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ATRIBUTOS FUNCIONAIS DE INDIVÍDUOS JOVENS DE *Euterpe edulis* EM FLORESTA MONTANA E SUBMONTANA

ILHÉUS -BA
2025

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Dissertação apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação da Biodiversidade.

Área de concentração: Ecofisiologia e Ecologia de Populações.

Orientador: Prof. Marcelo Schramm Mielke
Coorientadora: Prof.ª Amanda Freitas Cerqueira
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Ilhéus, 21 de fevereiro de 2025.

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"*É o olhar da terrível conscientização*, ela pensou, *de alguém obrigado a conhecer a própria mortalidade.*"

Frank Herbert

ATRIBUTOS FUNCIONAIS DE INDIVÍDUOS JOVENS DE *Euterpe edulis* EM FLORESTA MONTANA E SUBMONTANA

RESUMO

Compreender os fatores ambientais que influenciam a sobrevivência de indivíduos em estágios iniciais de desenvolvimento de plantas tropicais é essencial para a conservação dessas espécies. Contudo, a maioria dos estudos sobre atributos funcionais em plantas focam em comparações baseadas em um único estágio de desenvolvimento, limitando o conhecimento sobre a variação desses atributos entre estágios e em diferentes condições ambientais. Este estudo busca investigar os atributos funcionais morfológicos e fisiológicos de indivíduos de dois estágios ontogenéticos iniciais de *Euterpe edulis* (Jovem I e Jovem II) oriundos de dois ambientes de altitude, uma floresta submontana e outra montana e identificar quais traços funcionais contribuem para o agrupamento dos indivíduos amostrados. Foram amostradas folhas de 30 indivíduos de cada estágio em cada ambiente, totalizando 120. Atributos morfológicos e fisiológicos de fluorescência da clorofila foram obtidos. Análises de agrupamento, discriminante e ANOVA de dois fatores ou Kruskal-Wallis foram realizadas. Os atributos morfológicos e fisiológicos demonstraram dependência em relação à altitude e ao estágio de desenvolvimento. Indivíduos no estágio Jovem I e Jovem II da floresta montana exibiram valores semelhantes para os atributos fisiológicos. Em contraste, na floresta submontana, indivíduos Jovem I mostraram respostas fisiológicas distintas dos Jovem II, que indicaram maior estresse. As análises de agrupamento e discriminante indicaram maior similaridade entre indivíduos do estágio Jovem II, independentemente do ambiente. A floresta montana apresenta-se como um ambiente menos estressante para *E. edulis*. Com o aumento previsto na frequência e intensidade de secas devido às mudanças climáticas, florestas montanas úmidas podem servir como refúgio para espécies dependentes de ambientes úmidos, como *E. edulis*. Considerando a menor susceptibilidade de indivíduos Jovem II às condições ambientais, mudas nesse estágio ontogenético podem apresentar taxas de sobrevivência maiores em programas de repovoamento, em comparação com indivíduos Jovem I, no campo.

Palavras-chave: Ecofisiologia Vegetal. Fluorescência da clorofila a. Palmeiras. Eventos climáticos extremos.

FUNCTIONAL TRAITS OF *Euterpe edulis* YOUNG PLANTS IN MONTANE AND SUBMONTANE FORESTS

ABSTRACT

Understanding the environmental factors that influence the survival of individuals in the early developmental stages of tropical plant species is essential for the conservation of these species. However, most studies on functional traits in plants focus on comparisons based on a single developmental stage, limiting knowledge about trait variation across stages and in different environmental conditions. This study aims to investigate the morphological and physiological functional traits of individuals from two early ontogenetic stages of *Euterpe edulis* (Juvenile I and Juvenile II) originating from two altitudinal sites, a submontane forest and a montane forest, and to identify which functional traits contribute to the clustering of the sampled individuals. Leaves from 30 individuals of each stage in each environment were sampled, totaling 120. Morphological and chlorophyll fluorescence physiological traits were measured. Cluster analysis, discriminant analysis, and either two-way ANOVA or Kruskal-Wallis tests were performed. Morphological and physiological traits exhibited dependency on altitude and developmental stage. Juvenile I and Juvenile II individuals from the montane forest showed similar physiological trait values. In contrast, in the submontane forest, Juvenile I individuals displayed distinct physiological responses compared to Juvenile II, indicating higher stress levels. Cluster and discriminant analyses indicated greater similarity among Juvenile II individuals, regardless of the environment. The montane forest appears to be a less stressful environment for *E. edulis*. With increasing drought frequency and intensity due to climate change, humid montane forests may serve as refugia for moisture-dependent species such as *E. edulis*. Given the lower susceptibility of Juvenile II individuals to environmental conditions, seedlings in this ontogenetic stage may exhibit higher survival rates in reforestation programs compared to Juvenile I individuals in the field.

Keywords: Plant Ecophysiology. Chlorophyl a Fluorescence. Palms. Extreme Climatic Events.

SUMÁRIO

Introdução geral

As mudanças climáticas impactam espécies e ecossistemas ao redor do globo (BELLARD et al., 2012; BROWNE et al., 2021; IPCC, 2023; SCARANO e CEOTTO, 2015; THUILLER et al., 2005). Um dos principais desafios, enfrentados por cientistas interessados na conservação da biodiversidade, é prever como as espécies serão afetadas por essas mudanças (AHRENS et al., 2020). Plantas, em particular, são especialmente vulneráveis, pois, devido à sua natureza séssil, não conseguem migrar para habitats mais adequados à sua sobrevivência (SCHNEIDER, 2022). Uma vez estabelecidas em determinado ambiente, as plantas devem lidar com as condições ambientais presentes naquele local, independentemente de sua severidade.

Uma abordagem eficaz para compreender e prever as respostas das espécies às mudanças climáticas é a análise de atributos funcionais (HEILMEIER, 2019), que são características do fenótipo das plantas que refletem as suas interações com fatores bióticos e abióticos no ambiente (CARUSO et al., 2020; DÍAZ et al., 2013; REICH et al., 2003). Entre os atributos funcionais, os foliares são amplamente utilizados, não apenas devido à relativa facilidade de medição, mas também porque a folha é o principal órgão de interação da planta com o ambiente, onde ocorrem processos como a fotossíntese (BEYSCHLAG e RYEL, 2007; FREITAS, et al. 2024).

O palmito-juçara (*Euterpe edulis* Mart.) é uma espécie de distribuição ampla. Ocorre desde o sul do Brasil, onde temperaturas baixas são registradas, até o Nordeste, que possui verões muito quentes, desde terras baixas, a nível do mar, até 1400m de altitude (SOUZA e PREVEDELLO, 2019). Porém, apesar da ampla distribuição geográfica *E. edulis* ocorre em maior abundância em florestas úmidas bem preservadas (CERQUEIRA et al., 2021). Parece ser capaz de suportar diferentes temperaturas e condições de luminosidade (CERQUEIRA et al., 2022; GATTI et al., 2008; NAKAZONO et al., 2001), porém é uma espécie que precisa de ambientes úmidos para germinar e se estabelecer (ANDRADE, 2001; GATTI et al., 2014).

As florestas montanas são formações particularmente sensíveis as mudanças climáticas. São ambientes muito heterogêneos, confinados em espaços pequenos, geralmente rodeados por pastagens e outros tipos de uso da terra (BERGAMIN et al., 2024; MARTINELLI, 2007). São formações presentes no sul da Bahia, em locais como a Serra Bonita (ROCHA e AMORIM, 2012; MARTINELLI, 2007). A variação altitudinal no local é responsável por criar também um gradiente de temperatura e umidade (DIAS et al., 2014) onde *E. edulis* ocorre em abundância (ROCHA e AMORIM, 2012). Se tornando, assim, interessante objeto de investigação para o compreender como os atributos funcionais de uma palmeira ameaçada de extinção estão mudando entre estágios ontogenéticos iniciais em locais com diferentes cotas altimétricas.

Assim, objetivou-se investigar os atributos funcionais morfológicos e fisiológicos de indivíduos de dois estágios ontogenéticos iniciais de *E. edulis* oriundos de dois ambientes de altitude, uma floresta submontana e outra montana e identificar quais traços funcionais contribuem para o agrupamento dos indivíduos amostrados.

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Functional Traits of *Euterpe edulis* young plants in Montane and Submontane Forests

Abstract: Understanding the environmental factors that influence the survival of individuals in the early developmental stages of tropical plant species is essential for the conservation of these species. However, most studies on functional traits in plants focus on comparisons based on a single developmental stage, limiting knowledge about trait variation across stages and in different environmental conditions. This study aims to investigate the morphological and physiological functional traits of individuals from two early ontogenetic stages of *Euterpe edulis* (Juvenile I and Juvenile II) originating from two altitudinal sites, a submontane forest and a montane forest, and to identify which functional traits contribute to the clustering of the sampled individuals. Morphological and physiological traits exhibit dependency on altitude and developmental stage. Juvenile I and Juvenile II individuals from the montane forest show similar physiological trait values. In contrast, in the submontane forest, Juvenile I individuals display distinct physiological responses compared to Juvenile II, indicating higher stress levels. Cluster and discriminant analyses indicate greater similarity among Juvenile II individuals, regardless of the environment. The montane forest appears to be a less stressful environment for *E. edulis*. With increasing drought frequency and intensity due to climate change, humid montane forests may serve as refugia for moisture-dependent species like *E. edulis*. These findings suggest that seedlings at the Juvenile II stage, with their enhanced resistance to water stress, are better suited for reforestation and conservation efforts, as they are likely to achieve higher survival rates in the field compared to Juvenile I seedlings.

