



Trait variability in Bromeliaceae species from high-elevation habitats of the Atlantic Forest: morphoanatomical and biochemical responses to environmental factors

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Abstract

The interaction between abiotic factors and plant traits is central to ecological strategies and species distribution, especially in environments with climate variability. It is reflected in morphoanatomical and biochemical traits that influence growth and survival. Widely distributed, species-rich families are models for understanding how environmental filters shape plant traits and foster innovation. Bromeliaceae, a diverse Neotropical family, exemplifies this dynamic, bringing together species with multiple habits (epiphytic, rupicolous, saxicolous, and terrestrial) and remarkable morphological diversity. Given Bromeliaceae significance in the Brazilian Atlantic Forest, particularly in high-elevation regions, we investigated environmental parameters potentially influencing trait variation in three widely distributed species: *Aechmea vanhoutteana*, *Pitcairnia carinata*, and *Quesnelia kautskyi*, occurring in distinct areas within *Parque Nacional do Caparaó* (MG/ES), Brazil. PCA analyses confirmed that temperature, humidity, and light intensity were the primary filters shaping functional trait space, possibly influencing niche differentiation and species coexistence. *Aechmea vanhoutteana* exhibits a generalist ecological strategy, thriving across all three life habits with minimal morphoanatomical and biochemical content adjustments. *Pitcairnia carinata*, confined to rocky outcrops, exhibited notable anatomical specializations likely balancing thermal tolerance and water conservation. *Quesnelia kautskyi* demonstrated the greatest trait variation, particularly between terrestrial and epiphytic individuals, with humidity emerging as the main driver of anatomical and biochemical differences. While morphological traits were relatively stable across conditions and functioned as “effect traits”, anatomical and biochemical traits acted as “response traits”, adjusting dynamically to environmental stimuli. Altogether, the results highlight that morphoanatomical and biochemical plasticity is critical for ecological performance and persistence in heterogeneous montane landscapes. Furthermore, approaches incorporating multiple traits can offer key insights into how environmental pressures potentially drive plant adaptation, specialization, and evolution in Neotropical ecosystems.

Keywords Abiotic factors · *Aechmea vanhoutteana* · Phenotypic variability · *Pitcairnia carinata* · *Quesnelia kautskyi* · Trait–environment relationships

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1 Introduction

The interaction between abiotic factors and plant traits is a key driver of ecological strategies and species distribution, particularly in environments with pronounced climatic variability. In the last decades, increasing attention has been given to distinct plant traits, such as morphoanatomical and biochemical, as they reflect characteristics that influence critical population processes such as growth, reproduction and survival (Dickison 2000; Violle et al. 2007; Crang et al. 2018; Dias-Pereira et al. 2022; Liu et al. 2023; Pereira et al. 2025). Furthermore, these traits play a potential role in

elucidating the mechanisms underlying plant lineages diversification and speciation (Pierce et al. 2013; Vamosi et al. 2018; Skeel and Cardillo 2019). In this context, species-rich families with widely distributed genera serve as important model groups for understanding how plant traits are shaped by environmental filters across different ecosystems, which, to some extent, can lead to the appearance of key innovations (Vamosi et al. 2018). Among the most species-rich angiosperm lineages, Bromeliaceae stands out as a highly diverse Neotropical family, encompassing species that occupy a wide range of niches, including epiphytic, rupicolous, saxicolous, and terrestrial habitats, exhibiting a remarkable morphological diversity (Smith and Downs 1974; Benzing 2000). The family comprises ca. 3794 species distributed across 82 genera (Gouda et al. 2025, continually updated), resolved into eight subfamilies: Bromelioideae, Brocchioidae, Hechtioideae, Lindmanioideae, Navioideae, Puyoidae, Pitcairnioideae s.s. and Tillandsioideae, based on molecular phylogenies (Givnish et al. 2007, 2011).

Among the 82 genera of Bromeliaceae, those in the subfamilies Bromelioideae and Pitcairnioideae are particularly prominent in Brazilian vegetation due to their species richness and the diversity of ecological niches they occupy. In Pitcairnioideae, the genus *Pitcairnia* L'Her. (408 spp.) (POWO 2025) is commonly found in high-elevation grasslands (campos de altitude) within the Atlantic Forest, rocky outcrops (campos rupestres) in the Cerrado, and rocky habitats along rivers in the Amazon Rainforest (Saraiva et al. 2015, 2025). In Bromelioideae, genera, such as *Aechmea* Ruiz & Pav. (252 spp.) and *Quesnelia* Gaudich. (25 spp.) (POWO 2025), species diversity is notable and occupy a wide range of ecological niches, from epiphytic to terrestrial environments. These genera belong to lineages that have undergone significant diversification in Latin America's biodiversity hotspots, particularly in the Brazilian Cerrado and Atlantic Forest (Myers et al. 2000; Simon et al. 2009; Givnish et al. 2011). *Quesnelia*, for instance, is native and endemic in the Atlantic Forest Domain of Brazil (FFB 2025; POWO 2025), underscoring the importance of targeted conservation efforts to ensure the species' long-term survival (Versieux and Wendt 2007).

Regarding the habitats constituting the Atlantic Forest, high-elevation environments are remarkable for their unique species adaptations, making them ideal habitats for studying trait-environment interactions. In southeastern Brazil, high-elevation areas along the Serra do Mar and Serra da Mantiqueira Mountain ranges originate distinct vegetation mosaics that vary with elevation (Safford 1999; Vasconcelos 2011). Forests dominate the valleys up to 2000 m, supporting a high diversity of epiphytes (Safford 1999), while higher elevations are marked by exposed rocky areas, where xeromorphic herbs and subshrubs prevail (Safford 1999). These high-elevation regions also play a critical role in the

diversity of the Bromeliaceae, hosting many endemic species (Versieux and Wendt 2007). The combination of these diverse habitats, along with the high endemism of bromeliad species, makes the high-elevation environments in the southeastern Atlantic Forest an ideal setting for studying plant trait variation shaped by abiotic filters (Safford 1999; Ribeiro et al. 2007).

The variation in morphoanatomical traits is quite remarkable in Bromeliaceae, with several traits that are relevant in characterize bromeliad species, primarily associated with vegetative organs (i.e., Monteiro et al. 2011; Silva et al. 2018; Resende et al. 2020), particularly leaf traits (Monteiro et al. 2011; Dias-Pereira et al. 2022; Rapnouil et al. 2023). These include variations in leaf shape and rosette phyllotaxy, which form reservoir tanks, along with key anatomical adaptations, mainly related to water and nutrient absorption (Benzing 2000). Notable features include water storage tissues, scale-like trichomes, a well-developed aquiferous hypodermis, air channels and CAM photosynthetic metabolism (Tomlinson 1969; Benzing 2000; Pereira et al. 2011; Pereira-Dias and Santos 2015; Dias-Pereira et al. 2022). The morphoanatomical and biochemical variability, combined with the broad range of niches and habitats occupied by bromeliad species, underscores the potential influence of microclimatic variables on these traits. While investigating the effects of abiotic factors on morphoanatomical and biochemical traits is highly relevant, it is equally important to understand these traits from a functional perspective, investigating how they respond to environmental variables and how they contribute to adaptive strategies, species persistence and niche differentiation (Pierce et al. 2013, 2017). Such perspective mainly considers the plasticity of leaf traits, playing a key role in plant ecological strategies, as they directly influence the allocation of photosynthetic products (Mathur et al. 2018; Leroy et al. 2019; Rapnouil et al. 2023). For that, leaf traits can be classified as either 'effect' traits, which actively modify environmental conditions, or 'response' traits, which vary according to such conditions (Violle et al. 2007). In other words, morphoanatomical and biochemical plant traits play distinct roles in shaping the functional space that species occupy within a given environment, providing valuable perspectives into which characteristics actively shape ecosystems, contributing to their integrity, and which are influenced by environmental conditions, driving patterns of specialization and differentiation (Violle et al. 2007; Vamosi et al. 2018).

Therefore, considering the variation in traits and niches occupied by bromeliad species across high-elevation habitats, this study aims to investigate how environmental factors influence the expression of morphoanatomical and biochemical traits, contributing to niche differentiation among Bromeliaceae species occurring in distinct microenvironmental conditions. This objective is

addressed through three guiding questions: (1) How do environmental parameters, particularly light, humidity and temperature, influence the expression of morpho-anatomical and biochemical traits across species? (2) Do species with more restricted distributions tend to exhibit specialized traits? (3) How do morphological, anatomical, and biochemical traits differ in their response to specific abiotic factors and microclimatic variation? Through an integrative analysis, these questions aim to clarify the role of trait variability in bromeliads species, emphasizing the importance of studies that combine multiple traits to better understand the ecological strategies, which in turn, drive the success of Bromeliaceae in diverse environments.

2 Materials and methods

2.1 Study area

Plant material was collected in the *Parque Nacional do Caparaó* (PNC), which covers approximately 31,800 ha, located in the States of Espírito Santo and Minas Gerais (20°19' S 20°37' S 41°43' W 41°53' W). Approximately 80% of the area belonging to the National Park is situated in the Espírito Santo State, while 20% lies in Minas Gerais (ICMBIO 2019). According to Ab'Saber's classification (2003), The National Park belongs to the Morphoclimatic Domain of the Atlantic Forest. The climate is classified as Cwb (Köppen classification) (Alvares et al. 2013), a high-elevation tropical climate, with an average annual temperature ranging from 19 to 22 °C and average annual rainfall between 1000 and 1500 mm, mainly occurring from November to January (ICMBIO 2019).

