

Assessing occurrence, specificity, and mechanisms of plant facilitation in terrestrial ecosystems

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Abstract Plants alter environmental conditions enhancing the recruitment of other species. In spite of prior reviews of facilitation, the variability of its occurrence, mechanisms, and specificity across terrestrial ecosystems has not yet been assessed. In this article, we analyze facilitative mechanisms and the distribution of specific traits, such as nitrogen fixation and the presence of fleshy fruits, across ecosystems. A comprehensive database including 2,080 cases of facilitation among higher plants from 539 articles was analyzed with descriptive statistics for occurrences of positive interactions and underlying mechanisms in different terrestrial ecosystems. Positive interactions by plant-induced environmental changes are widespread in a range of ecosystems and not limited to conditions of chronic abiotic stress such as semiarid, alpine, and wetland ecosystems. The capability to act as nurse largely varied among different growth forms, and was observed more frequently for

woody than for herbaceous plants. Nitrogen fixers occur much more frequently as nurse plants than as beneficiary plants in facilitation cases due to increasing soil fertility. As known for Mediterranean ecosystems, fleshy-fruited species appear more dependent on facilitative interactions than other plants, being more frequent among beneficiaries than among nurses. The pattern can be extended worldwide being consistent in wetland, temperate, and alpine ecosystems as well. Our description of the relationship between distribution, mechanisms, and specificity of facilitation in terrestrial ecosystems has implications for the understanding of plant community organization considering that plant nursing capacity is affected by their size, architecture, and life span.

Keywords Competition · Fleshy fruit · Nitrogen fixer · Nurse · Positive interactions · Stress gradient hypothesis

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Introduction

Historically, competition has been considered the major interaction process in the regulation of natural plant community dynamics (Tilman 1988). In recent years, the significance of environmentally mediated positive, non-trophic species interactions (i.e., facilitation) in shaping natural plant communities has been re-evaluated (reviews in Callaway 1995;

Brooker et al. 2008). Facilitative interactions have been reported for a variety of ecosystems worldwide, including deserts (Yeaton 1978), Mediterranean mountains (Gómez-Aparicio et al. 2004), freshwater and saline wetlands (Bertness and Hacker 1994), temperate (Bonanomi et al. 2010), and alpine ecosystems (Callaway et al. 2002). The importance of facilitation as a cohesive force driving the organization of ecological communities has been re-evaluated (e.g., Bruno et al. 2003) focusing on the intensity of abiotic stressors (Maestre et al. 2006), the underlying mechanisms (Holzapfel and Mahall 1999) and the consequences for community species diversity (Hacker and Gaines 1997) by such positive interactions.

In this context, the specificity of facilitation has been considered a crucial issue (Callaway 1998), ranging from species-specificity, with facilitation occurring between either conspecifics or heterospecifics (Bonanomi et al. 2010), to broader levels, as in the case of functional guilds when different growth forms are compared (Gómez-Aparicio 2009). The classification of plant structural and functional traits has been attempted for a long time by plant ecologists (Warming 1909) and the subdivision based on plant size, architecture and life span in trees, shrubs, perennial and annual herbaceous plants, cacti and vines has been early and widely accepted. In the frame of facilitation studies, this approach has been proven useful in predicting plant occurrences as either nurse or beneficiary (Gómez-Aparicio 2009). In a recent review, based on 1,521 case studies, Bonanomi et al. (2010) reported that shrubs were the most common nurse growth form, followed by trees, herbaceous perennials, cacti, and annual plants. However, the variation of growth forms occurrences, as nurse and beneficiary, across different ecosystems remains to be clarified.

Another key issue requiring better assessment is the variability of the facilitative mechanisms. These have been extensively analyzed, reviewed (Callaway 1995, 2007), and classified as either direct, when a beneficiary is facilitated by modification of environmental conditions straight due to the nurse, or indirect, when the process operates by intermediating species (Callaway 2007). Common direct mechanisms that ameliorate the above-ground environment include the reduction of direct solar radiation and photo-inhibition by shading (Bader et al. 2007), the

buffering of extreme temperatures and the protection from wind (Callaway et al. 2002), and the mechanical shielding from water runoffs (Levine 2000). Below-ground mechanisms have been also reported, including the local increase of resources such as nitrogen (Maron and Connors 1996) and water (Kennedy and Sousa 2006), and the amelioration of abiotic conditions, such as the reduction of salinity (Bertness and Shumway 1993), the oxygenation (Callaway and King 1996), and stabilization (Crain and Bertness 2005) of the substrate. Concerning indirect positive interactions, there have been reports on the protection from grazing by unpalatable plants (Rebollo et al. 2002), the improvement of mycorrhizas inoculum close to conspecific adults enhancing juvenile performance (Dickie et al. 2007), a positive-density dependence increasing pollination success (Roll et al. 1997), and some indirect positive effects among competing plants (Miller 1994). Some authors considered also seed accumulation under an established plant (i.e., seed trapping) as an important mechanism for interspecific facilitation (Flores and Jurado 2003). In spite of this well-established knowledge of facilitation mechanisms, their relationship with the structural and functional traits of both nurse and beneficiary species has not yet been investigated.

Finally, in addition to plant growth forms, two particular plant functional syndromes have been described as affecting facilitative interactions: nitrogen fixation (Callaway 2007) and fleshy fruits bearing (Valiente-Banuet et al. 2006). In the first case, it is well known that nitrogen-fixing plants lead to enhanced local nutrient recycling and organic matter accumulation (Belsky 1994), thus creating the so called “islands of fertility” (Schlesinger et al. 1996) which produce a widespread facilitating effect (Callaway 2007; Bonanomi et al. 2010). In the case of fruit type, Valiente-Banuet et al. (2006) reported that, in Mediterranean ecosystems, the establishment of species bearing fleshy fruits was much more dependent on facilitative interactions compared to other plants. The occurrence of both nitrogen-fixing and fleshy-fruited plants within nurses and beneficiaries is another unresolved issue to be analyzed in relation to different growth forms and across ecosystems.

