



FACILITATION BETWEEN PLANTS AND THE USE OF FACILITATING SPECIES AS AN ECOLOGICAL RESTORATION STRATEGY

REVIEW ARTICLE

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ABSTRACT

Ecosystems subject to extreme abiotic factors are privileged places for studies of positive interactions between plants, such as facilitation mechanisms, which, from biotic or abiotic modifications, generate benefits to the environment. Due to the increase in the number of articles on facilitation in recent decades and the indication of the use of facilitating species in recovery and ecological restoration projects, the present study presents a literature review on facilitation between plant-plant and its applicability between the years 2011 and 2020. A total of 64 studies were considered that encompass the facilitation theme, and the text was composed of an introduction and two sections: i) studies on the facilitation mechanism – advances in the last decade and ii) facilitation as a strategy for ecological restoration. This review indicates that the best understanding of facilitation mechanisms occurs from the combination of knowledge at different levels, such as knowledge of species, ecological organization, phylogenetics and environmental conditions. Thus, this approach enables a better understanding of the community dynamics and demonstrates how the use of facilitating species in restoration areas, especially in regions with severe environmental conditions and/or more vulnerable to climate change, has been considered an effective strategy in the ecological restoration process.



Keywords: Extreme environments, Facilitation mechanism, Positive interactions.

1. INTRODUCTION

Facilitation mechanisms defined by positive interactions between plants allow that, on a time scale, benefits occur for one or both associated species (BRUNO; STACHOWICZ; BERTNESS, 2003; BROOKER *et al.*, 2008; O'BRIEN *et al.*, 2019). These interactions can occur due to environmental modifications, which favor the establishment or development of species (CALLAWAY, 1995; NAVARRO-CANO *et al.*, 2015; ABIYU *et al.*, 2017; LUCAS *et al.*, 2022), as well as by other organisms, leading to increased pollination (LOSAPIO *et al.*, 2021). The presence of a facilitator species allows the colonization of environments with low regeneration and extreme environmental conditions, positively modifying the dynamics and structure of the community, from the formation of microenvironments (PUGNAIRE; HAASE; PUIGDEFABREGAS, 1996; PUGNAIRE; ARMAS; MAESTRE, 2011; VALIENTE-BANUET; VERDÚ, 2013; MCINTIRE; FAJARDO, 2014; CAVIERES *et al.*, 2016; LIANCOURT; DOLEZAL, 2021).

Studies of positive interactions between plant-plant began to be highlighted in the literature after the reviews by Bertness and Callaway (1994) and Callaway (1995), in which the topic began to be discussed and integrated into general models of dynamics and organization of the community. The study by Bertness and Callaway (1994) made it possible to clarify how positive interactions affect recruitment, the spatial distribution of species, reduce physical stress and consumer pressure, thus controlling the process of ecological succession. The authors formulated the Stress Gradient Hypothesis (SGH), in which they considered that the actions of facilitating species are intensified with an increase in the stress level. Callaway's (1995) review, on the other hand, became a milestone in the facilitation theme, as it presented a table that brought together several studies produced since the early 1900s, expanding knowledge about the meaning of facilitation mechanisms and their role in communities. With these surveys, studies prior to the nineties gained visibility.



Niering, Whittaker and Lowe (1963), for example, in a desert environment in Arizona, mentioned that species of different bushes, mainly “palo-verde” individuals, sheltered juveniles of “giant cacti” saguaros under their canopies, acting effectively for the survival and development of cacti. In this study, the term “nurse plant” (facilitating plants) was cited for the first time in the literature, designated for the perennial species that housed the cacti under their canopy. Other research carried out in the same environment confirmed the importance of the shade of the bushes for the survival of cactus individuals, and affirmed the term “nurse plant” for the “palo-verde” bushes, due to their ability to improve the development of cacti (HASTINGS; TURNER, 1965; TURNER *et al.*, 1966). Connell and Slatyer (1977) expanded the knowledge about positive interactions, presenting a set of data on the dynamics of the community, raising questions about the processes of changes in the dynamics and ecological succession. These authors suggested three models of succession: tolerance, inhibition and facilitation, explaining how communities are formed and how they are modified over time.