2.2 Collection site and plant material

The collection sites are represented and described in Table 1, with four sites (A, B, C, and D) belonging to the State of Minas Gerais and three (E, F, and G) included in the State of Espírito Santo. The studied species, collection sites and features, as well as life habits per species, are detailed in Table 1. Species identification was conducted by comparing live specimens with Machado's field guide (Machado et al. 2016).

Aechmea vanhoutteana (Van Houtte) Mez, *Pitcairnia carinata* Mez and *Quesnelia kautskyi* C. Vieira were collected between November 2012 and March 2013 for traits analysis. Regarding life habits, for *A. vanhoutteana*, we collected five individuals for each habit (rupicolous, terrestrial and epiphyte). For *Pitcairnia carinata* we collected 15 rupicolous individuals and for *Q. kautskyi*, a survey of 11 terrestrial and eight epiphyte individuals was performed. During the same period, a survey of morphoanatomical and biochemical traits, as well as environmental parameters, were performed and described below. The studied species are key components of high-elevation habitats in the Brazilian Atlantic Forest (Versieux and Wendt 2007; FFB 2025; POWO 2025) and exhibit distinct growth habits and morphological traits. Therefore, they are considered promising models for investigating the influence of environmental factors on trait variability in bromeliad species.

2.3 Morphological traits analysis

Morphological traits were assessed by measuring the leaf and leaf sheath areas. Three leaves from the middle of the rosette were collected from each individual. Due to the strong curvature of the leaves, precise measurements required templates to be made by firmly pressing the blades onto paper. The area (cm²) of the cut templates was

Table 1 Collection sites with coordinates, landscape features and altitude from *Parque Nacional do Caparaó*, along with the species of Bromeliaceae collected, categorized by their life habits (R=rupicolous, T=terrestrial, E=epiphytic)

Collection sites	Coordinates	Landscape features	Altitude (m)	Species collected (habit)
A. Vale Verde (MG)	20°25'160" S/41°50'900" W	Dense forest with a river flowing beneath boulders	1.300	<i>Aechmea vanhoutteana</i> (R/T/E) <i>Quesnelia kautskyi</i> (T/E)
B. Vale encantado (MG)	20°24'697" S/41°50'062" W	Rocky cliff in a valley with rapids	2.019	<i>Pitcairnia carinata</i> (R)
C. Estrada para Tronqueira (MG)	20°24'575" S/41°50'945 W	Forest with plants collected from rocky cliffs	1.502	<i>Pitcairnia carinata</i> (R)
D. Cachoeira Bonita (MG)	20°24'21" S/41°50'16" W	Waterfall nestled within forest	1.827	<i>Quesnelia kautskyi</i> (T/E)
E. Pedra escorada (ES)	20°33'852" S/41°45'857" W	Dense forest	1.147	<i>Quesnelia kautskyi</i> (T/E)
F. Rio Norte (ES)	20°26'43,8" S/41°44'0,8" W	Forest	1.161	<i>Quesnelia kautskyi</i> (T/E)
G. Cachoeira Sete Pilões (ES)	20°28'58" S/41°49'51" W	Waterfall within forest, with plants collected from open rocky areas	1.844	<i>Pitcairnia carinata</i> (R)

measured using the Leaf Area Measurement System (Delta Co.).

2.4 Anatomical analysis

For the anatomical analyses, leaves from the middle portion of the rosette were collected from all sampled individuals of each species and habit. In total, 15 individuals of *Aechmea vanhoutteana* (5 per habit), 15 of *Pitcairnia carinata* (rupicolous), and 19 of *Quesnelia kautskyi* (8 epiphytic and 11 terrestrial) were anatomically processed. For each individual, three blocks were prepared, four slides per block, and four cross-sections per slide were measured. Midsection leaf samples were fixed in FAA50 (Johansen 1940) for 48 h and stored in 70% ethanol for further analysis. For micromorphometric analysis of the thickness (μm) of chlorenchyma and aquiferous parenchyma, the plant material was embedded in historesin and three blocks were prepared for each individual. Transverse sections of 5 μm thickness were obtained using a rotating microtome at the *Laboratório de Anatomia Vegetal* in the *Universidade Federal de Viçosa* (Viçosa, MG-Brazil). The sections were stained with Toluidine Blue, pH 4.0 (Kraus and Arduin 1997; modified) and photographed using a photomicroscope (model AX70TRF Olympus Optical®, Tokyo, Japan). Analyses were performed using AnatiQuanti 2.0 software (Aguiar et al. 2007).

To analyse stomatal density and scale density, leaf fragments were subjected to the diaphanization process (Kraus and Arduin 1997). Three fragments from the abaxial and three from the adaxial leaf surfaces, stored in 70% ethanol, were washed in water, and treated with a 10% sodium hydroxide solution. After rinsing in distilled water, the fragments were immersed in 20% sodium hypochlorite until fully cleared. The material was then stained with fuchsin, mounted in gelatin, and analyzed using AnatiQuanti 2.0 software (Aguiar et al. 2007). The entire photographic record was captured using a photomicroscope (model AX70TRF Olympus Optical®, Tokyo, Japan) equipped with a U-photo system and a Spot Insight Color 3.2.0 camera (Diagnostic Instruments Inc., New York, USA) at the *Laboratório de Anatomia Vegetal* in the *Universidade Federal de Viçosa*.

2.5 Biochemical analysis

Biochemical analyses included determining leaf pigment and phenol content. These analyses were performed only once for each species. Pigment and phenolic contents were quantified using pooled leaf discs collected from sampled individuals of each species/habit. As these measurements were based on pooled material and did not include independent biological replication at the individual level, the biochemical data were used primarily as exploratory trait descriptors and interpreted with caution. Fresh leaf material

was used by collecting 6 mm discs from the midsection of leaves from the middle of the rosette. For the determination of chlorophyll *a*, chlorophyll *b* and carotenoid pigments, four leaf discs were immersed in 7 mL of dimethyl sulfoxide (DMSO) in sealed tubes wrapped in aluminium foil. The tubes were incubated in a water bath at 65 °C for 48 h. Absorbance was measured at 470, 646, and 663 nm using a double-beam spectrophotometer at the *Laboratório de Nutrição e Metabolismo* in the *Universidade Federal de Viçosa* (Hiscox and Israelstam 1979).

For phenol determination, four leaf discs were macerated with an MCA extract (methanol, chloroform and water) and centrifuged. The resulting eluates were collected in glass tubes, mixed with distilled water and Folin–Ciocalteu solution, and left for 15 min. Subsequently, alkaline reagent “A” (prepared with 2% sodium carbonate in 0.1 N sodium hydroxide) was added, and the solution was manually stirred. Absorbance was measured at 760 nm using a double-beam spectrophotometer (Genesys 2 PC, Thermo Spectronic) (Bielecki and Turner 1966; modified). The standard curve was prepared using known amounts of tyrosine.

2.6 Environmental parameters

2.6.1 Luminosity

Irradiation on exposed plants was measured using hemispherical photography, with one recording taken per individual. Images were obtained using a Nikon UR-E12 camera with a Nikon FC-E9 fisheye lens mounted on a tripod above each individual. Photographs were taken without direct sunlight, with the camera's top facing magnetic north. Images were analysed using Gap Light Analyzer (GLA) software, which provided total light intensity data ($\text{photons.m}^{-2}.\text{day}^{-1}$) (Frazer et al. 1999).

2.6.2 Micrometeorological variables

Micrometeorological variables at the growth sites (A to G)—air temperature (°C), relative air humidity (%), and wind speed (m/s)—were recorded repeatedly during the field sampling campaigns between November and March 2013, using the Kestrel 4300 Wind and Weather Tracker (Nielsen-Kellerman USA). Environmental parameters (temperature, relative humidity, light intensity, and wind speed) were measured in situ during each field sampling campaign at the collection sites and life habits, rather than through continuous monitoring. The values presented in Table 2 represent mean measurements calculated for each life habit (or collection site, in the case of *Pitcairnia carinata*), reflecting the local microenvironment during the sampling period rather than single punctual records.

Table 2 Environmental parameters recorded for different life habits of *Aechmea vanhoutteana* and *Quesnelia kautskyi*, as well as for different collection site of the exclusively rupicolous species *Pitcairnia carinata* in the areas from Parque Nacional do Caparaó

	Temperature (°C)	Relative air humidity (%)	Light intensity (photons.m ⁻² .day ⁻¹)	Wind speed (m/s)
<i>Aechmea vanhoutteana</i>				
Life habit				
Epiphytic	23.46	71.70	12.07	0.44
Rupicolous	23.62	72.92	10.08	0.14
Terrestrial	23.28	72.72	10.74	0.08
<i>Pitcairnia carinata</i>				
Collection site				
Vale encantado (MG)	20.84	60.05	95.68	1.14
Estrada para Tronqueira (MG)	26.40	57.58	70.07	0.47
Cachoeira Sete Pilões (ES)	17.72	66.74	67.79	0.83
<i>Quesnelia kautskyi</i>				
Life habit				
Epiphytic	20.29	86.70	13.44	0.14
Terrestrial	22.23	80.91	12.40	0.01

2.7 Statistical analyses

To assess how environmental gradients influenced plant attributes (aquiferous and chlorenchyma thickness, stomatal and scale densities, pigment and phenolic contents, leaf and sheath areas), a Generalized Linear Model (GLM) was applied for each species. Functional traits were considered dependent variables, while environmental factors were independent variables. Models also included interactions between independent variables and life habits. After conducting a normality test, a Gaussian error distribution was applied to all models. To identify the best combinations of variables explaining variations in functional traits, the most suitable models were selected based on the Akaike Information Criterion of Second Order (AICc) values, using the dredge function from the MuMIn package. The best model was determined by the lowest AICc value, and models with $\Delta AICc < 2$ were considered equally plausible. Only results with $p < 0.05$ were considered significant. Because multiple GLMs were conducted across biologically related traits, models were interpreted within an integrative ecological framework rather than as independent tests. Thus, we retained the conventional significance threshold ($p < 0.05$), interpreting marginal p-values cautiously and supporting ecological inferences primarily through consistent patterns across traits and multivariate (PCA) analyses.

