

Bromeliads increase herbivory in an ecological restoration area in Restinga, southeastern Brazil

APARICIO DA CRUZ[✉]; IZABELA FERREIRA RIBEIRO; MARCEL MERLO MENDES & LUIS F. TAVARES DE MENEZES

Federal University of Espírito Santo. Vitória, Espírito Santo, Brasil.

ABSTRACT

1. We examined the effects of herbivory in a coastal sandbank (Restinga) restoration area by studying how the environment influences insect-plant interactions.
2. Four plant species were evaluated under three conditions: control, fertilization, and proximity to the bromeliad *Aechmea blanchetiana* (Baker) L.B.Sm. Leaf analysis using ImageJ software was performed to measure herbivory.
3. Bromeliad presence increased the herbivory rate on surrounding plants.
4. Conversely, less favorable conditions — characterized by high light intensity, temperature and low humidity — resulted in lower foliar herbivory in the control and fertilization treatments.
5. These results support the resource availability hypothesis, which posits that plants in resource-rich environments are more susceptible to herbivory, as *A. blanchetiana* facilitates the establishment of shaded microenvironments with milder temperatures that favor herbivore presence.
6. Implications. In restoration initiatives for fallow areas, it is essential to include species that provide physical facilitation and mediate biological interactions like herbivory, which can influence plant establishment success. This study demonstrates the potential of restoration projects to recover ecosystem services and key ecological interactions, such as those between insects and plants.

[Keywords: bromeliad, environmental factors, folivory, herbivores, environmental restoration]

RESUMEN. Las bromelias aumentan la herbivoría en una zona de restauración ecológica en la Restinga, al sureste de Brasil

1. Examinamos los efectos de la herbivoría en un área de restauración de Restinga (dunas costeras) estudiando cómo el ambiente influye en las interacciones insecto-planta.
2. Se evaluaron cuatro especies de plantas bajo tres condiciones: control, fertilización y proximidad a la bromelia *Aechmea blanchetiana* (Baker) L.B.Sm. Se realizó un análisis foliar utilizando el software ImageJ para medir la herbivoría.
3. La presencia de la bromelia aumentó la tasa de herbivoría en las plantas circundantes.
4. Por el contrario, condiciones menos favorables — caracterizadas por alta intensidad lumínica, temperatura y baja humedad — resultaron en una menor herbivoría foliar en los tratamientos control y de fertilización.
5. Estos resultados respaldan la hipótesis de la disponibilidad de recursos, que postula que las plantas en ambientes ricos en recursos son más susceptibles a la herbivoría, ya que *A. blanchetiana* facilita el establecimiento de microambientes sombreados con temperaturas más suaves que favorecen la presencia de herbívoros.
6. Implicancias. En iniciativas de restauración de áreas en descanso, es esencial incluir especies que provean facilitación física y que medien interacciones biológicas como la herbivoría, lo cual puede influir en el éxito del establecimiento de las plantas. Este estudio demuestra el potencial de los proyectos de restauración para recuperar servicios ecosistémicos e interacciones ecológicas clave, como aquellas entre insectos y plantas.

[Palabras-clave: bromelias, factores ambientales, folivoría, herbívoros, restauración ambiental]

INTRODUCTION

Successful environmental restoration isn't limited to planting trees (Holl and Brancalion 2020; Mendes et al. 2025; Menezes et al. 2025b); it is crucial to recreate the biotic interactions that model habitats/ecosystems (Holl and Brancalion 2020; Menezes et al. 2025b). In this sense, analyzing trophic interactions —such as herbivory— and facilitation interactions (among plants) that affect the process of recolonization of the environment by plant species is critical (Del-claro and Torezan-Silingardi 2012; Endara et al. 2017; Silva et al. 2025). Herbivory, influenced by biotic and abiotic factors, can hinder regeneration by consuming young plants, while facilitation among species can mitigate the adverse environmental conditions and may help in the establishment of new individuals (Endara et al. 2017; Wittingham et al. 2023). Therefore, it is vital to investigate how these interactions occur in restoration areas to develop more effective approaches and predict future directions (Holl and Brancalion 2020; Wittingham et al. 2023; Mendes et al. 2025; Rodrigues et al. 2025; Silva et al. 2025).

Herbivory is one of the main interactions between plants and animals, characterized by the removal of living plant tissue and, in turn, is influenced by biotic (e.g., chemical and physical defenses of plants, as well as biotic interactions) (Del-claro and Torezan-Silingardi 2012; Endara et al. 2017) and abiotic factors (e.g., light, soil nutrients and temperature) (Zhang et al. 2020). Coley et al. (1985) analyzed plants that evolved in environments with different levels of available resources (e.g., water, soil nutrients and light intensity). The results showed that plants from environments with more abundant resources were more susceptible to herbivory, as they directed more energy to growth in detriment of defenses. These observations led to the formulation of the Resource Availability Hypothesis (RAH), which has been widely tested (Endara and Coley 2011).

The Resource Availability Hypothesis (RAH) suggests that plants evolved in resource-rich environments tend to be more vulnerable to herbivory, since they allocate more energy to growth than to defense. In contrast, plants from resource-poor environments presented opposite characteristics, prioritizing defense mechanisms over growth (Endara and Coley 2011). Although RAH was initially formulated to explain patterns of interspecific variation,

studies have identified variations in growth rate and defense mechanisms within the same species, in accordance with RAH principles. However, some studies show conflicting results to these predictions (Hahn et al. 2019; Lowry et al. 2019). Studies on intraspecific RAH have been carried out in several environments, such as Ombrophilous Forest and Restinga (Da Silva and Medeiros 2005), Salt Marsh (with nutrient-enhanced beds) (Wittingham et al. 2023), intermountain pastures (characterized by low productivity and low precipitation) and prairie remnants (characterized by higher productivity and precipitation) (Hahn et al. 2019). In all cases, leaf herbivory was always associated with greater resource availability.

Restinga form strips of sand and dunes on the Brazilian coast, which have their origin in the processes of deposition of marine sandy sediments during the Quaternary (Scarano 2002; Pereira and Menezes 2023; Menezes et al. 2025a, 2025b). This ecosystem is characterized by sandy soil with low fertility, high salinity, intense luminosity and high incidence of winds, which filter out the species capable of withstanding such environmental conditions (Melo Jr. and Boeger 2015; Pereira and Menezes 2023; Menezes et al. 2025b; Rodrigues et al. 2025; Silva et al. 2025). Due to the intense anthropization of Restinga, ecological restoration strategies have been created to conserve this ecosystem (Brancalion et al. 2015; Menezes et al. 2025b). One of the strategies adopted is facilitation, where elements such as logs, rocks and plants are used to mitigate adverse environmental conditions and promote the establishment of other plant species (Brancalion et al. 2015; Menezes et al. 2025b). Plants capable of modifying environmental conditions and favoring the recruitment of other species are called facilitators (Kleinhesselink et al. 2014; Yelenik et al. 2015).

