

ORIGINAL ARTICLE

Facilitation by *Aechmea blanchetiana* (Baker) L.B.SM. (Bromeliaceae) in the establishment and development of plants in a coastal dune ecosystem

Facilitação por *Aechmea blanchetiana* (Baker) L.B.SM. (Bromeliaceae) no estabelecimento e desenvolvimento de plantas em ecossistema de restinga

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ABSTRACT

Terrestrial bromeliads are reported as facilitating the establishment of plants in coastal dunes (restinga). Still, their action on establishment and/or development of other plants is not well understood. We evaluated the effect of *Aechmea blanchetiana* (Baker) (Bromeliaceae) on the germination and development of shrub/tree species occurring in a restinga area. Seeds of *Clusia hilariana*, *Eugenia astringens*, *Guapira pernambucensis*, *Myrcia ilheosensis*, *Myrcia neuwiediana*, and *Protium heptaphyllum* were tested in a randomized experiment: T1 - germination in the axils of the bromeliad leaves; T2 - germination under bromeliad; and TC - control treatment: germination under the soil, without bromeliad. Soil fertility below and far from the bromeliad was evaluated to understand the chemical modifications in the soil promoted by *A. blanchetiana*. The presence of bromeliads favored the percentage and index germination speed, average germination time, and survival of germinated species. The biometry and biomass of the seedlings of the germinated species were positively influenced by the presence of the bromeliad, in addition to *A. blanchetiana* enriching the soil with organic matter and nutrients. Our results allowed us to classify *A. blanchetiana* as a facilitating plant in structuring restinga vegetation formations and suggest its use in environmental restoration projects of degraded restinga areas.

Keywords: Coastal dunes; Extreme environments; Facilitation mechanism; Positive interactions; Restinga restoration.

RESUMO

Bromélias terrestres são relatadas como plantas facilitadoras em dunas costeiras (restinga). Ainda assim, sua ação no estabelecimento e/ou desenvolvimento em outras plantas não é bem compreendida. Avaliamos o efeito de *Aechmea blanchetiana* (Baker) (Bromeliaceae) na germinação e desenvolvimento de espécies arbustivas/árvores ocorrentes em uma área de restinga. Sementes de *Clusia hilariana*, *Eugenia astringens*, *Guapira pernambucensis*, *Myrcia ilheosensis*, *Myrcia neuwiediana* e *Protium heptaphyllum* foram testadas em um experimento randomizado: T1 – germinação nas axilas das folhas da bromélia; T2 – germinação sob bromélia; e TC – tratamento controle: germinação sob o solo, sem bromélia. A fertilidade do solo abaixo e longe da bromélia foi avaliada para entender as modificações químicas no solo promovidas por *A. blanchetiana*. A presença de bromélias favoreceu a porcentagem e o índice de velocidade de germinação, o tempo médio de germinação e a sobrevivência das espécies germinadas. A biometria e a biomassa das plântulas das espécies germinadas foram influenciadas positivamente pela presença da bromélia, além de *A. blanchetiana* enriquecer o solo com matéria orgânica e nutrientes. Nossos resultados permitiram classificar *A. blanchetiana* como uma planta facilitadora na estruturação de formações vegetais de restinga e sugerir sua utilização em projetos de restauração ambiental de áreas degradadas de restinga.

Palavras-chave: Dunas costeiras; Ambientes extremos; Mecanismo de facilitação; Interações positivas; Restauração de restinga.



1. INTRODUCTION

Positive plant-plant interactions (here referred to as facilitation), where some plants protect others from abiotic stressors, are widely recognized (He et al., 2013), especially in harsh environments, and constitute the main driver of plant community dynamics and structuring (Reis et al., 2014). Their effects have been widely described for desert and grassland ecosystems, forests, wetlands, and more recently, alpine and restinga systems (Menezes et al., 2017; O'Brien et al., 2019; Saraiva et al., 2023; Silva et al., 2024).

The structure of plant populations in harsh environments is closely linked to recruitment, seed germination, and seedling establishment, which are high-risk periods in the plant life cycle and must occur at the right time and under appropriate conditions (Saraiva et al., 2023; Silva et al., 2024). In restingas, for example, the establishment of some species may depend on a complex double propagule dispersal system (Menezes et al., 2017) or even on facilitation by keystone species (Scarano et al., 2001). Restingas are low-resilience ecosystems with severe abiotic conditions that negatively impact the establishment and development of plants (Ribeiro et al., 2023), such as sandy soils of marine origin with low water and nutrient retention capacity, high temperatures and salinity of the soil and air, intense light and intense wind action (Shumway, 2000; Scarano et al., 2001). On the other hand, these factors favor competition for resources and intensification of facilitation among plant individuals (Brancaion et al., 2009), where some of them play a crucial role in the establishment and development of other plants, by offering protection against winds, reducing water evaporation, decreasing competition for resources and reducing predation (Correia et al., 2010; Menezes et al., 2017; Zani et al., 2023).