Key-words: Plant Ecophysiology; Chlorophyl a Fluorescence; Palms; Extreme Climatic Events; Brazilian Atlantic Forest.

1. Introduction

Euterpe edulis Mart. (Arecaceae) is a palm species (Henderson et al., 1995) considered a keystone species of the Brazilian Atlantic Forest, primarily because it fruits during periods of low resource availability for wildlife (Galetti et al., 2013; Silva and Reis, 2019; Tres et al., 2020). It is currently listed as an endangered species, primarily due to the intense exploitation of its meristem for human consumption (Galetti and Fernandez, 1998; Leitman et al., 2013). It occurs throughout the Atlantic Forest, up to 1400 m in altitude, and in riparian forests of the Cerrado (Henderson et al., 1995; Leitman et al., 2015; Souza and Prevedello, 2019; Silva et al., 2024). It is shade-tolerant (Gatti et al. 2011) and adult individuals are typically found in the mid-canopy of the forest (Fávaro et al., 2021). However, when seedlings and juvenile individuals of the species were analyzed under different light availabilities, they exhibited increased values of relative growth rate and net assimilation rate in response to higher light availability (Nakazono et al., 2001; Cerqueira et al., 2022). This suggests that light alone does not determine the species' presence in shaded forest interiors and its absence in more deforested landscapes (Cerqueira et al., 2021; Leal et al., 2021).

Water availability plays a fundamental role in the occurrence of *E. edulis*, as individuals are typically found in very humid locations (Gatti et al., 2014). Additionally, its seeds require high water content to remain viable and to germinate, as they are recalcitrant (Bovi and Cardoso, 1975; Matos and Watkinson, 1998; Andrade, 2001). This dependence on water apparently makes the species particularly vulnerable during its early developmental stages, a concern amplified by the fact that juvenile phases shape the future structure of ecosystems. Furthermore, higher mortality rates due to drought-induced stress have been reported in the early stages of development in tropical forests (Browne et al., 2011).

Droughts, which impose water stress on plants, are expected to intensify in the coming years due to rising temperatures and decreasing precipitation in various parts of the world (Phillips et al., 2010; Hajek and Knapp, 2022; IPCC, 2023). Palms (Arecaceae family), such as *E. edulis*, are known for their low tolerance to water deficit (Henderson et al., 1995), so the occurrence of droughts can be particularly concerning. This vulnerability is further exacerbated in mountain forests, where microclimatic conditions vary considerably over short distances due to altitudinal gradients (Motzer, 2005; Bergamin et al., 2024). Furthermore, these forests are often confined to small areas and surround by human-modified landscapes, such as agriculture fields and pastures (Martinelli, 2007; Bergamin et al., 2024). In southern Bahia, submontane and mountain forests such as those in Serra Bonita exhibit pronounced altitudinal variations in temperature and humidity (Martinelli, 2007; Rocha and Amorim, 2012; Dias et al., 2014), where *E. edulis* occurs abundantly (Rocha and Amorim, 2012).

The complexity of the interactions between species and their environment is an ongoing topic for moist tropical forests, primarily due to the high species diversity in these ecosystems (Begon et al., 2006; Rezende et al., 2018). Therefore, investigating species-specific responses can help understand the extent of variation in functional traits and the environmental factors that influence these variations (McGill et al., 2006). The use of functional traits to understand how individuals and populations of tree and palm species may respond to environmental pressures resulting from global climate change is extremely valuable (Heilmeier, 2019; Ahrens et al., 2020). This is because functional traits are phenotypic characteristics of plants that reflect their interactions with biotic and abiotic factors in the environment, thereby influencing reproduction, survival, and growth (Reich et al., 2003; Díaz et al., 2013; Caruso et al., 2020). Comparing functional traits of individuals in different environmental conditions allows the establishment of relationships between abiotic factors, survival, and the occurrence of plants in specific locations (Díaz et al., 2013; Reich, 2014; Freitas et al., 2024). This information helps predict how individuals will be affected by the occurrence of extreme events (Ahrens et al., 2020), such as droughts, which are projected to increase in frequency and intensity over the coming years (IPCC, 2023).

Despite the importance of understanding the environmental factors that affect the survival of individuals in the early stages of development in tropical forests, studies on functional traits in plants are generally focused on comparisons using a single developmental stage of the species, and little is known about the variation of these traits across stages and under different environmental conditions (Caruso et al., 2020). To bridge this gap, physiological indicators such as chlorophyll fluorescence can be used to assess plant responses to environmental stress (Kalaji et al., 2016; Toro-Tobón et al., 2022). The in vivo analysis of chlorophyll a fluorescence is an excellent indicator of photosynthetic efficiency (van Heerden et al., 2007; Baker, 2008), as it provides information about the transformation of light energy into chemical energy and the electron transfer in the photosynthetic electron transport chain, especially in photosystem II (PSII) (Papageorgiou e Govindjee, 2004). By applying this approach to *E. edulis* juveniles along an altitudinal gradient, it is possible to gain deeper insights into the species' functional responses to environmental variation and climate change.

In light of the above, understanding how the functional traits of an endangered palm species are changing between early ontogenetic stages at locations with different altitudinal levels will provide pioneering insights into the management challenges faced by populations of this species in montane and submontane forests. Thus, the present study aims: (1) to investigate the morphological and physiological functional traits of individuals from two early ontogenetic stages of *E. edulis* originating from two altitudinal sites, a submontane forest and a montane forest, and (2) to identify which functional traits contribute to the clustering of the sampled individuals. We hypothesize that physiological and morphological functional traits are dependent on both ontogenetic stage and altitudinal site.

2. Materials and Methods

2.1. Study Area

Fieldwork was performed at Reserva Particular do Patrimônio Natural (RPPN) Serra Bonita (15°24'3"S, 39°33'59"W), located in the municipality of Camacan, in the southern region of Bahia state, Brazil. The RPPN is situated in the highest central area of the Serra Bonita

Mountain range (Rocha and Amorim, 2012). Camacan has a predominant Af climate type (wet equatorial) according to the Köppen-Geiger classification system (Koppen, 1936; Instituto Uiraçu, 2019). There are no well-defined seasons, with the coldest month's temperature around 17.6°C or higher and an annual maximum temperature of approximately 33°C. Precipitation in the Serra Bonita RPPN region ranges from 1200 to 1400 mm annually, with a monthly average of 160.9 mm, high cloud cover, and 80% relative humidity (Dias et al., 2014; Instituto Uiraçu, 2019; Arnfield, 2024). The reserve is in the Atlantic Forest and features dense ombrophilous forest with submontane and montane formations. Submontane forests are formations found between 100 and 600 meters above sea level, while montane forests are situated between 600 and 1500 meters (IBGE, 2012). Both formations in the reserve have a history of exploitation and are classified as altered Submontane/Montane Tropical Moist Forest. In the site where the field work was conducted, both forests are in an advanced stage of regeneration (Rocha and Amorim, 2012; Instituto Uiraçu, 2019). Prior to the fieldwork, the region experienced dry periods, with monthly precipitation falling below 100 mm. However, during the fieldwork, precipitation remained high, exceeding 600 mm in April (Fig. 1).

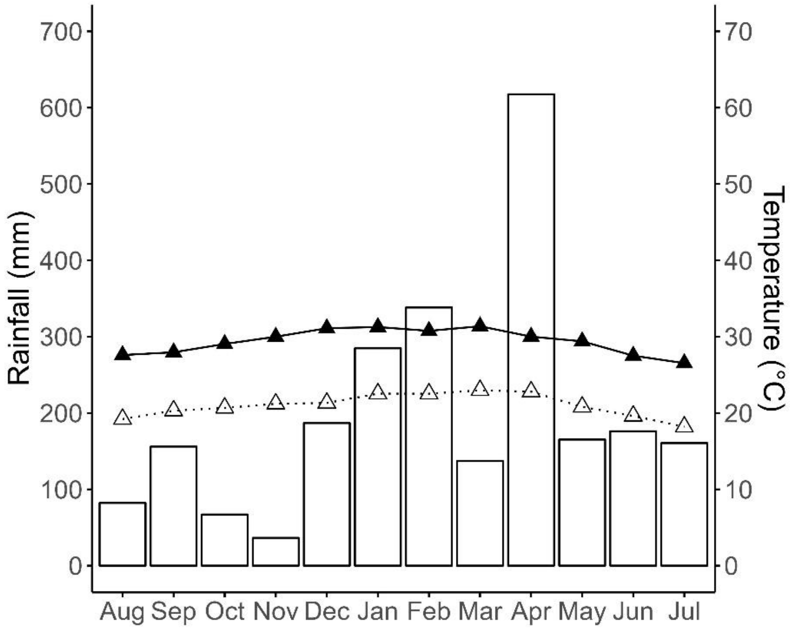

Fig. 1. Meteorological data collected from August 2023 to July 2024 using an automatic weather station (INMET) located in Ilhéus, Brazil. Δ: minimum temperature; ▲: maximum temperature.

2.2. Field Sampling

Leaves from young individuals of *E. edulis* were collected from March to July 2024. The samplings were conducted through active searching along two interpretive trails on the east-facing slope of the mountain, each approximately 1.5 km long, one in each environment: submontane (15°25'19"S, 39°32'30"W; 200 m a.s.l.) and montane forest (15°23'6"S, 39°34'17"W; 850 m a.s.l.) (Fig. 2). One temperature and relative humidity sensor (M2301, Onset, USA) was installed at each altitude level in May 2024 and remained in the field for 32 days. Leaves from thirty individuals in the ontogenetic stage Juvenile I were sampled at each altitude level, ensuring a minimum distance of 20 m between individuals. The same was done for individuals in the Juvenile II stage. Individuals in the Juvenile I stage typically have two to four palmate leaves, with an insertion height of less than 15 cm, while individuals in the Juvenile II stage have pinnate leaves and an insertion height ranging from 15 to 60 cm (Silva et al., 2009).