In addition to univariate analyses, a Principal Component Analysis (PCA) was performed to assess overall patterns of trait-environment relationships and functional differentiation among species. The PCA matrix included the following traits: leaf area, sheath area, chlorenchyma and aquiferous parenchyma thickness, stomatal and scale densities, chlorophyll a, chlorophyll b, total phenolics, carotenoids, and chlorophyll a/b ratio. PCA was conducted using PC-ORD

version 6.0 (McCune and Mefford 2011). The first two axes explaining the greatest variance were interpreted. To test the significance of PCA axes, a Monte Carlo permutation test was applied. The PCA scores were then interpreted as representing functional gradients across species and environments. The statistical significance of PCA axes indicates that the ordination explains more variance than expected by chance, but does not necessarily imply separation among predefined groups, as variation may be continuous in multivariate space. All statistical analyses were performed using R version 3.0.2 (R Core Team 2022).

3 Results

3.1 Anatomy

The studied species exhibit a similar leaf anatomical structure across the three habits (terrestrial, epiphytic and rupicolous) (Figs. 1, 2). The epidermis is uniseriate with a reduced cell lumen due to U-thickening of the anticlinal and inner periclinal cell walls (Fig. 2c), except in *Pitcairnia carinata* (Fig. 2a). Additionally, a silica body is present in each epidermal cell (Fig. 2c). All species exhibit peltate trichomes on both epidermal surfaces (Fig. 2f). The stomata are located only on the abaxial side of the leaf blade (Fig. 1), below the level of the epidermal cells in *Aechmea vanhoutteana* (Fig. 1c) and *Quesnelia kautskyi* (Fig. 1e) and at the same level in *Pitcairnia carinata* (Fig. 1f). The stomata guard cells feature a stomatal ridge, and their lumen is reduced due to the thickening of the inner and outer cell walls (Fig. 2e). The subsidiary cells are narrow and project below the guard cells (Fig. 2e), except in *Pitcairnia carinata*, where the guard cells are at the same level as the other epidermal cells

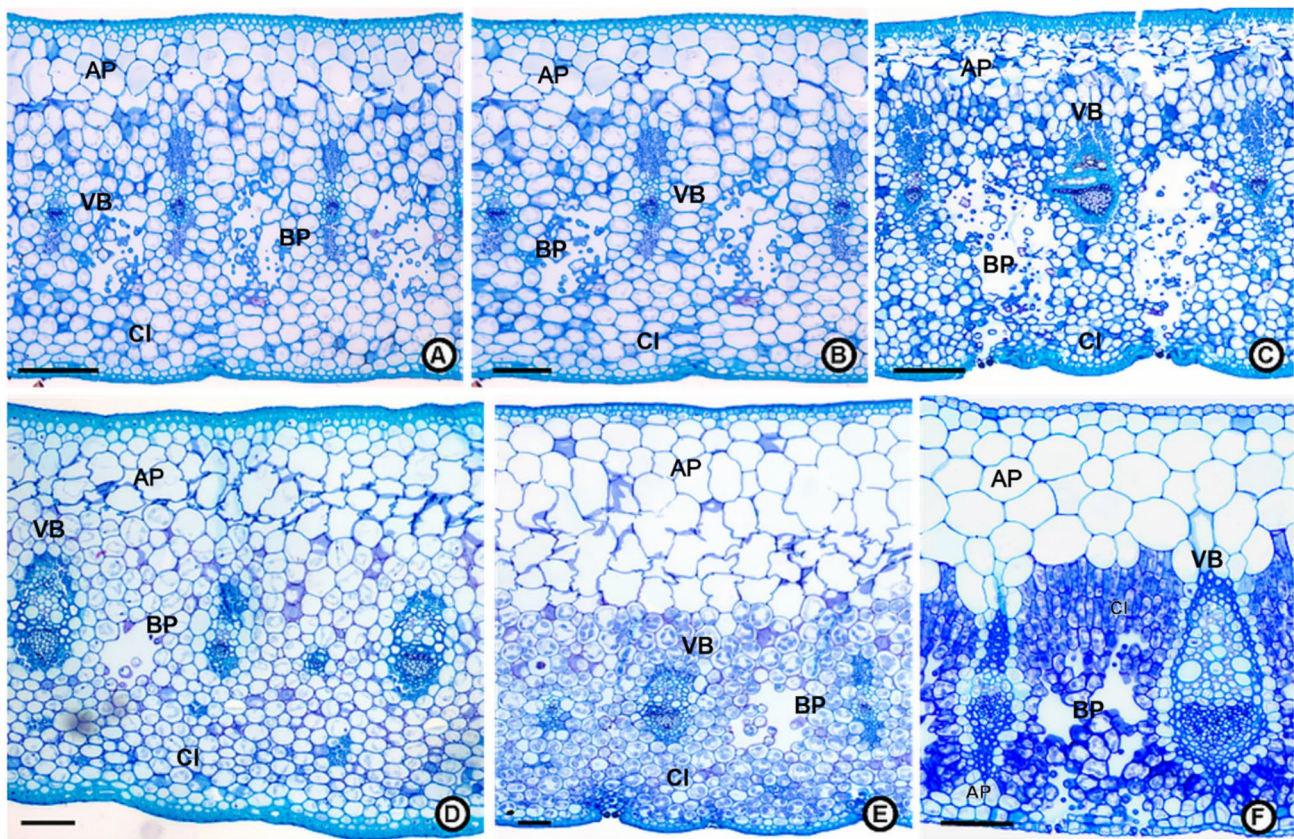


Fig. 1 Leaf anatomy (transverse sections) of the studied species from Parque Nacional do Caparaó. **A–C** *Aechmea vanhoutteana*. **D, E** *Quesnelia kautskyi*. **F** *Pitcairnia carinata*. **A, D** Terrestrial habit. **B, E** Epiphytic habit. **C, F** Rupicolous habit. AP: aquiferous parenchyma; BP: Brachiform parenchyma; Cl: Chlorenchyma; VB: Vascular bundle. Bar in A–F, 100 μ m

(Fig. 2g). In the aeration channels positioned between the vascular bundles, the presence of brachiform parenchyma can be observed (Figs. 1, 2b, h).

The vascular bundles are arranged alternately with smaller and larger bundles (Figs. 1, 2b), surrounded by a fiber sheath (Fig. 2h). Below the epidermis, in *Aechmea vanhoutteana* (Fig. 1a–c) and *Quesnelia kautskyi* (Fig. 1d, e) an aquiferous parenchyma with concertina-shaped cells is observed on the adaxial side (Fig. 2d). This parenchyma includes idioblasts containing raphides (Fig. 2d detail). In *Pitcairnia carinata*, one or two layers of aquiferous parenchyma can also be observed on the abaxial side (Figs. 1f, 2b). Above the abaxial epidermis, a chlorenchyma with isodiametric cells is found (Fig. 1); which in *Pitcairnia carinata*, the chlorenchyma is located between the aquiferous parenchyma (Figs. 1f, 2b).