Several studies in restingas have shown that the performance of plants established in the vicinity of other plants is greater than in open areas (Shumway, 2000; Martínez, 2003; Forey et al., 2009; Castanho & Prado, 2014; Souza et al., 2016). However, the occurrence and intensity of facilitation in restingas are also high variables within and between studies (Forey et al., 2009; Castanho et al., 2012), suggesting that facilitation depends on local environmental conditions or gradients (He et al., 2013) and also on the characteristics of the interacting plants (Soliveres et al., 2014).

Some specific plant characteristics can enhance the facilitation process. For example, species with large canopies and dense crowns are reported as facilitators (Castanho et al., 2012), because they reduce incident radiation and soil temperature and promote increased nutrient availability (Saraiva et al., 2023; Schneider et al., 2023). In addition, species with fleshy fruits attract seed dispersers and act as perches, increasing seed rain under their canopies (Schneider et al., 2023). Thus, shrubs with these characteristics can improve local conditions and receive propagules through the attraction of animal dispersers, increasing seedling recruitment under their canopy (Castanho et al., 2012; Ribeiro et al., 2023; Schneider et al., 2023).

The bromeliads are a group of plants with peculiar characteristics that play a fundamental role in structuring plant formations in restingas (Freitas et al., 2000). In addition, some species of bromeliads play a facilitating role, helping to retain sediments and increase the availability of nutrients in the soil, from the organic matter accumulated below their rosettes (Hay & Lacerda, 1980; Pereira et al., 2005; Tsuda & Castelani, 2015). Another possible facilitation pathway is through the germination of seeds of shrub and tree species within their rosettes (Fialho, 1990; Fialho & Furtado, 1993; Scarano, 2002), favoring the establishment of these plants in restingas (Souza et al., 2016), but this process has been little studied, being based on empirical observations.

Understanding the ecological processes that lead to the structuring of plant communities in restingas has direct applicability, especially

in environmental restoration programs for these ecosystems, which are classically understood as having low resilience and are difficult to restore (Souza et al., 2016; Pinheiro et al., 2023). In degraded areas, facilitator plants are recommended to guide the succession process of species (Ren et al., 2008), in addition to improving soil quality, making it more fertile and capable of supporting a greater diversity of plant species (Mendes et al., 2022; Ribeiro et al., 2023) and improving seedling survival and growth rates (Padilla & Pugnaire, 2006).

This study evaluated the influence of the bromeliad *Aechmea blanchetiana* (Baker) L.B.Sm., common in the restingas of northern Espírito Santo, on the germination and establishment of shrub/tree species present in a restinga area of the Environmental Protection Area (APA) of Conceição da Barra - Conceição da Barra - ES, to understand the process of structuring restinga plant communities and guiding mechanisms for restoring degraded restinga areas through the use of facilitating plants.

2. MATERIAL AND METHODS

2.1 Study area

This study was developed, partly in the APA of Conceição da Barra (18°39'59.36"S; 39°47'23.67" W) and partly in the experimental area of the Federal University of Espírito Santo (UFES) – São Mateus campus (18°40'34.91"S; 39°51'36.66" W), 6 km apart. The climatic characteristics are the same for both areas.

The region's climate is type "Af" (rainy tropical, without a dry season in winter), according to the Köppen classification (Alvares et al., 2014). The average temperature of the hottest month (February) is 26.8 °C and the coldest month (July) is 21.9 °C, with an annual average of 24.4 °C. The average annual rainfall is 1,175.1 mm, with the highest volume of rainfall from October to April (847.9 mm) and lower volumes between May and September (327.1 mm) (INCAPER, 2020).

2.2 Plant material

A. blanchetiana was selected because it is considered a facilitating plant (Ribeiro et al., 2023) and because seeds and seedlings of other species are often seen in the axils of its leaves. Its distribution is restricted to the restingas of Bahia and Espírito Santo, forming clumps, in areas exposed to the sun and in places with partial shade. Its individuals can reach 1.20 m in height and 1.5 m in diameter and its occurrence is widespread in the Conceição da Barra APA (Herbarium voucher 12569) (Monteiro et al., 2014).