In this study, we explored the occurrences in different ecosystems and the specificity, at growth form level, by the analysis of available literature. The specific questions that we address are:

- (1) In which ecosystems do positive interactions occur and according to what mechanisms?
- (2) Are there differences in the capability of acting as nurse among different growth forms?
- (3) Do facilitation mechanisms vary between different growth forms in different ecosystems?
- (4) Are nitrogen-fixing and fleshy-fruited plants differentially occurring among nurses and beneficiaries, and are these traits related to growth forms and are they specific to certain ecosystems?

Materials and methods

Data collection

The extensive data set compiled by Bonanomi et al. (2010) was updated including articles published between 1909 and 2011. Data were obtained from 539 articles with a total of 2,080 reported cases of facilitation among higher plants. The bibliographic search was carried out in all indexed international ecological journals by online access to Biological Abstract, Science Citation Index, ISI Web of Knowledge, Science Direct, and JSTOR. Used keywords were “beneficiary,” “facilitation,” “nurse,” “positive feedback,” “positive interaction,” “commensalism,” “symbiosis,” “beneficiary,” and “protégée.” Many articles were identified from the references of previously collected papers.

Only papers reporting taxonomic identification of the considered species were taken into account. Therefore, studies not referring to specific nurse and beneficiary plants were excluded from the analysis. Documentation of both direct and indirect positive interactions, such as experimental works and spatial associations between species, were included as evidence of facilitation (Callaway 1995) though spatial association might be also due to external factors (e.g., patchy distribution of soil resources). Relative abundances and/or performances at individual scale (e.g., survival, growth, and reproductive output) were considered as facilitation measures if assessed either in the proximity of conspecific, heterospecific or in gaps with no vegetation cover. Measures at species scale were also considered, as in the case of fire-effects studies reporting of species gaining benefits by increasing fire frequency.

Ecosystems, as described in the original papers, were classified following Gómez-Aparicio (2009)

into (a) tropical, (b) water-limited systems with different types of climate (hereafter indicated as semiarid) including desert, semidesert, and Mediterranean, (c) temperate, (d) wetland, and (e) alpine. Such a classificatory approach, not based on proper quantitative climatic data, could appear questionable. However, given that the original ecosystem descriptions were a miscellany of qualitative and quantitative data, this approach was considered as the most practical and suitable to the objective of the study.

The growth forms of nurses and beneficiaries were classified into trees, shrubs, herbaceous perennials and annuals (including forbs and grasses), cacti and lianas. Nitrogen-fixing species were considered within each growth form, whereas fleshy-fruited species were identified only among shrubs and trees, since this trait is considered as discriminating for beneficiaries, depending on sheltering requirements (Valiente-Banuet et al. 2006). The data set does not include epiphytic plants because of their unique life style.

The mechanisms producing facilitative interactions, as reported in the original papers, were classified into (1) improvement of above-ground microclimate (e.g., reduction of solar radiation by shading, mitigation of extreme temperatures, protection from frost in cold climate); (2) modification of soil nutrient fertility (either increase or decrease); (3) modification of soil water availability (either increase or decrease); (4) improvement of soil abiotic conditions (e.g., pH buffering, reduction of soil salinity, substrate stabilization, and oxygen increase); (5) modification of soil biotic conditions (e.g., enhanced mycorrhizal inoculum and shifts in soil microbial communities composition), identified as positive or negative as proposed in the source papers; (6) protection from grazing, hereafter indicated as associational refuge; (7) modification of fire regime (either increase or decrease); (8) seed trapping (i.e., seed transport to favorable sites for establishment, growth or reproduction, see Callaway 2007); (9) physical support; and (10) reduction of interspecific competition. Evidence of facilitation mechanisms were derived from both experimental and correlative studies (Callaway 2007). However, only correlative studies reporting evidence of plant spatial association with nurse plants or gaps in vegetation cover with differences in environmental conditions (e.g., air temperature or relative humidity, soil water content,

soil nutrient availability, soil salinity, changes of soil microbial soil communities, herbivore damage, etc.) have been included in the analysis. Facilitative interactions related to pollinators activity have not been considered since not mediated by environment modifications.

Results

Facilitation occurrence across terrestrial ecosystems

A total of 2,080 cases of facilitative interactions were analyzed (Table S1—Supplementary material). The majority were recorded in semiarid ecosystems ($n = 1,189$), followed by temperate ($n = 330$) and alpine ($n = 320$) habitats, with relatively few reported cases of facilitation in tropical ($n = 177$) and wetlands ($n = 64$) (Fig. 1).

In general, shrubs, trees, and herbaceous perennials were the most common nurse growth forms (Fig. 2). Shrubs were the most common nurse in semiarid (53.6% of total cases), temperate (40.6%), and alpine (64.0%) ecosystems. Trees and herbaceous perennials were the most common nurse in tropical habitats (84.7%) and wetlands (89.1%), respectively. The prevalence of herbaceous perennials in wetlands can be likely explained by the low abundance of woody species in this environments. On the other hand, trees were the most common nurse in tropical environments probably because the majority of tropical studies focused on woody plants colonizing

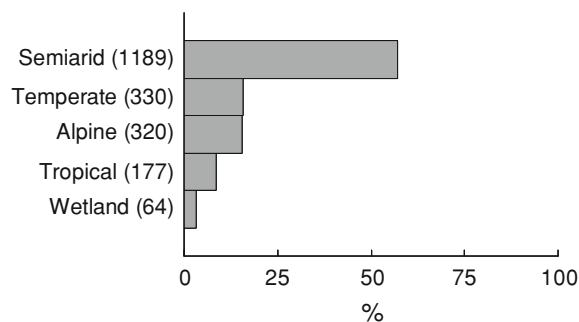


Fig. 1 Relative occurrences of facilitative interaction in five different ecosystems. Numbers in bracket indicate the total cases recorded

