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FACILITATION BETWEEN HIGHER PLANT SPECIES IN A SEMIARID ENVIRONMENT[1]

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Abstract. A major role of facilitation between higher plant species, particularly in stressful environments, has recently been reported in several papers that suggest that beneficial interactions could be more important in the dynamics of plant communities than has been recognized to date. In a semiarid region in southeastern Spain we determined the effect of a leguminous shrub, *Retama sphaerocarpa,* on its environment, testing the hypothesis that facilitation by the shrub of one species of its understory, *Marrubium vulgare,* is reciprocal and that the shrub benefits from sheltering herbs beneath its canopy.

Marrubium plants under *Retama* had greater specific leaf area, leaf mass, shoot mass, leaf area, more flowers, a higher nitrogen (N) concentration in leaf tissue, and more N per plant than isolated plants, suggesting a facilitative effect of *Retama* on *Marrubium* including increased availability of resources. Biomass of 1-yr-old cladodes, total biomass, total nitrogen content of 3-yr-old branches, and shoot water potential at midday were higher for *Retama* shrubs with *Marrubium* beneath them than in shrubs without *Marrubium.*

Retama strongly improved its own environment, facilitated the growth of *Marrubium* and other species underneath its canopy, and at the same time obtained benefits from sheltering herbs underneath. The interaction between these two species was indirect, associated with differences in soil properties and with improved nutrient availability under shrubs compared with plants growing on their own.

We propose that the mutual benefit of the association between *Retama* and *Marrubium* is best termed a facultative mutualism. Each partner benefits from greater availability of resources in the "island of fertility" that results from their association. If beneficial plant–plant interactions as described here are widespread, positive relationships may have a major role in determining the pattern and structure of plant communities.

Key words: arid zones; facilitation; island of fertility; Marrubium; *mutualism;* Retama; *species interactions.*

INTRODUCTION

Recent papers have emphasized the role of positive feedbacks in the dynamics of plant communities (Hobbie 1992, Wilson and Agnew 1992), in particular the ability of plant species to improve their environment by enhancing nutrient availability or resource capture. Some papers have also reported a major role of facilitation among higher plants, particularly in stressful environments such as salt marshes (Bertness and Shumway 1993, Callaway 1994), arctic regions (Walker and Chapin 1986, Carlsson and Callaghan 1991, Chapin et al. 1994), and desert environments (McAuliffe 1988, Franco and Nobel 1989). This suggests that positive relationships between species are more important than recognized to date in the dynamics of plant communities (e.g., Bertness and Shumway 1993).

Ever since Clements' work (1916), facilitation, i.e., the modification of the environment by one species that makes it more suitable for other species, has been considered to be merely a mechanism for succession (e.g., Connell and Slatyer 1977, Van Andel et al. 1993), of far less importance than competition in structuring plant communities. For this reason, the best example of facilitation involves fungi rather than higher plants (Van Andel et al. 1993). Bertness and Callaway (1994) proposed that the buffering of environmental harshness enhances positive interactions in communities under high physical stress, while competition predominates in more mesic habitats. Interaction among species should then lie somewhere on a continuum between facilitation and competition.

Facilitation could be important in semiarid environments, in which shrubs often have a layer of annual and perennial herbs underneath their canopies (Went 1942, Muller 1953, Fowler 1986). Herbs may benefit from greater availability of water under the canopy (Richards and Caldwell 1987, Joffre and Rambal 1988, 1993, Dawson 1993) as well as from greater availability

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of nutrients (Callaway et al. 1991, Rostagno et al. 1991, Gutiérrez et al. 1993). It is also possible that the shrub benefits from the effect of herbs on the soil, for example, protecting the soil from erosion, direct insolation, and over-heating. However, the effect of the herb layer on the shrub has not yet been reported to our knowledge.

