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An overview on epiphytism as a direct mechanism of facilitation in tropical forests

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Abstract: Direct facilitation is characterized by the positive effect of one individual on the other through changes in abiotic conditions and the creation of novel habitats. We aimed to present a systematic review of the literature about direct facilitation in tropical forests, emphasizing knowledge gaps and suggesting future lines of inquiry. We asked: (1) What is the existing literature about direct facilitation in tropical forests? (2) What kind of methodological approach (experimental or observational) has been more used? (3) What kind of study, pairwise species or community level, are more common? (4) What vegetative habits are more common between facilitators and facilitated species? (5) What hypotheses are more commonly tested? (6) How often epiphytism has been approached as facilitation? Based on literature search, we found thirty-five studies examining direct facilitation in plants mainly in the Neotropics (69%). The number of observational and experimental studies was similar. Most studies were based on pairwise comparisons of species. Trees were the most common nurse plants representing 51% of the studies, followed by shrubs (20%). This was the same for facilitated plants: trees corresponded to 48% and shrubs to 21%. The most common facilitation mechanism in tropical forest was the improvement of aboveground microclimate conditions (43%). Epiphytism is still marginally explored (11%, only 4 out of 35 studies) as a direct mechanism of facilitation. Given that about nine per cent of the world vascular flora are epiphytes that demand facilitators to survive, it is timely to widen the scope of field studies about facilitation towards such direct mechanisms.

Key words: Commensalism, Neotropical, plant community, plant-plant interaction, positive interaction, systematic review.

Introduction

Interactions between plants are positive (e.g., facilitation) or negative (e.g., competition) and they simultaneously play key roles in the organization and functioning of plant communities (Callaway & Walker 1997; Holmgren *et al.* 1997). The balance between the positive and negative effects that one individual plant causes on the other in growth, survival or reproduction, is the basis for such distinction (Bertness & Callaway 1994). For instance, Anthelme *et al.* (2011) studied the effect of

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the grass *Setaria sphacelata* (Poaceae) on palm tree seedlings in cloud forests of Ecuador. The shade provided by the grass considerably reduced above and belowground water stress. This effect counterbalanced the negative effects of competition, resulting in a positive effect of grass on palm seedlings.

Facilitation between plants may be thus defined as a positive, non-trophic, interaction, between physiologically independent plants, which benefits at least one of the organisms involved (species or individuals) (Brooker *et al.* 2008). It can occur when the presence of a facilitator modifies local micro-environment more favorable to other (facilitated) plants (Brooker *et al.* 2008; Bruno *et al.* 2003; Callaway 1997), improving reproduction, growth and survival of at least one of the involved organisms (Callaway 2007). Facilitation can result in positive, neutral or negative effects for the facilitator plants (Bronstein 2009; Callaway 2007). Therefore, facilitative interactions between species may occur through mutualism, commensalism or parasitism (Bronstein 2009; Callaway 2007; Lin *et al.* 2012). Commensalism between plants is demonstrated by epiphytism (Burns 2007; Flores-Palacios 2016). It comprises those plant species that use trees (phorophytes) as structural support. The phorophytes are facilitators for providing a vital space above the forest floor for the establishment of epiphytes and the facilitated plants generally (or supposedly) has a neutral effect on phorophytes. This is a reasonable case of facilitation (Ewel & Hiremath 2005; McIntire & Fajardo 2014). These facilitated plants need the support of phorophytes to survive, but not nutrients and water that are provided by moist air or rainwater (Benzing 1990; Burns 2007). Importantly, there is a large array of studies about epiphytism in tropical systems and they have not been synthesized yet under the scope of facilitation theory.

