical models and discussions (e.g., Chen et al., 2009; Lortie and Callaway, 2006; Maestre et al., 2006, 2009, 2005b; Malkinson and Tierlbörger, 2010) are paving the way for new and important advances to develop a more general and predictive theory. Studies carried out in SE Spain have been highly influential to shape these

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developments, and we believe that facilitation research from this region will continue playing an important role in this important ecological topic.

We need a good understanding of natural processes to be able to properly manage natural habitats, prevent environmental risks, and secure the continued supply of ecosystem services. Complex processes like plant–plant interactions are at the base of ecosystem structure in semi-arid environments and knowing them in detail can substantially improve our understanding of ecosystem functioning and its responses to the ongoing environmental change. We hope this review illustrated research carried out in SE Spain on plant–plant interactions and will foster additional research efforts on this exciting and important ecological topic.

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