Some regions of southeastern Spain, with ≈250 mm of annual rainfall, resemble desert ecosystems in which biomass is concentrated around individual or grouped shrubs, to form "islands of fertility" (García-Moya and McKell 1970, Barth and Klemmedson 1982, Virginia and Jarrel 1983, Garner and Steinberger 1989). In southeastern Spain, the leguminous shrub, *Retama sphaerocarpa* (L.) Boiss., is a dominant species over large areas of rangeland and abandoned land (Losa and Rivas-Goday 1974). *Retama* is a practically leafless, N-fixing shrub with photosynthetic stems, called cladodes, and a deep root system that may draw water from a depth of ≤20–30 m (Haase et al., 1996) that successfully colonizes perturbed habitats. Typically, there is an undergrowth of annual and perennial herbs associated with *Retama.* One of the most conspicuous species at our field site is *Marrubium vulgare* L. (Lamiaceae), a mesic, woolly perennial herb ≤80 cm tall that often accounts for most of the understory biomass but also occurs in the open independently of *Retama.*

In this paper we investigate the association between *Retama* and the understory herb *Marrubium vulgare* in a semiarid region. We performed a natural, rather than manipulative, experiment, testing the hypothesis that *Retama* improves its own environment and facilitates the growth of *Marrubium* and other species while at the same time benefits from the sheltering herbs underneath it.

FIELD SITE

Our field site is located in the Rambla Honda, a valley near Tabernas, Almería, Spain (37°08′ N, 2°22′ W; 630 m altitude) with an ephemeral water course that only carries water after heavy rains. Rambla Honda is in the southern foothills of the Sierra de Los Filabres mountain range. The local climate is semiarid with a mean annual precipitation of 218 mm and a pronounced dry season from June to September, broken only by occasional thunderstorms, but with little rain in most years. The mean annual temperature at Tabernas (490 m altitude, 9 km south of the field site) is 17.9°C with monthly means of 10.7°C in January and 27.1°C in August (R. Lázaro, *personal communication*). Vapor pressure deficits are high during summer months, reaching >4 kPa (Pugnaire et al., 1996).

The mostly flat, sandy bottom of the valley is disturbed by sporadic floods, and may best be described as a desert-like environment because of the low availability of water, the very low water holding capacity of the soil, and the sparse vegetation. This area is dominated by *Retama,* with a density of ≈500 plants/ha covering ≈40% of the surface. The largest shrubs may reach >4 m in height, but most are between 2 and 3 m tall. Gaps between shrubs are almost bare of vegetation, with only occasional patches of winter annuals and negligible cover of other shrub species.

METHODS

Five pairs of *Retama* shrubs were selected in the valley bottom; each pair had one shrub with *Marrubium* plants naturally occurring in the understory and another one without *Marrubium.* The two shrubs of each pair were similar in size, growing close to each other, did not differ significantly in pre-dawn water potential, and most likely had similar-sized root systems. Five *Marrubium* plants growing alone were selected in the same area as well. Gas exchange of both species was measured for each plant with a portable, solid-state, infrared gas analyzer and a 12-cm^3 leaf chamber (Analytical Development Company Limited, Hoddesdon, England) within a 2-h period around solar noon in late April 1993. Three 1-yr-old *Retama* cladodes were enclosed in the chamber during each measurement; three cladodes were measured because of their small area. Projected cladode area of *Retama* and leaf area of *Marrubium* were measured destructively with an area meter (Delta-T Devices, Cambridge, England).

To compare the performance of both species in association and isolation, the following parameters were measured: dry mass (of *Retama* cladodes per branch and of *Marrubium* leaves per shoot), specific leaf area (area of cladode or leaf per unit dry mass), and nitrogen content. Concentrations of N and naturally occurring ^{15}N were measured by an elemental analyzer and mass spectrometer (Europa Scientific, Crewe, United Kingdom) using traceable plant material (SRM 1572 of the U.S. National Bureau of Standards) as reference; results are expressed on a dry mass basis. Total N content was calculated as mass per 3-yr-old branch for *Retama* and per aboveground plant for *Marrubium,* and $\delta^{15}N$ was calculated following Ehleringer and Osmond (1989).

Measurements of biomass of *Retama* and *Marrubium* growing in association or alone were also made. For *Marrubium,* total plant biomass (average branch biomass times the number of branches, 10 branches per plant, $n = 5$ pairs) was determined; for *Retama,* the biomass of the 3-yr-old portion of branches (10 branches per shrub, $n = 5$ pairs) was determined. Pre-dawn and midday plant water potentials (ψ) were determined for two to three shoots per plant ($n = 5$ pairs per species) with a pressure chamber (Skye Instruments, Limited, Llandrindod Wells, United Kingdom).