Facilitation has a key role in maintaining and promoting the diversity of plant communities (Hacker & Gaines 1997; McIntire & Farjado 2014). These positive effects occur through a wide variety of direct mechanisms (see Callaway 1995; Callaway 2007) caused by facilitator species in changing conditions and resources favoring facilitated species (Bertness & Callaway 1994; Brooker *et al.* 2008; McIntire & Farjado 2014). The direct mechanism is characterized by the effect of one species over another, i.e., it does not require another, third, species (Callaway 1995; Callaway 2007). For instance, the shade provided by the canopy of trees and shrubs can protect plants from extreme temperatures, winds, solar radiation, reducing water loss, and increasing soil moisture to other plant species, thus promoting microclimate conditions (Callaway 1995; Callaway 2007). Although poorly documented, facilitator plants also directly modulate the availability of resources to other organisms, creating new habitats at which many species depend on (Jones *et al.* 1997). Especially in tropical forests, trees can be facilitators by providing habitat through structural support for various taxa (e.g., nonvascular epiphytes such as lichens and mosses, vascular epiphytes such as ferns, orchids, bromeliads, aroids, climbing plants, among others) allowing the establishment and survival of these groups (Burns 2007; Garbin *et al.* 2012; McIntire & Fajardo 2014). In this way, direct interactions can occur in plant communities and have an important role in species coexistence (Lang *et al.* 2012) influencing the structure (Filazzola & Lortie 2014) and promoting diversity in plant communities (Garbin *et al.* 2012; Hacker & Gaines 1997; McIntire & Fajardo 2014). While most known examples of facilitation in plants come from systems with stressful environmental conditions (e.g., salt marsh, arid and semi-arid environments, deserts, and alpine environments, see Bronstein 2009), facilitation may also be important in many other ecosystems, particularly in the tropics. However, there are relatively few studies in these environments (Bonanomi *et al.* 2011; Castanho *et al.* 2015).

We aimed to prepare a systematic review about direct facilitation in tropical forests, emphasizing knowledge gaps and directing future research. We asked: (1) What is the existing literature about direct facilitation in tropical forests? (2) What kind of methodological approach (i.e., experimental or observational) has been more used? (3) What kind of study, pairwise species or community level, are more common? (4) What vegetative habits (trees, shrubs, herbs, climbers) are more common among facilitators and facilitated species? (5) Which hypotheses are more commonly tested? (6) How often epiphytism (as a commensal +/0 interaction) has been approached as facilitation? The role of epiphyte-phorophyte interactions as a key facilitative process, especially in tropical forests, in promoting and maintaining species diversity has been seldom studied. We argue that the inclusion of epiphytism into facilitation theory expands the