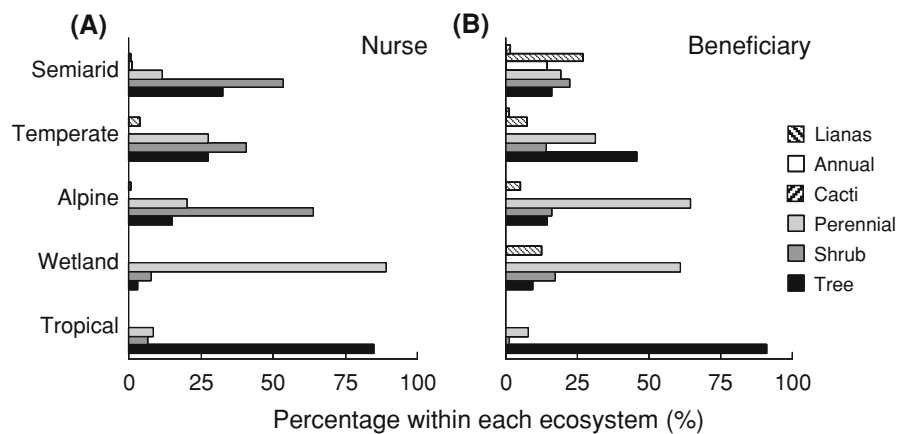
abandoned pastures (e.g., Slocum 2001). Herbaceous annuals and lianas nurses are very rare, being observed in <5.0% of total cases in all ecosystems (Fig. 2). Cacti, mainly occurring in semiarid ecosystems, are rarely observed as nurse (1.3%; Fig. 2). Concerning beneficiaries, herbaceous perennials are the most facilitated in alpine and wetland ecosystems (64.4 and 60.9% of total cases, respectively) followed by shrubs in the same environments (15.9 and 17.2%). Trees and herbaceous perennials are the most common beneficiaries in temperate conditions (45.8 and 31.2%, respectively) and also in tropical ecosystems, but with different relative occurrences in such environments (91.0, and 7.9%, respectively) (Fig. 2). In semiarid environments, all growth forms are frequently facilitated with the exception of lianas (Fig. 2). Cacti, which are very rarely reported as nurses, commonly occur as the beneficiary species in semiarid environments (14.5%; Fig. 2).

Specificity of nurse and beneficiary

Overall, nurse occurrences are heterogeneously distributed among different growth forms: shrubs showing highest frequencies ($n = 993$), followed by trees ($n = 678$), herbaceous perennials ($n = 364$), annuals ($n = 27$), cacti ($n = 16$), and vines ($n = 2$). About the specificity of nurse growth forms, shrubs assist all plants in similar proportion, with the exception of the rarely reported cacti and vines (Fig. 3). A similar pattern was found for trees, but with more cases of assistance provided to other trees and shrubs (Fig. 3). Herbaceous perennial and annual nurses showed a totally different distribution. For such plants, the assistance was mainly provided to individuals of the same growth form, with annual plants specifically providing benefit only to other herbs (Fig. 3). In the few cases of cacti acting as nurses, the beneficiaries were mostly other cacti, and very rarely shrubs, trees, or herbaceous perennials (Fig. 3). Finally, the nursing specificity of lianas was not assessed, due to insufficient data availability.

From the reverse point of view, trees and shrubs mostly benefit from other woody plants (Fig. 3). Herbaceous perennials showed a slightly distinct pattern, being facilitated also by other perennials (Fig. 3). Finally, annual herbs and cacti were mainly assisted by shrubs and less frequently by trees and herbaceous perennials (Fig. 3).

Fig. 2 Relative occurrences of nurse (a) and beneficiary (b) species classified in six growth form within each ecosystem. Values are percentage calculated within each ecosystem



Facilitation mechanisms

Mechanisms in terrestrial ecosystems

A total of 2,086 cases of facilitation mechanisms were analyzed (Table S1—Supplementary material). In some studies, two or more mechanisms were associated to the observed cases of facilitative interaction. In detail, one explanatory mechanism was considered in 34.5% of the total cases, and two, three, four, and even five complementary processes were claimed in 43.8, 18.5, 0.8, and 2.4% of the studies, respectively.