Facilitation represents a beneficial relationship between plants, where one species (the facilitator) alters its surroundings to reduce abiotic or biotic pressures, creating regenerative spaces that favor the establishment and development of other species (Mendes et al. 2022, 2025; Souza et al. 2025). In Restinga, where factors such as high light, lack of water and infertile soils create significant environmental barriers, these positive relationships become essential for the evolution and recovery of local flora (Brancalion et al. 2015; Holl and Brancalion

2020; Souza et al. 2025). Therefore, by using species that aid in restoration projects, we are in effect harnessing and enhancing natural ecological processes, promoting the transition from a degraded environment to a more diverse and self-sustaining ecosystem (Mendes et al. 2022, 2025).

Research indicates that the bromeliads such as, *Aechmea blanchetiana* and *Neoregelia cruenta* (R.Graham) L.B.Sm (Bromeliaceae), play a fundamental role in the Restinga ecosystem, driving a significant increase in soil organic matter and nutrients under its cover, in contrast to surrounding areas without vegetation (Pereira et al. 2005; Souza et al. 2016; Souza et al. 2025). In addition, bromeliads interact with local fauna, contributing considerably to the increase in biological diversity of communities (Martinelli et al. 2008; Scarano 2009; Souza et al. 2025). Given the diversity of taxa that use bromeliads as habitat (Fravetto et al. 2011). Their ability to alter soil nutritional properties, it is crucial to analyze their impact on ecosystem functions in the environments in which they are present, leading to the hypothesis that they may have a significant impact on the foliar herbivory of plant species that surround them. Based on this knowledge, this work has the objective of evaluating the percentage of foliar herbivory of four plant species in an ecological restoration experiment, considering the Resource Availability Hypothesis and the role of bromeliads that live associated with these species.

MATERIAL AND METHODS

Study area

The study was carried out in an experimental area of environmental restoration, implemented in an oil exploration well base in the Restinga area in São Mateus, Espírito Santo, Brazil (UTM 24K: 416533.22 m E, 7925979.37 m S) (Figure 1). The climate of the municipality in the region is classified as Aw according to Köppen, characterized as humid tropical, with dry winters and maximum rainfall concentrated in the summer (INCAPER 2023). The average annual rainfall in the municipality totals 1279.9 mm. During the rainy season, which covers the months of October to April, the average rainfall is 976.8 mm and during the dry season between the months of May and September, there is a lower incidence of rainfall, with an average of 303.1 mm and the temperature in the region has an annual average of 24.1 °C according to INCAPER (2023).

Experimental design

The restoration experiment was carried out with the species *Aechmea blanchetiana* (Baker) L.B.Sm (Bromeliaceae), *Inga laurina* Willd (Fabaceae), *Psidium cattleianum* Sabine (Myrtaceae), *Schinus terebinthifolia* Engler (Anacardiaceae) and *Dalbergia ecastophyllum* (L.) Taub (Fabaceae). According to Mendes et al. (2022), all species in this experiment are perennial and native to the Atlantic Forest,

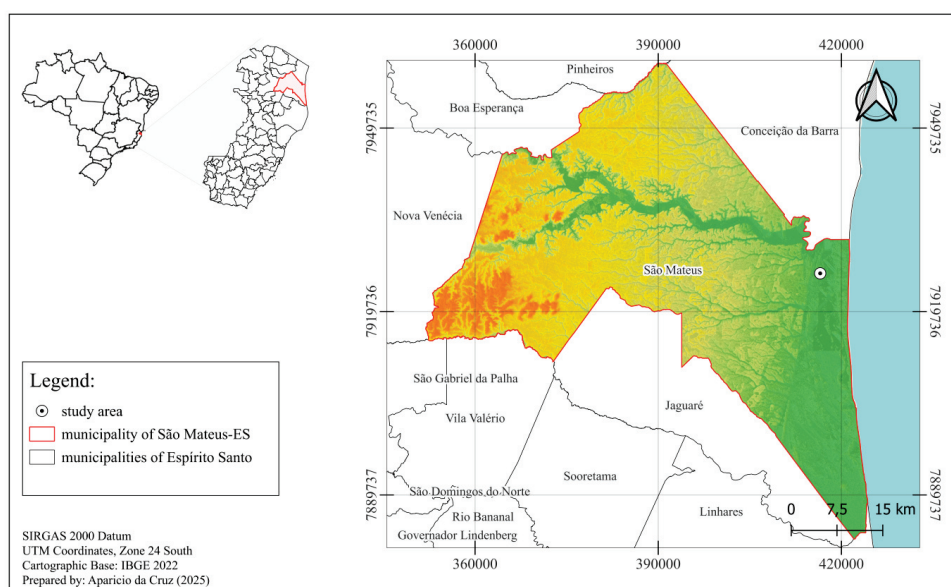


Figure 1. Study area. Municipality of São Mateus, ES, Brazil.

Figura 1. Área de estudo. Município de São Mateus, ES, Brasil.

also occurring in Restinga vegetation. In their restoration work, the authors divided the four species into two functional groups: nitrogen-fixing (*I. laurina* and *D. ecastophyllum*) and non-nitrogen-fixing (*P. cattleianum* and *S. terebinthifolia*). The individuals were arranged in nucleations (Figure 2) and distributed into three treatments: control, fertilizer and bromeliad (Figure 3). Each treatment consisted of five nucleations, where each nucleation

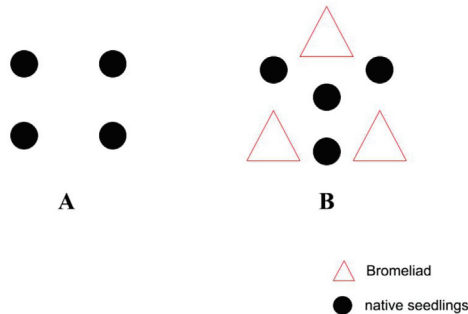


Figure 2. Distribution of plant species in the nucleations of treatments with and without the presence of the bromeliad *Aechmea blanchetiana* (Baker) L.B.Sm (Bromeliaceae). A) Nucleations without *A. blanchetiana*. B) Nucleations with *A. blanchetiana*.

