

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

#### **REVIEW ARTICLE**

RIBEIRO, Izabela Ferreira<sup>1</sup>, MENEZES, Luis Fernando Tavares de<sup>2</sup>, NASCIMENTO, Marcelo Trindade<sup>3</sup>

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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 and/or abiotic modifications, generate benefits in the environment. Due to the increase in the number of articles in recent decades and the indication of the use of these species in ecological recovery and restoration projects, the present study presents a review of the literature on plant-plant facilitation and its applicability between 2011 and 2020. A total of 64 studies involving the theme facilitation were considered, 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 a better 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 allows a better understanding of 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 benefits for one or both associated species (BRUNO; STACHOWICZ; BERTNESS, 2003; BROOKER et al., 2008; O'BRIEN et al., 2019). These interactions may occur due to environmental changes, which favor the establishment and/or development of species (CALLAWAY, 1995; NAVARRO-CANO et al., 2015; ABIYU et al., 2017; LUCAS et al., 2022), as per other organisms, leading to increased pollination (LOSAPIO et al., 2021). The presence of a facilitating 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 microenvironments (PUGNAIRE; HAASE; PUIGDEFABREGAS, of 1996: PUGNAIRE; WEAPONS; MAESTRE, 2011; VALIENTE-BANUET; VERDÚ, 2013; MCINTIRE; FAJARDO, 2014; CAVIERES et al., 2016; LIANCOURT; DOLEZAL, 2021).

Studies of positive plant-plant interactions began to have highlights in the literature from the reviews of Bertness and Callaway (1994) and Callaway (1995), in which the theme began to be discussed and integrated into general models of community dynamics and organization. The study by Bertness and Callaway (1994) allowed us to clarify how positive interactions affect the recruitment, spatial distribution of species, reduces 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 the facilitating species are intensified with the increase of the stress level. The review of Callaway (1995) became a milestone in the theme of facilitation, 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 studies, studies prior to the 1990s gained visibility. Niering, Whittaker and Lowe (1963), for example, in a desert environment in Arizona,



mentioned that species of different shrubs, mainly "palo-verde" individuals, harbored juvenile saguaros "giant cacti" under their canoses, acting effectively for the survival and development of cacti. In this study, the term "nurse plant" was first mentioned in the literature, assigned to the perennial species that harbored cacti under its canopy. Other research carried out in the same environment confirmed the importance of shade of the bushes for the survival of cactus individuals, and affirmed the term "nurse plant" for the shrubs of "palo-verde", due to the ability to improve the development of cacti (HASTINGS; TURNER, 1965; TURNER *et al.*, 1966). Connell and Slatyer (1977) expanded their knowledge about positive interactions, presenting a data set on community dynamics, raising questions about the processes of changes in ecological dynamics and succession. These authors suggested three models of succession: tolerance, inhibition and facilitation, explaining how community formations occur and how they are modified over time.

Studies that contemplate this theme continued to be published, mainly from the 2000s, as cited by Brooker *et al.* (2008). Due to the presence of an individual facilitator to mitigate severe environmental conditions (BANNISTER *et al.*, 2020), allowing a better 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 gained greater visibility, being considered an effective technique, by reducing 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.*, 2019).

Thus, focusing on a greater understanding of the relations of the facilitating species with the dynamics of the communities, where these processes occur, and their application in environmental restoration projects in recent years, a literature review on these themes was carried out between 2011 and 2020.



### 2. MATERIAL AND METHODS

In December 2020, the publications were researched in four bibliographic databases: 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 "facilitation mechanism" and "vegetation" or "plant" were used, and in the second section, the keywords "facilitation", "restoration" or "restored" and "vegetation" or "plant" were used.

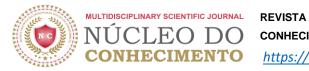
For each topic, a screening of the articles was performed, in which repeated articles were excluded and articles directed to the themes were excluded, from the reading of these, considering the criteria: research involving evaluations of facilitating species and facilitated species, both in Brazil and in the world; studies of facilitating species inserted in ecological restoration projects; and the use of these species in empirical projects.

### 3. RESULTS

Of a total of 1,811 publications, 64 publications were selected for analysis. After screening and exclusion of repeated articles, it is evident the low number of articles that encompass the proposals of this study. 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.

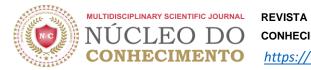
## 4. STUDIES ON FACILITATION MECHANISMS - ADVANCES IN THE LAST DECADE

Review articles that have evaluated studies on the facilitation mechanism in recent years confirm that positive interactions, such as plant facilitation, can benefit



community biodiversity by mitigating abiotic stresses, forming micro-habitats and generating heterogeneity in the environment, especially in places under extreme environmental conditions (PUGNAIRE; WEAPONS; 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 allow to assist in the understanding of biodiversity and in the functioning of the ecosystem, leading to an understanding of how diversity affects functions in a given environment (WRIGHT *et al.*, 2017).