Studies that contemplate this theme continued to be published, mainly from the 2000s, as mentioned by Brooker *et al.* (2008). Due to the presence of a facilitating individual, severe environmental conditions are alleviated (BANNISTER *et al.*, 2020), allowing the understanding of the dynamics of communities (VEGA-ÁLVAREZ; GARCÍA-RODRÍGUEZ; CAYUELA, 2018; NAVARRO-CANO *et al.*, 2019; LIANCOURT ; DOLEZAL, 2021), the use of facilitating species in ecological restoration projects has gained greater visibility, being considered an effective technique, as it reduces costs where human interventions, throughout the projects, are reduced by the benefits generated by the facilitating plant (HE; BERTNESS; ALTIERI, 2013; GÓMEZ-RUIZ; LINDIG-CISNEROS; VARGAS-RÍOS, 2013; SILLIMAN *et al.*, 2015; SOLIVERES; SMIT; MAESTRE, 2015; ALDAY *et al.*, 2016; FEDRIANI *et al.*, 2019).

Thus, with a focus on a better understanding of the relationships between facilitating species and the dynamics of communities, where these processes occur, and the



application of these species in environmental restoration projects in recent years, a literature review on these topics was carried out between 2011 and 2020.

2. MATERIAL AND METHODS

The search for publications was carried out, in December 2020, in four bibliographic bases: Web of Science, Scielo, ScienceDirect, Scopus and in a personal database. For each section, different words were searched, present in the title and/or in the keywords and/or in the abstract, which were redefined between 2011 and 2020. For the first section, the keywords were used: "facilitation mechanisms" and "vegetation" or "plant", and in the second section, the keywords "facilitation", "restoration" or "restored" and "vegetation" or "plant" were used.

A screening of the articles was carried out, in which repeated articles were excluded and articles directed to the themes were selected, based on their reading.

3. RESULTS

From a total of 1,811 publications, 64 publications were selected for analysis. After sorting and excluding repeated articles, the low number of articles that encompass the proposals of this study is evident. In the topic Studies on facilitation mechanisms – advances in the last decade, 28 out of 708 articles were used, and in the topic Facilitation, as a strategy for ecological restoration, 36 out of 592 were used.

3.1 STUDIES ON FACILITATION MECHANISMS – ADVANCES IN THE LAST DECADE

Review articles that evaluated studies on the facilitation mechanism in recent years confirm that positive interactions, such as facilitation between plants, can benefit community biodiversity by mitigating abiotic stresses, forming microhabitats and generating heterogeneity in the environment, especially in places under extreme environmental conditions (PUGNAIRE; ARMAS; MAESTRE, 2011; VALIENTE-



BANUET; VERDÚ, 2013; CAVIERES *et al.*, 2014; MCINTIRE; FAJARDO, 2014; CAVIERES *et al.*, 2016; LIANCOURT; DOLEZAL, 2021). It is noteworthy that positive interactions also help in understanding biodiversity and ecosystem functioning, leading to an understanding of how diversity affects functions in a given environment (WRIGHT *et al.*, 2017).