3.2 Environmental parameters

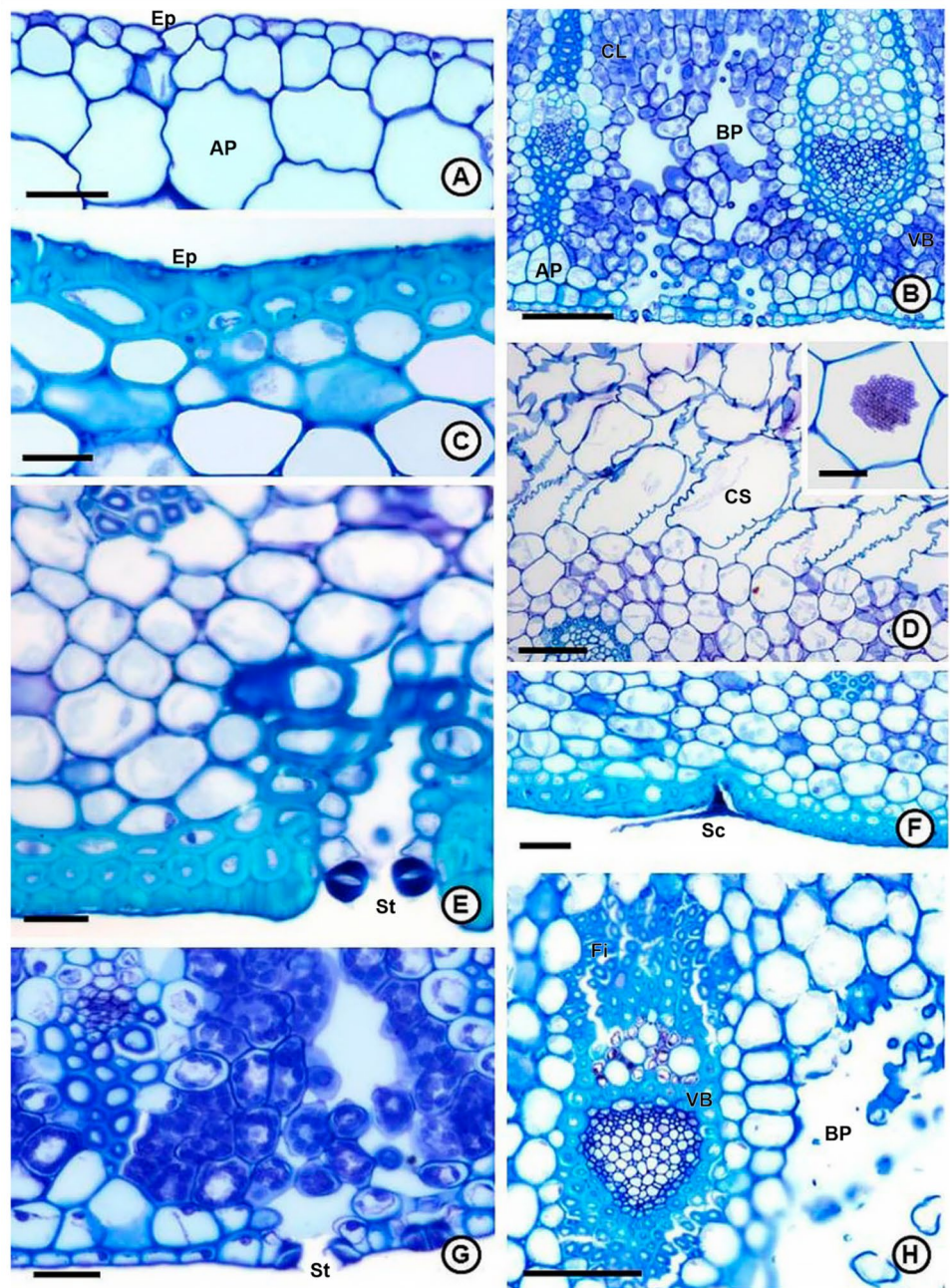
The morphoanatomical and biochemical features of the studied species exhibit variations concerning the abiotic factors analysed, such as temperature, relative air humidity

and light intensity (Table 2). Except the wind speed that did not act as a significant factor in the determination of anatomical and biochemical characters in any of the species (Table 2). The detailed result for each species is described below:

Aechmea vanhoutteana—According to the statistical survey, only the leaf sheath area showed significant variation due to relative air humidity ($P = 0.0437$), where a decrease in the leaf sheath area occurred with increasing relative air humidity (Fig. 3). Furthermore, no differentiation was observed between the different life habits.

Pitcairnia carinata—Among the collection sites of *Pitcairnia carinata* individuals, Vale Encantado location exhibits the highest light intensity (Table 2), as it is an open area without surrounding slopes. The Estrada para Tronqueira location recorded the highest temperature and the lowest relative air humidity (Table 2). Although it is situated in a forest area with mainly tree species, this is the only site without a nearby water source, which contributes to the higher temperatures. Cachoeira Sete Pilões location exhibited the highest relative air humidity, although the

Fig. 2 Leaf anatomy (transverse sections) of the studied species from *Parque Nacional do Caparaó*. **A, B, G** *Pitcairnia carinata*. **C–F, I** *Quesnelia kautskyi*. **H** *Aechmea vanhoutteana*. **A** Detail of the uniseriate adaxial epidermis. **B** Vascular bundles alternating between smaller and larger calibers, with air channels interposed by bractiform parenchyma. Note the stomata at the same level of the epidermis (arrow). **C** Detail of the uniseriate epidermis with thickened walls and a silica body in its lumen. **D** Aquiferous parenchyma with concertina cells (detail of idioblast containing raphides). **E** Sunken stomata with guard cells featuring thickened walls and reduced lumens. **F** Peltate scale trichome (arrowhead). **G** Stomata with guard cells featuring thickened walls. **H** Vascular bundle surrounded by a fiber cap. AP: aquiferous parenchyma; BP: Bractiform parenchyma; CL: Chlorenchyma; CS: Concertina cell; Ep: Epidermis; Sc: Scale; St: Stomata; VB: Vascular bundle. Bar in **C–E**, 25 μm ; **A, F**, 50 μm ; **B, G, H**, 100 μm



lowest temperatures and light intensity (Table 2), possibly due to the presence of a waterfall.

Regarding the trait–environmental parameter interaction, temperature appeared to influence the leaf sheath area ($P=0.0145$) (Fig. 4a), chlorenchyma thickness ($P=0.0099$) (Fig. 4b), and phenol content ($P=0.0103$) (Fig. 4c). Both phenol content and leaf sheath area increased with rising temperature (Fig. 4a, c), while chlorenchyma thickness decreased (Fig. 4b). An increase in relative air humidity showed a tendency to reduce chlorophyll *a* content ($P=0.00271$) (Fig. 4d). For the scales on the adaxial surface, the location with the highest temperature, *Estrada*

para Tronqueira, had individuals with higher scale density ($P=0.0351$) (Table 3). However, the scales on the abaxial surface exhibited lower values when relative air humidity was higher, as seen at *Cachoeira Sete Pilões* ($P=0.0129$) (Table 3). GLM analysis revealed a trend of increased stomatal density with higher light intensity ($P=0.00318$) (Table 3).

Quesnelia kautskyi—The species exhibit individuals with terrestrial and epiphytic habits, with the former exhibiting a higher influence by light intensity (Fig. 5). *Quesnelia kautskyi* showed a trend toward a decrease in leaf area as relative air humidity increased (Fig. 5a),

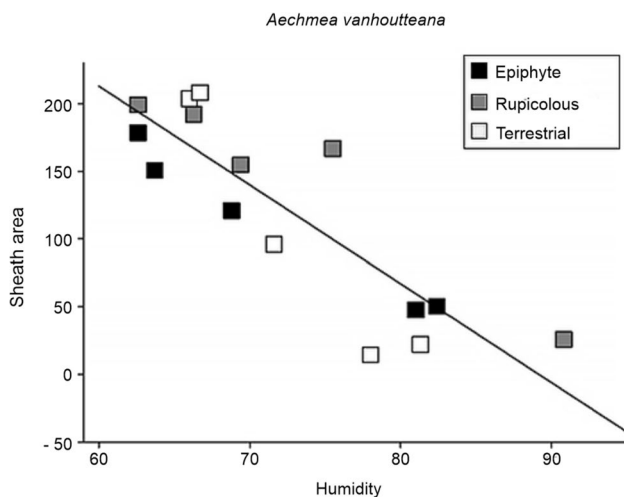


Fig. 3 GLM relating relative air humidity (%) to leaf sheath area in *Aechmea vanhoutteana* across different life habits (epiphytic, rupicolous, and terrestrial). The line represents the fitted GLM ($p=0.0437$), indicating the statistical significance of the relationship ($p<0.05$)

while the leaf sheath area increased with rising temperature ($P=0.00215$) (Fig. 5b). The thickness of the aquiferous parenchyma decreased as relative air humidity increased ($P=0.0276$) (Fig. 5c). Terrestrial individuals had a greater average aquiferous parenchyma thickness compared to epiphytic plants (Fig. 5d), which may be attributed to higher light intensity at the terrestrial collection sites ($P=0.0096$) (Fig. 5d). Chlorenchyma thickness was influenced by temperature (Fig. 5e), light (Fig. 5f), and relative air humidity (Fig. 5g), with the tissue thickness decreasing with increasing temperature or relative air humidity ($P=0.0358$) (Fig. 5e, g), but increasing in terrestrial individuals ($P<0.001$) (Fig. 5f), likely due to higher light intensity at their collection sites.

Considering biochemical characteristics, chlorophyll *b* content was influenced by temperature and light. The lowest chlorophyll *b* levels were found in environments with higher temperatures ($P<0.001$) (Fig. 6a). As light intensity increased, chlorophyll *b* content decreased ($P=0.0251$) (Fig. 6b). Chlorophyll *a* content decreased with rising relative air humidity ($P=0.0265$) (Fig. 6c), and this factor contributed to the differentiation between individuals with different life habits, with epiphytic individuals exhibiting the lowest chlorophyll *a* values ($P=0.0299$) (Fig. 6d). The chlorophyll *a/b* ratio increased as temperature rose (Fig. 6e). Additionally, carotenoid content was higher in terrestrial individuals, though no direct relationship with any environmental factor was identified ($P=0.0396$) (Fig. 6f). Phenol content increased with rising relative air humidity (Fig. 6g).

3.3 Principal component analysis

The Principal Component Analysis (PCA) including all species revealed a separation of functional groups (Fig. 7A) (Axis 1: $p=0.001$; Axis 2: $p=0.001$), as indicated by the clustering of individuals from each species according to correlations among their morpho-physiological traits. *Pitcairnia carinata* appeared most distant from the other species (Fig. 7A). In contrast, while *Aechmea vanhoutteana* and *Quesnelia katuskyi* also showed functional separation, they were positioned closer to each other in the PCA space (Fig. 7A). In the PCA of *Aechmea vanhoutteana* alone (Fig. 7B), no functional differentiation was detected among the three growth habits in which the species was found (epiphytic, rupicolous, terrestrial), although Axis 2 ($p=0.011$) and Axis 3 ($p=0.003$) were significant. For *Pitcairnia carinata*, no group formation was observed (Fig. 7C), as all individuals sampled shared the same rupicolous habit (Axis 1: $p=0.007$; Axis 2: $p=0.001$). In *Q. katuskyi*, epiphytic individuals remained more clustered (Fig. 7D), while terrestrial individuals were more dispersed and distant from the epiphytes, although some terrestrial individuals were positioned near the epiphytic group (Axis 1: $p=0.001$; Axis 2: $p=0.001$).