In recent years, publications addressing the theme of facilitation between plant species have been divided into bibliographic reviews and field evaluations. The bibliographic reviews focus on the evaluation of a particular species or a set of these, allowing the global understanding of the dynamics of a given area and/or community, as seen in the article by Pugnaire, Armas and Maestre (2011). The authors gathered 15 years of studies conducted in desert areas of southeastern Spain, explaining the theme of positive interactions and their relationship with the community. Field evaluations are performed 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, floristic surveys aim to verify the occurrence of possible facilitation mechanisms, how they work and what are the implications of these species and 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; TIELBORGER, 2011; QUON; BOBICH; QUESTAD, 2019) and/or seedlings, with the inclusion of facilitating and/or facilitated species, with the purpose of evaluating the facilitation mechanisms in isolated forms (AVENDAÑO-YÁÑEZ et al., 2014; VAN ZONNEVELD; GUTIÉRREZ; HOLMGREN,

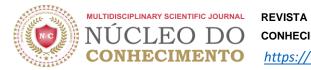


2012; BADANO et al., 2016). It should be considered that, when the studies mentioned above are quantified, the predominance of observational studies is highlighted. This preference makes it difficult to identify facilitation processes and facilitating species, because field activities are considered more effective methodologies to identify facilitation mechanisms, due to the ability to evaluate and test (BROWN; OLIVE TREE; 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 community dynamics occur (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 phylogenetics (VALIENTE-BANUET; VERDÚ, 2013; VEGA-ÁLVAREZ; GARCÍA-RODRÍGUEZ; CAYUELA, 2018; DUARTE et al., 2021). Losapio et al. (2021) mention that facilitating plants increase the phylogenetic and functional diversity of floral visitors, indicating that the facilitation mechanisms between plants can support the functioning of the ecosystem, both directly (improvement of micro-habitat) and indirectly (effects of diversity). For the phylogenetic diversity of plants, Valiente-Banuet and Verdú (2013) mention that the maintenance of phylogenetic diversity can occur when species, in a given environment, present lineages with different evolutionary histories. Due to the optimal environment, there is a reduction in the competition process and an increase in facilitation. Data also cited by Duarte et al. (2021), in an experiment that sought to test SGH, they describe a positive relationship between facilitation and elevation, mainly for interactions involving 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 most pronounced. Several authors use the SGH proposed by Bertness and Callaway (1994) as a basis for evaluating facilitation mechanisms (KIKVIDZE et al., 2011; BEDUSCHI;

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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). With regard to environments with severe climatic conditions, different authors conclude that the mechanisms of facilitation and competition 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 an individual facilitator in these environments has an important effect on maintaining community diversity, in which facilitating species can alter climate filters, allowing the establishment and recruitment of species, increasing diversity and contributing to the distribution of these gradients 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 can occur due to the decreasing effect of species facilitation, while the change from facilitation to competition can 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 in interactions between plant species.

With the increasing number of studies considering plant-plant interactions, researchers began to correlate these processes with climate change. According to O'Brien *et al.* (2019), in some cases, the facilitating species allowed greater survival of individuals in the face of rising temperatures, because they offer shelter and more favorable conditions for the development of other individuals. Thus, the authors conclude that the use of species that minimize the effects of climate change, such as global warming, could create refuges for many individuals who, without assistance, will not be able to resist climate change.



# 5. FACILITATION AS A STRATEGY FOR ECOLOGICAL RESTORATION

With the increasing change of natural environments around the world, mainly motivated by anthropization, the creation and development of techniques for the recovery of degraded areas have become essential (BURKE *et al.*, 2011). Ecological restoration, whose focus is to form 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, c2023), 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, c2023), 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 the reduction of physiological stress of plant individuals, by easing extreme environmental conditions (BANNISTER *et al.*, 2020), make the soil more nutritious (NAVARRO-CANO *et al.*, 2015; ABIYU *et al.*, 2017), inhibit the growth of the coverage of exotic species (MARTINEZ; DORNBUSH, 2013; GALINDO *et al.*, 2017) and increase local fauna (LOSAPIO *et al.*, 2021). These modifications make the medium more favorable, allowing the formation of the composition of the soil seed bank (ERFANZADEH; PALAYE; GHELICHNIA, 2020; FORONDA *et al.*, 2020), seed 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 the reduction of costs in the 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 most often used in restoration projects in environments with extreme conditions, with lower regeneration capacity, mainly due to abiotic factors (MENDOZA-HERNÁNDEZ *et al.*, 2013; BROWN; OLIVE TREE; PRADO, 2015, SER, c2023). However, the inclusion of biotic interactions in restoration projects in mild environmental conditions, such as atlantic forest areas and riparian forest, should be considered. When forest areas suffer 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 simply fail, indicating that this tool may be limited by climate (MICHALET *et al.*, 2014; GONZALEZ; GHERMANDI, 2019).