Figura 2. Distribución de especies vegetales en las nucleaciones de los tratamientos con y sin presencia de la bromelia *Aechmea blanchetiana* (Baker) L.B.Sm (Bromeliaceae). A) Nucleaciones sin *A. blanchetiana*. B) Nucleaciones con *A. blanchetiana*.

contained four individuals of the same shrub species, totaling 20 individuals per native species per treatment (Figure 3).

In the control treatment, there was no intervention. In the fertilizer treatment, the individuals received chemical fertilizer (100 g of NPK 04-14-08 at the bottom of the hole) and organic fertilizer (2 liters of cattle manure at the bottom of the hole) at the time of planting. Finally, in the bromeliad treatment, the nucleations had three individuals of *A. blanchetiana*, with the aim of analyzing their facilitating potential in Restinga areas (Figures 2 and 3). Considering the aims in this experiment, the treatments follow a resource availability gradient (from highest to lowest): 1) bromeliad treatment; 2) fertilizer treatment, and 3) control treatment, which represents the natural conditions of low fertility and high stress typical of Restinga vegetation. This sequence allows us to evaluate RAH predictions regarding resource distribution and vulnerability to herbivory at the intraspecific level.

Data collection

To assess the percentage of leaf herbivory, 14 individuals (young plants ± 2 years old in vegetative phase) of each species were selected in each treatment. Leaf collections



Figure 3. Aerial view of the experimental area, containing the species *Inga laurina* Willd (Fabaceae), *Psidium cattleianum* Sabine (Myrtaceae), *Schinus terebinthifolia* Engler (Anacardiaceae) and *Dalbergia ecastophyllum* (L.) Taub (Fabaceae) in the control, fertilizer and bromeliad treatments. The treatments are arranged vertically and the species are arranged horizontally.

Figura 3. Vista aérea del área experimental, que contiene las especies *Inga laurina* Willd (Fabaceae), *Psidium cowtanium* Sabine (Myrtaceae), *Schinus terebinthifolia* Engler (Anacardiaceae) y *Dalbergia ecastophyllum* (L.) Taub (Fabaceae) en los tratamientos de control, fertilizante y bromelia. Los tratamientos están dispuestos de forma vertical, y las especies, horizontal.

were performed at two times, the first during the rainiest period of the year (February) and the second during the period with the lowest average rainfall (August). From the selected individuals, five leaves arranged in the third or fourth node were collected and analyzed, counting from the apex to the base. For species with compound leaves, such as *I. laurina* and *S. terebinthifolia*, the leaflets were treated as simple leaves, following the method described by Bongers and Popma (1990).

The collected leaves were digitized at high resolution (1698 × 2336 pixels) on graph paper. They were subsequently processed in the ImageJ software to calculate both the total leaf area and the herbivorous leaf area. The calculation of the herbivory value of each leaf was based on the comparison between the compromised area —referring to the leaf area removed by insects— and the total area of the leaves, as illustrated in Figure 4. To determine the percentage of herbivory, the leaf measurements obtained were applied to Equation 1.

$$\% \text{ Herbivory} = (\text{Compromised Area} / \text{Total Area}) \times 100$$

Equation 1

These results were used to compare species individually and identify the scenarios of greatest consumption. For a general analysis, the leaves collected in the different treatments were grouped without considering the species, allowing the evaluation of the treatments with the highest incidence of herbivory.

The environmental parameters examined were air temperature (°C), relative humidity (%) and light intensity (lm/m²). Using Hobo dataloggers, data collection was conducted on individuals in each treatment, which employed nine devices, configured to record data every hour, from 8:00 AM to 4:00 PM, during a sunny day. The Hobo records were later extracted using Hoboware software.

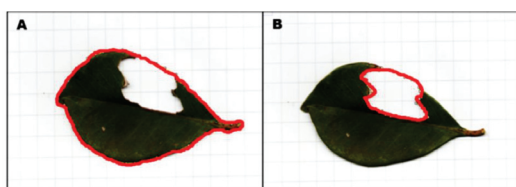


Figure 4. Illustration of the leaf herbivory analysis process. A) Total area. B) Compromised area.

Figura 4. Ilustración del proceso de análisis de la herbivoría foliar. A) Área total. B) Área comprometida.

Statistical analysis

The distribution of leaf herbivory data was initially assessed in relation to the ANOVA assumptions. However, due to non-compliance with these assumptions, the Kruskal-Wallis test was chosen ($P < 0.05$). Subsequently, the Dunn post-hoc test was used to compare treatments. All analyses were performed using RStudio software, version 4.2.2, and the table was created using Microsoft Excel (2023). The environmental parameters (air temperature [°C], luminosity [m²] and relative humidity [%]) were also assessed by ANOVA analysis. These data were collected throughout the day (8 h, 10 h, 12 h, 14 h and 16 h) during the same period of leaf sampling, comparing with bromeliad and without bromeliad treatments. Assumptions were confirmed and Tukey's post-hoc were performed when factor effect was significant. Since there was no statistically significant difference between the control and fertilizer treatments for the environmental variables, both treatments were merged in the category Without bromeliad and compared with the bromeliad treatment (With bromeliad).

The data obtained were subjected to multivariate principal component analysis (PCA) to identify the correlations between herbivory and microenvironmental parameters in an attempt to explain the ecological strategies (animal-plant) in the presence and absence of *A. blanchetiana* considering the assumption of the resource availability hypothesis (RAH). All analyses were performed using RStudio 4.2.2, with graphs created in Excel 2023.

RESULTS

In the comparison between treatments, the highest percentage of leaf herbivory was observed in the bromeliad treatment, followed by the fertilizer treatment and, consequently, the lowest percentage of leaf damage by insects was observed in the control treatment (Table 1). The results showed that for the species *I. laurina*, *P. cattleianum* and *S. terebinthifolia*, individuals in the bromeliad treatment were more consumed than control and fertilizer treatments, which did not vary between them. For *D. ecastaphyllum*, there was no difference in herbivory percentage between the fertilizer and bromeliad treatments, but the individuals were more consumed than the control treatment (Table 1).

The environmental parameters analyzed revealed that relative humidity did not present

Table 1. Mean and standard deviation of the percentages of leaf herbivory of plant species in the control, fertilizer and bromeliad treatments. The letters indicate whether or not there was statistical variation between treatments.

Tabla 1. Media y desviación estándar de los porcentajes de herbivoría foliar de las especies vegetales en los tratamientos control, fertilizante y bromelias. Las letras indican si hubo variación estadística entre los tratamientos.