The two most explanatory axes of the PCA including all species (Axis 1 and Axis 2) were significant (Fig. 8), and environmental factors were incorporated into the same model. Along Axis 1, sites with high light intensity were associated with the development of *Pitcairnia carinata* individuals, which exhibited higher stomatal density, chlorophyll *a/b* ratio, and phenolic content (Fig. 8A) (GLM $t=-6.098$; $p<0.001$). As light intensity decreased, *Quesnelia katuskyi* and *Aechmea vanhoutteana* individuals became more frequent (Fig. 8A), with increased values of functional traits such as leaf and sheath area, trichome density on both leaf surfaces, chlorenchyma thickness, and chlorophyll *b* content (Fig. 8A). This graph also highlights the clear functional distance between *Aechmea vanhoutteana* and *Quesnelia katuskyi* relative to *Pitcairnia carinata*. Temperature was another environmental factor that affected functional traits (Fig. 8B) (GLM $t=2.018$; $p=0.0496$). Individuals from warmer sites showed increased leaf and sheath area, higher trichome density on both leaf surfaces, thicker chlorenchyma, and elevated chlorophyll *b* content. In contrast, individuals from cooler sites had higher stomatal density, greater chlorophyll *a/b* ratios, and higher phenolic content (Fig. 8B). Along Axis 2, reduced light intensity (Fig. 8C) (GLM $t=3.908$; $p<0.001$), increased temperature (Fig. 8D) (GLM $t=-6.201$; $p<0.001$), and higher wind speed (Fig. 8E) (GLM $t=-5.579$; $p<0.001$) were associated with increased thickness of the water-storage parenchyma and reduced chlorophyll *a* and carotenoid content (Fig. 8C–E).

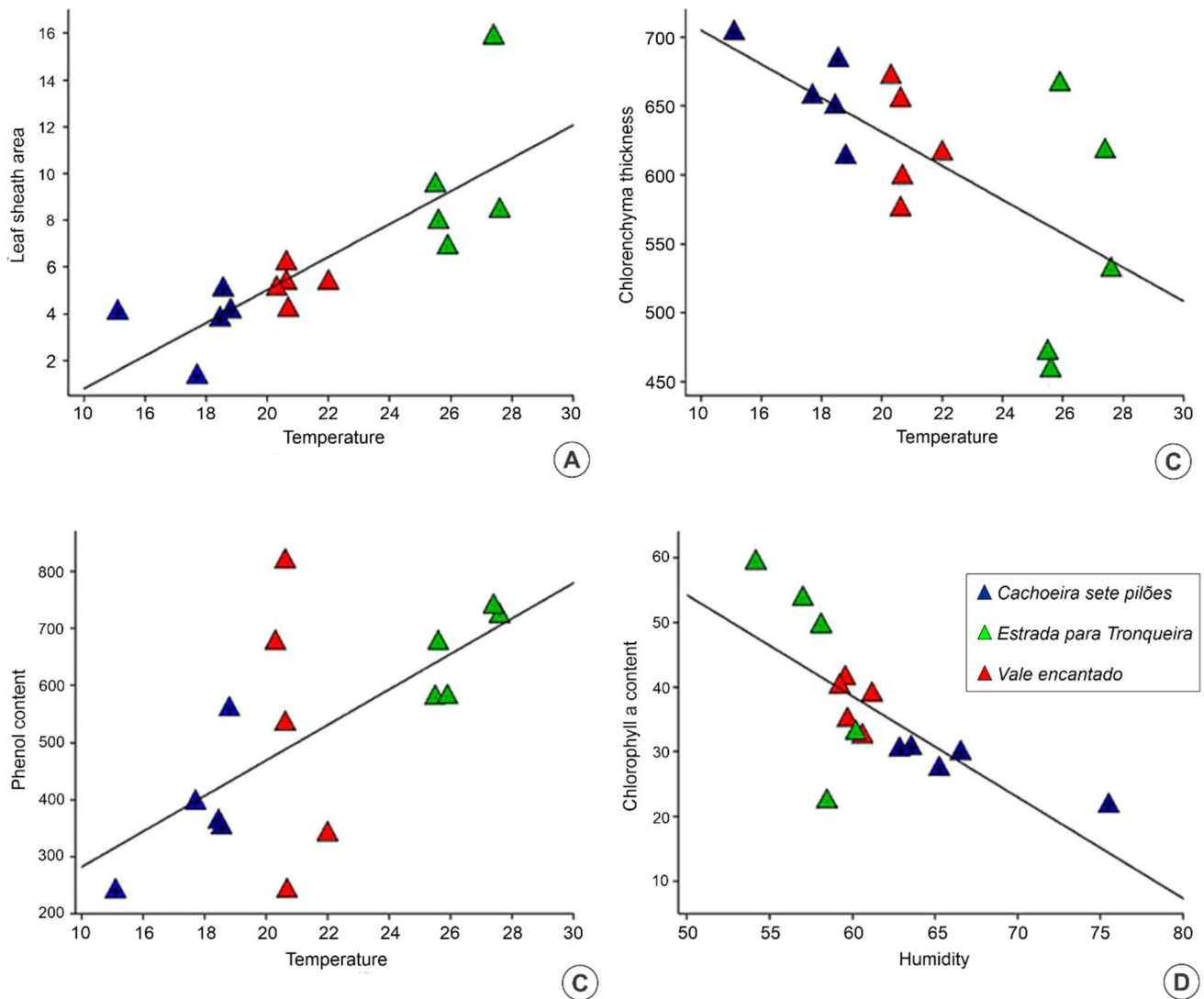


Fig. 4 Significant GLM analysis relating to environmental factors to the morphology (**A** leaf sheath area related to temperature), anatomy (**B** chlorenchyma thickness related to temperature) and metabolism (**C** phenol content related to temperature and **D** Chlorophyll *a* content related to humidity) of *Pitcairnia carinata*. The coloured triangles indicate the collection sites

The results reinforce the association of *Pitcairnia carinata* with high light environments (Fig. 8C).

The PCA analyses conducted for each species separately were interpreted considering the statistically significant axes from the best-fit models: Axis 3 for *Aechmea vanhoutteana* (Fig. 9A), Axis 1 for *Quesnelia kautskyi* (Fig. 9B), and Axis 2 for *Pitcairnia carinata* (Fig. 9C–E). In *A. vanhoutteana*, total light availability was the main environmental factor influencing functional trait variation (GLM $t = 2.478$; $p = 0.0291$). Plants in warmer environments tended to have higher chlorophyll *a/b* ratios, smaller leaf area, and fewer trichomes on the abaxial epidermis (Fig. 9A). For *Q. kautskyi*, only relative humidity significantly influenced trait variation (GLM $t = -3.783$; $p = 0.0015$) (Fig. 9B). As previously observed in the general PCA for this species (Fig. 7D), there

was a clear distinction between epiphytic and terrestrial individuals, now confirmed to be associated with differences in humidity. Individuals in drier environments exhibited higher levels of chlorophyll *a*, carotenoids, chlorophyll *a/b* ratios, leaf area, sheath area, and stomatal density.

In *Pitcairnia carinata*, three covarying environmental factors significantly influenced functional traits: light intensity (GLM $t = 3.442$; $p = 0.0055$; Fig. 9C), relative humidity (GLM $t = 6.736$; $p < 0.001$; Fig. 9D), and wind speed (GLM $t = -2.882$; $p = 0.0168$; Fig. 9E). Higher light levels were recorded at Vale Encantado (Fig. 9C), an exposed site lacking surrounding slopes that would otherwise create shade—unlike other sampled locations. Relative humidity was highest at Sete Pilões Waterfall (Fig. 9D), where plants grew on rock walls near a

Table 3 GLM values for the number of leaf scales and stomata in *Pitcairnia carinata* across different collection sites

Collection site	Scales on the adaxial face	Scales on the abaxial face	Stomata
<i>Estrada para Tronqueira</i> (MG)	5.00	8.30	347.26
	0.67	4.00	282.87
	3.50	2.00	340.82
	0.67	2.00	334.38
	0.00	2.67	321.50
<i>Vale encantando</i> (MG)	1.3	4.80	203.02
	0.33	3.25	210.75
	2.00	6.00	267.41
	1.00	4.25	251.56
	0.00	2.30	254.53
<i>Cachoeira Sete Pilões</i> (ES)	0.75	1.33	334.38
	1.00	2.30	308.62
	0.33	2.00	276.43
	0.00	4.00	257.11
	0.33	0.33	218.47
Standard error	0.08**	0.09**	1.22***
Environmental parameter	Temperature	Relative air humidity	Light intensity

Values represent means, with standard errors provided at the bottom of the table. Statistical significance levels are indicated as $P < 0.01$ (**) and $P < 0.001$ (***). Environmental parameters (temperature, relative air humidity, and light intensity) influenced the variation in plant structure

waterfall, creating constant mist from water droplets. Wind speed did not vary significantly between locations (Fig. 9E), yet its effect on functional traits was well-defined. Strong relationships were observed between anatomical, morphological, and biochemical traits and wind exposure. Individuals exposed to higher light (Fig. 9C), higher humidity (Fig. 9D), and lower wind speeds (Fig. 9E) exhibited thicker chlorenchyma, but reduced leaf and sheath area, lower trichome density on the adaxial surface, and decreased phenolic content.