The collection of fruits of the species used in the experiment was carried out in August 2021, in the Conceição da Barra APA area. The species were chosen based on the availability of fruits at the time of collection. Seeds of six species were used: *Clusia hilariana* Schltdl. (Clusiaceae), *Eugenia astringens* Cambess. (Myrtaceae), *Guapira pernambuncensis* (Casar.) Lundell (Nyctaginaceae), *Myrcia ilheosensis* Kiaersk., *Myrcia neuwiediana* (O. Berg) E. Lucas & C.E. Wilson (Myrtaceae) and *Protium heptaphyllum* (Aubl.) Marchand (Burseraceae) (vouchers no SAMES Herbarium: 11814, 11815, 11816, 11817, 11819, 11820, respectively).

The fruits were collected while still on the mother plant, considering the color pattern that corresponded to ripening, similar to the placement of the fruits found on the ground. A maximum number of 5 fruits per individual was stipulated to ensure maximum genetic diversity in the seeds for the experiment and minimize possible genetic problems that could prevent germination.

The fruits and seeds underwent a manual processing process to remove undesirable materials, such as empty, immature, and broken seeds, pieces of fruit, and leaves (Silva et al., 1993). Seed germination was assessed over 30 days. Seeds that showed rupture of the teguments and emergence of the main root were considered germinated (Brasil, 2009). After germination assessment, plant survival up to five months of age was evaluated in T1 and T2. The germination percentage, mean germination time (MGT), and germination speed index (GSI) were evaluated. To assess seedling development, biometric measurements of shoot length and root length were performed using a digital caliper with an accuracy of ± 0.01 mm. In addition, analyses of biomass attributes of surviving seedlings were performed, where individuals were weighed on a digital precision scale with an accuracy of 0.01 g to obtain fresh weight. Then, the seedlings were placed in paper bags and placed in an oven with forced air circulation at a temperature of 70°C for 72 hours. After this period, the seedlings were reweighed, obtaining dry weight.

2.3 Experimental design and statistical analysis

The facilitation tests were carried out in the experimental area of the Federal University of Espírito Santo - São Mateus campus, with exposure to sunlight for most of the day and shade in the final two hours of the afternoon (4:00 p.m. and 5:00 p.m.). These conditions are similar to those found in the non-flooded open shrub formation of the restinga of the Conceição da Barra APA and where the *A. blanchetiana* populations occur.

In the experimental area of UFES - São Mateus, 60 individuals of *A. blanchetiana* with a height of 80 cm (± 10) and a diameter of 100 cm (± 10) were placed in 25 L plastic pots filled with sand from restinga. This sand was sieved to remove seeds, branches, and leaves. *A. blanchetiana* plants used in this study were donated by the Palmarum Botanical Garden of the Federal University of Espírito Santo - São Mateus campus. The experimental design was in randomized blocks, with one control and two treatments per block. Three blocks were established in an east-west direction, so the shading would affect all treatments equally. Each block consisted of 30 pots spaced 1 m apart. In each block, 10 pots were used for each treatment: (T1) germination in the axils of the bromeliad leaves, (T2) germination under bromeliad, and control treatment (TC) germination under the soil, without bromeliad. For each block, 150 seeds of each of the studied species were used, with five seeds of each species for each replicate. In the TC and T2 pots, aluminum dividers were used to separate the seeds by species, and plastic plates were used for identification.

The seeds were sown at a depth of 1.5 cm in the TC pots. In T1, the seeds were placed in cheesecloth bags, tied with nylon thread, and introduced into the axils of the bromeliad leaves. In T2, the seeds were sown in the soil, under the bromeliad, at a depth of 1.5 cm. Sowing was ordered clockwise so that all species had at least one replicate exposed for each of the cardinal points.

Temperature (°C), humidity (%), and luminosity (lux) measurements were taken using the HOBO data logger U12-001 equipment, at one-hour intervals, between 8:00 am and 5:00 pm, on the days August 18th and 19th, October 3rd, 4th, 5th and 10th, 2022, cloudless.

To understand the soil modifications caused by the presence of *A. blanchetiana*, 20 simple soil samples were collected from the non-flooded open shrub formation of the Conceição da Barra APA, at a depth of 20 cm, just below the bromeliad and in open areas 2 and 3 meters away from the plant. To avoid the influence of one bromeliad on another, a minimum distance of 50 m between them was arbitrarily stipulated for soil collection. These samples were

homogenized, resulting in a composite sample containing 200 g of soil for each collection point.