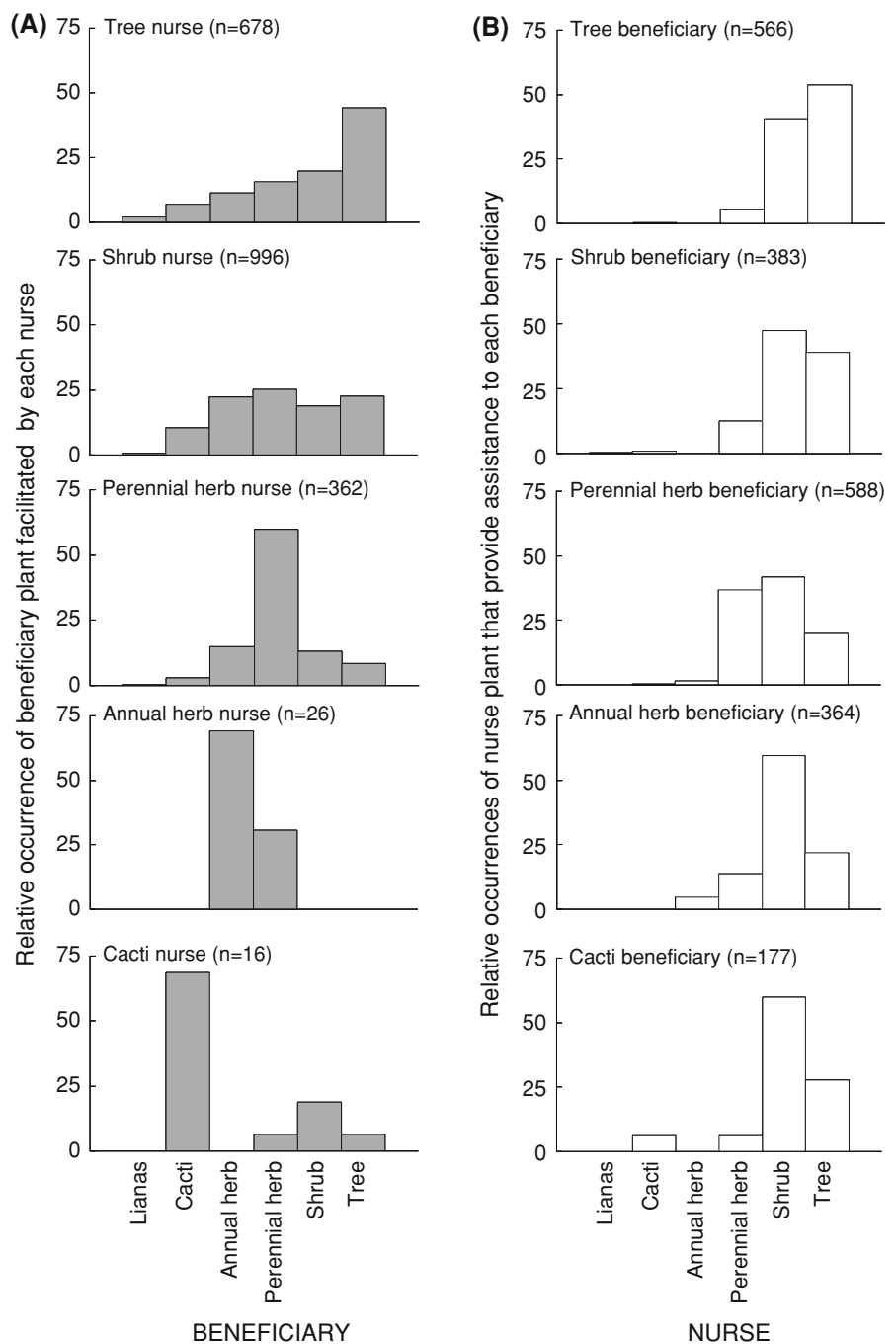
The most reported ($n = 714$) mechanism of facilitation was an improvement of above-ground microclimate. Other frequent mechanisms included a modification of soil nutrient fertility ($n = 536$), associational refuge ($n = 256$), soil water availability ($n = 240$), soil abiotic ($n = 93$) and biotic ($n = 50$) conditions, seed trapping ($n = 77$), and reduction of interspecific competition ($n = 87$). Few cases were attributed to a modification of fire regime ($n = 28$) and to the provision of physical support ($n = 5$). The mechanisms were differently prevailing across terrestrial ecosystems. In semiarid environments improvement of above-ground microclimate, increase of soil fertility and associational refuge were the most common (Fig. 4). Surprisingly, an increase of soil water content was more often observed in alpine and temperate ecosystems compared to semiarid (Fig. 4). In alpine environment, the most common mechanisms were the improvement of above-ground microclimate, increase of soil nutrient fertility and enhance of soil watering conditions (Fig. 4). In temperate ecosystems associational refuge, reduction of

interspecific competition, and improvement of above-ground microclimate, soil fertility, soil biotic conditions, and soil water content were reported with similar frequencies (Fig. 4). A different pattern was observed in wetlands, where the most common mechanism was an improvement of soil abiotic conditions, followed by an increase of soil fertility and associational refuge (Fig. 4). In tropical ecosystems, the most reported mechanism was the improvement of above-ground microclimate followed by the increase of soil fertility and associational refuge (Fig. 4). Seed trapping showed its highest relative occurrence in tropical ecosystems (Fig. 4). An alteration of fire regime was rarely observed in all ecosystems and was absent in wetlands, occurring in more than 5.0% of the cases only in tropical environments (Fig. 4).

Specificity of facilitation mechanisms

Trees and shrubs mainly facilitated beneficiaries by providing favorable above-ground microclimate and soil fertility, with overall observed frequencies equal to 70.6 and 63.1% of the respective total cases. For trees and shrubs, the mechanisms related to the increase of soil water content, associational refuge, and seed trapping were also frequent, while all other mechanisms were far less important (Fig. 5). Herbaceous nurses showed a substantially different pattern. The perennials mostly provided assistance by improving soil abiotic conditions and above-ground microclimate, as well as by associational refuge (Fig. 5). The improvement of soil biotic conditions and the modification of fire regimes, rarely observed for woody nurses (1.4% of total cases), were more common for