Samples of soil were collected from the upper 5 cm of soil underneath and at the edge of five *Retama* canopies not associated with *Marrubium,* and the <2-mm fraction was retained for analysis. Similarly, soil samples were collected under the canopies of a different set of shrubs ($n = 6$ pairs) with and without *Marrubium*

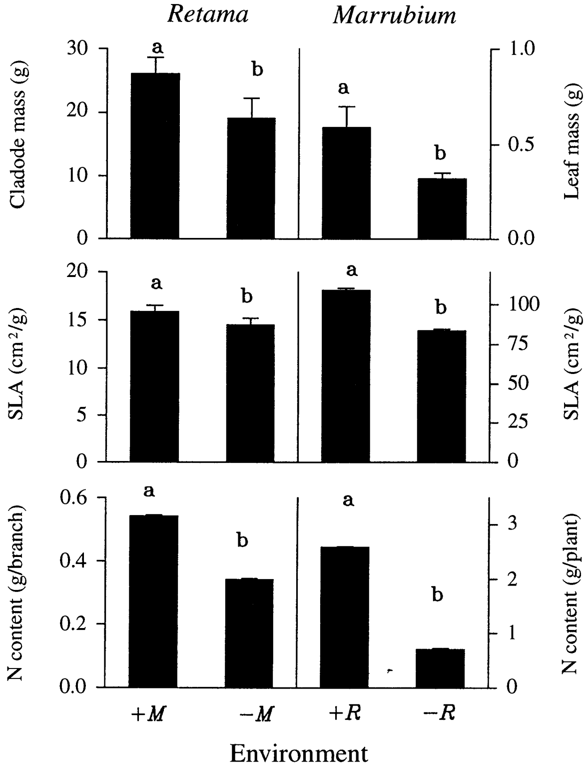

FIG. 1. Dry mass of cladodes or leaves per branch, specific leaf area (SLA), and nitrogen content in *Retama sphaerocarpa* (*R*) and *Marrubium vulgare* (*M*) growing in association (+*R*, +*M*) or alone (−*R*, −*M*) at Rambla Honda, Almería, Spain. Nitrogen content is expressed as mass per 3-yr-old branch in *Retama* and per plant in *Marrubium*. Data represent means; error bars represent 1 SE; those with different letters are significantly different at $P < 0.05$ (*t* test).

beneath them and the <1-mm fraction was analyzed. Because of the low clay content and the absence of gypsum and other salts, organic matter content was determined by combustion at 430°C. The fine particle fraction in the soil (clay plus silt) was obtained by passing samples that had been treated with hydrogen peroxide to destroy organic matter through a 0.05-mm sieve. Water content at field capacity was determined at 333 kPa with a pressure membrane apparatus (Soil Moisture Equipment Corporation, Santa Barbara, California). Bulk density was obtained by weighing a known volume of soil that had been dried at 110°.

The number of flowers per *Marrubium* plant was calculated as the product of the mean number of individual flowers per inflorescence, the mean number of inflorescences per branch, and the number of branches per plant. The number of flowers per branch in *Retama* was calculated as the product of the mean number of flowers per 2-yr-old cladode and the number of 2-yr-old cladodes per branch.

When repeated measurements were made on the same plant (i.e., cladode biomass and ψ), the results were averaged for each plant and the means of those growing alone or in association were compared by *t* tests.

RESULTS

In the sandy bottom of the valley, there were significantly more flowers on *Marrubium* growing underneath *Retama* than on isolated plants (7900 ± 1100 vs. 2500 ± 400 flowers, mean ± 1 SE; $t = 4.61$, $n = 10$, $P < 0.01$). *Marrubium* plants under *Retama* had greater specific leaf area, more leaf dry mass (Fig. 1), and therefore greater leaf area, as well as more shoot dry mass (Fig. 2) than plants in the open. They also differed significantly in N content per plant (Fig. 1), because in understory plants, N concentration was significantly higher (28.1 ± 2.2 vs. 23.6 ± 1.3 g/kg, mean ± 1 SE; $t = 2.7$, $n = 10$, $P < 0.05$) and there was much more aboveground dry biomass per plant than in isolated *Marrubium* plants (Fig. 2).

Despite the significant reduction in midday incident photon flux density reaching the *Marrubium* plants under the diffuse *Retama* canopy, their photosynthetic rate and leaf conductance were not reduced (Table 1) and ψ was similar in both situations (Fig. 2).