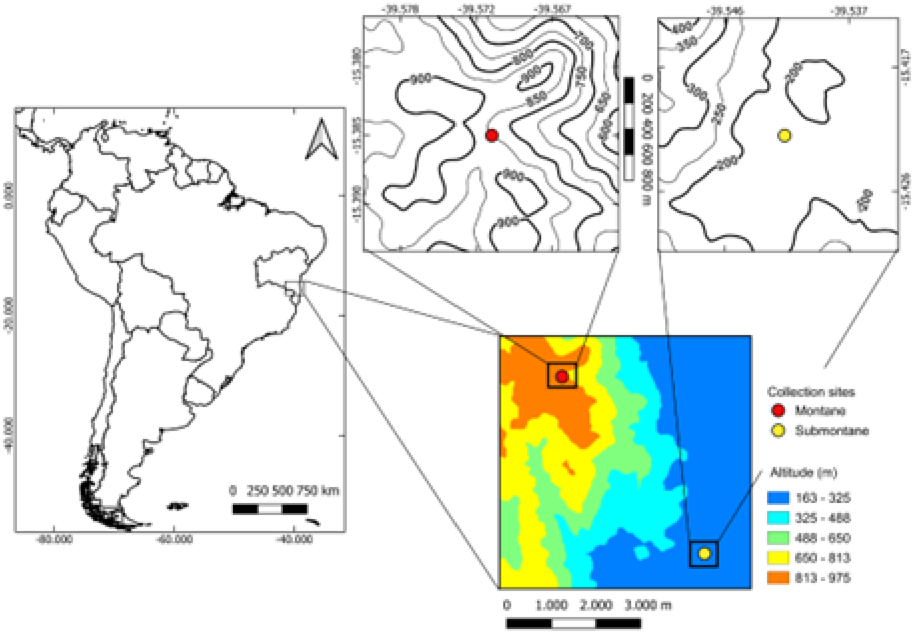

Fig. 2. Location of the starting points of the two trails used for plant material sampling. The submontane forest is located at approximately 200 meters above sea level, while the montane forest is situated at around 850 meters.

2.3. Morphological and Physiological Traits

All plants and leaf morphological and physiological traits are shown in Table 1. Initially, for each individual, height was measured with a ruler and stem diameter was measured using a digital caliper. After this, fully expanded leaves, that did not show apparent signs of pathogen and herbivore attacks, were collected and placed in ziplock plastic bags and moistened with water. The bags were then placed in a cooler with ice until the leaf physiological and morphological traits were measured in the Plant Ecophysiology Laboratory at the Universidade Estadual de Santa Cruz (UESC), located in Ilhéus, BA, Brazil (14°45′15″S, 39°13′59″W). These procedures were carried out to ensure that the leaves were well-hydrated and did not suffer any damage to their tissues before the leaf dehydration assays.

Leaf dehydration assays were conducted based on adaptations of the methodology described by Trueba et al. (2019) and Mielke et al. (2024). On the morning following the field sampling, the ziplock bags were removed from the cooler. For Juvenile I individuals, a leaflet was separated, while for Juvenile II individuals, a pinna was selected from each leaf for the leaf dehydration process and chlorophyll a fluorescence measurement (to facilitate understanding both will be referred as "leaflet" from now on). The leaflets were placed on the laboratory bench with a clip on each leaflet to ensure sample adaptation to darkness. After a period of 30 minutes, chlorophyll a fluorescence was measured in the median region of the leaflet, avoiding the main vein, using a Pocket PEA portable fluorometer (Hansatech Instruments, UK). Immediately after measuring fluorescence, each leaflet was weighed on an analytical balance to obtain the saturated leaflet fresh mass (LMs). Digital images were also captured, which were then analyzed using ImageJ software to calculate the leaflet area (LA) (Schneider et al., 2012). Chlorophyll index was also measured in the median region of the leaflet, using a portable chlorophyll meter Soil Plant Analysis Development (SPAD) (Minolta, Japan). After these procedures, the leaflets were placed back on the bench and dehydrated under laboratory conditions. Chlorophyll a fluorescence was measured again at intervals of 2, 4, 6, 8, 10, and 12 hours. After each measurement, the leaflets were weighed to obtain the current fresh mass decrease during dehydration (LMde). At the end of the dehydration cycle, the leaflets were placed in an oven with forced air circulation at 60°C for 48 hours to obtain the dry mass (LMd). The relative water content (RWC) was calculated from the values of LMs, LMde and LMd for each measurement time using $RWC = (LMde - LMd)/(LMs - LMd)$. The percentages of loss of maximum quantum yield of photosystem II on dehydration ($\mathrm{PL}_{[\mathrm{Fv/Fm}]}$) was calculated using the equation $PL_{[Fv/Fm]} = 100 \times 1 - ([Fv/Fm]de/[Fv/Fm]s)$, where *[Fv/Fm]de* is the value of the Fv/Fm ratio at each LMde value, and *[Fv/Fm]s* is the value of Fv/Fm at full hydration, that is, at the beginning of the assay. The absolute water content (AWC) was calculated using the following equation: $AWC = 100 \times (LMs - LMd)/LMd$. The slenderness index (HDR) was determined as the ratio between plant height (H) and stem diameter (D). The leaflet dry matter content (LDMC) and leaflet mass per area (LMA) were calculated through the respective following formulas (Garnier et al., 2001): $LDMC = 100 \times (LMd/LMs)$ and $LMA = LMd/LA$.

The JIP test represents the translation of the original data recorded from chlorophyll a fluorescence into biophysical parameters that quantify the energy flow at various stages through the PSII (Strasser et al., 2004; Lazár, 2006; van Heerden et al. 2007). We used JIP test parameters to understand the physiological responses of the photochemical stage of photosynthesis in individuals from different ontogenetic stages and altitudes. Performance indices indicate energy conservation through the reduction of electron acceptors between the photosystems (PI_{abs}) and the reduction of the final electron acceptors of photosystem I (PSI) (PI_{total}) (Strasser et al., 2004; Oukarroum et al., 2007; Gonçalves et al., 2010). Both PI_{abs} and PI_{total} are excellent parameters for analyzing the photosynthetic performance of plants, as they take into account energy conservation beyond PSII (Guimarães et al., 2022). The variables ABS, TR_0, ET_0 and DI_0 provide information on how photosystem II (PSII) is handling the incoming photons and how the transformation of the light energy into chemical energy and the electron flow within PSII occur (Gonçalves et al., 2010). We used the specific fluxes of energy per reaction center (RC), i.e., ABS/RC, TR_0/RC, ET_0/RC e DI_0/RC (Table 1).

Table 1. Abbreviations and units for morphological and physiological traits.

Traits	Abbreviature	Unit
Morphological traits		
Plant height	*H*	cm
Stem diameter	*D*	mm
Slenderness index	*HDR*	cm mm^{-1}
Leaflet dry matter content	*LDMC*	%
Leaflet mass per area	*LMA*	g m^{-2}
Absolute water content	*AWC*	%
Physiological traits		
Relative water content (*RWC*) at 50% of F_v/F_m loss	$RWC_{PL[Fv/Fm]50}$	%
Time to reach $RWC_{PL[Fv/Fm]50}$	$Time\_RWC_{PL[Fv/Fm]50}$	hours
Soil plant analysis development (*SPAD*) — Measures the chlorophyll index in leaves	*SPAD* index	unitless
Performance index (potential) for energy conservation from exciton to the reduction of intersystem electron acceptors	PI_{abs}	unitless
Performance index (potential) for energy conservation from exciton to the reduction of PSI end acceptors	PI_{total}	unitless

Absorption flux (of antenna Chlorophylls) per RC — It indicates the efficiency of light absorption relative to the number of active RC	ABS/RC	unitless
Trapping per RC — It reflects the efficiency of electron transport during photosynthesis	TR_0/RC	unitless
Electron transport flux (further than Q_A^-) per RC — It indicates fraction of absorbed energy that is successfully transferred through the photosynthetic system per RC	ET_0/RC	unitless
Dissipation per RC — The amount of energy dissipated "lost as heat" per RC during the photosynthetic process; higher values may indicate stress in the plant.	DI_0/RC	unitless

PSI: photosystem I; F_v/F_m: maximum quantum yield of of photosystem II; RC: reaction center; Q_A^-: reduced quinona A. Definitions based on Strasser et al., 2004: Gonçalves et al., 2010; Gonçalves et al., 2012; Toro-Tobón et al., 2022.

2.4. Microclimatic Variables

Canopy cover was assessed using a smartphone and the CanopyCapture app (Lusk 2022), which provided the canopy cover instantly, ensuring that the individuals are under similar local light availability conditions. The M2301 temperature and relative humidity sensors (Onset, USA), installed in each altitudinal site, record environmental variables every hour. We used the records from 05/21/2024 to 06/21/2024 and calculated a daily mean temperature for each of the 32 recorded days. From these 32 daily means, we calculated an overall daily mean temperature for each location (Submontane and Montane). For the daily maximum and minimum temperatures, we obtained the highest and lowest temperature values recorded each day and subsequently calculated the mean maximum and minimum temperatures for each location. For the difference between the daily maximum and minimum temperatures (ΔT), we also calculated the mean from the 32 daily values obtained for each location.