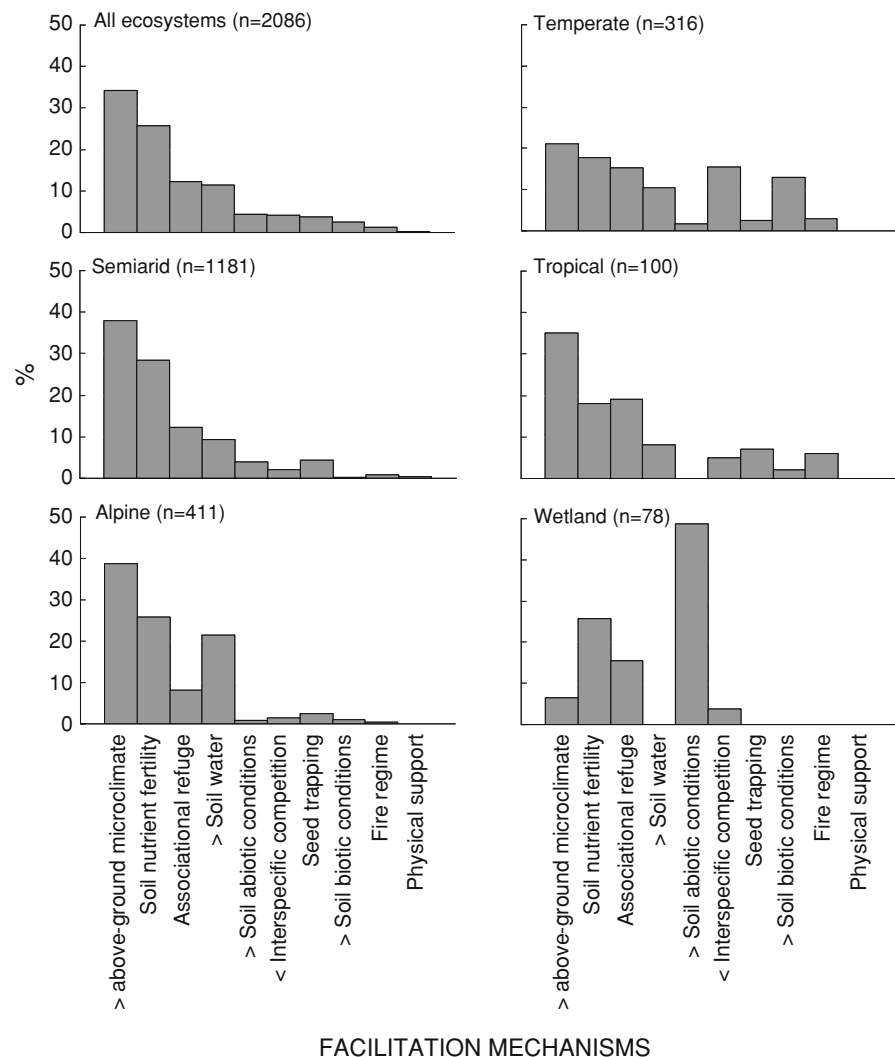
Fig. 3 **a** Relative occurrence of beneficiaries facilitated by different nurse growth forms (*left gray bars*) and **b** relative occurrence of nurses facilitating different beneficiary growth forms (*right open bars*). Values in *brackets* indicate the total number of cases



herbaceous perennials (13.6%). Annual herbs act as nurses mainly by reducing interspecific competition, and improving soil abiotic condition (Fig. 5). Finally, in the few cases reported in semiarid environment, cacti provide assistance by improving above-ground microclimate, enhancing soil fertility, promoting associational refuge and seed trapping (Fig. 5).

Independent of their growth form, beneficiaries were mainly facilitated by improving above-ground microclimate and enhancing soil fertility (Fig. 5). These two mechanisms jointly accounted for more than 55.0% of the total occurrences for all beneficiary growth forms, with a maximum of 71.3% in the case of cacti (Fig. 5). Improvement of soil abiotic

Fig. 4 Relative occurrences of different facilitation mechanisms within five ecosystems. Values in *brackets* indicate the total number of cases



conditions (for annual herbs) and associational refuge (for all other growth forms) were the third most common mechanisms (Fig. 5). Seed trapping was relatively frequent only in the cases of cacti (10.0% of total cases), shrubs (6.4%) and annual beneficiaries (4.8%), and the improvement of soil biotic condition was relevant only for herbaceous perennials and trees (5.8 and 1.4%, respectively).

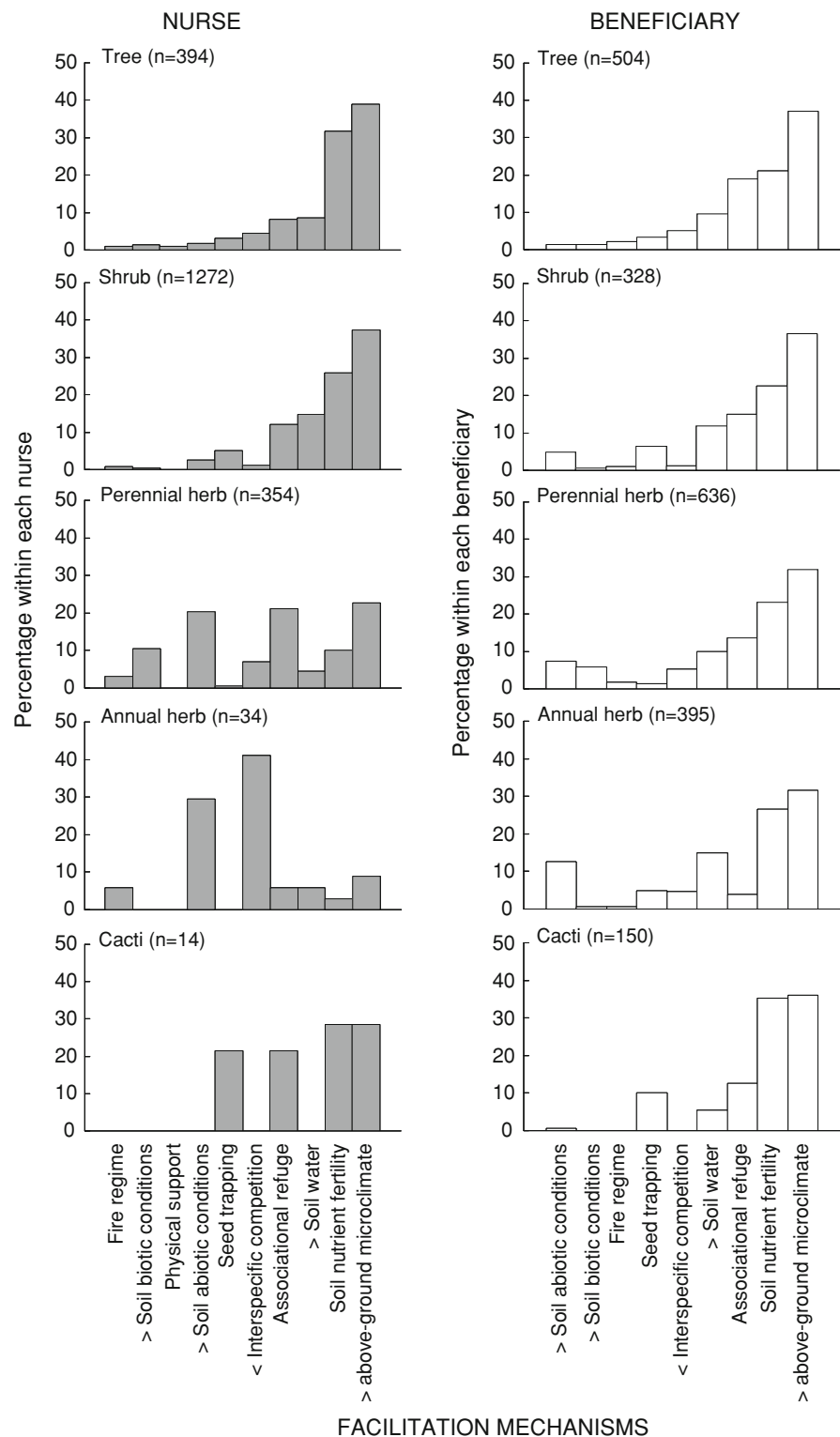
Nitrogen fixers and fleshy-fruited plants among nurses and beneficiaries