Analysis of variance (ANOVA) was performed to verify significant differences between the treatment means, considering the following variables: seed germination, biometry and biomass of seedlings, percentage of organic matter, chemical characterization of nutrients present in soil samples, and environmental variables. After verifying significant differences between treatments through ANOVA, the Tukey test ($p < 0.05$) was performed to identify which treatments differed statistically. The majority of statistical analyses were performed using the Sisvar program (Ferreira, 2011). On the other hand, multivariate analysis (PCA) was performed using the following packages: tidyverse version 1.3.1 (Wickham et al., 2019), FactoMineR version 2.3 (Le et al., 2008), factoextra version 1.0.7 (Kassambara & Mundt, 2020) using R software version 4.2.1 (R Core Team, 2022).

3. RESULTS

There was no seed germination in TC, and all species tested germinated in T1 and T2, with significant differences in germination percentage and GSI between treatments (Table 1). The species *C. hilariana*, *M. ilheosensis*, and *G. pernambucensis* were more successful in germinating within the axils of the bromeliad leaves and *P. heptaphyllum*, *M. neuwiedeana* and *E. astringens* below the bromeliad's plants. The highest germination percentage in T1 occurred in *C. hilariana* and in T2 in *P. heptaphyllum*. Only in *M. neuwiedeana* and *M. ilheosensis* the TMG did not show significant differences between T1 and T2.

Only *M. neuwiedeana* (58%), *C. hilariana* (50%), *M. ilheosensis* (22%) and *E. astringens* (16%) managed to survive in T1. On the other hand, all tested species survived in T2, with *E. astringens* being the most successful (90%), followed by *M. neuwiedeana* (58%), *P. heptaphyllum* (48%), *G. pernambucensis* (20%), *M. ilheosensis* (14%) and *C. hilariana* (4%).

Except for *M. ilheosensis*, the other species presented significant differences in the biometry and biomass estimators between treatments (Table 2). In T1, *C. hilariana*, *E. astringens*, and *M. neuwiedeana* presented greater root development, differing significantly from T2. On the other hand, *G. pernambucensis*, *M. ilheosensis*, and *P. heptaphyllum* had greater root development in T2, differing significantly from T1. Regarding shoot growth, only *M. neuwiedeana* had significantly higher values in T1. The other species had significantly greater shoot development in T2. Biomass accumulation was more expressive in T2.

No significant differences were observed in temperature, humidity, and luminosity between T1 and T2 (Table 3), but they differed when compared with TC, where the highest temperatures were recorded, with values ranging from 32°C to 35°C, together with the highest luminosities, ranging from 2,000.0 to 16,000.0 lux.

A decrease in humidity was observed as the temperature increased. On the other hand, under the canopy of *A. blanchetiana* and in the axils of its leaves, the lowest temperatures were recorded, ranging from 30°C to 31°C. In these areas, the highest humidity values were also observed.

To confirm and visualize the relationships of the six species with the best twinning and development site (within or on) *A. blanchetiana*, a principal component analysis (PCA) was performed (Figure 1).

Based on the results, the two principal components explained the total variance in the dataset respectively in Figure 1A - *G. pernambucensis* 83.2%, Figure 1B - *M. neuwiedeana* 86.8%, Figure 1C - *P. heptaphyllum* 90.9%, Figure 1D - *C. hilariana* 84.3%, Figure 1E - *M. ilheosensis* 89.5%, Figure 1F - *E. astringens* 87.6%. The overlapping areas between ellipses distinguish the performances and highlight the particularities of the

Table 1. Germination speed index (GSI), mean germination time (MGT), and germination percentage (%) of seedlings of six native species of the restinga submitted to germination in the axils of the bromeliad leaves (T1), germination under bromeliad (2) and germination under the soil, without bromeliad (TC).