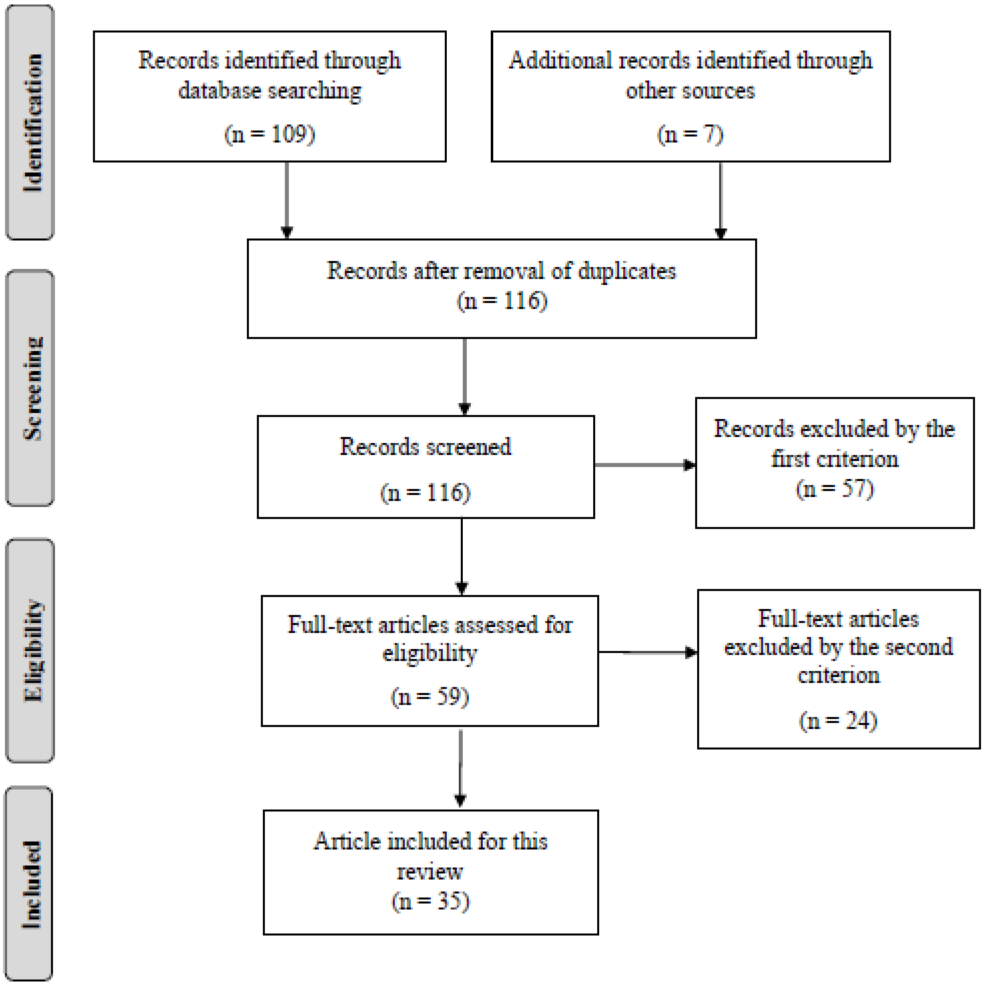

Fig. 1. Flow diagram describing the search protocol and the articles included for the systematic review. Adapted from Moher *et al.* (2009). See text for criteria used for exclusions.

scope of positive interactions adding an important vertical dimension to the mechanism.

Methods

Literature research method

A literature review was conducted including research articles published and indexed between 1945-2015 that examined and provided evidence about direct facilitation between plants in tropical forests. The literature was consulted using the ISI database Web of Science® on November 4, 2015 using a combination of three groups of terms: (1) "*facilitation*" or "*positive interaction**" or "*commensalism**" or "*commensal interaction**" and (2) "*plant**" or "*tree**" or "*shrub**" or "*herb**" or "*climb**" or "*epiphyte**" and (3) "*tropical rain forest**" or "*tropical rainforest**" or "*tropical forest**" or "*tropical dry forest**" or "*tropical wet forest**". The search was made in the topic field "topic terms" of the database that searches for words in the title, abstract, keywords, articles and keywords. Articles in all languages were included in this search. The review included a personal database with additional references (Fig. 1).

From ISI, 109 research articles were found. For the first criterion (Fig. 1), an initial screening of titles, abstracts and keywords was conducted, and the articles were excluded if: (1) they comprised literature reviews, 2) the interacting organisms were not plants (e.g., animal-plant interactions), (3) they were related to indirect facilitation, when a third species was required (e.g., potential competitive elimination or involved organisms of other trophic levels such as soil mycorrhizae, pollinators or herbivores), and (4) they were not conducted in tropical forests. For those articles where the location of the studied site was not