4 Discussion

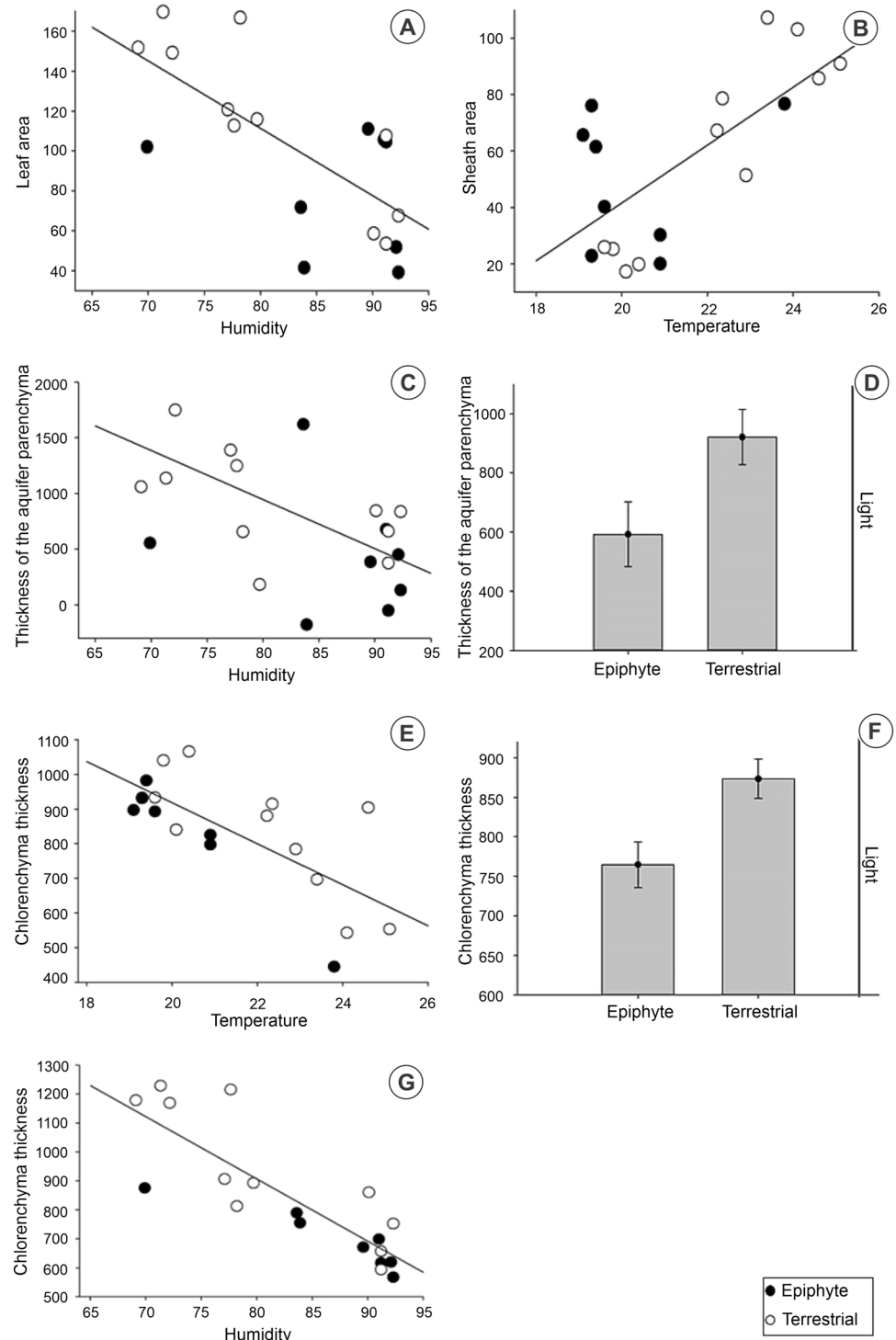
This study provides relevant insights into the role of abiotic factors in shaping the expression of morphoanatomical and biochemical traits in Bromeliaceae species. By integrating species with contrasting life habits (terrestrial, epiphytic, and rupicolous) and different distribution ranges, we assessed how environmental variables: light intensity, altitude, temperature, relative humidity and wind speed, influence trait variation. Below, we discuss three main aspects: (1) how do environmental parameters, particularly light, humidity, and temperature, influence the expression of different trait types; (2) whether species with restricted distributions exhibit more specialized traits; and (3) how morphoanatomical and biochemical traits differ in their responses to abiotic factors and microclimatic conditions.

4.1 How do environmental parameters influence the expression of morphoanatomical and biochemical traits across species?

Among the abiotic factors analysed (light intensity, altitude, temperature, relative air humidity and wind speed), temperature and relative air humidity had the most pronounced interaction with species traits, followed by light intensity. In contrast, wind speed did not have a significant effect on the traits of the studied species. Although wind is often considered an important selective factor in high-elevation rocky environments (Leuschner 2000) it showed no significant effect in our analyses, suggesting that temperature, humidity, and light may be more influential drivers of trait expression in this system. It is also possible that local topographic complexity reduces direct wind exposure at the microsite level, buffering its effect on leaf structure. This interpretation should be made cautiously given the microclimatic heterogeneity of montane habitats. Environmental variables were recorded during discrete field campaigns (November–March), representing a limited temporal window. Therefore, they should be interpreted as a specific temporal framework rather than a full characterization of seasonal variability.

Trait responses varied across species depending on trait type and microenvironmental condition and Principal component analysis (PCA) further reinforced the functional differentiation among species in response to environmental drivers. *Pitcairnia carinata* exhibited traits adapted to open rocky habitats with intense radiation, thermal fluctuation,

Fig. 5 Significant GLM analysis relating environmental factors to the morphology (**A** leaf area and **B** leaf sheath area) and anatomy (**C** aquiferous parenchyma thickness related to humidity, **D** aquiferous parenchyma thickness related to light intensity and habits; **E** Chlorenchyma thickness related to temperature, **F** Chlorenchyma thickness related to light intensity and habits, **G** Chlorenchyma thickness related to humidity) of *Quesnelia kautskyi*. Standard error: D=19.56, F=5.227



and water-deficit stress. This species presented high stomatal density, elevated phenolic and carotenoid content, and smaller leaf area compared to the other species, features typically associated with a resource-acquisition strategy, enabling rapid adjustment to environmental variation (Reich 2014; Wright et al. 2004). In contrast, *Aechmea vanhoutteana* and *Quesnelia kautskyi* appeared to follow a

resource-conservative strategy, exhibiting thicker aquiferous parenchyma, larger leaf and sheath areas, lower stomatal density, and higher chlorophyll *b* content. In these species, trait expression seemed more influenced by low light availability than by water-deficit stress. This trait configuration ensures both resource acquisition and efficient use, contributing to functional stability commonly found in species

Fig. 6 Significant GLM analysis relating environmental factors to the metabolism (**A** Chlorophyll *b* concentration related to temperature, **B** Chlorophyll *b* concentration related to light intensity, **C** Chlorophyll *a* concentration related to humidity, **D** Chlorophyll *b* concentration related to humidity and habits, **E** Chlorophyll *a/b* ratio related to temperature, **F** Carotenoid concentration related to habits, **G** Phenol concentration related to humidity) of *Quesnelia kautskyi*. Standard error: D=0.2914, F. Standard error=1,601