From the relative humidity and temperature values, we calculated the water vapor pressure deficit (VPD) for each hour of the day over all 32 days of records using the following formula (Grossiord et al., 2020): $VPD = e_s - e_a$, where: $e_s = 613.75 \times e^{(17.502T)/(240.97+T)}$ and $e_a = e_s \times (RH/100\%)$. The variable e_s is the saturation water vapor pressure at ambient temperature, where T represents the temperature in °C registered at a given moment, while e_a is the current water vapor pressure, where RH represents the recorded relative humidity. Therefore, VPD is the difference between e_s and e_a. For the calculation of the mean daily VPD we used the same approach as with temperature but filtered the recorded values only between 6:00 AM and 6:00 PM, considering that the nighttime records mostly showed VPD values equal to 0 kPa.

2.5. *Relative Phenotypic Plasticity Index (PPR)*

The relative phenotypic plasticity index (PPR) was calculated to quantify the degree of plasticity in both physiological and morphological traits across two plant stages (Juvenile I or Juvenile II) at different altitudinal sites (submontane and montane). The PPR was calculated for each trait in the two plant stages (Juvenile I or Juvenile II) as the ratio between the absolute difference of all possible combinations of each repetition of the two altitudinal sites (submontane *versus* montane) and the maximum observed value (Eq. 1):

$$PPR_i = \frac{1}{n} \sum_{j=1}^{n} \left(\frac{|X_{ij,Submontane} - X_{ij,Montane}|}{\max{(X_{ij})}} \right), \qquad (1)$$

where, PPR_i is the relative phenotypic plasticity index for trait i; $X_{ij,Submontane}$ and $X_{ij,Montane}$ represent the observed values of trait i in the repetition j for the Submontane and Montane altitudinal sites, respectively; max (X_{ij}) is the maximum observed value of the trait i at all sites and repetitions; n is the total number of possible combinations between replicates of the two altitudinal sites; and $\sum_{j=1}^{n}(\dots)$ indicates the sum of all possible combinations of repetitions between sites. PPR standardizes plasticity values, making them comparable between traits with different units of measurement, and since it is a permutation of all possible pairs of repeat combinations between sites, a mean and 95% confidence interval can be calculated.

2.6. Data Analysis

The relative water content at which 50% of the maximum quantum yield of photosystem II is lost ($RWC_{PL[Fv/Fm]50}$) were determined for each dehydrated leaflet by fitting the relationship between $PL_{[Fv/Fm]50}$ and RWC using best fit of three shaped functions: linear, $y = a + b \times x$; logarithmic, $y = a \times \ln(x) + b$ and exponential, $y = a \times e^{(-b \times x)}$. This resulted in 120 differently shaped functions and values of $RWC_{PL[Fv/Fm]50}$. The same approach was used to determine the time needed for each leaflet to reach the $RWC_{PL[Fv/Fm]50}$ value ($Time\_RWC_{PL[Fv/Fm]50}$) by fitting the relationship between RWC and the dehydration time in hours (Mielke et al. 2024). All functions were compared using the coefficient of determination (R^2) and the Akaike information criterion corrected for small samples (AICc, Berk, 2018), with the best fit selected based on the highest R^2 and the lowest AICc.

All morphological and physiological traits from the two altitudinal elevation sites (submontane or montane) and plant stages (Juvenile I or Juvenile II) were evaluated by two-way analysis of variance (Fisher's ANOVA) or Kruskal-Wallis's test, *a priori* checking the statistical assumptions (*i.e.* normality of residuals by Shapiro-Wilk's test, Shapiro & Wilk, 1965; and homogeneity of variances by Bartlett's test, Barlett, 1937). The detection of the difference between means was by the least significant difference test (*LSD*, $P<0.05$). The Tukey's honestly significant difference test was performed following the two-way ANOVA, while Dunn's test for multiple comparisons was applied after the Kruskal-Wallis test. A Kruskal-Wallis's test was also used to evaluate canopy cover.

To explore the correlation patterns among the morphological and physiological traits across different altitudinal sites and plant stages, a hierarchical clustered heatmap was generated. The data matrix was standardized using log_{10} and then z-scores to ensure comparability between traits with different units (Gu et al., 2016). Hierarchical clustering was performed using Ward's method (Ward, 1963), with Euclidean distance serving as the metric to quantify dissimilarities between traits.

To further elucidate the differentiation of groups based on altitudinal sites and plant stages, a Linear Discriminant Analysis (LDA) was conducted using the measured morphological and physiological traits. The dataset was standardized to a mean of zero and unit variance prior to LDA to meet the assumptions of the analysis (Fisher, 1936).

Statistical differences in PPR for physiological and morphological traits between the two plant stages were assessed using independent t-student tests for traits meeting the assumptions of normality and homogeneity of variances. For traits that did not meet these assumptions, the *Mann-Whitney U* test was employed as a non-parametric alternative. Results were presented as means ± 95% confidence intervals (CI).

All statistical analyses and data visualizations were performed using the R programming language (*version* 4.4.1; R Core Team, 2024). The "*pheatmap*" package was utilized for heatmap generation (Kolde, 2019), and the "*MASS*" package was employed for *LDA* implementation (Venables & Ripley, 2002).

3. Results

3.1. Microclimate

The results obtained for the microclimatic variables support empirical observations of differences in the microclimate of the environments where the samplings were conducted (submontane and montane forests). The mean temperature in the submontane was higher than in the montane environment. The submontane forest exhibited higher daily maximum temperature, daily minimum temperature, and ΔT (Table 2). The mean daytime water vapor pressure deficit was also higher in the submontane environment compared to the montane, with daily values exceeding 0.30 kPa in the submontane (Fig. 3). The daily maximum VPD values in the submontane forest were three times higher than those in the montane (Table 2). The values of saturation water vapor pressure at ambient temperature (e_s) and current water vapor pressure (e_a) were higher in the submontane forest (Table 2).

The canopy cover was similar among the study sites ($\chi^2 = 4.29$, df = 3, $P > 0.05$). The mean values of canopy cover were as follows: Juvenile I Submontane, 83%; Juvenile II Submontane, 76%; Juvenile I Montane, 83%; and Juvenile II Montane, 85%.

Table 2. Microclimatic characterization of submontane and montane forest environments in Southern Bahia.

Variable	**Submontane**	**Montane**
Mean temperature (ºC)	21.24 ± 0.10	18.31 ± 0.08
Daily maximum temperature (ºC)	23.94 ± 0.19	19.29 ± 0.11
Daily minimum temperature (ºC)	19.14 ± 0.20	17.27 ± 0.11
ΔT (ºC)	4.80 ± 0.32	2.02 ± 0.13
Mean diurnal DPV (kPa)	0.07 ± 0.02	0.02 ± 0.007
Maximum DPV (kPa)	0.20 ± 0.04	0.05 ± 0.01
e_s (kPa)	2.69 ± 0.02	2.15 ± 0.01
e_a (kPa)	2.62 ± 0.01	2.12 ± 0.01

The values are presented as mean ± standard error. ΔT: mean daily temperature difference; DPV: water vapor pressure deficit; e_s: saturation water vapor pressure at ambient temperature and e_a: current water vapor pressure.

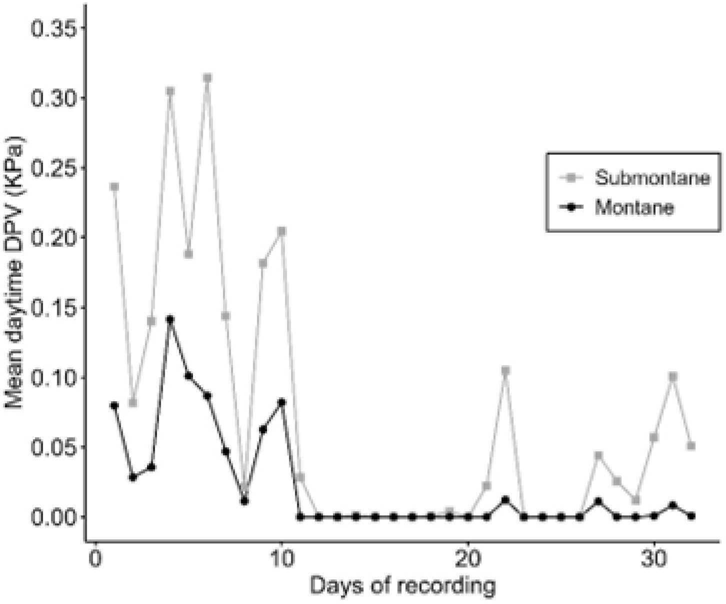

Fig. 3. Mean water vapor pressure deficit (VPD) values during the daytime period (6:00 AM to 6:00 PM) in the two sampling environments (Submontane and Montane forests) over the 32 days of recording.

3.2.Morphological and Physiological Traits

Both morphological and physiological traits showed a dependence on altitude and stage of development, with significant differences between sites and stages. Within the same altitude, individuals at ontogenetic stages Juvenile I and Juvenile II exhibited different functional trait values; however, these responses varied depending on the altitude at which they were collected. Within the same ontogenetic stage, functional traits differed according to altitudinal site, and these differences were more pronounced in the Juvenile I stage.

For individuals in the Juvenile I stage of development, slenderness index (HDR), leaflet dry matter content (LDMC), absorption flux per reaction center (ABS/RC), trapping per reaction center (TR$_0$/RC), and dissipation per reaction center (DI$_0$/RC) were higher in the submontane forest. In the montane forest, a higher stem diameter (D), absolute water content (AWC), time required to reach the relative water content at which 50% loss of F$_v$/F$_m$ occurs (Time_RWC$_{PL[Fv/Fm]50}$), chlorophyll index (SPAD index), performance index (PI$_{abs}$) and total performance index (PI$_{total}$) were found, while plant height (H), leaflet mass per area (LMA), relative water content at 50% of F$_v$/F$_m$ loss (RWC$_{PL[Fv/Fm]50}$), and electron transport flux per reaction center (ET$_0$/RC) showed no differences between sites (Table 3).