In recent years, publications that addressed the issue of facilitation between plant species were divided into bibliographic reviews and field evaluations. Bibliographic reviews focus on the evaluation of a particular species or a set of these, allowing a global understanding of the dynamics of a particular area and/or community, as seen in the article by Pugnaire, Armas and Maestre (2011). The authors brought together 15 years of studies carried out in desert areas of southeastern Spain, explaining the theme of positive interactions and their relationship with the community. Field evaluations are carried out by floristic surveys and experiments. With a focus on quantifying the abundance and richness of species with and/or without the presence of a possible facilitator, the floristic surveys aim to verify the occurrence of possible facilitation mechanisms, how they work and what are the implications of these for the species and for the environment (VAN ZONNEVELD; GUTIÉRREZ; HOLMGREN, 2012; BADANO *et al.*, 2016; LYU *et al.*, 2016; TSUDA; CASTELLANI, 2016; AL-NAMAZI; EL-BANA; BONSER, 2017; DALOTTO *et al.*, 2018; FILAZZOLA *et al.*, 2018; VEGA-ÁLVAREZ; GARCÍA-RODRÍGUEZ; CAYUELA, 2018; O'Brien *et al.*, 2019; PELÁEZ *et al.*, 2019). The second approach is the experiments, carried out by planting methodologies. In this approach, different techniques are used, such as the use of seeds (LIANCOURT; TIELBÖRGER, 2011; QUON; BOBICH; QUESTAD, 2019) and/or seedlings, with the inclusion of facilitating and/or facilitated species, in order to evaluate the facilitation mechanisms in isolated ways (AVENDAÑO-YÁÑEZ *et al.*, 2014; VAN ZONNEVELD; GUTIÉRREZ; HOLMGREN, 2012; BADANO *et al.*, 2016). It should be considered that, when the studies cited above are quantified, the predominance of observational studies stands out. This preference makes it difficult to identify facilitation processes and facilitating species,



because field activities are considered more effective methodologies to identify facilitation mechanisms, due to the ability to evaluate and test (CASTANHO; OLIVEIRA; PRADO, 2015; CHAIEB *et al.*, 2021).

Regardless of the technique used to describe facilitation processes and facilitating species, studies indicate that positive effects go beyond facilitating and benefiting other individuals. The evaluation of these effects allows answers about how the community dynamics occurs (VALIENTE-BANUET; VERDÚ, 2013; MCINTIRE; FAJARDO, 2014; WRIGHT *et al.*, 2017; LIANCOURT; DOLEZAL, 2021) and how much diversity is changed, including functional diversity (LOSAPIO *et al.*, 2021) and phylogenetic diversity (VALIENTE-BANUET; VERDÚ, 2013; VEGA-ÁLVAREZ; GARCÍA-RODRÍGUEZ; CAYUELA, 2018; DUARTE *et al.*, 2021). Losapio *et al.* (2021) mention that facilitator plants increase the phylogenetic and functional diversity of floral visitors, indicating that facilitation mechanisms between plants can support ecosystem functioning, both directly (microhabitat improvement) and indirectly (diversity effects). For the phylogenetic diversity of plants, Valiente-Banuet and Verdú (2013) cite that the maintenance of phylogenetic diversity can occur when species, in a given environment, have lineages with different evolutionary histories. Due to the optimal environment, there is a reduction in the process of competition and an increase in facilitation. Data cited by Duarte *et al.* (2021), in an experiment that sought to test SGH, where the authors describe a positive relationship between facilitation and elevation, mainly for species interactions with distant evolutionary lineages.

In addition to verifying the occurrence of facilitation in a given community, scientists seek to understand how this process is triggered and where it is more pronounced. Several authors use the SGH proposed by Bertness and Callaway (1994) as a basis for evaluating facilitation mechanisms (KIKVIDZE *et al.*, 2011; BEDUSCHI; CASTELLANI, 2013; CAVIERES *et al.*, 2014; MICHALET *et al.*, 2014; LYU *et al.*, 2016; AL-NAMAZI; EL-BANA; BONSER, 2017; O'BRIEN *et al.*, 2019). Regarding environments with severe climatic conditions, different authors conclude that



facilitation and competition mechanisms vary with climate change, and that environments with severe environmental conditions are positively related to facilitation mechanisms (KIKVIDZE *et al.*, 2011; CAVIERES *et al.*, 2014; AL-NAMAZI; EL-BANA; BONSER, 2017; O'BRIEN *et al.*, 2019). The presence of a facilitator individual in these environments has an important effect on maintaining community diversity, in which facilitator species can alter climate filters, allowing the establishment and recruitment of species, increasing diversity and contributing to their distribution along these gradients, however, Michalet *et al.* (2014) warn that the evaluation of species composition related to the facilitation process and tested by the SGH approach can become complex. These authors cite that, at a certain threshold of climate change, processes such as the collapse of facilitation, the change from facilitation to competition and null mechanisms of interactions can occur. The collapse of facilitation may occur due to the decreasing effect of species facilitation, while the shift from facilitation to competition may be driven by environmental conditions and species response strategies, as corroborated by Liu *et al.* (2020). On the other hand, null mechanisms of interactions can occur in situations of extreme stress, in which environmental changes can directly interfere with interactions between plant species.