Species	Fertilizer treatment	Bromeliad treatment	Control treatment
<i>Dalbergia ecastaphyllum</i>	4.81±10.90 A	4.64±10.86 A	2.13±6.48 B
<i>Inga laurina</i>	3.53±13.20 B	4.03±10.53 A	2.15±7.83 B
<i>Psidium cattleianum</i>	4.76±9.45 B	10.92±15.72 A	3.50±8.93 B
<i>Schinus terebinthifolius</i>	3.77±11.03 B	20.52±25.66 A	1.12±5.63 B
Leaf herbivory	4.94±10.47 B	11.99±20.6 A	1.72±6.74 C

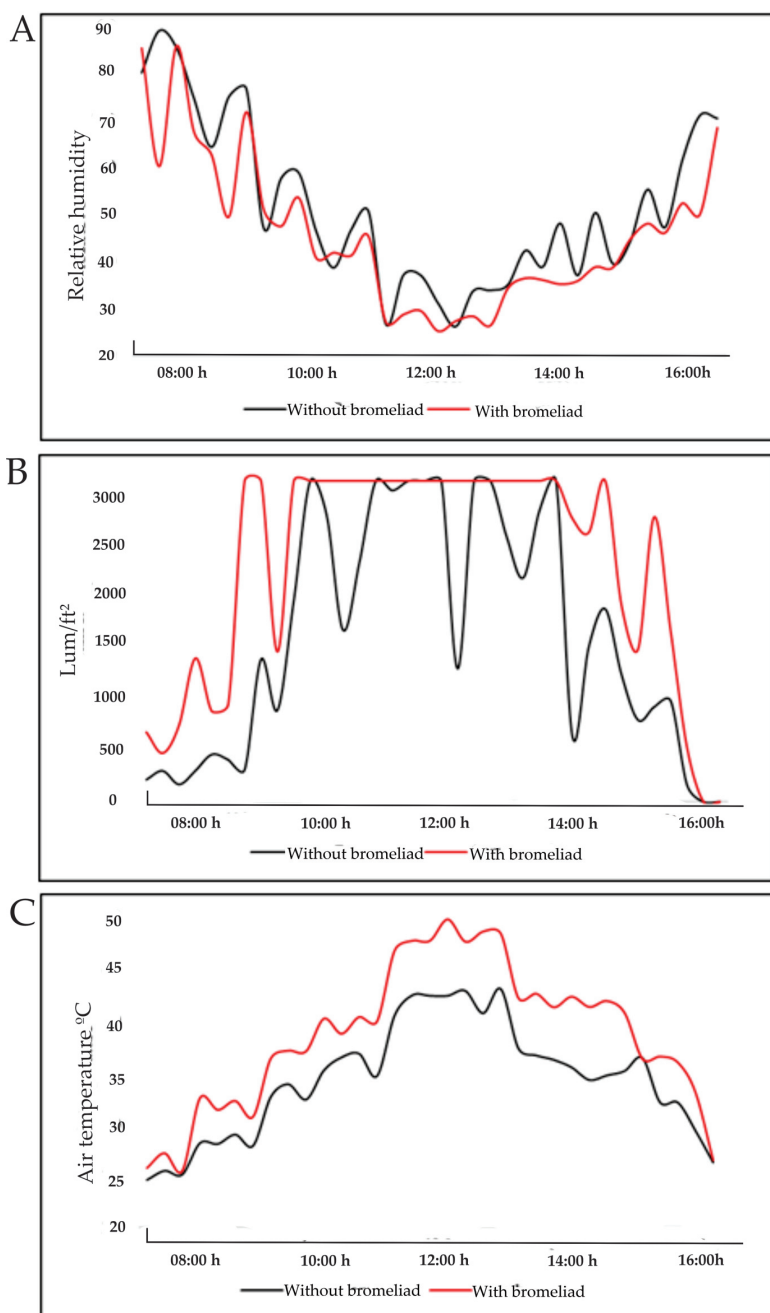


Figure 5. Variation of environmental parameters analyzed over a period of one day in the treatment with the bromeliad *Aechmea blanchetiana* (Baker) L.B.Sm. and in the treatments without *A. blanchetiana*. A) Relative air humidity. B) Luminosity. C) Air temperature.

Figura 5. Variación de los parámetros ambientales analizados a lo largo de un día en el tratamiento con la bromelia *Aechmea blanchetiana* (Baker) L.B.Sm. y en los tratamientos sin *A. blanchetiana*. A) Humedad relativa del aire. B) Luminosidad. C) Temperatura del aire.

statistical difference between treatments ($P=0.107$) (Figure 5A). Light intensity varied significantly between treatments, being higher in the groups without bromeliad (control and fertilizer) compared to the treatment with bromeliad ($P=0.008$) (Figure 5B). Regarding air temperature, the treatments without

bromeliad recorded higher temperatures than the treatment with bromeliad ($P=0.0175$) (Figure 5C).

The principal component analysis (PCA) was performed for each environmental data collection time (8 h, 10 h, 12 h, 14 h and 16 h).