Individuals at the Juvenile II stage showed only AWC higher in the montane forest. In the submontane forest, higher LDMC and RWC$_{PL[Fv/Fm]50}$ were found, while H, D, HDR, LMA,

$Time\_RWC_{PL[Fv/Fm]50}$, SPAD index, PI_{abs} and PI_{total}, ABS/RC, TR_0/RC, ET_0/RC, and DI_0/RC showed no differences between sites (Table 3).

Table 3. Comparison of morphological and physiological parameters between plant stages (Juvenile I or Juvenile II) and altitudinal elevation sites (Submontane or Montane) was conducted using two-way analysis of variance (ANOVA) or Kruskal-Wallis's test, as appropriate.

Parameter	**Juvenile I**		**Juvenile II**		$F^{(\S)}$ **or** KW	R^2	P_{model}
	Submontane	**Montane**	**Submontane**	**Montane**			
Morphological traits							
H	20.8 ± 1.3 **Ba**	24.8 ± 1.5 **Ba**	48.3 ± 2.4 **Aa**	48.5 ± 2.0 **Aa**	92.5	---	***
D	3.29 ± 0.26 **Bb**	5.56 ± 0.26 **Ba**	7.07 ± 0.50 **Aa**	6.99 ± 0.23 **Aa**	87.6	---	***
HDR	2.79 ± 0.52 **Aa**	1.04 ± 0.07 **Bb**	1.33 ± 0.17 **Ba**	1.29 ± 0.08 **Aa**	68.9	---	***
LDMC	40.1 ± 1.5 **Aa**	37.8 ± 1.1 **Ab**	40.9 ± 1.5 **Aa**	37.9 ± 0.8 **Ab**	$25.8^{\S}$	---	***
LMA	29.9 ± 1.5 **Ba**	30.5 ± 1.1 **Ba**	39.1 ± 2.1 **Aa**	39.8 ± 2.2 **Aa**	70.4	---	***
AWC	59.9 ± 1.5 **Ab**	62.2 ± 1.1 **Aa**	59.1 ± 1.5 **Ab**	62.1 ± 0.8 **Aa**	25.8	---	***
Physiological traits							
$RWC_{PL[Fv/Fm]50}$	11.3 ± 0.7 **Ba**	12 ± 0.55 **Aa**	20 ± 1.18 **Aa**	14.1 ± 0.69 **Ab**	44.7	---	***
$Time\_RWC_{PL[Fv/Fm]50}$	8.65 ± 0.4 **Bb**	14.3 ± 0.7 **Aa**	11.4 ± 0.5 **Aa**	13.2 ± 0.5 **Aa**	33.4	---	***
SPAD index	36.7 ± 2.2 **Bb**	42.7 ± 2.3 **Aa**	40.8 ± 2.6 **Aa**	43.9 ± 3.1 **Aa**	18.5	---	***
PI_{abs}	1.73 ± 0.24 **Bb**	2.96 ± 0.30 **Aa**	2.73 ± 0.34 **Aa**	2.80 ± 0.34 **Aa**	$14.2^{\S}$	0.27	***
PI_{total}	0.22 ± 0.04 **Bb**	0.41 ± 0.05 **Aa**	0.38 ± 0.07 **Aa**	0.39 ± 0.06 **Aa**	29.2	---	***
ABS/RC	1.36 ± 0.07 **Aa**	1.15 ± 0.05 **Ab**	1.18 ± 0.04 **Ba**	1.22 ± 0.09 **Aa**	26.2	---	***
TR_0/RC	1.08 ± 0.05 **Aa**	0.95 ± 0.04 **Ab**	0.97 ± 0.03 **Ba**	1.00 ± 0.07 **Aa**	20.0	---	***
ET_0/RC	0.38 ± 0.01	0.38 ± 0.01	0.38 ± 0.01	0.39 ± 0.01	2.2	---	*n.s.*
DI_0/RC	0.28 ± 0.02 **Aa**	0.20 ± 0.01 **Ab**	0.21 ± 0.01 **Ba**	0.22 ± 0.02 **Aa**	37.8	---	***

Uppercase letters indicate statistically significant differences between plant stages within the same altitudinal elevation site (Submontane or Montane; *LSD*, $P < 0.05$), while lowercase letters denote statistically significant differences between altitudinal elevation sites within the same plant stage (Juvenile I or Juvenile II; *LSD*, $P < 0.05$). Refer to Table 1 for the meaning of abbreviations. Mean ± error standard; $F^{(\S)}$: Fisher's value; *KW*: Kruskal-Wallis value; R^2: coefficient of determination; P_{model}: model probability; *n.s.*: not significant, $P>0.05$; *: $P<0.05$; **: $P<0.01$; and ***: $P<0.001$.

Comparing the stages of development within the submontane forest, Juvenile I individuals had higher HDR, ABS/RC, TR_0/RC, and DI_0/RC, while Juvenile II had higher H, D, LMA, $RWC_{PL[Fv/Fm]50}$, Time_$RWC_{PL[Fv/Fm]50}$, SPAD index, PI_{abs} and, PI_{total}. LDMC, AWC, and ET_0/RC showed no significant difference. Within the montane forest, Juvenile II individuals had higher H, D, HDR and LMA. All other traits II (LDMC, AWC, $RWC_{PL[Fv/Fm]50}$, Time_$RWC_{PL[Fv/Fm]50}$, SPAD index, PI_{abs}, PI_{total}, ABS/RC, TR_0/RC, ET_0/RC, and DI_0/RC) did not differ significantly between Juvenile I and Juvenile II (Table 3).

3.3. Trait Variation: Clustering and Discriminant Analysis

The resulting heatmap visualizes the relative trait expression (Fig. 4A), this approach enabled the visualization of trait co-expression patterns and their clustering across the environmental gradients, revealing key trait associations specific to each altitudinal site and developmental stage. In order of altitudinal site and developmental stage, Juvenile II plants were very similar between the montane and submontane forests, followed by Juvenile I from the montane, lastly, Juvenile I from the submontane. With respect to the traits, four clusters were observed, with high values with AWC, LMA, LDMC, SPAD, H, and $RWC_{PL[Fv/Fm]50}$, and then grouping with low values with DI_0/RC, PI_{total}, and ET_0/RC, lastly two groupings with intermediate values: D and Time_$RWC_{PL[Fv/Fm]50}$, and PI_{abs}, HDR, ABS/RC, and TR_0/RC.

The LDA model aimed to maximize the separation between predefined groups while minimizing within-group variance (Fig. 4B). Ellipses with 95% confidence intervals around the group centroids indicate the dispersion and separation of groups based on different altitudinal sites and plant ontogenetic stages. The resulting biplot displays the projection of trait variables onto the first two linear discriminants, LD1 and LD2, which account for 78.2% and 18.4% of the total variability, respectively (96.6% cumulative variance explained). This approach enabled the identification of key traits contributing to the differentiation of plant responses across varying environmental and developmental conditions, as illustrated in the heatmap and LDA biplot. The LD1 axis, which explains most of the variability, is strongly influenced by physiological traits such as PI_{abs}, PI_{total}, ET_0/RC, and H; these traits have greater weight in the separation of Juvenile I and Juvenile II stage plants at both sites. On the other hand, the LD2 axis, with lower contribution to the total variability, discriminates mainly based on D, ABS/RC, HDR, DI_0/RC, and TR_0/RC, which most effectively differentiate Juvenile I plants between the altitudinal sites.

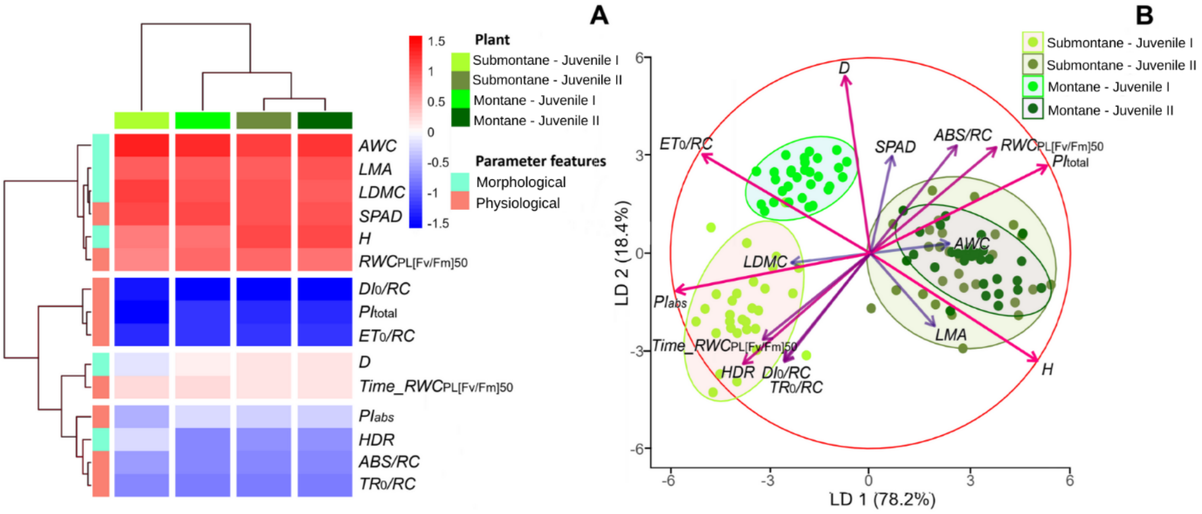

Fig. 4. A) Hierarchical clustered heatmap showing the correlation patterns of morphological and physiological traits across different altitudinal elevation sites (Submontane or Montane) and plant stages (Juvenile I or Juvenile II). The color gradient from red (high values) to blue (low values) highlights the variation in trait expression across the sites and plant stages; and **B)** Linear discriminant analysis (LDA) biplot projecting morphological and physiological traits onto the LD1 and LD2 axes, which explain 78.2% and 18.4% of the variability, respectively (96.6% cumulative variance explained). The ellipses with 95% confidence intervals represent distinct groups based on different altitudinal elevation sites (Submontane or Montane) and plant stages (Juvenile I or Juvenile II), capturing their separation in multivariate trait space. Vector arrows (with cos^2 adjustment) indicate the direction and magnitude of each trait's contribution to group separation. Refer to Table 1 for the meaning of abbreviations.