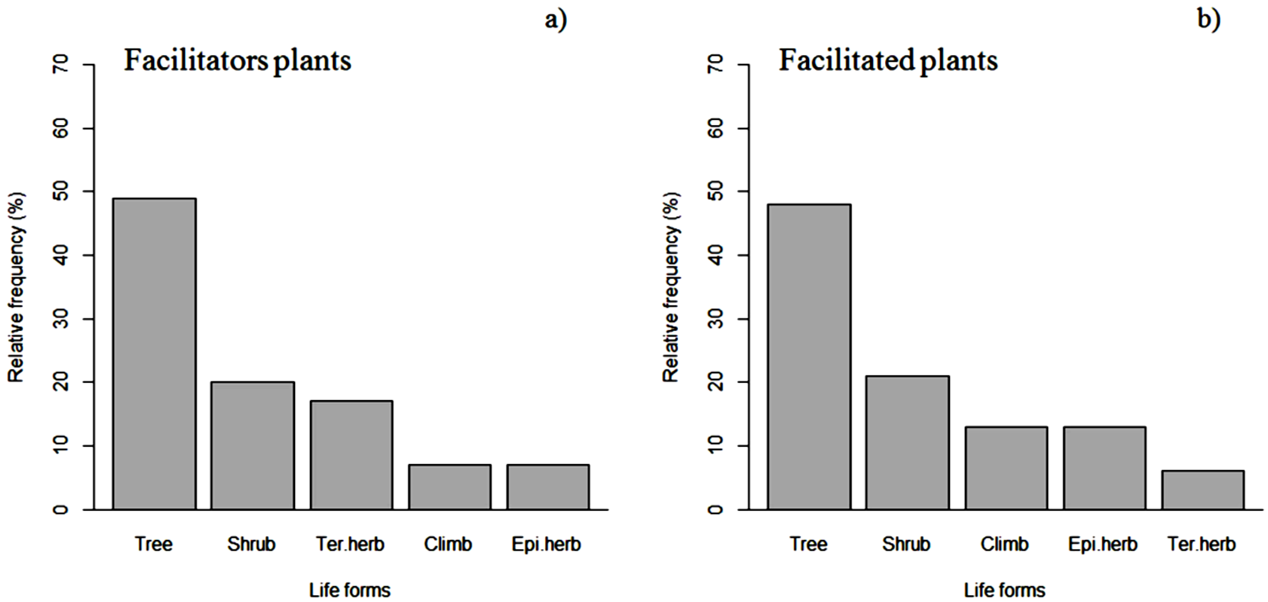

Fig. 2. Relative frequency of facilitators and facilitated plants in each vegetative habits in tropical forests. (a) Vegetative habit of facilitators. (b) Vegetative habit of facilitated plants. Epi.herb: Epiphyte herbs; Ter.herb: Terrestrial herbs; Climb: Climbing plants. Woody and non-woody climbers were included. (Table S2).

indicated in the abstract, the methods section was checked and the location retrieved. Olson *et al.* (2001) was consulted to check whether study sites were within the domain of tropical forests. Therefore, for the second inclusion criterion, the articles selected by these six criteria above were assessed. In summary, this review used those articles addressing the following criteria: (1) observational or experimental studies testing the effects of direct facilitation, (2) articles addressing facilitation versus competition were only included when facilitation was the predominant interaction, and (3) articles that resulted in both interactions were excluded, since the focus of the study are the positive interactions and not making inference on these two interactions.

Analysis of the literature

The following data were extracted from each selected reference: a description of the facilitator mechanism; the location of the study area (country and geographical coordinates) including the type of habitat studied (types of forests); the type of methodological approach (whether experimental or observational) and research areas (general ecology, restoration, regeneration, biological invasions, ecological succession). Experimental approaches comprised those studies in which the performance of facilitated species in two conditions was compared, i.e., in the absence and in the presence of facilitator species. Observational studies were those based on spatial associations between facilitated and facilitator species. We also extracted variables measured for the facilitated plant species (target-species), as growth (including biomass and height growth), survival, abundance and density. Community level attributes were species richness and composition. We also retrieved whether studies were conducted for pairwise species (only two species) or if they were made at the community level (several species involved in the interaction).

The vegetative habits (e.g., tree, shrub, herbs, climber and epiphytes) of facilitators and facilitated plant species, and the type of direct mechanisms of facilitation, whether inter- or intraspecific, were also recorded. The vegetative habits of facilitators and facilitated species were classified in tree, shrub, epiphytes herbs (vascular- orchids, bromeliads, and other fern and nonvascular- mosses and lichens), terrestrial herbs (terrestrial bromeliads, terrestrial ferns, grasses) and climbers (voluble and woody). The herbs were subdivided according to substrate preference: terrestrial plants that live directly on the soil surface and plants living on other plants (epiphytes) without emitting haustoria (Table S1 and S2). Direct mechanisms of facilitation between plants (according to Callaway 2007) were classified as: (1) improving the microclimate above the ground (e.g., reduction of excessive temperature or solar radiation by shading, increased humidity, etc.); (2) modification of soil nutrients; (3) increasing the availability of water in the soil; (4) improvement of abiotic soil conditions; (e.g., pH buffering, reducing soil salinity, substrate stabilization, increased oxygen, etc.) and (5) supporting structure (Table S1 and S2).

Results

From the 109 retrieved articles, 28 (26%) met the selection criteria and were included in this review (Fig. 1 and Table S1). Approximately 74% (81 articles) showed no direct facilitation in tropical forest environments, and they were excluded from the review. Seven articles from a personal database (Fig. 1 and Table S1) addressing direct facilitation in tropical forests were included. Thus, this review made use of 35 articles from empirical studies.