Species	Treatment	GSI	MGT	Germination (%)
<i>C. hilariana</i>	TC	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T1	0.23 ± 0.10 a	15.54 ± 4.23 a	3.83 ± 1.09 a
	T2	0.01 ± 0.02 b	2.67 ± 8.14 b	0.30 ± 0.79 b
<i>E. astringens</i>	TC	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T1	0.02 ± 0.05 b	3.52 ± 9.19 b	0.57 ± 1.55 b
	T2	0.23 ± 0.07 a	21.69 ± 3.96 a	4.33 ± 0.92 a
<i>G. pernambucensis</i>	TC	0 ± 0 b	0 ± 0 c	0 ± 0 b
	T1	0.24 ± 0.09 a	18.45 ± 4.17 a	3.53 ± 1.36 a
	T2	0.01 ± 0.03 b	5.73 ± 11.17 b	0.13 ± 0.43 b
<i>M. ilheosensis</i>	TC	0 ± 0 c	0 ± 0 b	0 ± 0 c
	T1	0.36 ± 0.19 a	13.53 ± 6.97 a	4.63 ± 2.37 a
	T2	0.03 ± 0.05 b	9.86 ± 13.35 a	0.80 ± 1.30 b
<i>M. neuweideana</i>	TC	0 ± 0 c	0 ± 0 b	0 ± 0 c
	T1	2.44 ± 1.24 a	2.09 ± 1.08 a	4.90 ± 2.48 a
	T2	1.97 ± 0.59 b	2.42 ± 1.05 a	4.13 ± 1.01 b
<i>P. heptaphyllum</i>	TC	0 ± 0 c	0 ± 0 c	0 ± 0 c
	T1	0.37 ± 0.52 b	1.18 ± 1.68 b	0.87 ± 1.12 b
	T2	1.21 ± 0.52 a	2.71 ± 1.66 a	2.73 ± 1.23 a

Means followed by the same letter in the column, within each species, do not differ, according to the Tukey test ($p < 0.05$).

Table 2. Biometric estimators: root length and aerial part and biomass: fresh weight and dry weight of seedlings of six native species of the restinga submitted to germination in the axils of the bromeliad leaves (T1), germination under bromeliad (2) and germination under the soil, without bromeliad (TC).

Species	Treatment	Root length (cm)	Shoot length (cm)	Fresh weight (g)	Dry weight (g)
<i>C. hilariana</i>	TC	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T1	7.65 ± 13.79 a	9.89 ± 12.47 a	0.04 ± 0.06 a	0.01 ± 0.01 a
	T2	0.51 ± 3.40 b	0.92 ± 5.89 b	0.01 ± 0.02 b	0 ± 0 b
<i>E. astringens</i>	TC	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T1	3.26 ± 6.97 b	4.26 ± 9.68 b	0.01 ± 0.02 b	0 ± 0.01 b
	T2	64.39 ± 43.37 a	50.28 ± 33.50 a	0.11 ± 0.14 a	0.07 ± 0.09 a
<i>G. pernambucensis</i>	TC	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T1	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T2	9.05 ± 26.43 a	9.67 ± 25.63 a	0.03 ± 0.13 a	0.02 ± 0.06 a
<i>M. ilheosensis</i>	TC	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T1	7.64 ± 16.83 a	5.68 ± 12.30 a	0.01 ± 0.02 ab	0 ± 0.01 ab
	T2	10.82 ± 34.54 a	8.87 ± 27.83 a	0.02 ± 0.06 a	0.01 ± 0.05 a
<i>M. neuweideana</i>	TC	0 ± 0 b	0 ± 0 c	0 ± 0 c	0 ± 0 c
	T1	10.60 ± 12.53 b	16.82 ± 17.55 b	0.05 ± 0.06 b	0.01 ± 0.02 b
	T2	57.54 ± 97.66 a	37.32 ± 39.02 a	0.08 ± 0.09 a	0.06 ± 0.07 a
<i>P. heptaphyllum</i>	TC	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T1	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
	T2	38.56 ± 49.95 a	51.41 ± 59.66 a	0.09 ± 0.13 a	0.09 ± 0.09 a

Means followed by the same letter in the column, within each species, do not differ, according to the Tukey test ($p < 0.05$).

Table 3. Microclimatic variables temperature (°C), humidity (%), and luminosity (lux) of TC (control treatment – open area, without the presence of bromeliads), T1 (axils of the bromeliad leaves) and T2 (under the bromeliad).

Treatment	Temperature	Humidity	Luminosity
TC	33.57 ± 19.34 b	55.39 ± 13.93 b	42884.74 ± 708.41 b
T1	30.32 ± 5.68 a	59.29 ± 11.91 a	17292.23 ± 647.06 a
T2	29.87 ± 4.70 a	61.79 ± 10.02 a	15644.50 ± 333.52 a

Means followed by the same letter in the column, within each species, do not differ, according to the Tukey test ($p < 0.05$).