Considering all data pooled, nitrogen-fixing plants occurred much more frequently as nurse (27.1% of 2,080 cases) than as beneficiary (5.0%). Shrubs and

trees showed 19.5 and 50.6% of nitrogen fixers within nurses, and 6.2 and 6.4% within beneficiaries, respectively (Fig. 6a). Contrarily, in the cases of annual and perennial herbs, nitrogen fixers were relatively rare (<10% of total cases) both among nurses and beneficiaries (Fig. 6a). Considering its distribution across ecosystems, nitrogen fixation was not observed in wetlands, and rarely in all other environments, except for semiarid and tropical habitats, where 40.0 and 22.1% of nurses were nitrogen-fixing plants, respectively (Fig. 6b).

Plants bearing fleshy fruit were more frequent among beneficiaries than among nurses, both considering jointly the growth forms and the ecosystems (Fig. 7). This pattern is consistent across disaggregated data, with the only exception of shrubs bearing

Fig. 5 Relative occurrence of facilitation mechanisms of different nurse growth forms (*left gray bars*) and relative occurrence of facilitation mechanisms required by different beneficiary growth forms (*right open bars*). Values in *brackets* indicate the total number of cases



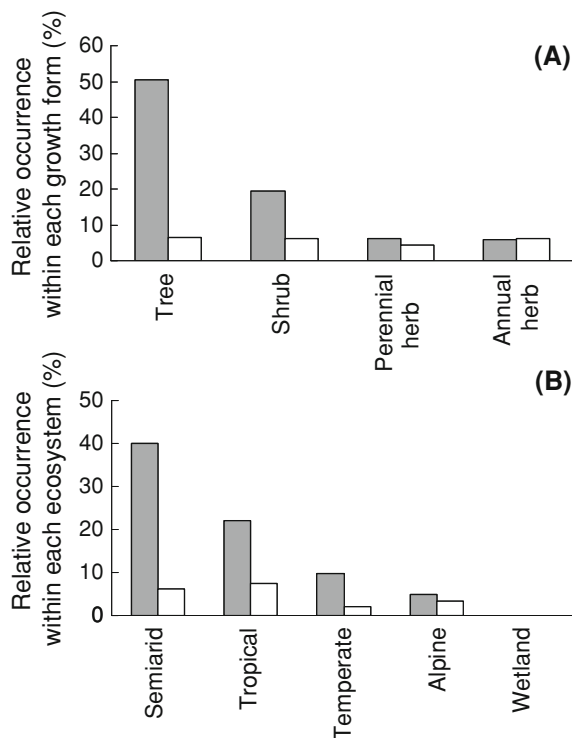


Fig. 6 Relative occurrence of nitrogen fixers among nurses and beneficiaries within each growth form (a) and within each ecosystem (b). In wetlands, nitrogen fixation was neither observed among nurses, nor among beneficiaries

fleshy fruit in tropical systems, observed more often among nurses than among beneficiaries (Fig. 7).

Discussion

This work provided a comprehensive synthesis on the relationships between distribution, mechanisms, and specificity of facilitation in terrestrial ecosystems. It also assessed the occurrence of nitrogen-fixing and fleshy-fruited plants as nurses and beneficiaries. As such, our findings improve the understanding of plant community organization in different ecosystems.

Plant facilitation: specificity and mechanisms across the ecosystems

The large majority of facilitative interactions occur in arid and semiarid ecosystems, consistently with the findings, based on a smaller data set, of Flores and Jurado (2003). Many cases of facilitation are also

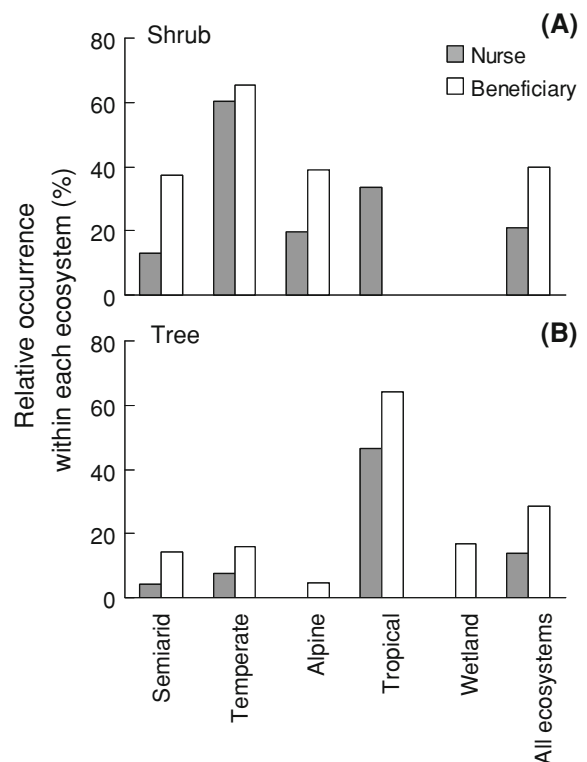


Fig. 7 Relative occurrence of fleshy-fruited shrubs (a) and trees (b) among nurses and beneficiaries within each ecosystem, and for all data pooled