3.4. Relative Phenotypic Plasticity Index for Plant Stages

The PPR values provided insights into the capacity of the plant to adaptively respond to environmental variations at different altitudinal sites, highlighting significant plasticity differences between developmental stages in response to altitudinal gradients (Fig. 5). In terms of morphological traits, significantly greater plasticity was observed in HDR, D and H in Juvenile I than in Juvenile II ($P<0.001$), while for LMA, greater plasticity was found in Juvenile II ($P<0.05$). No significant differences between plant stage ($P>0.05$) were found for LDMC and AWC. For physiological traits, PI_{total}, PI_{abs}, $RWC_{PL[Fv/Fm]50}$, DI_0/RC, ABS/RC, and TR_0/RC significantly greater plasticity was observed in Juvenile I than in Juvenile II, with exception

SPAD, Time_RWC$_{PL[Fv/Fm]50}$, and ET$_0$/RC which showed no significant differences between plant ontogenetic stage.

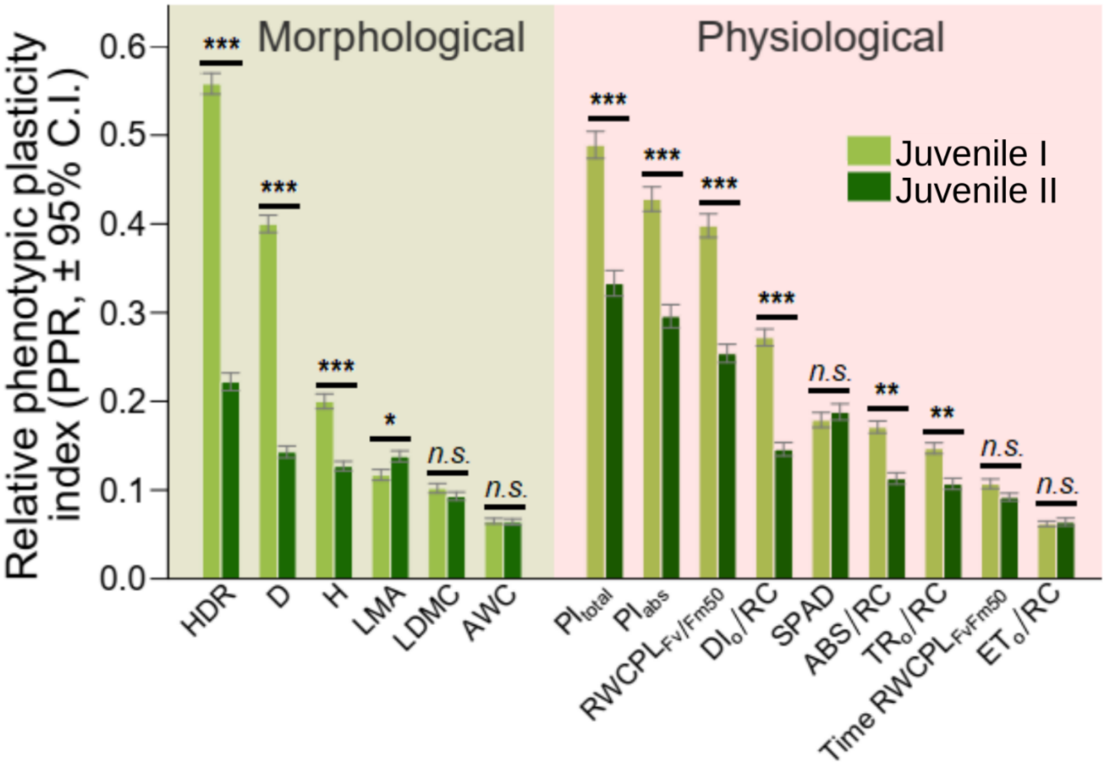

Fig. 5. Relative phenotypic plasticity index (PPR) for physiological and morphological traits in plant stages (Juvenile I or Juvenile II) across different altitudinal elevation sites (Submontane or Montane). Two plant stages (Juvenile I and Juvenile II) were compared based on their response to environmental variation between the altitudinal elevation sites. Asterisks indicate statistically significant differences between plant stages (Young 1 or Young 2); $P>0.05$, *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, and *n.s.*: not significant. Refer to Table 1 for the meaning of abbreviations. Mean ± 95% I.C. (confidence interval).

4. Discussion

We found that morphological and physiological functional traits responded to both ontogenetic stage and altitudinal site. This indicates that juvenile *E. edulis* plants can adjust their functional traits according to both altitudinal site and their ontogenetic stage. Comparative studies on the early stages of *E. edulis* are scarce. Our findings provide novel insights into the behavior of this endangered species (Leitman et al., 2013) at two early ontogenetic stages (Juvenile I and Juvenile II). Additionally, we provide valuable information on two sites with altitudinal differences (submontane and montane forest) in an important region for species conservation in the state of Bahia (Amorim et al., 2009; Dias et al., 2014).

4.1.Microclimate

The mean temperature registered at 200 m a.s.l. and 850 m. a.s.l. in our study (Table 2) were consistent with those collected by Rocha (2016) at RPPN Serra Bonita between April 2014 and March 2015. They registered the average temperature of 20.70º C and 18.44º C at 513 m. a.s.l. and 894 m a.s.l., respectively. We recorded a higher average temperature at 200 m a.s.l., which is lower than the altitude sampled by Rocha (2016), and the same average temperature at 850 m a.s.l. (Table 2). The mean DPV we recorded at 200 m a.s.l. was similar to that recorded by Rocha (2016) at 513 m a.s.l., which was 0.08 kPa. The same pattern occurred at higher altitudes, where the author recorded a DPV of 0.01 kPa (Table 2). On the other hand, the maximum DPV values recorded in our study were lower than those reported by Rocha (2016), who recorded maximum DPV values of 1.30 and 1.14 kPa at 513 m a.s.l. and 894 m a.s.l., respectively.

The difference in altitude in the Serra Bonita region (200 m a.s.l. to 950 m a.s.l.) is responsible for creating a gradient of humidity and temperature (Dias et al., 2014; Bergamin et al., 2024). At lower altitudes, there is a tendency for temperature to be higher and precipitation lower compared to higher altitudes, with an estimated decrease of 0.59° C for every 100 m increase in altitude (Rocha and Amorim, 2012; Rocha, 2016). As the soil in the region is similar along the gradient, it is likely that temperature and air humidity are the main environmental factors influencing species distribution at this site (Rocha e Amorim, 2012).

The canopy cover was similar among the study sites. This indicates that all plants were exposed to similar light availability conditions, which is a crucial factor for the development of *E. edulis*, as shown by the increase in relative growth and net assimilation rates in response to increased light availability (Nakazono et al., 2001; Cerqueira et al., 2022). This consistency in light conditions across sites suggests that the plant responses are unlikely to be related to differences in light availability.

4.2.Morphological and Physiological Traits

For *E. edulis* juveniles, both morphological and physiological traits varied according to altitudinal site and ontogenetic stage. Significant differences were observed both between altitudinal sites within the same ontogenetic stage and between ontogenetic stages within the same altitudinal site.

The altitudinal site influenced several traits of Juvenile I individuals. Although height (H) was not affected, individuals from the montane forest exhibited a greater stem diameter (D), which contributed to a lower slenderness coefficient (HDR). Portela et al. (2021) reported that *E. edulis* individuals from larger forest fragments had lower H and greater D compared to those from smaller fragments. Since *E. edulis* is highly sensitive to habitat loss (Benchimol et al., 2017; Cerqueira et al., 2021), larger forest fragments likely provide more favorable conditions for the species, allowing individuals to allocate more resources to stem diameter growth as an adaptive strategy. A similar pattern can be expected in relation to water availability, given the strong dependence of juveniles *E. edulis* individuals on this factor (Andrade, 2001; Gatti et al., 2014). The higher precipitation and lower VPD in the montane forest create a more favorable environment for establishment, potentially enabling individuals to invest more in stem diameter growth. The slenderness coefficient (HDR) was lower in Juvenile I individuals from the montane forest. Lower values of this trait indicate greater stability (Oladoye et al., 2020). The greater D observed in the montane forest explains the lower HDR in this environment.

Juvenile I individuals from the submontane forest had higher leaf dry matter content (LDMC) and lower absolute water content (AWC). Lower values of LDMC are associated with rapid biomass production and higher values with efficient conservation of nutrients (Garnier et al., 2001; Silva et al., 2021). The ability to conserve nutrients is often linked to adaptations to high temperatures and drought resistance (Silva et al., 2021). Thus, the higher LDMC observed in Juvenile I individuals from the submontane forest may reflect an adaptive response to the drier and hotter conditions of this site compared to the montane forest. This is reinforced by lower AWC in the submontane. LDMC and AWC exhibited an inverse relationship, representing distinct strategies for coping with drought. Leaves with higher LDMC have, generally, lower capacity for water storage meaning that drought resistance in these individuals is primarily achieved through structural reinforcement rather than water retention (Toro-Tobón et al., 2022). Our results suggest that, in the submontane, individuals may adopt a strategy based on increased structural resistance, whereas in the montane forest, higher AWC provides greater short-term water reserves.