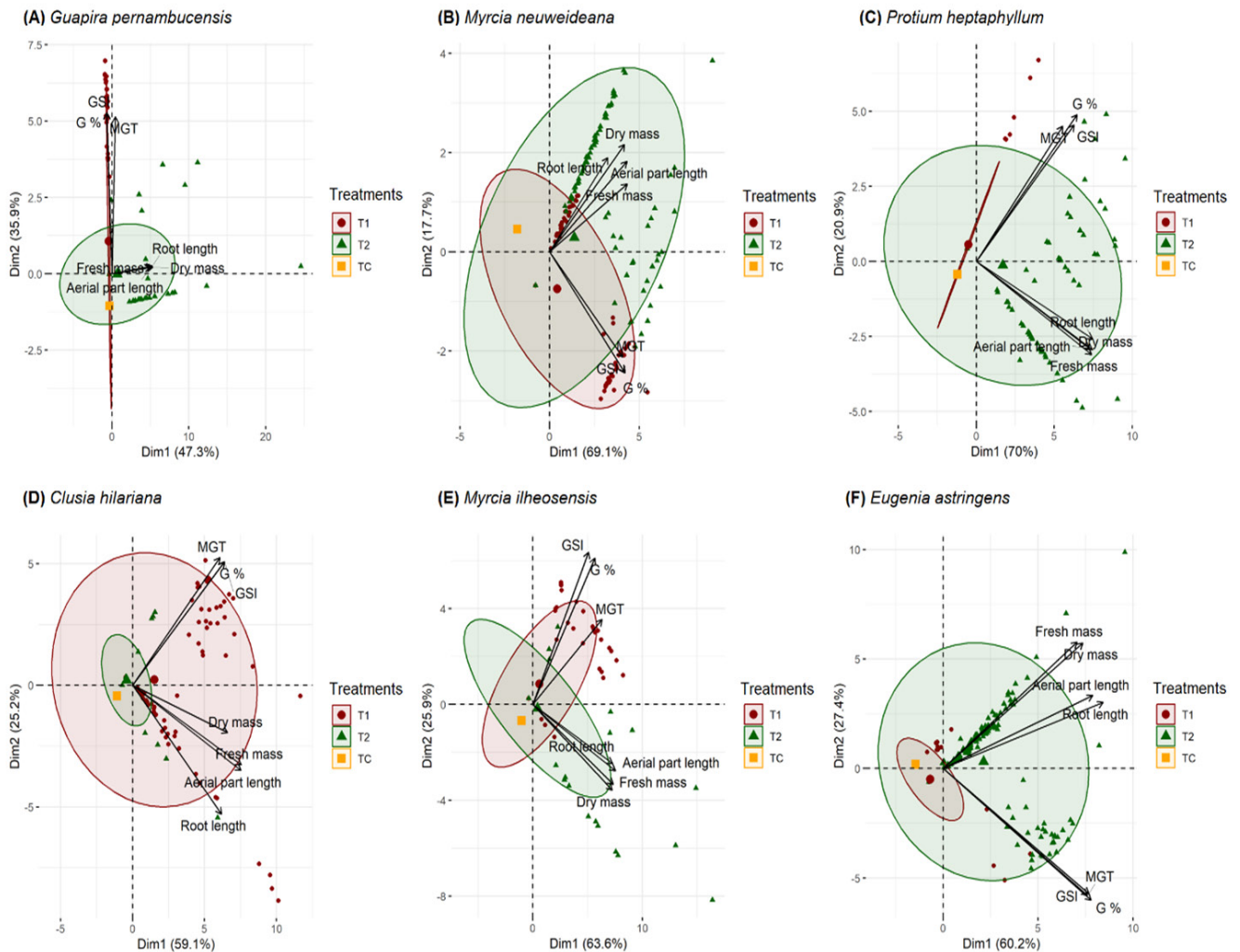


Figure 1. Principal component analysis of morphophysiological traits related to germination in the axils of the bromeliad leaves (T1), germination under bromeliad (T2), and germination under the soil, without bromeliad (TC).

effects of the germinated seeds in T1 (germination in the axils of the bromeliad leaves) and T2 (germination under bromeliad). Four behaviors can be visualized: plants that germinate and develop better in T1 (*C. hilariana*), plants that germinate and develop better in T2 (*E. astringens* and *P. heptaphyllum*), plants that do this in both T1 and T2 (*M. neuweideana* and *M. ilheosensis*) and plants that do not develop well in any treatment (*G. pernambucensis*).

The analyses of soil samples obtained in the field revealed higher percentages of organic matter in those below the *A. blanchetiana*, compared to the samples collected in the open areas, 2 and 3 m away from the bromeliad. The chemical characterization of the soil showed significant differences between these samples (Table 4). Significantly higher concentrations of phosphorus (P), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), and boron (B) were observed in the soil below the bromeliads. The values of the sum of the bases, aluminum (Al) saturation and cation exchange capacity (CEC) were also significantly higher under the bromeliad.