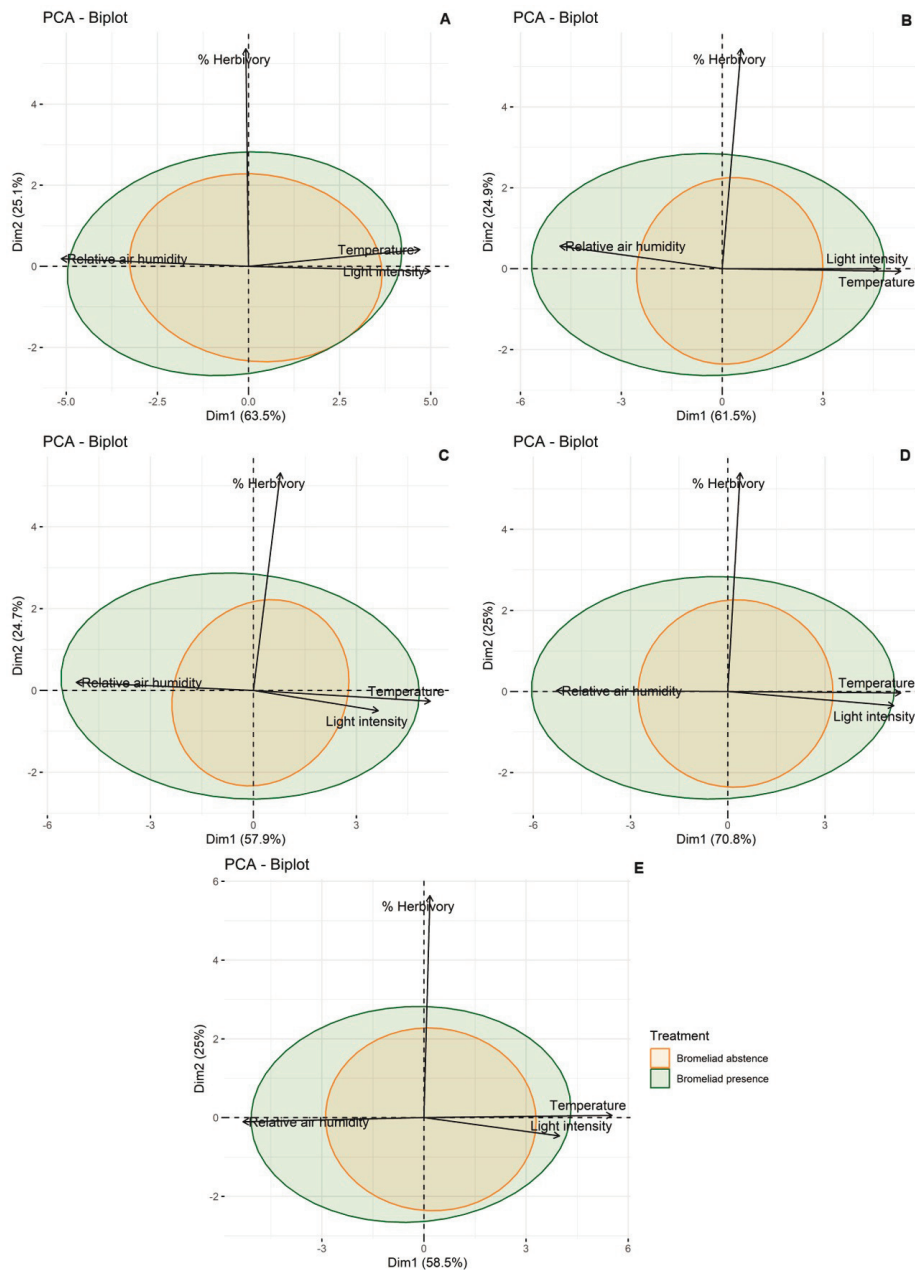


Figure 6. Principal component analysis (PCA) showing the relationship between microenvironmental variables and the percentage of herbivory. The ellipses represent confidence intervals (95%) for the two treatments: bromeliad absence (orange) and bromeliad presence (green). Each graph (A-E) corresponds to different times throughout the day (8 h, 10 h, 12 h, 14 h and 16 h, respectively).

Figura 6. Análisis de componentes principales (PCA) que muestra la relación entre variables microambientales y el porcentaje de herbivoría. Las elipses representan intervalos de confianza (95%) para los dos tratamientos: ausencia de bromelias (naranja) y presencia de bromelias (verde). Cada gráfico (A-E) corresponde a diferentes horarios a lo largo del día (8 h, 10 h, 12 h, 14 h y 16 h, respectivamente).

It was possible to observe patterns between environmental factors and herbivory at all times throughout the day (Figure 6). The principal axis (Dim1) explained 57.9% to 70.8% of the total variance, with temperature and light intensity inversely correlated with relative humidity. The second axis (Dim2) accounted for ~25% of the total data variance, and herbivory correlated with this axis. At all times analyzed, distinct clusters were observed among treatments. The treatment that included *A. blanchetiana* (Bromeliad presence) demonstrated a positive relationship with the highest indices of leaf herbivory, especially in the principal components during the hours of 8 h, 10 h and 12 h. This correlation was significant throughout the day. The greater amplitude of this cluster is due to the strong correlation between these treatments and environmental variables. Even during the hottest hours of the day (Bromeliad presence), the air humidity remained higher.

DISCUSSION

The literature states that bromeliads such as *A. blanchetiana* are key species in ecological restoration processes in Restinga environments (Brancalion 2015; Holl and Brancalion 2020; Souza et al. 2025). The main goal of restoration is to return a degraded ecosystem to its original condition, or as close as possible (Brancalion 2015; Holl and Brancalion 2020; Mendes et al. 2022, 2025). Thus, restoration projects are not limited to planting trees, but also to recovering ecosystem services and ecological relationships (Brancalion; Holl and Brancalion 2020; Antonetti et al. 2021). In our study, we aimed to understand how the presence of the bromeliad (a facilitator species) could influence insect-plant interactions, considering changes in microenvironmental variables and resource availability, while testing the Resource Availability Hypothesis (RAH).

Our findings (PCA) indicate that the presence of bromeliads (*A. blanchetiana*) is a key element in altering herbivory patterns, particularly those observed in restoration experiments. In our study, this occurred independently of microclimatic fluctuations throughout the day. The relationship between bromeliad treatment and high percentages of leaf damage (herbivory) supports the RAH (Coley et al. 1985; Endara and Coley 2011; Wittingham et al. 2023), suggesting that this facilitator species makes other plants susceptible to herbivory. From the perspective of ecological restoration,

herbivory is not inherently bad; in fact, one of the goals of this process is to return a degraded ecosystem to its original condition, including the return of negative ecological relationships (predation/herbivory). This demonstrates the success of the techniques applied for this purpose. In the present study, the higher percentage of herbivory found in the fertilizer treatment when compared to the control treatment indicates that organic chemical fertilization may have resulted in more robust individuals (Paiva et al. 2009; Biagiotti et al. 2017; Barea et al. 2020). Consequently, this influenced the feeding preference of insects, since plants present in environments with greater nutrient availability are more herbivorous, as described in interspecific RAH (Coley et al. 1985; Wittingham et al. 2023).

According to data collected by Martins (2020), the presence of *A. blanchetiana* did not influence the nutritional quality of the soil, contrary to what was observed in studies with *N. cruenta* in Restinga (Pereira et al. 2005; Souza et al. 2016; Souza et al. 2025). The leaf damage recorded in the bromeliad treatment was not attributed to soil nutrients, suggesting that environmental factors, such as lower temperatures and lower light intensity, may have played a significant role in leaf herbivory. It is worth noting that herbivory is strongly influenced by variations in abiotic factors (Abdala-Roberts 2016). When exposed to high light intensities, plants can adjust their morphoanatomy, resulting in thicker leaves and a lower specific leaf area (SLA), which is the ratio between leaf area and dry mass (Milaneze-Gutierrez et al. 2003). These adaptations negatively affect insect feeding (González-Esquivel et al. 2019). In environments with high light and high temperatures, which can harm organisms, protected microhabitats are expected to become vital resources for insects.