Most of these articles (68%) were published in the last five years (2010–2015). Articles on direct facilitation in tropical forests addressed interactions in the context of ecological succession, biological invasions, regeneration and restoration systems, mainly. Most studies were concentrated in the neotropical countries (69% - 24), eight of them (23%) were conducted in Brazil. The second country in the number of articles was China with five (14%), followed by Mexico with four (11%), while most tropical countries (11) had one or two studies.

There was almost equivalence in the number of observational (51%) and experimental studies (49%; Table S1). When comparing the level of the organisms involved in the studies, based on the pair of species facilitators and facilitated plant (target-species) or community level (several individuals and/or species involved in the interaction), 27 studies addressed the interaction at the community level. In general, the most common facilitator plants were trees, representing 51% of the results, followed by shrubs 20%. The same was true for facilitated plants with trees corresponding to 48%, followed by shrubs with 21% (Fig. 2). However, it was possible to detect seven studies (21%) that identified herbs as facilitators, especially of tree and shrub species.

The mechanism by which the facilitation operates in tropical forests is well represented by the improvement of above ground microclimate environment, which was evident in 22 studies, representing 43% (Fig. 3 and Table S2). Structural support as a facilitating mechanism appeared in eight (16%) of the studies (Fig. 3), of which only 4 articles (11%) addressed the epiphytism (Table S1 and S2).

Discussion

In this review, we synthesized mechanisms of direct facilitation in tropical forests and the existing literature on direct facilitation through epiphytism. Although empirical studies of direct facilitation in tropical forests broadened our understanding about the implications of facilitation on community assembly, our results indicate that the role of epiphytism as a facilitation mechanism is still underestimated in tropical forests. Not surprisingly, the focus is on the effects of organisms in ameliorating abiotic conditions. However, this is only a fraction of the direct mechanisms comprised as facilitation. The positive effects of plants that provide vital substrate for other plants (as the epiphyte-phorophyte interaction) was addressed in only 11% of the studies, even though about nine per cent of all vascular flora of the world (Zotz 2013) necessarily need this facilitative mechanism to survive. Trees and shrubs are mostly studied as both, facilitated and facilitators – epiphytes comprise a minor component of the species classified as facilitated.

The experimental approach is considered as the most robust way to make inferences about facilitation by providing ways of distinguishing the biological effects of the facilitators from the local environmental effects, that is, to detect the mechanisms behind the phenomenon (Callaway 1995; Callaway 2007). Consequently, a relatively high number of experimental studies contributed to the understanding of facilitation in plant communities (Gould *et al.* 2013; Lang *et al.* 2012). Nevertheless, Castanho *et al.* (2015) identified a predominance of observational over experimental studies in a systematic review of facilitation in coastal dune plant communities. Observational studies based on the quantification of positive spatial associations indicate that facilitation is an important determinant of community structure and diversity (Callaway 1995; Castanho *et al.* 2012). Here, there was almost equivalence between the number of observational and experimental studies. This may be attributed to the eight studies that addressed facilitation through its direct effect as structural support which were conducted through the observation of associative patterns among phorophytes-lianas and epiphytes. All studies addressing the epiphyte-phorophyte relationship were observational. They showed, in most cases, that the association between epiphytes and phorophytes is nonrandom (e.g. Wagner *et al.* 2015) due to differences in the structural properties of

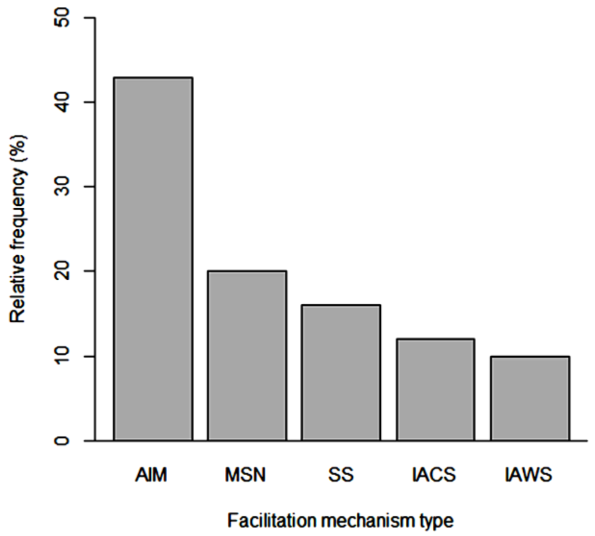

Fig. 3. Relative frequency of direct mechanisms of facilitation found in tropical forest environments all over the world. AIM, aboveground improved microclimate conditions; MSN, modification of soil nutrients; SS, structural support; IACS, improved abiotic conditions of soil; and IAWS, increasing the availability of water in soil (see method) (Table S2).