4. DISCUSSION

The positive and significant effect of the germination percentage, the Germination Speed Index, and the Average Germination Time of the

seeds of the tested species, in the leaf axils and below the rosette of *A. blanchetiana*, indicate that the bromeliad provides the necessary abiotic requirements for seed germination, such as the ideal temperature and humidity range. Studies by Larcher (2003) and Brancalion et al. (2010) indicated that the temperature range between 20 and 30°C is ideal for the germination of subtropical and tropical species. This temperature range includes that recorded in T1 and T2, where the seeds of all species germinated. The temperature has a great influence on both the percentage and the speed of germination, altering the speed of water absorption and modifying the speed of chemical reactions that will mobilize or degrade stored reserves and the synthesis of various substances for seedling growth (Ribeiro et al., 2023; Zani et al., 2023).

In contrast to the microclimatic conditions present in T1 and T2, the absence of bromeliads in TC drastically modified the air temperature, humidity, and light conditions, nullifying the basic requirements for seed germination. In open restinga areas. Seeds that remain on the soil surface are quickly damaged by desiccation and high temperatures, often reaching 70°C at the soil surface (Mantovani & Iglesias, 2001; Scarano, 2002; Menezes et al., 2017; Pinheiro et al., 2023), indicating that the colonization of these areas involves complex ecological processes, for example, mutualism in seed dispersal, where seeds are buried at depths where soil temperature and humidity meet the adequate requirements for germination (Menezes et al., 2017).

Table 4. Soil variables (mean \pm standard deviation) under the of *Aechmea blanchetiana* (Baker), 2 and 3 m away from the plant, respectively, in the APA of Conceição da Barra (ES).

Chemical properties	Unit	Under bromeliad	2 meters away from the bromeliad	Areas devoid of bromeliads
Phosphorus (P)	mg/dm ³	3.20 \pm 1.64 a	1.20 \pm 0.45 a	1.00 \pm <0.05 a
Potassium (K)	mg/dm ³	33.60 \pm 10.29 a	12.00 \pm 3.00 b	6.00 \pm <0.05 b
Calcium (Ca)	cmol _c /dm ³	0.76 \pm 0.46 a	0.40 \pm 0.84 ab	0.20 \pm <0.05 b
Magnesium (Mg)	cmol _c /dm ³	1.00 \pm 0.19 a	0.24 \pm 0.11 b	0.20 \pm <0.05 b
Sodium (Na)	mg/dm ³	36.40 \pm 13.63 a	11.80 \pm 4.66 b	6.00 \pm <0.05 b
Aluminum (Al)	cmol _c /dm ³	1.64 \pm 0.36 a	1.20 \pm 0.40 ab	0.80 \pm <0.05 b
Sulfur (S)	mg/dm ³	8.20 \pm 4.60 a	2.80 \pm 0.84 b	4.00 \pm <0.05 ab
pH	cmol _c /dm ³	4.24 \pm 0.15 a	4.40 \pm 0.23 a	4.70 \pm <0.05 a
Manganese (Mn)	mg/dm ³	2.60 \pm 0.89 a	1.60 \pm 0.55 ab	1.00 \pm <0.05 b
Boron (B)	mg/dm ³	0.36 \pm 0.12 a	0.16 \pm 0.06 b	0.10 \pm <0.05 b
Sums of Bases (SB)	cmol _c /dm ³	2.04 \pm 0.56 a	0.74 \pm 0.34 b	0.40 \pm <0.05 b
Cation exchange capacity (CEC)	cmol _c /dm ³	3.68 \pm 0.76 a	1.94 \pm 0.74 b	1.20 \pm <0.05 b
Organic matter (OM)	dag/dm ³	8.16 \pm 3.64 a	2.72 \pm 1.65 b	2.60 \pm <0.05 b
Aluminum Saturation (m)	%	45.36 \pm 6.67 b	63.20 \pm 3.55 a	64.40 \pm <0.05 a

Means followed by the same letter in the column, within each species, do not differ, according to the Tukey test ($p < 0.05$).

Depending on the species, the most favorable conditions for germination may be between the axils of the bromeliad or below its rosette. This is directly related to the water requirement that each species needs for germination. Those which require greater humidity will be more successful in the axils of the bromeliad leaves, where the accumulation of water is greater. However, the presence of water for a long period can result in the death of the seedling, due to the lack of oxygenation in the roots, as observed with *P. heptaphyllum* and *G. pernambucensis*, which had seeds germinated in the axils of the bromeliad leaves but the seedlings did not survive. Furthermore, it is possible that the reduction in light caused by the presence of *A. blanchetiana* in T1 and T2 contributed to the seedling survival rate. Ecophysiological studies have shown that the reduction in light helps plant growth, making it slower, and contributing to the adequate development of leaves, flowers, and fruits (Mendes et al., 2022; Pinheiro et al., 2023).