Retama shrubs with and without *Marrubium* beneath them differed in the amount of photosynthetic tissue since biomass of 1-yr-old cladodes and biomass of 3-yr-old branches were greater in plants associated with *Marrubium* (Figs. 1 and 2). *Retama* shrubs associated with *Marrubium* had a higher area of cladode per unit dry mass (Fig. 1). The measured environmental variables for the *Retama* branches were not affected by the

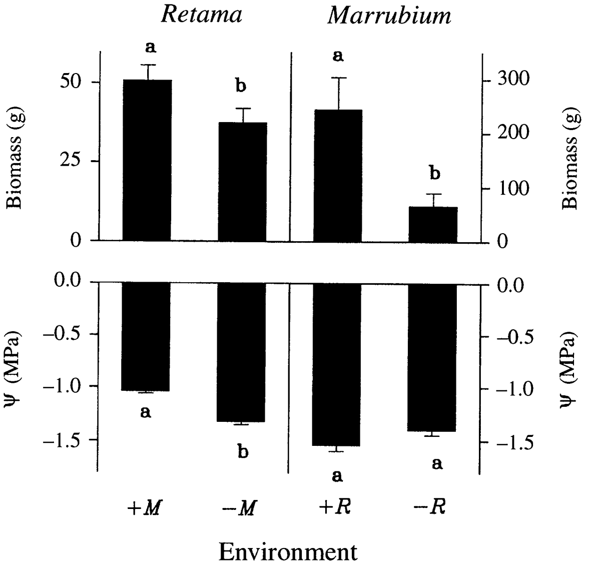

FIG. 2. Dry biomass of 3-yr-old branches of *Retama* ($n = 5$), total plant biomass of *Marrubium*, and midday water potential (ψ) in *Retama sphaerocarpa* (*R*) and *Marrubium vulgare* (*M*) growing in association (+*R*, +*M*) or alone (−*R*, −*M*) at the Rambla Honda, Almería. Data represent means; error bars represent 1 SE. Statistical comparisons as in Fig. 1.

TABLE 1. Air and leaf temperatures (*T*), incident photon flux density (PFD), net CO_2 assimilation rate (*A*), and leaf diffusive conductance (*g*) for *Retama sphaerocarpa* and *Marrubium vulgare* growing in association and alone. Data represent means ± 1 SE ($n = 5$ plants). For differences (*t* test): * significant at $P < 0.05$, NS = not significant.

Plant	Association	Air *T* (°C)	Leaf *T* (°C)	PFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	*A* ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	*g* ($mol \cdot m^{-2} \cdot s^{-1}$)
Retama sphaerocarpa	*Marrubium* present	27.0 ± 0.3	26.7 ± 0.3	1400 ± 80	27.9 ± 0.4	0.32 ± 0.02
	Marrubium absent	27.2 ± 0.8	26.6 ± 0.6	1350 ± 80	27.6 ± 0.7	0.34 ± 0.04
	Difference	NS	NS	NS	NS	NS
Marrubium vulgare	Under canopy	26.8 ± 0.3	26.6 ± 0.3	950 ± 100	26.9 ± 0.4	0.19 ± 0.02
	Outside canopy	26.4 ± 0.1	25.9 ± 0.1	1170 ± 60	27.2 ± 0.1	0.26 ± 0.01
	Difference	NS	NS	*	NS	NS

presence of *Marrubium,* nor was their gas exchange reduced (Table 1).

Because their branches were larger, *Retama* shrubs with *Marrubium* beneath them had more nitrogen per 3-yr-old branch (Fig. 1) than shrubs in isolation, although N concentration was identical (26.0 ± 2.0 g/kg). In shrubs with and without *Marrubium* present, $\delta^{15}N$ was similar (−2.23‰ and −2.87‰, respectively), indicating that atmospheric N was fixed in the root system of all *Retama* shrubs (Shearer et al. 1983) and that *Marrubium* does not affect N fixation. *Retama* shrubs with *Marrubium* underneath them had a higher ψ at midday (Fig. 2).

Because there were more 2-yr-old cladodes per branch (data not shown) and equal numbers of flowers per unit cladode mass, *Retama* shrubs with *Marrubium* beneath them tended to have more flowers per 3-yr-old branch than shrubs without *Marrubium,* but differences were not significant (1600 ± 250 vs. 1300 ± 200 flowers per branch, respectively, mean ± 1 SE; $t = 1.71$, $n = 10$, $P = 0.13$).