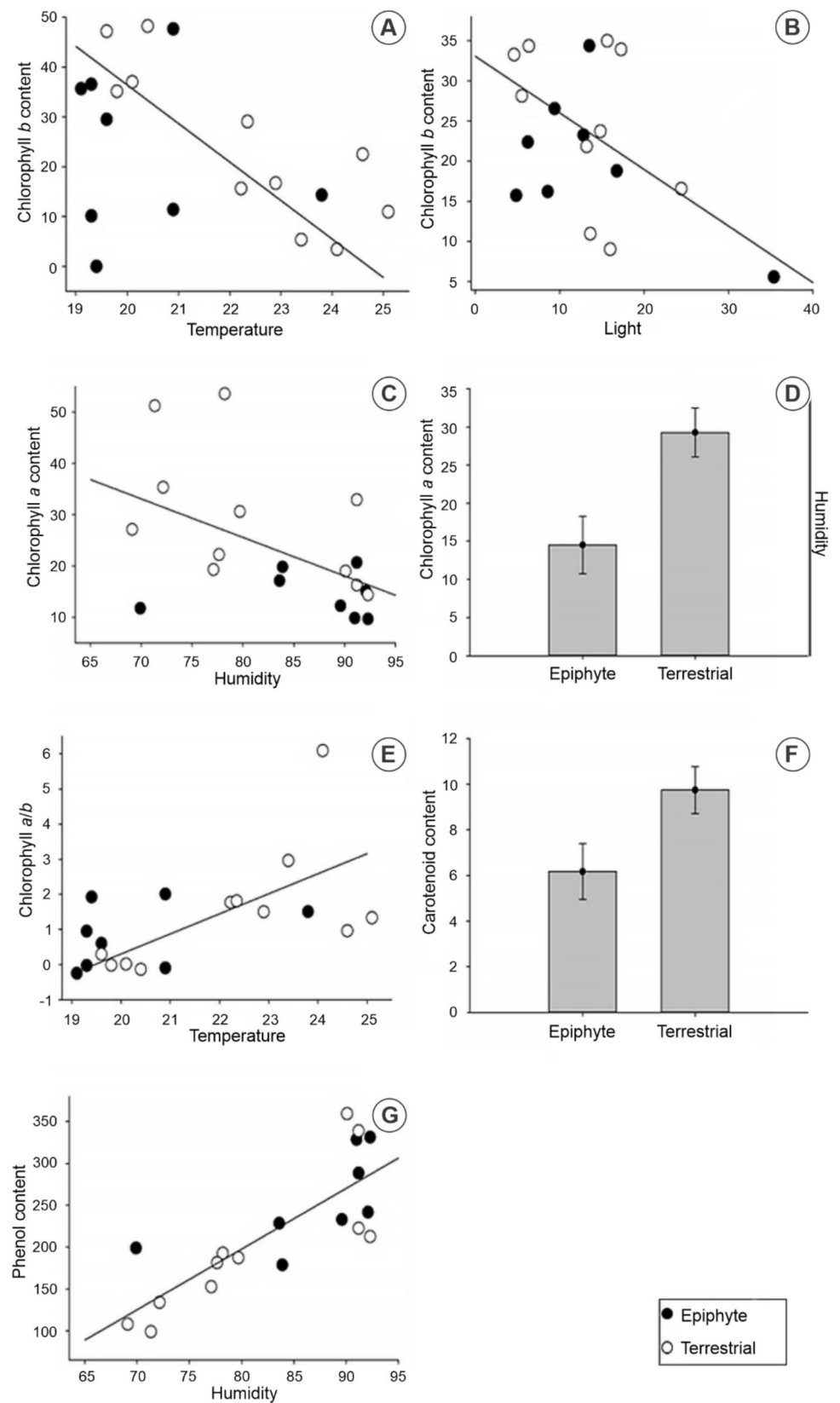
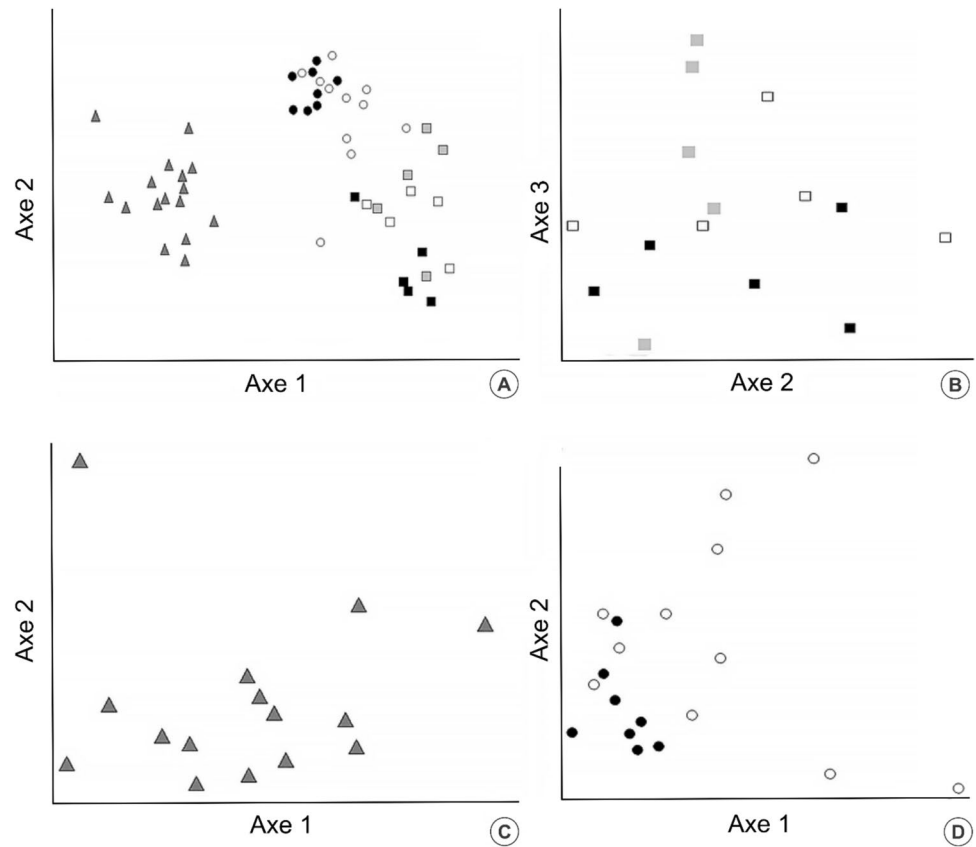


Fig. 7 Principal Component Analysis (PCA) of species and environmental variables, showing the two axes that best explained the variance in the environmental and functional trait dataset. **A** All species. **B** *Aechmea vanhoutteana*. **C** *Pitcairnia carinata*. **D** *Quesnelia kautskyi*. Squares represents: *Aechmea vanhoutteana*. Circle: *Quesnelia kautskyi*. Triangle: *Pitcairnia carinata*. Habits are represented by black: epiphytic; grey: rupicolous; white: terrestrial



inhabiting shaded, humid environments (Reich et al. 2003; Wright et al. 2004; Valladares & Niinemets 2008; Cayssials and Rodríguez 2013).

Among morphological traits, leaf sheath area was the most influenced by abiotic factors, especially temperature and humidity. There was a tendency for increased leaf sheath area with rising temperatures, as observed in *Pitcairnia carinata* and *Q. kautskyi*, while higher humidity was associated with reduced sheath area in *A. vanhoutteana*. This morphological adjustment contributes to larger tank formation, enhancing water storage and improving survival under dry conditions (Scarano et al. 2002; Voltolini and Santos 2011). Although no significant relationship was observed with light intensity, other studies report that increased light levels can lead to larger leaves and more compact rosettes (Barberis et al. 2017; Cavallero et al. 2009, 2011). At the anatomical level, temperature, humidity and light intensity again emerged as key predictors of variation. *Aechmea vanhoutteana* and *Quesnelia kautskyi* exhibited similar features, including uniseriate epidermis with U-thickened cell walls, sunken stomata and aquiferous parenchyma, traits potentially related to water retention and transpiration control (Dickison 2000; Dias-Pereira et al. 2022). In contrast, *Pitcairnia carinata* displayed unique anatomical features, such as aquiferous parenchyma on both leaf surfaces, with chlorenchyma interspersed between layers. This configuration suggests

a balance between water storage and photosynthesis, protecting chlorenchyma from damage caused by intense light (Smith and Downs 1974; Dias-Pereira et al. 2022; Pereira et al. 2025). Rather than relying on classic water-saving adaptations like sunken stomata, *Pitcairnia carinata* may cope with temperature and light fluctuations by investing in structural modifications that protect photosynthetic tissues. This strategy suggests adaptation to the daily thermal oscillations of rocky outcrops, where buffering temperature extremes may be more important than strict water conservation (Bandurska 2022; Münchinger et al. 2023; Chaves et al. 2024).

Biochemical responses also appeared to be linked to environmental drivers. In *Pitcairnia carinata* and *Q. kautskyi*, chlorophyll content decreased under higher light and temperature, which in terms may be related to changes in gene expression in the chlorophyll biosynthesis pathway, reducing enzymatic activity and impairing chlorophyll synthesis (Maxwell et al. 1995; Gratani et al. 2006; Niinemets 2010; Rapnouil et al. 2023). Conversely, carotenoid levels increased, mainly in terrestrial individuals of *Q. kautskyi*, consistent with previous findings that high light intensity and temperatures lead to chlorophyll reduction and carotenoid increase in plants (Yang et al. 2018; Rapnouil et al. 2023). This pigment profile helps limit excessive light absorption, reducing oxidative stress caused by light saturation (Königer