The PCA is a statistical tool widely used in ecophysiological studies (Díaz et al., 2016; Mendes et al., 2022; Martins et al., 2023; Martins et al., 2024). The improved nutritional conditions of the soil below the bromeliads are of fundamental importance in the complex process of plant colonization in the restinga, after the critical stage of seed germination, contributing to the development of seedlings (Carvalho & Nakagawa, 2012). This condition was also observed below *Neoregelia cruenta* in the Maricá restinga (RJ) (Hay & Lacerda, 1980), where soil organic matter was higher compared to open areas. Organic matter plays a crucial role in water retention and can lead to a greater nutrient storage capacity, while water reductions can compromise the soil's ability to meet the nutritional needs of plants (Ferreira et al., 2012; Paterson & Sim, 2013). Furthermore, the CEC values above 24 cmol_c/dm³ found in soils below the *A. blanchetiana*, added to the high values of the sum of bases and aluminum saturation, contribute greatly to the greater capacity for nutrient and moisture retention (Mendes et al., 2022). In the soil, cation exchange acts to stabilize pH, allowing the exchange of elements such as Ca, Mg, and K between the soil and plants. This helps maintain soil pH at a level suitable for plant nutrition, providing ideal conditions for the growth and development of plant species (Hay & Lacerda, 1980). Thus, soil CEC has a direct impact on the rate of nutrient loss by leaching, especially in restingas, where soils are sandy and have low cation retention capacity (Mendes et al., 2022).

In this study, the presence of high and significant concentrations of P, K, Mg, Mn, and B in the soil below the bromeliad, in addition to the high CEC and organic matter contents indicate that *A. blanchetiana* strongly influenced the chemical composition of the soil, rendering essential nutrients to be available to the plants. These nutrients, in higher concentrations, play a crucial role in several stages of the germination process, such as water absorption by the seeds, formation of the reserve organs and the tegument, as well as for the growth and development of the embryo and supply of energy and protein synthesis (Pereira et al., 2018). In an ecosystem where nutrients are rapidly leached, the presence of *A. blanchetiana* assumes a nutrient conservation role, making them available to other plants around it for a longer time. This strategy has already been observed in *Quesnelia quesneliana* (Brongn.) L.B.Sm. and *N. cruenta* in the Marambaia restinga (RJ), which showed higher concentrations of K, N, and P in the soil below their rosettes, originating from the decomposition of their leaves (Souza et al., 2016). Bromeliad leaves are leathery and rich in sclerenchyma, which makes their decomposition difficult, releasing nutrients gradually in restinga environments (Pereira et al., 2005; Souza et al., 2016).

These microclimatic and soil quality changes have already been reported for *Neoregelia cruenta* (R. Graham) L.B.Sm. (Bromeliaceae) (Hay & Lacerda, 1980; Souza et al., 2016) and *Allagoptera Arenaria* Gomes Kuntze (Arecaceae) (Carvalho et al., 2014), creating favorable conditions for the establishment of other species. Such evidence has suggested the recommendation of these species for restoration projects of degraded restinga areas, as they are considered to be facilitating plants that contribute to the secondary succession process, helping with the establishment of other species and structuring of communities (Ribeiro et al., 2023).

5. CONCLUSIONS

Our results confirmed that the *A. blanchetiana* bromeliad plays a facilitating role in the process of establishing plant development in restinga environments in northern Espírito Santo, through the microclimatic conditions within the axils of its leaves and below its rosette. In these locations, unlike open restinga areas, the requirements for seed germination and seedling development are present. This bromeliad mitigates adverse abiotic conditions, such as high air

and soil temperatures and high light intensity, while increasing the availability of soil resources, such as moisture, organic matter, and nutrients. The benefits provided by *A. blanchetiana* make it a viable option in projects to restore degraded restinga areas between southern Bahia and northern Espírito Santo, together with the shrub/tree species tested here. Thus, it is expected that this system will provide the essential impetus for ecological restoration and promote increased biodiversity in the areas under restoration.

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AUTHOR CONTRIBUTIONS

KJS: investigation, writing – original draft.
 MMM: formal analysis, writing – original draft, writing – review & editing.
 EMA: writing – review & editing, supervision.
 LFTM: conceptualization, supervision, funding acquisition, writing – original draft.