In addition, to mitigating severe environmental conditions, *A. blanchetiana* may have other characteristics that enhance the presence of insects in its surroundings. Several species belonging to the Bromeliaceae family establish complex interactions with organisms that depend on water at some stage of their development (Del-claro and Torezan-Silingardi 2012). Some bromeliad species, such as *A. blanchetiana*, accumulate water in their tanks, creating microhabitats with moderate temperatures and high humidity levels compared to the surrounding areas (Rocha et al. 2000). These conditions favor the colonization of local fauna, giving bromeliads

the role of multipliers of biodiversity in ecosystems (Jorge et al. 2020). It is important to highlight that, in environments with scarce water availability, the water accumulated in the leaves of bromeliads may represent the only source of fresh water for the local fauna (Silva et al. 2011), highlighting the relevance of the Bromeliaceae family in the environments where they occur. According Ribeiro (2023) the morphological analysis revealed statistically significant differences between the treatments with and without *A. blanchetiana*. In the height parameter, significant differences were observed in all five evaluations, with higher values for individuals planted with *A. blanchetiana*. This indicates that the presence of the bromeliad had a positive effect on the height growth of *D. ecastophyllum* plants, in the same environmental conditions.

The results of this study may indicate that in the bromeliad treatment, insects occupied microenvironments with lower light and mild temperatures (Lopez and Rios 2001; Frank and Lounibos 2009; Antonetti et al. 2021). These conditions directly influence the feeding and development of insects (Araújo 2013). Seasonal fluctuations, population dynamics and species succession, in addition to the presence of more generalist species, may explain the occupation of herbivores on plants whose growth is facilitated by *A. blanchetiana*. In addition, bromeliads provide ideal places for shelter and reproduction (Del-claro and Torezan-Silingardi 2012), resulting in a higher incidence of herbivory in these individuals. Thus, the properties of bromeliads, including their favorable microenvironments, play a significant role in the herbivory of the plants around them (Araújo 2013). Considering that temperature is one of the main environmental elements that affect the distribution of living organisms (Doming et al. 2012; Mendes et al. 2022, 2025; Menezes et al. 2025a, 2025b). The microhabitats provided by the bromeliad in the experiment, with moderate temperatures and lower exposure to light, become crucial resources for insects (Doming et al. 2012; Endara et al. 2017, 2023). In environments where such environmental factors can impair insect feeding, sites that mitigate these effects gain significant importance. This strengthens the relevance of the Resource Availability Hypothesis, especially given the higher incidence of herbivory observed in the bromeliad-associated treatment.

Bromeliads function as ecosystem engineers not only by altering abiotic conditions (Pereira

et al. 2005; Souza et al. 2016; Souza et al. 2025), but also by creating microhabitats that directly affect biotic (plant-animal) interactions, especially between plants and herbivores. The persistence of the association between bromeliads and herbivory during the hottest and driest periods suggests a possible attraction and retention of species specialized in herbivory, in addition to long-term microclimatic changes in the understory. These findings have significant implications for ecological restoration initiatives, suggesting that facilitator species such as *A. blanchetiana* can accelerate ecological processes but also introduce important trade-offs with increasing herbivory pressure. Considering these complex interactions when developing restoration strategies is critical to establishing resilient and ecologically functional plant communities (Mendes et al. 2025; Menezes et al. 2025b; Silva et al. 2025). Due to the robust database collected over the years, the resource availability hypothesis (RAH) is considered the hypothesis that best explains and predicts plant defense and growth investments in an interspecific approach (López-Goldar et al. 2020; Forrister et al. 2023; Endara et al. 2023). As for intraspecific RAH, a review study revealed divergent results: while some support the findings of interspecific RAH, others contradict them, indicating an opposite pattern (Hernán et al. 2019). These findings highlight the need and importance of collecting new data to understand RAH, especially in the context of intraspecific variations.

CONCLUSIONS

Based on the data from our study, it was confirmed that the bromeliad *A. blanchetiana* acts as a key facilitator in Restinga restoration. The increased foliar herbivory on neighboring plants demonstrates the return of ecological relationships that were previously absent. The observed pattern strongly corroborates the RAH at an intraspecific level, showing that plants in microhabitats with more favorable environmental conditions become susceptible to consumption by insects. *A. blanchetiana* created a microenvironment with lower light intensity and milder temperatures, generating a favorable microhabitat that attracted, sheltered and sustained herbivore activity. These new findings highlight that effective ecological restoration goes beyond mere plant survival and growth; it involves restoring complex biotic interactions, such as herbivory, long perceived as solely negative.

The presence of *A. blanchetiana* accelerated the reestablishment of this crucial trophic interaction, signaling the return of ecological functionality. However, this also reveals an important trade-off: while facilitator species help reduce abiotic stress and promote faunal recolonization, they can simultaneously intensify herbivory pressure on target plants. Thus, restoration approaches in Restinga

and similar stressful ecosystems should deliberately include facilitator species like *A. blanchetiana*, but their use must be planned considering their dual role in shaping both the physical environment and biotic networks. Future studies should explore the long-term outcomes of this facilitation-herbivory dynamic on plant community establishment and resilience.