found in alpine ecosystems, while relatively few are the records in wetlands and tropical conditions. Interestingly, a large number of positive interactions was also found in temperate ecosystems, mainly grasslands and encroaching scrublands, indicating facilitative interactions as an issue of global interest, not limited to abiotically stressed systems such as wetlands, alpine, and semiarid plant communities. In temperate ecosystems, cases attributed to reduction of interspecific competition, improvement of soil biotic conditions, and associational refuge, include 43.7% of all positive interactions, a very high value compared to other ecosystems. This result suggests that in the absence of chronic abiotic stressors, facilitation is likely to be driven by biotic-related mechanisms. For example, a large number of cases of facilitation in temperate grasslands was related to indirect positive interactions occurring in nursed microsites (Table S1). On this issue, Bonanomi et al. (2005a) proposed a mathematical model showing the emergence of indirect positive

interactions between plants in beneficial microsites, relatively free of either soilborne pathogens or autotoxic litter, and created by the occurrence of different species. More recently, Callaway (2007, p. 160) pointed out that such plant–soil negative feedback has not been explicitly considered in the context of plant facilitation. New evidence from studies carried out in temperate grasslands (e.g., Klironomos 2002; Bonanomi et al. 2005b) indicates that plant species can produce a mosaic of microsites detrimental to conspecifics, but beneficial to other species (review in Mazzoleni et al. 2007; Kulmatisky et al. 2008). The effects of such facilitative mechanism are cryptic, and can be assessed only by specific experiments (Klironomos 2002; Bonanomi et al. 2005b). In ecosystems with continuous vegetation cover, positive interactions can be more difficult to observe compared to environments with discontinuous plant cover. In other words, the association between different species can be easier to note in the case of patchy vegetation which is common in semiarid and alpine environments (Garner and Steinberger 1989). On this base, we suggest that the occurrence of facilitation in temperate and tropical ecosystems might be underestimated.

In general terms, the mechanisms underlying facilitative interactions are remarkably different across ecosystems. In semiarid environments facilitation is mostly mediated by the amelioration of above-ground microclimate through shading, whereas few cases have been attributed to an increase of soil water content. This is somewhat surprising, as water availability is the most limiting factor in these ecosystems. However, the shade cast by the nurse canopy can well improve the water balance of beneficiaries without enhancing the soil water content because of reduced air temperature and by protecting from direct sunlight (Callaway 2007). In fact, a plant canopy may even reduce the water content of underlying soil by competition for moisture and/or rainfall interception, especially for limited precipitation events (<10–20 mm) under dense plant canopies (Valladares et al. 2008; Holmgren and Scheffer 2010). Interestingly, soil water content is instead a limiting factor in alpine ecosystems, especially in the cases of coarse-grained substrates of primary succession processes (Cavieres et al. 2002) where the increasing soil organic matter under nurse canopy may enhance the soil water retention capability.

Wetlands show very different facilitative mechanisms compared to all other ecosystems, with higher occurrences of amelioration of substrate abiotic conditions, including salinity reduction (Bertness and Shumway 1993), oxygenation (Callaway and King 1996), and substrate stabilization (Fogel et al. 2004). Bertness and Hacker (1994) noted that in saline wetlands positive interactions are enhanced by the synergy between reduced soil salinity and decreasing water evaporation by nurse canopy shading.

With regards to specificity of nurse growth forms across terrestrial ecosystems, two different patterns were observed: in tropical, semiarid, and temperate environments woody plants were the dominant nurses. On the other hand, herbaceous nurses were highly frequent in wetland and alpine plant communities. Such pattern in part reflects the abundance of the different growth forms in each ecosystem, with herbaceous perennial often dominating wetlands. In addition, while woody plants are found to provide assistance to many different growth forms, cacti and herbaceous plants are very rarely beneficial to woody plants, supporting in most cases either individuals of the same growth form or smaller species (herbaceous perennials and annuals). These patterns can be clearly related to the mechanisms producing the facilitative interactions. Woody plants facilitation in all ecosystems is mostly due to the improvement of above-ground microclimate, increases of soil fertility and protection from herbivores. These types of mechanisms require suitable traits for casting shade, sheltering from wind and/or grazing, implying an adequate size and architecture of nurses, and, in the case of fertility islands, a sufficient time for the appearance of the facilitation effect, i.e., life span of decades or even centuries. Facelli and Brock (2000) reported increasing concentration of organic matter, N, P, and S under the canopy of *Acacia papyrocarpa* with tree aging and a subsequent decline after their death. Evidently, the above-mentioned mechanism rarely occurs for herbaceous plants and annuals because of their small size and short-life span. In this context, it is worth noting that annual plants, in contrast to woody plants, cannot selectively favor single individuals, but frequently provide facilitation at stand scale, either for conspecifics or heterospecifics. Examples include the increase of fire regime by the so called “fire-grass cycle” (D’Antonio and

Vitousek 1992), or the enhancement of soil salinity (Vivrette and Muller 1977) providing an ecological advantage to fire adapted or halophytes plants because of the reduced interspecific competition.