With the increase in the number of studies that consider plant-plant interactions, researchers have begun to correlate these processes with climate change. According to O'Brien *et al.* (2019), in some cases, facilitating species allowed greater survival of individuals in the face of increased temperatures, by offering shelter and more favorable conditions for the development of other individuals. Thus, the authors cite that the use of an individual that minimizes the effects of climate change, such as global warming, can create refuges for many individuals who, without assistance, will not be able to resist climate change.



3.2 FACILITATION AS A STRATEGY FOR ECOLOGICAL RESTORATION

With the increasing modification of natural environments around the world, motivated mainly by anthropization, the creation and development of techniques for the recovery of degraded areas have become essential (BURKE *et al.*, 2011). Ecological restoration aims to form the necessary conditions for the restoration of the environment over the years, favoring abiotic and biotic flows in the matrix and making the environment not dependent on long-term human interventions (TEMPERTON *et al.*, 2004; SER, 2023), and began to be inserted in recovery projects in the mid-twentieth century, in which different strategies and techniques were created and tested over the years (BRANCALION *et al.*, 2015; SER, 2023), such as the use of biotic interactions. Among biotic interactions, the use of facilitating species (e.g., positive interactions between plant species) has been tested and considered an effective strategy.

A facilitating species can lead to a reduction in the physiological stress of plant individuals, by mitigating extreme environmental conditions (BANNISTER *et al.*, 2020), and can make the soil more nutritious (NAVARRO-CANO *et al.*, 2015; ABIYU *et al.*, 2017), inhibit the growth of exotic species cover (MARTINEZ; DORNBUSH, 2013; GALINDO *et al.*, 2017), increase the local fauna (LOSAPIO *et al.*, 2021), form seed banks below the canopy (ERFANZADEH; PALAYE; GHELICHNIA, 2020; FORONDA *et al.*, 2020), allow germination (FEDRIANI *et al.*, 2019) (Figure 1: A-B), survival and growth of plant species (URRETAVIZCAYA; DEFOSSÉ, 2013; ENCINO-RUIZ *et al.*, 2013; DOMÍNGUEZ *et al.*, 2015; TORROBA-BALMORI *et al.*, 2015; SUN *et al.*, 2017) (Figure 1: C). Thus, in environmental restoration projects, facilitating individuals allow cost reduction in projects, by positively modifying the community and making the environment more favorable for the development of other individuals, without the need for major human interventions (HE; BERTNESS; ALTIERI, 2013; GÓMEZ-RUIZ; LINDIG-CISNEROS; VARGAS-RÍOS, 2013;



SILLIMAN *et al.*, 2015; SOLIVERES; SMIT; MAESTRE, 2015; ALDAY *et al.*, 2016; FEDRIANI *et al.*, 2019).

Biotic interactions are more frequently used in restoration projects in environments with extreme conditions, with less regeneration capacity, mainly due to abiotic factors (MENDOZA-HERNÁNDEZ *et al.*, 2013; CASTANHO; OLIVEIRA; PRADO, 2015, SER, 2023). However, the inclusion of biotic interactions in restoration projects in mild environmental conditions, such as areas of Atlantic forest and riparian forest, should be considered. When forest areas undergo deforestation, drastic environmental changes occur that generate an imbalance in the environment, making the use of positive interactions an appropriate technique (ANTHELME; GÓMEZ-APARICIO; MONTÚFAR, 2014; AVENDAÑO-YÁÑEZ *et al.*, 2014; LAMEIRA *et al.*, 2019; PEREA *et al.*, 2019). It should be considered that, in certain arid areas, under severe drought conditions, with high water stress, the positive effects can be suppressed by competition (JANKJU, 2013; NOUMI *et al.*, 2015), or will simply fail, indicating that this tool can be limited by the climate (MICHALET *et al.*, 2014; GONZALEZ; GHERMANDI, 2019).