phorophytes (e.g. Sáyago *et al.* 2013). Although positive spatial association studies are not as powerful as the experimental evidence, they provide relevant information on the relative importance of positive interactions in the organization of plant communities. In which half of the information we have about direct facilitation between plants in the tropical region is based on this type of approach.

Many studies were conducted at the community level and these studies showed that the structural support provided by facilitators allow the existence of numerous species of epiphytes and lianas. However, most of our knowledge of facilitation is based on studies among species pairs (Travis *et al.* 2005; Yamamura *et al.* 2004). It is known that communities take emergent properties when many species interact (Filotas *et al.* 2010) and species are involved in complex networks of interactions that encompass many species (Bascompte & Jordano 2007).

Different vegetative habits can exert positive effects on other plants. The most common facilitators were the woody plants (trees and shrubs). Bonanomi *et al.* (2011) in a systematic review about facilitation mechanisms in terrestrial ecosystems found that woody plants were the most frequent facilitators in tropical environments. This pattern reflects, in part, the abundance of different growth forms in each ecosystem. For example, shrubs can be important facilitators in coastal dune environments (Castanho *et al.* 2015). In forest ecosystems, trees composed the main component, and their interactions with other plants represent a key role in structuring forest communities. Trees can regulate environmental heterogeneity and create, maintain or modify biotic and abiotic characteristics in all temporal and spatial scales (Jones *et al.* 1997). For example, their canopy can soften aboveground microclimate conditions resulting in an improvement in the physiological performance of the plants that grow under this influence (Holmgren *et al.* 1997; Pugnaire *et al.* 1996). Woody plants provide benefits to many different vegetative habits, while herbs were rarely observed benefiting woody plants. In most cases, they facilitate individuals and species with the same growth form (Callaway 2007; Jian *et al.* 2013; Zotz *et al.* 2005). However, we found seven studies that identified herbs as facilitators, especially of tree and shrub species (Anthelme *et al.* 2011; Gómez-Ruiz *et al.* 2013; Gould *et al.* 2013; Maza-Villalobos *et al.* 2011; Rocha *et al.* 2015; Wan *et al.* 2014) (Table S2). For instance, Rocha *et al.* (2015) observed that the presence of *Bromelia balansae* Mez (Bromeliaceae), a terrestrial herb in forest and ecotone area, facilitates tree seedlings by improving the above ground microclimate conditions and soil nutrients. Moreover, epiphytes can facilitate each other, promoting greater biodiversity in tropical ecosystems, such as forest (Jian *et al.* 2013; Zotz *et al.* 2005). Such interactions are important in maintaining the epiphytic diversity. For example, Jian *et al.* (2013) found a positive interspecific association between two species of vascular epiphytes in tropical and subtropical forests and suggested that the interaction through drought mitigation is an important mechanism that helps epiphytes to survive and grow on phorophytes. Therefore, this is an important process in maintaining epiphyte diversity in tropical and subtropical regions with water restriction events, especially in the context of climate change. The outcome of interactions between plants is highly variable, because it implies a balance between positive and negative effects that may change depending on various factors such as the characteristics of the interacting species and environmental conditions. The effectiveness of the facilitator necessarily depends on its structural properties. These vary in response to the environmental conditions which organisms are subjected, as well as the life stages of the facilitator species and other aspects of their life histories (Brooker *et al.* 2008; McIntire & Farjado 2014).