By looking at the specificity of facilitation mechanisms from the beneficiary point of view, all growth forms appear very similar in the type of assistance required to the nurse. We showed that over 50% of observed cases were beneficiaries facilitated by improved above-ground microclimate and increased soil fertility. Why beneficiaries are so similar in their requirements independently from their growth form? A possible explanation is that both adults herbaceous plants and juveniles of cacti, shrubs, and trees can be advantaged from improved conditions, particularly in harsh environments. It should be noted that most studies reporting woody plants as beneficiary considered such plants at seedling and sampling stages, i.e., individual sizes much smaller than their nurse. In this context, many studies reported a shift from commensalic to competitive effects of beneficiary on nurse plants during their ontogenetic cycle (Miriti 2006; Soliveres et al. 2010), even resulting in the nurse replacement (McAuliffe 1988; Valiente-Banuet et al. 1991; Callaway 2007; Bonanomi et al. 2010).

Another frequent mechanism for all beneficiaries, but for herbaceous perennials, is the associational refuge. Again, long-lived and large-sized woody plants could likely provide a more efficient refuge compared to smaller, short-lived plants, at least excluding other biological defensive strategies (e.g., spines and chemical toxins). Interestingly, associational refuge was reported in all ecosystems with moderately high frequencies, ranging from a minimum of 8.1% in alpine to a maximum of 19.0% in tropical ecosystem. Such similar spreading of this mechanism across terrestrial ecosystems may possibly be related to synergistic interactions between associational refuge and different limiting factors in different ecosystems, producing local specific conditions for the emergence of facilitative interactions.

Nitrogen fixation and fleshy fruit syndrome

It is commonly accepted that nitrogen fixation is widespread among nurse plants but not among beneficiaries (Callaway 2007). This consideration is based on the observation that soil fertility under the canopy of perennial nitrogen-fixing plants is higher

compared to its neighborhood (Facelli and Brock 2000; Bonanomi et al. 2008). Our findings support previous observations with quantitative evidence, given that nitrogen fixers occur much more frequently as nurse than as beneficiary (Bonanomi et al. 2010). This pattern is mainly due to the high frequency of nitrogen fixation among woody nurse species, such as *Olneya tesota*, which is reported as facilitating 161 beneficiaries, and many other species of *Acacia*, *Mimosa*, *Myrica*, *Prosopis*, *Retama*, and *Ulex*. Interestingly, the frequency of nitrogen-fixing nurses drops to 5.0% among herbaceous growth forms, consistently with the lower occurrences of increased soil fertility mediated by these growth forms, with respect to trees and shrubs. However, nitrogen fixation was observed also in herbaceous nurses, as in the case of several well-known nurse species of *Lupinus*, *Medicago*, and *Trifolium*. We suggest that the higher occurrences of nitrogen fixers among woody nurses, compared to the herbaceous, may be related again to their larger size and especially to their longer life span, likely allowing to built-up wider and longer-lasting islands of fertility (Facelli and Brock 2000). In some cases, nitrogen-fixing perennial species may create dense vegetation thickets that strongly compete with other plants by reducing light availability at ground level (Walker et al. 2003). Hence, their facilitative effect due to increased soil fertility does become evident only after their die-back (Gosling 2005).

In semiarid ecosystems, the commonness of nitrogen fixers is consistent with the frequent cases of facilitation mediated by an increase of soil fertility, thus suggesting that limiting factors such as water and nutrient shortage are often coupled. In this regard, it is worth noting that water shortage, indirectly, leads to a decreased soil fertility by limiting the circulation of soil solutions and the diffusion of mineral nutrients (Schulze 1991). In such conditions, nitrogen fixation by woody plants appears as a strategy evolved not only to survive in a harsh environment, but also to indirectly promote the coexistence of less tolerant species, by mitigating the stress factors.

In wetlands, soil nutrient increase is a frequently reported mechanism of facilitation, but there is no evidence of nitrogen-fixing nurses. This result could appear surprising, because in waterlogged conditions the reduced mineralization of organic matter limits nitrogen availability too. Under such condition,

nitrogen fixation could also improve plant performances, as reported for legumes by Saur et al. (2000) and Koponen et al. (2004). However, the interactive actions of multiple stressors such as water logging, substrate salinity, low temperature, and oxygen availability could possibly reduce the competitiveness of nitrogen-fixing plants in such ecosystem.

Concerning the fleshy fruit syndrome, Valiente-Banuet et al. (2006) reported that, in semiarid Mediterranean ecosystems, fleshy-fruited species seem much more dependent on facilitative interactions than other plants. Our findings quantitatively confirm their result with fleshy-fruited frequency significantly higher among beneficiaries than among nurses, both for shrubs and trees. Moreover, this pattern can be extended worldwide being consistent in wetland, temperate, and alpine ecosystems as well.

Conclusions

It is well known that all plants are able to modify the surrounding physical environment (Jones et al. 1997), thus changing their own performances and those of coexisting species. In the last century, Clements' (1916) succession to climax, Watt's (1947) cyclic successional dynamics and Connell and Slatyer (1977) facilitation successional processes have all been theories incorporating the concept of plants altering environmental conditions enhancing the recruitment of other species. Our analysis carried out on a comprehensive data set of facilitation cases, consistently with previous findings (Brooker et al. 2008; Holmgren and Scheffer 2010), indicates that positive interactions by plant-induced environmental changes are widespread in a range of ecosystems and not limited to specific conditions of chronic abiotic stress. Moreover, this study shows that the ability to provide facilitation is highly dependent on plant structural and functional traits, being specific among different growth forms, with higher frequency for woody than herbaceous plants. This is consistent with the recent meta-analysis carried out by Gómez-Aparicio (2009) reporting that trees and especially shrubs are by far the most promising nurse growth forms to be used in restoration ecology. The ability of woody plants to modify the surrounding environment likely relies on their size, architecture, and life span. However, a large nursing variability exists within

each growth form (Callaway 1998). For instance, Gómez-Aparicio et al. (2004) found significant differences in the magnitude of interactions mediated by several nurse shrub species, with nitrogen-fixing legumes and *Cistus* spp. showing the best and worst performances, respectively. Consequently, studying plant facilitation at growth form level can be useful to analyze occurrences and mechanisms across ecosystems, but further work, focused on the species level, is necessarily required to investigate the specificity of positive interaction with more detail.

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