The assessment of functional identity (NAVARRO-CANO *et al.*, 2019), taxonomic and phylogenetic, of facilitating and facilitated species is important to potentiate the use of this technique, and has been shown to be relevant in the results of interactions in restoration experiments (VERDÚ; A; HERNÁNDEZ-CUBA, 2011; NAVARRO-CANO *et al.*, 2016). It is noticed that the greater the phylogenetic distance between the species, the more they tend to present different phenotypes, therefore, different ecological requirements, reducing competition and maximizing the facilitation effect (VERDÚ; A; 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 the establishment of the seedlings (NAVARRO-CANO *et al.*, 2019). However, it should be considered that facilitating species do not necessarily pave the way to benefit all species 159



(LORTIE, 2017), and soil preparation, species choice and seedling selection for the efficient recovery of the environment are also relevant (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 field experiments, proving the efficiency of the use of 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 example of articles, including their authors, titles and the main results

Authors	Article title	Summary
Bannister <i>et</i> <i>al.</i> (2020)	Shrub influences on seedling performance when restoring the slow- growing conifer Pilgerodendron uvi ferum in southern bog forests.	In an experiment to evaluate the recovery of <i>Pilgerodendron uvfero</i> (D. Don) <i>Florin.</i> 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 p individuals. (measured as Fv/Fm), as well as greater height increment and greater vitality.
Foronda <i>et</i> <i>al.</i> (2020)	Substrate-specialist plants for restoring vegetation in post-mining gypsum substrates.	The authors evaluated the facilitating role of <i>Gypsophila strutthium Loefl.</i> germination and development of species in a deposit of rubble 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, growing individuals, improving soil and forming micro-habitats under its canopy.
Fedriani <i>et</i> <i>al.</i> (2020)	Combined effect of seed provenance, plant facilitation and restoration site on revegetation success.	This study evaluated the potential facilitator of three species of shrubby for <i>Pyrus bourgaeana</i> <i>Decne</i> , in an area in the process of environmental restoration in Spain. As a result, it was observed that although the shrubs have a positive effect on <i>P. bourgaeana</i> , the magnitude of the interactions changes both with the sowing site and with the provenance of the seeds.
Gonzalez and Ghermandi (2019)	Dwarf shrub facilitates seedling recruitment and plant diversity in semiarid grasslands.	The richness, emergence of seedlings and survival of <i>Festuca pallescens</i> (StYves) <i>Parodi</i> were evaluated with and without the presence of <i>Acaena</i> <i>splendens</i> , in an area of northwestern 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 dry



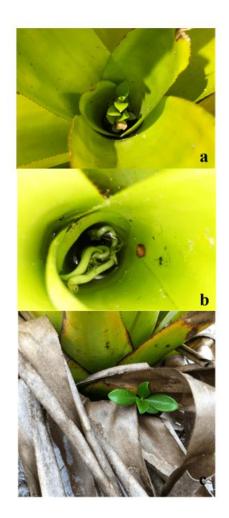
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		conditions, indicating to be a climate-limited restoration tool.
Martelletti <i>et</i> <i>al.</i> (2018)	Microsite manipulation in lowland oak forest restoration results in indirect effects on a corn predation.	The study that investigated <i>Cytisus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

#### Source: Author.

Figure 1 - Development of Clusia hilariana Schltdl. inside the bromeliad-tank Aechmea blanchetiana (Baker) LB Sm.: (A-B) seed germination within bromeliad tank; (C) growth and development within the bromeliad tank



Source: Author.



### 6. FINAL CONSIDERATIONS

This review highlights the importance of knowledge about the environment and climate 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 the dynamics of communities, both ecologically and phylogeneticly, and the understanding of the efficiency of the use of facilitating species in restoration projects of degraded areas. It is noteworthy that most of the studies cited are considered observational, and a small number of these were developed with planting methodologies. These data, together with the existence of a gray literature (*e.g.*, theses, dissertations, technical reports, unpublished data), generate gaps in the knowledge of the processes evaluated here.

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<sup>&</sup>lt;sup>1</sup> Master in Tropical Biodiversity. ORCID: 0000-0002-4868-6369. LATTES CURRICULUM: http://lattes.cnpg.br/7186707603292907.

 <sup>&</sup>lt;sup>2</sup> Co-advisor. PhD in Ecology (UFRJ). Post-doctorate from the Universidade Federal do Rio de Janeiro and the Estacion Experimental de Zonas Áridas - Spain (CAPES Scholarship). ORCID: 0000-0003-1854-2441. LATTES CURRICULUM: http://lattes.cnpq.br/4502113593775550.
<sup>3</sup> Advisor. PhD in Ecology, PhD, University of Stirling, Scotland in 1994 and Post-doctorate at the Royal Botanic Garden Edinburgh in 2013. ORCID: 0000-0003-4492-3344. LATTES CURRICULUM: http://lattes.cnpq.br/3704305950005564.