The assessment of the functional (NAVARRO-CANO *et al.*, 2019), taxonomic and phylogenetic identity of facilitating and facilitated species is important to enhance the use of this technique, and has been shown to be relevant in the results of interactions in restoration experiments (VERDÚ; NUMA; HERNÁNDEZ-CUBA, 2011; NAVARRO-CANO *et al.*, 2016). It is noticed that, the greater the phylogenetic distance between species, the more they tend to present different phenotypes, therefore, different ecological requirements, reducing competition and maximizing the facilitation effect (VERDÚ; NUMA; HERNÁNDEZ-CUBA, 2011; VERDÚ; GÓMEZ-APARICIO; VALIENTE-BANUET, 2012). The same occurs with the functional distance (morphological and physiological characteristics), in which, the greater the functional distance between the facilitator and the facilitated species, the greater the success of seedling establishment (NAVARRO-CANO *et al.*, 2019). However, it should be considered that facilitating species do not necessarily open



the way to benefit all species (LORTIE, 2017), soil preparation, choice of species and selection of seedlings being also relevant for the efficient recovery of the environment (DIAS *et al.*, 2014).

Finally, it should be considered that, although there are several studies that cite the use of facilitating species as alternatives in ecological restoration, few of them, especially in recent years, have carried out experiments in the field, proving the efficiency of using these species in restoration projects (Chart 1).

Table 1- Advances in research on the use of facilitating species in ecological recovery and restoration projects in the last three years, with examples of articles, including their authors, titles and main results

Authors	Article title	Abstract
Bannister et al. (2020)	Shrub influences on seedling performance when restoring the slow-growing conifer <i>Pilgerodendron uviferum</i> in southern bog forests.	In an experiment to evaluate the recovery of <i>Pilgerodendron uviferum</i> (D. Don) Florin. in swampy forests in Chile. The authors evaluated, for four years, the presence and absence of shrubs in the development of the species, and indicated that the presence of shrubs generated a reduction in the physiological stress of <i>P. uviferum</i> individuals (measured as Fv/Fm), as well as greater height increase and greater vitality.
Foronda et al. (2020)	Substrate-specialist plants for restoring vegetation in post-mining gypsum substrates.	The authors evaluated the facilitating role of <i>Gypsophila struthium</i> Loeffl. on the germination and development of species in a rubbish dump in Spain. As a result, the species was considered a pioneer shrub in the mine, increasing local diversity and having a positive effect on seed germination, individual growth, soil improvement and forming microhabitats under its canopy.
Fedriani et al. (2020)	Combined effect of seed provenance, plant facilitation and restoration site on revegetation success.	This study evaluated the facilitator potential of three shrub species for <i>Pyrus bourgaeana</i> Decne, in an area undergoing environmental restoration in Spain. As a result, it was observed that, although shrubs have a positive effect on <i>P. bourgaeana</i> , the magnitude of interactions changes both with the sowing location and with the provenance of the seeds.
Gonzalez and Ghermandi (2019)	Dwarf shrub facilitates seedling recruitment and plant diversity in semiarid grasslands.	The richness, seedling emergence and survival of <i>Festuca pallelescens</i> (St.-Yves) Parodi were evaluated with and without the presence of <i>Acaena splendens</i> , in an area of northwest Patagonia. In the results, the indices were higher with the presence of <i>A. splendens</i> , however, the seedlings died in the summer in both microsites, indicating that <i>A. splendens</i> acts as a kind of facilitator, however, the facilitation mechanism can fail