Soil properties under the canopy differed from those outside the canopy (Table 2). Under the canopy there was much more organic matter, more retention of water at field capacity, and lower bulk density, which increases soil aeration. Litter accumulated under the canopy (1.8 kg/m^2 under canopy vs. < 0.1 kg/m^2 outside canopy), as well as clay and silt (Table 2), forming a mound of soil with improved texture. When soils under *Retama* canopies with and without *Marrubium* were compared, the organic matter and silt plus clay fractions were found to be greater in the presence of *Marrubium.* However, water content at field capacity and bulk density were not significantly different (Table 3).

DISCUSSION

It is known that plants can modify their physical environment (Miles 1985) through feedbacks that encompass acquisition of resources, alteration of soil properties, or biological interactions (Hobbie 1992, Wilson and Agnew 1992). In the Rambla Honda, *Retama* and *Marrubium* appear to strongly influence their surrounding, infertile environment, leading to an increase in soil fertility and making it more suitable for their own growth.

For *Marrubium* located under *Retama* shrubs, the greater biomass, greater nutrient content, and greater number of flowers observed compared to isolated plants are consistent with the hypothesis that the shrub has a facilitative effect on *Marrubium.* This effect may arise from a greater availability of resources under the shrubs, such as nutrients and water. In studies that addressed similar issues, availability of water (Richards and Caldwell 1987, Joffre and Rambal 1988, 1993, Dawson 1993) as well as nutrients (García-Moya and McKell 1970, Garner and Steinberger 1989, Callaway et al. 1991, Gutiérrez et al. 1993) increased under shrub and tree canopies relative to the open because of the shrub's effect on soil properties and nutrient cycling (Hobbie 1992). The shrub may also improve physical conditions for the growth of herbs, perhaps by protecting them from direct insolation and over-heating (Valiente-Banuet and Ezcurra 1991).

The presence of *Marrubium* and other herbs under *Retama* may help to improve the water relations of the shrub. *Retama* has a small diurnal and seasonal change in ψ (Lansac et al. 1994), as noted in other phreatophytic shrubs (e.g., Nilsen et al. 1984, Foster and Smith

TABLE 2. Properties of soil under and outside the *Retama* canopy at the Rambla Honda. Data represent means ± 1 SE ($n = 5$).

Soil property	Outside		Underneath
Organic matter content (%)	1.4 ± 0.0	**	3.9 ± 0.7
Clay plus silt content (%)	9.6 ± 0.1	**	15.6 ± 0.2
Volumetric water content at field capacity (%)	14.7 ± 0.7	**	17.5 ± 0.5
Bulk density (g/cm^3)	1.8 ± 0.1	*	1.5 ± 0.0

* Difference between locations significant at $P < 0.05$ (*t* test).

** Difference between locations significant at $P < 0.01$ (*t* test).

TABLE 3. Properties of soils underneath *Retama* shrubs with and without *Marrubium* (*M*) beneath them. Data represent means ± 1 SE ($n = 6$).

Soil property	*M* absent		*M* present
Organic matter content (%)	2.6 ± 0.4	*	4.1 ± 0.2
Clay plus silt content (%)	12.2 ± 3.7	*	19.1 ± 3.9
Volumetric water content at field capacity (%)	12.2 ± 0.7	NS	12.8 ± 1.0
Bulk density (g/cm^3)	1.7 ± 0.0	NS	1.6 ± 0.1

* Difference between locations significant at $P < 0.05$; NS, not significant (*t* test).

1991). At our field site, all shrubs had the same predawn ψ, but those sheltering *Marrubium* had significantly higher ψ at midday (Fig. 2), despite having a larger biomass and evaporative area (Fig. 1). This suggests that the root systems of shrubs with *Marrubium* underneath are more efficient at maintaining a supply of water to their transpiring tissues. Since shrubs were not randomly assigned to treatments, factors other than the presence of *Marrubium* may be responsible for the observed patterns. For example, the shrubs with *Marrubium* beneath them may in fact be older and have deeper root systems than shrubs without *Marrubium,* potentially allowing them to reach deeper water stores. Differences in midday ψ of *Retama* cladodes, however, were seasonal and occurred in spring when water was available to the plant from the upper soil layers, but were not observed in the summer (*data not shown*), when the upper soil horizons were dry. This suggests that *Retama* may obtain a substantial proportion of water from the moister upper soil layers in spring, at the time of its maximum growth.