The chlorophyll fluorescence results suggest that Juvenile I individuals from the submontane forest are under greater stress compared to those from the montane forest, as indicated by their higher ABS/RC, TR_0/RC, and DI_0/RC values and lower PI_{abs} and PI_{total}. These differences point to an imbalance between light energy absorption (ABS) and the photosystem II (PSII) capacity to process electrons, leading to energy accumulation and the need for dissipation as heat

(DI_0/RC) to prevent oxidative damage (Strasser et al., 2004; Gonçalves et al., 2012; Toro-Tobón et al., 2022). Increased DI_0/RC reflects a protective strategy, as stressed plants tend to prevent photodamage by channeling excess energy away from photochemical pathways (Santos et al., 2009). Additionally, ABS/RC has been reported to increase under water stress conditions (van Heerden et al. 2007; Gomes et al., 2012; Guha et al., 2013). Similar patterns have been observed in other species. In *Euterpe oleracea*, a water deficit of -3 MPa led to a 33% increase in non-photochemical quenching (NPQ), a parameter equivalent to DI_o/RC, demonstrating that water stress enhances energy dissipation as heat (Oliveira et al., 2019). Similarly, Guha et al. (2013), studying *Morus indica*, found that under water stress, negative regulation of PSII activity was primarily driven by an increase in inactive reaction centers and enhanced energy dissipation. Meanwhile, Lage-Pinto et al. (2012) also documented a seasonal increase in heat dissipation in *Siparuna guianensis* and *Xylopia sericea* during the dry season, reinforcing the idea that this is a common response to environmental stress.

The reductions in PI_{abs} and PI_{total} observed in Juvenile I individuals from the submontane forest further support this interpretation. These parameters serve as key indicators of photochemical performance, as they take into account energy conservation beyond PSII (Guimarães et al., 2022). Lower PI_{abs} and PI_{total} values reflect reduced electron transport rates and the use of strategies for dissipating the energy captured by the light-harvesting systems in the form of heat (van Heerden et al. 2007; Toro-Tobón et al., 2022). A decline in photochemical efficiency were associated with lower net CO_2 assimilation rate which compromise the photosynthesis efficiency (Lopes Filho et al., 2021; Guimarães et al., 2022). Given that *E. edulis* at the Juvenile I ontogenetic stage requires efficient photosynthesis for development and growth, as all plants (Taiz and Zeiger, 2017), lower photochemical efficiency can affect these processes. Water stress is known to negatively affect photochemical performance causing reductions in PI_{abs} and PI_{total} (van Heerden et al., 2007; Guha et al., 2013). Lower values of PI_{abs} can be a consequence of the down-regulation of PSII under water-stress conditions and these consequences can be amplified by increase in leaf temperature, which is a consequence of having less water in the leaf tissues (van Heerden et al., 2007). Taken together, these findings suggest that individuals from the submontane forest are operating under more stressful environmental conditions, leading to physiological adjustments that prioritize stress tolerance over photosynthetic efficiency.

As with performance indices, chlorophyll index (SPAD index) was lower in Juvenile I individuals from the submontane forest. A decrease in chlorophyll content under water stress is commonly reported (Din, 2011; Ashraf and Harris, 2013; Guha et al., 2013). During drought the absorption of nutrients, such as nitrogen, can be limited, which can disrupt chlorophyll synthesis and lead to its degradation (Mody et al., 2009; Sharma, et al., 2020). Given that chlorophyll is an essential pigment for energy absorption in photosynthesis (Palta, 1990), chlorophyll content and chlorophyll fluorescence parameters can be correlated. For example, the maximum quantum yield of PSII (Fv/Fm) tends to decrease as chlorophyll content declines under water stress (Li et al., 2006; Gholamin and Khayatnezhad, 2011).

One possible explanation for the results found in Juvenile I is the influence of water stress, which is what we've been focusing. Physiological traits can respond to seasonal changes in environmental conditions (Larcher, 2003; van Heerden et al., 2007; Lage-Pinto et al., 2012), and although precipitation was high in Serra Bonita during the sampling period, the preceding dry season, which started in Augst and lasted until mid-December 2023, may have affected more the Juvenile I individuals from the submontane forest, leaving them still in the process of recovery. This prolonged water deficit could have triggered stress responses that persisted beyond the dry period (Xu et al., 2010; Li et al., 2019). The higher LDMC, ABS/RC, TR_0/RC, DI_0/RC, and lower AWC, PI_{abs}, PI_{total}, and SPAD index values in our study could be a consequence of water stress and the higher temperatures and lower air humidity present in the submontane forest when compared to the montane forest.

Another potential factor could be light availability. Cerqueira et al. (2022) found that in a greenhouse experiment, PI_{abs} and light availability were positive related in Juvenile I individuals. However, in our study, canopy openness was measured to ensure similar light conditions across all sampled individuals. Additionally, leaf mass per area (LMA), a key trait associated with light availability (Poorter et al., 2009; Cerqueira et al., 2021), did not differ between altitudinal sites. Shade-tolerant species such as *E. edulis* typically have lower LMA, as a greater distribution of photosynthetic biomass per unit area enhances light capture in understory environments with low irradiance (Niinemets, 2006; Poorter et al., 2009). Furthermore, Cerqueira et al. (2021) reported a positive relationship between canopy openness and LMA, showing that in Juvenile I individuals, LMA increased with greater canopy openness, which is associated with higher light availability. Since LMA remained consistent across altitudinal sites in our study, we believe that the observed differences in LDMC, AWC, and physiological traits are unlikely to be driven by variations in light availability.

Juvenile II individuals from submontane and montane forests showed very similar responses to each other. Twelve out of the fifteen traits analyzed showed no significant differences between the altitudinal sites, indicating that, at this ontogenetic stage, individuals are more alike, and the environment has less influence on their responses compared to Juvenile I individuals. The relationship between LDMC and AWC followed the same pattern observed in Juvenile I, with Juvenile II individuals from the submontane forest exhibiting higher LDMC and lower AWC. This reinforces the idea that *E. edulis* juveniles in the submontane forest, in both ontogenetic stages, display traits related to a more efficient nutrient conservation strategy (Garnier et al., 2001; Silva et al., 2021) compared to those in the montane forest. Juvenile II from the submontane forest adopt a strategy based on increased structural resistance, which favor a resistance to high temperatures and drought by providing greater resistance to wilting under water stress but reduces their ability to store water (Toro-Tobón et al., 2022). Since *E. edulis* is a shade-tolerant species, it must cope with light limitations. In this context, more conservative traits offer a greater adaptative advantage, prioritizing nutrient and biomass conservation over the allocation of energy to tissue growth (Reich et al., 2003). Moreover, stressful environmental conditions can influence resource-use strategies, and more conservative traits tend to provide competitive advantages for individuals in these conditions (Wright et al., 2004; Reich, 2014). This may explain the strategy of *E. edulis* juveniles in the submontane forest.

None of the chlorophyl fluorescence traits differ between Juvenile II individuals from the two altitudinal sites. All the processes involved in the photochemical phase of photosynthesis were similar in this ontogenetic stage and were unaffected by the environment during our sampling period.

In the submontane forest the morphological and physiological traits were influenced by the ontogenetic stage. Juvenile II individuals are taller and have a greater stem diameter than Juvenile I. With the growth and development of *E. edulis* individuals, an increase in H and D are expected, since the species can reach 20 m of heigh and 10-15 cm of stem diameter (Henderson et al., 1995). Two of the variables that did not show differences between ontogenetic stages were LDMC and AWC, the same ones that did respond to altitudinal site. Highlining that these traits were influenced by the environment and not by the development of plants.

A trait that did not respond to altitudinal site but respond to ontogenetic stage was LMA, which had higher values in Juvenile II. This leaf trait represents the amount of biomass required to form a unit of leaf area (Niinemets, 2006; Poorter et al., 2009). Leaves with higher LMA are more resistant (tougher) and thicker providing both structural reinforcement and greater resistance to herbivory (Larcher, 2003; Poorter et al., 2009). At this stage, individuals are better established in the environment and prioritize resource-use efficiency and leaf longevity, traits commonly associated with shade-tolerant forest interior species (Lusk et al., 2008; Reich, 2014). Therefore, the increase in LMA with ontogeny suggests a shift towards a more resource-conservative strategy in Juvenile II individuals. Tougher leaves with prolonged lifespans, as observed in *E. edulis*, are adaptive in low-light environments, reducing the need for frequent leaf replacement and promoting long-term survival, since LMA and leaf longevity are positively correlated (Wright et al., 2004; Gatti et al., 2011). Additionally, Carvalho et al. (1999) reported that, although similar herbivory attacks occur in infants and juveniles of *E. edulis*, these attacks did not result in leaf mortality in juveniles but caused 14.3% leaf mortality in infants. This suggests that the higher LMA observed in Juvenile II may also contribute to mitigating the impact of herbivory, as tougher leaves are less palatable and more resistant to damage (Poorter et al., 2009). Thus, leaf turnover can be greater for younger individuals, as herbivory attacks can lead to leaf loss. LMA can also have changed in Juvenile II individuals because they are taller. LMA can be influenced by the average light availability in the environment and ontogenetic changes, such as growth in height, in the species may alter the quantum interception efficiency of incident light (Niinemets, 2006; Poorter et al., 2009; Garcia et al., 2022). Which, in turn, can increase the biomass allocation to leaves.