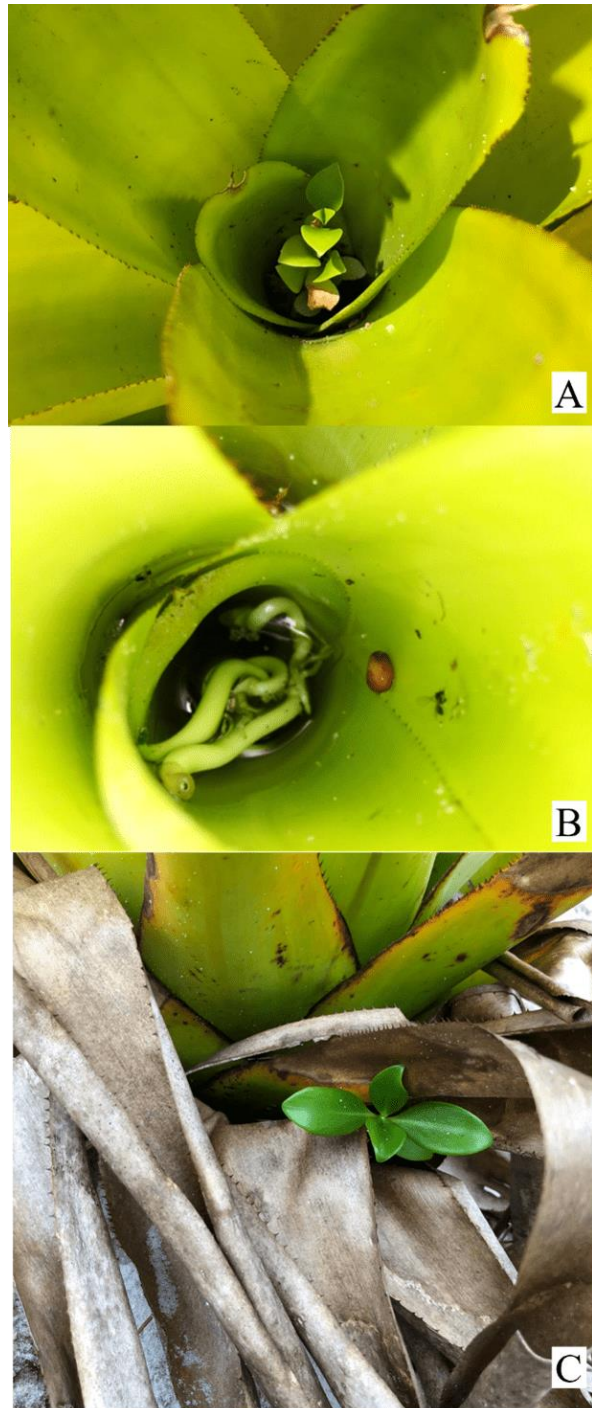


		in conditions drought, indicating that it is a climate-limited restoration tool.
Martelletti et al. (2018)	Microsite manipulation in lowland oak forest restoration results in indirect effects on a corn predation.	The study that investigated <i>Cytisus scoparius</i> (L.) Link. and artificial shade structures, as possible facilitation mechanisms, with and without prior soil improvement, in seed emergence and predation, in northern Italy, found no evidence of direct facilitation in emergence, however, indirect effects were detected in the form of seed predation, which were negatively affected by the presence of <i>C. scoparius</i> .

Source: Author.



Figure 1 - *Clusia hilariana* Schlttdl. in the rosette of the tank bromeliad *Aechmea blanchetiana* (Baker) LB Sm.: (A-B) Germination of *C. hilariana* in the rosette of the tank bromeliad; (C) Growth of *C. hilariana* in the tank bromeliad rosette



Source: Author.

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4. FINAL CONSIDERATIONS

This review highlights the importance of knowledge about the environment and climatic conditions for a better understanding of facilitation processes, as well as the responses of facilitating and facilitated species.

The articles selected in this study highlight the positive role of facilitating plants in community dynamics, both ecologically and phylogenetically, and understanding the efficiency of using facilitating species in restoration projects for degraded areas. It is noteworthy that most of the cited studies are considered observational, and a small number of these were developed with planting methodologies. These data, together with the existence of gray literature (e.g., theses, dissertations, technical reports, unpublished data), generate gaps in the knowledge of the processes evaluated here.

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