REFERENCES

- Abdala-Roberts, L., A. A. Agrawal, and X. Moreira. 2016. Biotic and abiotic factors associated with altitudinal variation in plant traits and herbivory in a dominant oak species. *American Journal of Botany* 103(12):2070-2078. <https://doi.org/10.3732/ajb.1600310>.
- Antonetti, D. A., E. Malfatti, and L. R. Pinto-Utz. 2021. Influence of environmental and morphological parameters on the microfauna community present in phytotelmata of a bromeliad in a fragment of Atlantic Forest, southern Brazil. *Neotropical Biology and Conservation* 16(1):59-70. <https://doi.org/10.3897/neotropical.16.e62317>.
- Araújo, W. S. 2013. A importância de fatores temporais para a distribuição de insetos herbívoros em sistemas neotropicais. *Revista da Biologia* 10(1):1-7. <https://doi.org/10.7594/revbio.10.01.01>.
- Barea, A. R., A. P. L. Lima, S. F. Lima, J. B. Leite Junior, and H. A. V. Meireles. 2020. Protetor físico, bioestimulante e adubação nitrogenada na emergência e crescimento inicial do paricá em campo. *Scientia Forestalis* 48(127):e3314. <https://doi.org/10.18671/scifor.v48n127.25>.
- Biagiotti, G., S. V. Valeri, M. C. P. Cruz, and R. T. Vasconcelos. 2017. Fertilização potássica na implantação de *Corymbia citriodora* (Hook.) K.D. Hill and L.A.S. Jonhson. *Scientia Forestalis* 45(113):129-137. <https://doi.org/10.18671/scifor.v45n113.10>.
- Bongers, F., and J. Popma. 1990. Leaf characteristics of the flora of the tropical rainforest of Los Tuxtlas, Mexico. *Botanical Gazette* 151(3):354-365. <https://doi.org/10.1086/337836>.
- Brancalion, P. H. S., S. Gandolfi, and R. R. Rodrigues. 2015. Restauração florestal. Oficina de Textos.
- Coley, P. D., and Chapin, F. S. 1985. Resource availability and plant antiherbivore defense. *Science* 230(4728):895-899. <https://doi.org/10.1126/science.230.4728.895>.
- Da Silva, L. D. S. A. B., and J. De Deus Medeiros. 2005. Herbivoria em *Psidium cattleyanum* Sab. (Myrtaceae). *INSULA Revista de Botânica* 34:83-94.
- Del-Claro, K., and H. M. Torezan-Silingardi. 2012. Ecologia das interações plantas-animais: Uma abordagem ecológico-evolutiva. Technical Books Editora.
- Endara, M.-J., and P. D. Coley. 2011. The resource availability hypothesis revisited: A meta-analysis. *Functional Ecology* 25(2):389-398. <https://doi.org/10.1111/j.1365-2435.2010.01803.x>.
- Endara, M.-J., P. D. Coley, G. Ghabash, J. A. Nicholls, K. G. Dexter, D. A. Donoso, and G. N. Stone. 2017. Coevolutionary arms race versus host defense chase in a tropical herbivore-plant system. *Proceedings of the National Academy of Sciences* 114(36):E7499-E7505. <https://doi.org/10.1073/pnas.1707727114>.
- Endara, M.-J., D. L. Forrister, and P. D. Coley. 2023. The evolutionary ecology of plant chemical defenses: From molecules to communities. *Annual Review of Ecology, Evolution, and Systematics* 54(1):107-127. <https://doi.org/10.1146/annurev-ecolsys-102221-045254>.
- Favretto, M. A., J. C. Santos, and E. G. Oliveira. 2011. Entomofauna em duas espécies de bromélias no oeste de Santa Catarina, Brasil. *Entomobrasilia* 4(1):10-12. <https://doi.org/10.12741/ebrazilis.v4i1.126>.
- Forrister, D. L., M.-J. Endara, A. J. Soule, G. C. Younkin, A. G. Mills, J. Lokvam, and P. D. Coley. 2023. Diversity and divergence: Evolution of secondary metabolism in the tropical tree genus *Inga*. *New Phytologist* 237(2):631-642. <https://doi.org/10.1111/nph.18554>.
- Frank, J. H., and L. P. Lounibos. 2009. Insects and allies associated with bromeliads: A review. *Terrestrial Arthropod Reviews* 1(2):125-153. <https://doi.org/10.1163/187498308X414742>.
- González-Esquivel, J. G., P. Cuevas-Reyes, and K. Oyama. 2019. Functional attributes of two *Croton* species at different successional stages of tropical dry forest: Effects on herbivory and fluctuating asymmetry patterns. *Tropical Ecology* 60(2):238-251. <https://doi.org/10.1007/s42965-019-00027-y>.
- Hahn, P. G., A. A. Agrawal, K. I. Sussman, and J. L. Maron. 2019. Population variation, environmental gradients, and the evolutionary ecology of plant defense against herbivory. *The American Naturalist* 193(1):20-34. <https://doi.org/10.1086/700838>.
- Hernán, G., M. J. Ortega, M. Gómez, and J. J. Vergara. 2019. Herbivory and resource availability change plant defense and herbivore choice in a seagrass system. *Oecologia* 189(3):719-732. <https://doi.org/10.1007/s00442-019-04364-6>.
- Holl, K. D., and P. H. S. Brancalion. 2020. Tree planting is not a simple solution. *Science* 368(6491):580-581. <https://doi.org/10.1126/science.aba8232>.
- Jorge, J. S., E. M. Santos, and M. M. Ribeiro. 2020. Living among thorns: Herpetofaunal community (Anura and Squamata) associated with the rupicolous bromeliad *Encholirium spectabile* (Pitcairnioideae) in the Brazilian semiarid. *Zoologia* 37:e46661. <https://doi.org/10.3897/zoologia.37.e46661>.
- Kleinhesselink, A. R., S. M. Magnoli, and J. H. Cushman. 2014. Shrubs as ecosystem engineers in an environmental gradient: Effects on species richness and exotic plant invasion. *Oecologia* 175(4):1277-1290. <https://doi.org/10.1007/s00442-014-2972-0>.