Measurements of gravimetric soil water content under *Retama* canopies at 5 and 20 cm depth over two years at our field site showed that the 5-cm layer was wetter than the 20-cm layer, especially in the moister periods of the year (J. Puigdefábregas and L. Gutiérrez, *unpublished data*). Similarly, a higher soil water content under the canopy than in the open is well documented in mediterranean trees (e.g., Joffre and Rambal 1988) as well as in other semiarid (Rostagno et al. 1991) and tropical species (Mordelet 1993), where it is associated with changes in soil properties. On the other hand, water may also be taken from deep stores by the root system and shed in higher soil layers (Richards and Caldwell 1987, Dawson 1993). These data support our view that *Retama* is able to tap water stored in the upper soil layers, the storage of which is in turn favored by the presence of a dense understory.

The dense understory also suggests that, though *Retama* has a high concentration of secondary metabolites, particularly alkaloids (Martín-Cordero et al. 1993), it does not appear to be allelopathic, and unlike other shrubs and trees in mediterranean environments (e.g., Callaway et al. 1991, Bartolome et al. 1994), *Retama* seems to facilitate growth under its canopy, despite possible competition for nutrients. Competitive interactions in an environment as infertile as this should have serious consequences, yet having *Marrubium* in its understory was not associated with poorer conditions for any of the properties measured. In fact, *Retama* shrubs with *Marrubium* beneath them showed traits indicating higher availability of resources, such as greater N content or larger biomass.

An improved cycling of nutrients in the understory could be a consequence of increased litter decomposition (Berendse 1994). The presence of *Marrubium,* usually with a large number of annual species, should enhance litter decomposition under *Retama* by keeping a higher moisture content under the shrub. Litter decomposition is increased by high humidity, as shown in related studies on other species (Cornejo et al. 1994, Erickson and Edmonds 1994, Schomberg et al. 1994). Enhanced decomposition would be of special importance in the case of *Retama,* since its litter (predominantly made up of its own cladodes) is more difficult to decompose than is herbaceous litter (Gallardo and Merino 1993).

Soil fertility in the understory may also be related with the accumulation of litter and fine mineral particles, which form a mound of soil with improved texture (Rostagno et al. 1991, Parsons et al. 1992). This property is enhanced by the presence of a dense understory (Table 3). Thus, we suspect that nutrient cycling is increased under *Retama,* as has been documented in arid and semiarid environments under the canopy of other species such as *Larrea* (Lajtha and Schlesinger 1986), *Prosopis* (Mazzarino et al. 1991), or different species growing in clumps (Rostagno et al. 1991). Since annual species are usually senescing by the time *Retama* has its major flush of growth in May, direct competition for nutrients may be avoided and the net effect of understory species could be to store nutrients, minimizing leaching of nutrients during the heavy rainstorms characteristic of semiarid environments.

Our results are consistent with the hypothesis that *Retama* provides a beneficial microclimate and that the presence of the understory vegetation, including *Marrubium,* somehow enhances availability of water to *Retama.* Nevertheless, causes other than facilitation could be responsible for the patterns observed. A higher performance of plants growing in association could be strictly correlative rather than causal, e.g., due to unmeasured factors such as differences in the properties of the deep underlying sediment or of the basement rock. In addition, we have only looked at a single point in time during the life of these two perennial plants.

The effect of *Marrubium* on *Retama,* however, appears weaker than the other way around, and we cannot be sure that the improved conditions beneath *Retama* with *Marrubium* lead to a better performance. Nevertheless, it is possible that over the years (or with larger sample sizes), the trend for higher number of flowers on branches could be significant. Clarifying these aspects through manipulative experiments and assessing the long-term persistence of this association and of its biological and edaphic properties should determine the validity of our hypothesis.

We propose that the relationship between *Retama* and *Marrubium* is mutualistic, since each partner appears to benefit from the greater availability of resources in the island of fertility that results from their association. Unlike other interactions commonly assumed to be mutualistic but in which the benefit for one partner has been seldom investigated (see Cushman and Beattie 1991, Bronstein 1994), benefits for both *Retama* and *Marrubium* can be quantitatively measured. Mutualism could also enable colonization by *Marrubium* of an otherwise extreme environment. Rather than being specifically associated with *Marrubium,* in these semiarid environments *Retama* can probably form similar facilitative associations with other herb species as well.

While facilitation is a well known and studied interaction, to our knowledge there have been no other demonstrations that it is *mutually* rather than unilaterally beneficial. Positive plant–plant interactions seem to be more widespread than previously thought, and underlying positive feedback processes could be major mechanisms determining the pattern and structure of plant communities (Wilson and Agnew 1992), especially in extreme environments.

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