Juvenile I individuals had lower PI_{abs} and PI_{total} and higher ABS/RC, TR_0/RC, and DI_0/RC values compared to Juvenile II. Lower PI_{abs} and PI_{total} indicate that Juvenile I individuals from the submontane forest presented lower energy conservation in the photosynthesis electron transport chain than Juvenile II individuals from the same forest (van Heerden et al. 2007; Toro-Tobón et al., 2022). Probably related to higher energy dissipation (i.e. high DI_0/RC) and more inactive RCs (Santos et al., 2009; Lage-Pinto et al., 2012). It has been reported that juveniles of oil palm (*Elaeis guineensis* Jacq.) can memorize the effects of water deficit events, since individuals submitted to more than one water deficit event had a better set of physiological responses to drought than those subjected to stress for the first time (Lopes Filho et al., 2021). The probability that Juvenile II individuals had already faced stress inducing conditions, such as drought, and developed a memory of how to respond to it are higher, because they are in the environment for more time than Juvenile I individuals. This way Juvenile II could be more able to deal with stress than Juvenile I individuals that could be facing stress for the first time. *E. edulis* is a slow-growing palm (Henderson et al., 1995) and, under greenhouse conditions, it toke around 225 days to reach the Juvenile I stage (Cerqueira et al., 2022), so the individuals in this stage from the submontane and montane forest could be facing their first drought between Augst until mid-December 2023.

Another factor that could have influenced the chlorophyll fluorescence results is the higher LMA in Juvenile II. Photosynthetic capacity in individuals of a species is strongly related to LMA, as it scales linearly with biomass investment in leaves, making leaf anatomy the main driver of the light-saturated rate of photosynthesis (Poorter et al., 2009). Regarding the SPAD index, Juvenile I exhibited lower values. When analyzing the SPAD values of the other sampled groups, we found that this difference was not due to an increase in the chlorophyll index in Juvenile II individuals from the submontane environment but rather to a decrease in Juvenile I individuals, as previously discussed in relation to the differences between Juvenile I individuals from the two altitudinal sites.

In the montane forest four traits were higher in Juvenile II individuals. H and D are ones related with the growth and development that is expected to the species (Henderson et al., 1995) and followed the results found in the submontane forest. LMA had the same response found in the submontane forest, probably for the same reasons. Since, leaves of older individuals tend to have higher LMA (Rijkers et al., 2000; Niinemets, 2006; Garcia et al., 2022), it can be expected in the *E. edulis* development an increase in biomass per leaf area, resulting in higher LMA in older individuals.

Unlike the submontane forest, in the montane forest, none of the chlorophyll fluorescence variables were influenced by ontogenetic stage, likely because this environment provides more favorable conditions for the species.

The conversion of excitation energy to the electron transport chain per reaction center (ET_0/RC) was a variable that did not respond to either the altitudinal site nor the ontogenetic stage. The physiological adjustments observed in Juvenile I individuals from the submontane forest likely acted as compensatory mechanisms to maintain normal electron transport in the still-active RCs, resulting in ET_0/RC values similar to those of the other individuals (van Heerden et al., 2007).

In the present study, we used a methodology reported by Trueba et al. (2019) and adapted by Mielke et al. (2024) to compare the susceptibility of juvenile individuals of tropical trees to leaf desiccation and, consequently, to severe water stress. According to this methodology, comparisons between individuals can be made using the RWC at which 50% of Fv/Fm is lost

($PL_{[Fv/Fm]50}$), meaning that leaves of species more susceptible to desiccation exhibit higher $PL_{[Fv/Fm]50}$ values at high RWCs. The $RWC_{PL[Fv/Fm]50}$ values found for the juvenile individuals of *E. edulis* in our study are similar to those found for all the species studied by Mielke et al. (2024), with the exception of *Garcinia gardneriana*, that exhibited the most tolerant photochemical phase of photosynthesis to desiccation with a $RWC_{PL[Fv/Fm]50}$ around 33%. However, we found that the leaflets of *E. edulis* reach $RWC_{PL[Fv/Fm]50}$ values in much less time compared to tropical tree species. For *E. edulis*, Juvenile I individuals from the submontane forest exhibited a Time_$RWC_{PL[Fv/Fm]50}$ of approximately 9 hours while the lowest Time_$RWC_{PL[Fv/Fm]50}$ value reported by Mielke et al. (2024) was approximately 16 hours for *Arapatiella psilophylla*. When comparing these two species, it is clear that the photosynthetic photochemical performance of *E. edulis* loses vitality very quickly with leaf desiccation. However, the differences become even more pronounced when comparing *E. edulis* with species such as *Gallesia integrifolia*, which took almost 90 hours to reach $RWC_{PL[Fv/Fm]50}$. These results reinforce the fact that *E. edulis* is a species highly susceptible to water stress, and that prolonged droughts can have a highly negative effect on the regeneration of this species compared to other tropical forest species.

4.3.Trait Variation: Clustering and Discriminant Analysis

The hierarchical clustering (heatmap) generated reveals patterns of similarity among variables within and between groups, while the linear discriminant analysis (LDA) assesses the effectiveness of the variables in discriminating the predefined groups (Chatfield, 1980; Gotelli e Ellison, 2011; Afifi et al. 2019). Variables such as AWC, LMA, LDMC, SPAD, H and $RWC_{PL[Fv/Fm]50}$ are more strongly associated with each other in the heatmap, indicating that these variables have similar response patterns, which may reflect aspects of the plant's morphology and physiology (Chatfield, 1980). The physiological responses observed in Juvenile I individuals from the submontane forest influenced the separation of this group from the others. They were the only ones that showed significant differences for the physiological variables (PI_{abs}, PI_{total}, SPAD, ABS/RC, TR_0/RC and DI_0/RC). In the clustering analysis, it was the most distant group from the others in the cluster, demonstrating that these individuals indeed behaved differently from the others. Juvenile II individuals are the most similar to each other, as shown by both the heatmap and the LDA.

4.4. Relative Phenotypic Plasticity Index for Plant Stages

Phenotypic plasticity is the ability of a genotype to express different phenotypes in response to different environmental conditions, without changes in its genetic constitution (Pigliucci, 2001; Gilbert, 2003). The greater relative phenotypic plasticity found in Juvenile I individuals for nine of the 15 traits analyzed was largely influenced by the responses of Juvenile I individuals from the submontane forest.

This is because, for Juvenile II individuals, 11 of the 15 traits evaluated were the same between the forests. The signs of stress in Juvenile I individuals from the submontane forest indicate that in this environment, the individuals had to employ strategies to cope with the adverse, stress-inducing conditions. This may involve physiological adjustments or the expression of a phenotype better adapted to this environment (Oliveira et al., 2019).

Although phenotypic plasticity is typically associated with something positive, this is not always the case (Schneider, 2022). In the case of the individuals analyzed in our study, the greater relative phenotypic plasticity is primarily related to the fact that Juvenile I individuals from the submontane forest exhibited a wider range of trait values, which can be associated with stress-related variables.

5. Concluding Remarks

Montane forests are priority areas for conservation (Martinelli, 2007). Serra Bonita is home to a rich biodiversity, including endemic species from southern Bahia and high-altitude regions (Amorim et al., 2009; Dias et al., 2014). Although our findings suggest that the Juvenile I individuals from the submontane forest of Serra Bonita are under more stressful conditions, *E. edulis* occurs in high abundance in both the submontane and montane forests (Rocha e Amorim, 2012). However, as demonstrated in our study, the montane forest is an environment that provides less stressful conditions for *E. edulis*, where juvenile individuals find ideal conditions for growth and development. This is likely due to higher precipitation and air humidity in the montane forest, which is influenced by lower temperatures and the presence of clouds and fog (Rocha e Amorim, 2012).

The populations of *E. edulis* in the submontane forests may be more vulnerable to extreme climatic events, such as occasional severe droughts, specifically the Juvenile I individuals. Therefore, conservation efforts should focus on these areas, aiming to minimize mortality among the more susceptible individuals. Montane forests, with their less stressful conditions for young individuals of *E. edulis*, can be prioritized as key areas for the conservation of the species, functioning as natural refuges, especially in the context of climate change. With predictions of increased frequency and intensity of droughts (IPCC, 2023), these moist montane forests could serve as a refuge for species like *E. edulis*, which depend on high humidity. This follows the trend, predicted for various species, of migration to higher altitudes due to climate change (Thuiller et al., 2005; Rumpf et al., 2018; Bergamin et al., 2024).

However, we must always bear in mind that, in addition to abiotic factors related to the occurrence of the species, which can be heavily affected by climate change (Portela et al., 2023), it is important to highlight that the threat to *E. edulis* is multifactorial, influenced by factors such as: palm heart extraction (Galetti e Fernandez, 1998), deforestation and habitat fragmentation (Benchimol et al., 2017; Cerqueira et al., 2021), and the extinction of pollinators and dispersers (Galetti et al., 2013; Carvalho et al., 2016; Portela et al., 2023). These factors interact, amplifying the risks to the species.

Considering the lower susceptibility of individuals in the Juvenile II stage to environmental conditions, for the repopulation of *E. edulis* or its use in reforestation programs, seedlings at this ontogenetic stage may have higher field survival rates compared to Juvenile I individuals. Therefore, not only is the maternal environment important in selecting seeds for the production of *E. edulis* seedlings used in repopulation and reforestation (Cerqueira et al., 2022), but also the age at which these seedlings are transplanted to the field. Furthermore, if introduced in submontane areas, it may be necessary to implement moisture retention measures or irrigation to ensure the successful establishment and growth of *E. edulis* regenerants in these environments.

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