- Lopez, L. C. S., and R. I. Rios. 2001. Phytotelmata faunal communities in sun-exposed versus shaded terrestrial bromeliads from southeastern Brazil. *Selbyana* 22(2):219-224. <https://doi.org/10.2307/41760099>.
- López-Goldar, X., R. Zas, and L. Sampedro. 2020. Resource availability drives microevolutionary patterns of plant defenses. *Functional Ecology* 34(8):1640-1652. <https://doi.org/10.1111/1365-2435.13610>.
- Lowry, D. B., J. M. Sobel, A. L. Angert, T. -L. Ashman, R. L. Baker, B. K. Blackman, and M. A. Streisfeld. 2019. Mechanisms of a locally adaptive shift in allocation among growth, reproduction, and herbivore resistance in *Mimulus guttatus*. *Evolution* 73(6):1168-1181. <https://doi.org/10.1111/evo.13699>.
- Martinelli, G., C. M. Vieira, M. Gonzalez, P. Leitman, A. Piratininga, A. F. Costa, and R. C. Forzza. 2008. Bromeliaceae da Mata Atlântica brasileira: Lista de espécies, distribuição e conservação. *Rodriguésia* 59(1):209-258. <https://doi.org/10.1590/2175-7860200859114>.
- Martins, J. K. D. 2020. Produção de mudas e revegetação de base de poço em áreas de exploração de petróleo no norte do estado do Espírito Santo [Dissertação de mestrado, Universidade Federal do Espírito Santo]. Repositório Institucional da UFES. <http://repositorio.ufes.br/handle/10/15130>.
- Melo, J. C. F., and M. R. T. Boeger. 2015. Riqueza, estrutura e interações edáficas em um gradiente de restinga do Parque Estadual do Acaraí, Estado de Santa Catarina, Brasil. *Hoehnea* 42(2):207-232. <https://doi.org/10.1590/2236-8906-40/2014>.
- Mendes, M. M., A. C. R. Pinheiro, F. R. Pires, A. A. Fernandes, L. F. T. D. Menezes, I. D. P. Pereira, V. F. D. Santos, L. D. A. Leite, D. Cassol, and A. R. Falqueto. 2022. Photosynthesis and leaf traits of tree species influenced by green manure associated with soil treatments. *Communications in Soil Science and Plant Analysis* 53(16):2064-2081. <https://doi.org/10.1080/00103624.2022.2070195>.
- Mendes, M. M., I. F. Ribeiro, V. D. F. Santos, F. R. Pires, A. A. Fernandes, L. F. T. D. Menezes, and A. R. Falqueto. 2025. Green manure can be an auxiliary factor against dynamic photoinhibition in *Dalbergia ecastophyllum* (L.) young trees in areas impacted by mining. *Photosynthetica* 63(2):129-139. <https://doi.org/10.32615/ps.2025.015>.
- Menezes, L. F. T. de, F. Z. Saiter, P. Dodonov, O. J. Pereira, E. L. Poelking, F. de D. Fonseca Neto, C. N. de Fraga, D. Piotto, H. M. Dias, et al. 2025a. Afogada no progresso: o dilema da Restinga no Brasil. *Boletim do Museu de Biologia Mello Leitão*, 2(2), 174-190. <https://doi.org/10.70525/2025.41>.
- Menezes, L. F. T. de, M. da C. Souza, M. M. S. Conde, M. M. Mendes, and D. S. D. de Araujo. 2025. Relação entre estrutura e topografia em uma floresta de duna na Restinga da Marambaia-RJ, Brasil. *Paubrasilia* 8:e214s. <https://doi.org/10.33447/paubrasilia.2025s.e0214s>.
- Paiva, A. V., F. Poggiani, J. L. M. Gonçalves, and A. V. Ferraz. 2009. Native tree seedling growth when fertilized with different amounts of dry sewage sludge and mineral fertilizer. *Scientia Forestalis* 37(84): 499-511. URL: tinyurl.com/yj5ajv7t.
- Pereira, M. G., O. J. Pereira, and A. M. Santos. 2005. Propriedades químicas de solos sob *Neoregelia cruenta* (R. Grah) L.B. Smith na restinga da Marambaia, RJ. *Floresta e Ambiente* 12(1):70-73.
- Pereira, O. J., and L. F. T. Menezes. 2023. Restinga no Espírito Santo: Vegetação, flora, distribuição geográfica das espécies. Editora Rupestre.
- Ribeiro, I. F. 2023. *Aechmea blanchetiana* (Baker) LBSm. (Bromeliaceae) como espécie facilitadora em áreas de restinga no Sudeste do Brasil. Tesis doctoral. Center for Biosciences and Biotechnology, State University of Northern Rio de Janeiro Darcy Ribeiro, Campos dos Goytacazes. Rio de Janeiro. Brazil. Pp. 65.
- Rocha, C. F. D., L. Cogliatti-Carvalho, D. R. Almeida, and A. F. N. Freitas. 2000. Bromeliads: Biodiversity amplifiers. *Journal of the Bromeliad Society* 50(2):81-83.
- Rodrigues, A. B., A. A. Bhering, J. M. Otero, L. L. Venetas, P. A. S. Marbach, and L. R. Zamith. 2025. Efeitos da temperatura e condição de luz na germinação e da colonização de isolados de *Trichoderma* sp. na promoção do crescimento de mudas de *Inga maritima* Benth. *Paubrasilia* 8:e205s. <https://doi.org/10.33447/paubrasilia.2025s.e0205s>.
- Scarano, F. R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Annals of Botany* 90(4):517-524. <https://doi.org/10.1093/aob/mcf189>.
- Scarano, F. R. 2009. Plant communities at the periphery of the Atlantic rain forest: Rare-species bias and its risks for conservation. *Biological Conservation* 142(6):1201-1208. <https://doi.org/10.1016/j.biocon.2009.02.027>.
- Scheffers, B. R., D. P. Edwards, A. Diesmos, S. E. Williams, and T. A. Evans. 2014. Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology* 20(2):495-503. <https://doi.org/10.1111/gcb.12439>.
- Silva, H. R., A. L. G. Carvalho, and G. B. Bittencourt-Silva. 2011. Selecting a hideout: Anuran diversity and bromeliad use in threatened coastal dune habitats in Brazil. *Biotropica* 43(2):218-227. <https://doi.org/10.1111/j.1744-7429.2010.00656.x>.
- Silva, T. R. da, T. J. Antunes, and L. F. S. Magnago. 2025. Influência do solo sobre a riqueza e composição em gradiente fitofisionômico de Restinga no Sudeste do Brasil. *Paubrasilia* 8:e206s. <https://doi.org/10.33447/paubrasilia.2025s.e0206s>.
- Souza, K. J., M. M. Mendes, E. M. Aoyama, A. R. Falqueto, and L. F. T. Menezes. 2025. Facilitation by *Aechmea blanchetiana* (Baker) L.B.Sm. (Bromeliaceae) in the establishment and development of plants in a coastal dune ecosystem. *Scientia Forestalis* 53:e4037. <https://doi.org/10.18671/scifor.v53.09>.
- Souza, R. C., M. N. Delgado, and M. G. Pereira. 2016. Papel de bromélias terrestres na ciclagem de nutrientes, restinga da Marambaia, Brasil. *Floresta e Ambiente* 23(2):161-169. <https://doi.org/10.1590/2179-8087.106414>.
- Wittingham, S. S., J. Carey, and D. S. Johnson. 2023. Resource availability and plant age drive defense against herbivory in salt marshes. *Oikos* (8):e09672. <https://doi.org/10.1111/oik.09672>.
- Yelenik, S. G., N. Dimanno, and C. M. D'Antonio. 2015. Evaluating nurse plants for restoring native woody species to degraded subtropical woodlands. *Ecology and Evolution* 5(2):300-313. <https://doi.org/10.1002/ece3.1294>.
- Zhang, P., D. M. Blumenthal, and J. K. Smith, J. K. 2020. Ectothermic omnivores increase herbivory in response to rising temperature. *Oikos* 129(7):1028-1039. <https://doi.org/10.1111/oik.07082>.