The main mechanism by which facilitation operates in tropical forests is well represented by improvement of above ground microclimate conditions. This mechanism has strong effects on germination and seedling establishment of juvenile individuals (e.g., Anthelme *et al.* 2011; Gould *et al.* 2013; Rocha *et al.* 2015), growth and survival (e.g., Gómez-Ruiz *et al.* 2013; Gould *et al.* 2013; Sánchez-Velásquez *et al.* 2004), as well as species richness and abundance (e.g., Fischer *et al.* 2009; Rocha *et al.* 2015). The improvement of microclimate conditions is the commonest forms of facilitation (Callaway 2007). They are detected in both tropical rainforests and dry forests, and thus different forest environments can show similar facilitative processes. Structural support is less explored than improvement of microclimate conditions as a mechanism of facilitation (Callaway 2007). Climbing plants, including lianas (woody climbers), even if they have their roots in the soil, use tree trunks as support to reach the canopy and they are almost obligatory organisms of facilitators effects (Campanello *et al.* 2007; Garbin *et al.* 2012; McIntire & Fajardo 2014), even though some climbing plants grow on rocks or other structures (Campanello *et al.* 2007). In tropical forests, besides trees, lianas are also facilitated by other lianas that provide structural support through their trunks, already established in a host tree (Campanello *et al.* 2007; Pérez-Salicrup & Sork 1998).

Only 11% of the articles addressed the commensal interaction as epiphyte-phorophyte interactions. According to Callaway (2007), there is a lack of studies that address the commensal interaction between plants, and this can be at least in part due to a disinterest by members of the scientific community more than a simple ecological artifact. Futuyma (1979) suggested that commensalism could be so common that is often not noticed. Commensalism between plants is evidenced by the interaction between epiphytes and phorophytes (Callaway 2007), a relationship easily observed in forest ecosystems throughout the tropics. Although it is recognized that facilitation may occur as commensalism (Bronstein 2009; Callaway 2007; Lin *et al.* 2012), no study in this review addressed directly the interactions between epiphytes and phorophytes in the context of facilitation theory. This may be due to an independent advance of the two concepts and an emphasis on the study of facilitation in gradients of stress.

There is a need for an integrative perspective for the concepts of facilitation and epiphytism. Plant-plant positive interactions are mostly focused on direct mechanisms related to the improvement of environmental conditions (by increasing the access to nutrients, reducing temperature and increasing humidity, etc.). This is commonest mechanism implicit behind the use of the term facilitation. Nevertheless, the structural support provided by trees in epiphyte-phorophyte relationships constitutes also a direct mechanism through the creation of a novel ecosystem (McIntire & Fajardo 2014). It is interesting that this structural support can also indirectly represent an improvement in environmental conditions (such as greater light availability, excessive temperature reduction by shading, increased humidity by intercepting the canopy, etc.). The integration of these concepts of facilitation and epiphytism implies strengthening the theory of facilitation in broader aspects, besides stress gradient studies. The broad definition of facilitation provided by McIntire & Fajardo (2014) as “any increase in a diversity measure that results directly or indirectly from the modifications of biotic and abiotic conditions caused by any and all species’ presence” satisfies this need. However, as showed here, there is a resistance to explicitly treat the interaction between epiphytes and phorophytes into the facilitation theory framework. Considering only the direct mechanisms of facilitation, structural support, allows numerous species of epiphytes (vascular and nonvascular), lianas and vines to persist, given that these groups are almost obligatory recipients for the facilitating effects of trees as structural support. This facilitative-epiphytism largely contributes to the high diversity of vascular and nonvascular plants in tropical forests. The study of facilitation, and its theory, needs to move beyond the study of changes in environmental conditions and explicitly include the interaction between epiphytes and phorophytes.

Conclusion

Different types of plants exhibit positive effects on other plants. Studies on direct facilitation between plants in tropical forests have been conducted to understand important ecological processes in the organization of plant communities and to apply this knowledge in the restoration of degraded ecosystems. Empirical studies on direct facilitation have expanded our understanding of the implications that facilitation has for community ecology. However, these studies underestimate the role of facilitation in plant communities, because the focus is primarily on the effect of organisms on moderating abiotic stress. This represents only a fraction of the direct mechanisms encompassed by facilitation. The provision of vital substrate to other plants (the epiphyte-phorophyte relationship) is responsible for the maintenance of about nine percent of all vascular flora of the world. From this renewed perspective of the epiphytes-phorophytes interactions, it becomes crucial to understand the role of host trees in explaining the ecology of structurally dependent plants, such as vascular epiphytes, especially in tropical forests.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. List of articles used for this systematic review of direct facilitation of global tropical forest environments.

Table S2. Experimental and observational studies that address facilitation between plants in tropical forests.