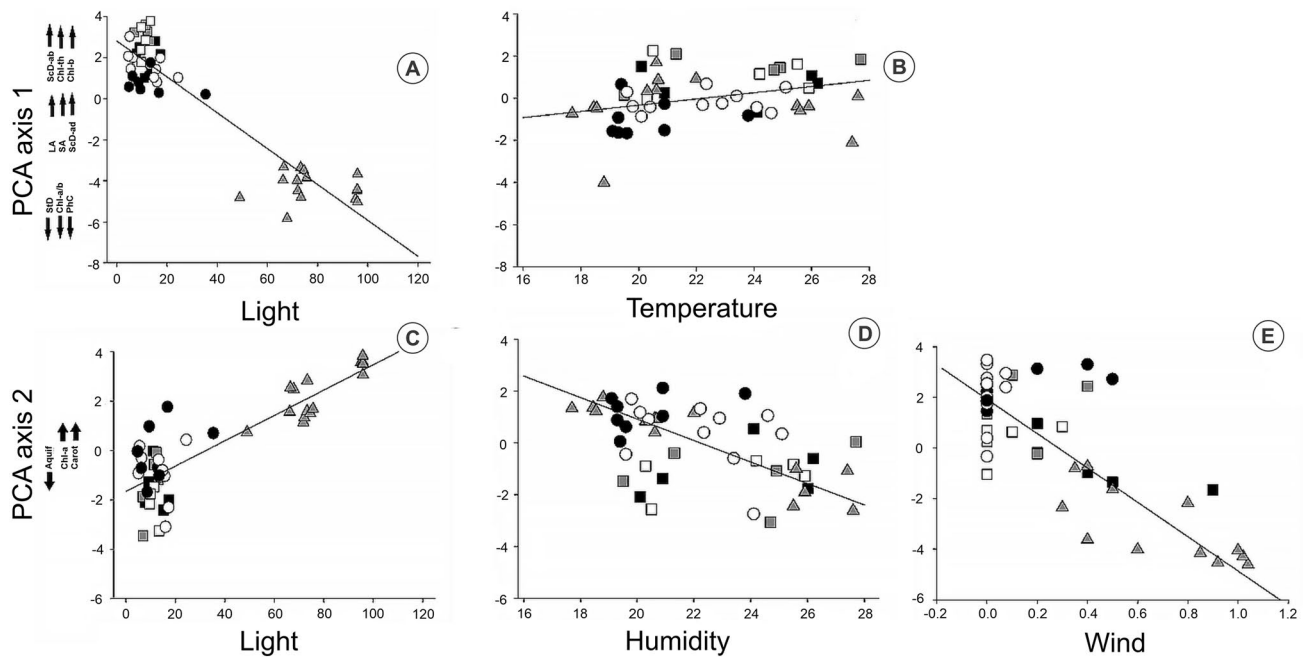


Fig. 8 PCA of the Bromeliaceae species based on the two significant axes. **A, B** Environmental variables light and temperature with Axis 1. **C–E** Environmental variables light, temperature, and wind with Axis 2. Square represents: *Aechmea vanhoutteana*. Circle: *Quesnelia kautskyi*. Triangle: *Pitcairnia carinata*. Habits are represented by black: epiphytic; grey: rupicolous; white: terrestrial. Aquif: aquiferous parenchyma thickness; Carot: carotenoid content; Chl-a/b: chlorophyll a/b ratio; Chl-a: chlorophyll a content; Chl-b: chlorophyll b content; Chl-th: chlorenchyma thickness; LA: leaf area; PhC: phenol content; SA: sheath area; ScD-ab: scale density on the abaxial surface; ScD-ad: scale density on the adaxial surface; StD: stomatal density. Arrows indicate the direction of trait increase

et al. 1995; Matsubara et al. 2009; Rosa-Manzano et al. 2014; González-Salvatierra et al. 2021). Additionally, phenolic content increased in response to high temperatures in both species, suggesting that phenolic compound synthesis is activated under heat and water-deficit stress, improving plant tolerance (Winkel-Shirley 2002; Pollastri and Tattini 2011). This aligns with evidence that secondary metabolites play critical roles in plant responses to environmental challenges, including UV radiation, light stress, extreme temperatures, drought, and salinity (Winkel-Shirley 2002; Pollastri and Tattini 2011). It is important to note that biochemical traits (photosynthetic pigments and phenolic compounds) were obtained from pooled samples and therefore should be interpreted as descriptive indicators of functional variation rather than strictly inferential responses.

PCA highlighted the role of key environmental filters in potentially shaping trait expression and driving niche partitioning. For *Pitcairnia carinata*, light was the most important factor explaining functional differentiation, correlating with variations in stomatal density, leaf size, and phenolic content. For this species stomatal opening during daytime coincides with peak light and temperature conditions, making traits such as high stomatal density and increased transpiration particularly advantageous for thermal regulation. This is a typical strategy in species with C3 photosynthetic

metabolism (Sage et al. 2012). In addition, high wind exposure in rocky outcrops reduces the leaf boundary layer, facilitating CO₂ diffusion and enhancing photosynthetic efficiency under intense radiation (Reinert et al. 2003; Ribeiro et al. 2012; Schock et al. 2014). In *Q. kautskyi*, humidity was most relevant, particularly in distinguishing terrestrial and epiphytic individuals. Epiphytes showed traits enhancing water retention, such as thicker aquiferous parenchyma and reduced stomatal density, reflecting greater dependence on atmospheric moisture. Terrestrial individuals showed greater variability in stomatal density, leaf area, and pigment content, indicating a greater functional plasticity. For *A. vanhoutteana*, despite some influence of light on leaf area and scale presence, PCA showed minimal trait differentiation across ecological habits, reinforcing its generalist strategy.

While our findings provide evidence of functional divergence and environmental filtering among bromeliad species, the framework presented here should be understood as a functional model based on a focused set of species and environmental gradients. Because multiple trait–environment relationships were examined, results are interpreted within an integrative perspective, emphasizing the consistency of patterns across traits and their support by multivariate analyses rather than isolated significant associations. This approach provides a replicable baseline for investigating

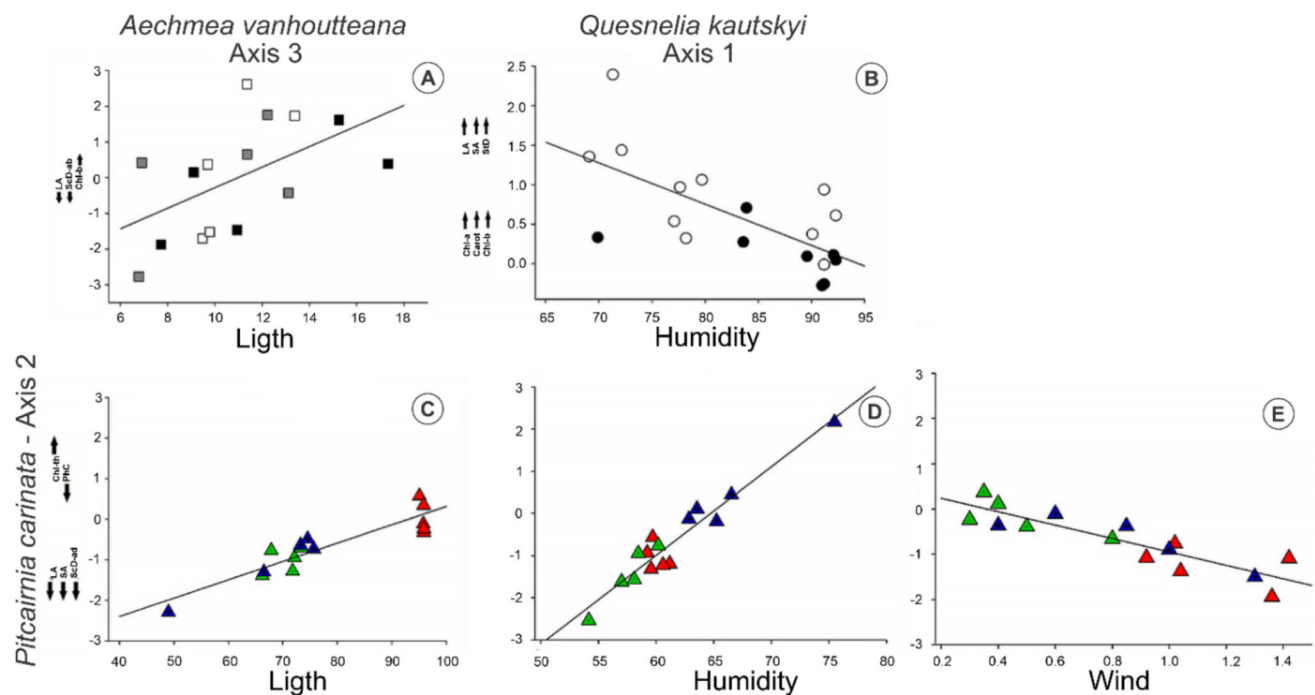


Fig. 9 Principal Component Analysis (PCA) of the Bromeliaceae species analyzed separately according to the significant axes. **A** Light as an environmental variable associated with Axis 3 of the PCA for *Aechmea vanhoutteana*. **B** Humidity associated with Axis 1 of the PCA for *Quesnelia kautskyi*. **C–E** Light, humidity, and wind associated with Axis 2 of the PCA for *Pitcairnia carinata*. Collection sites are represented by red triangles: Vale Encantado; green triangles: Road to Tronqueira; blue triangles: Sete Pilões waterfall. Habits are represented by black: epiphytic; grey: rupicolous; white: terrestrial. Aquif: aquiferous parenchyma thickness; Carot: carotenoid content; Chl-a/b: chlorophyll a/b ratio; Chl-a: chlorophyll a content; Chl-b: chlorophyll b content; Chl-th: chlorenchyma thickness; LA: leaf area; PhC: phenol content; SA: sheath area; ScD-ab: scale density on the abaxial surface; ScD-ad: scale density on the adaxial surface; StD: stomatal density. Arrows indicate the direction of trait increase

trait–environment relationships in other taxa and regions, contributing to broader assessments of functional plasticity and niche dynamics in heterogeneous montane ecosystems.

4.2 Do species with more restricted distributions tend to exhibit specialized traits?

Trait specialization was particularly evident in *Pitcairnia carinata*, a rupicolous species inhabiting exposed rocky environments. It displayed distinctive anatomical traits, such as aquiferous parenchyma on both leaf surfaces interspersed with chlorenchyma, which likely balances water storage with photosynthesis while protecting photosynthetic tissues from light damage (Smith and Downs 1974; Dias-Pereira et al. 2022; Pereira et al. 2025). This combination, along with increased scale and stomatal density, reflects structural specialization for thermal buffering, prioritizing temperature regulation over strict water conservation (Bandurska 2022; Münchinger et al. 2023; Chaves et al. 2024). Such traits allow *Pitcairnia carinata* to remain functional in highly variable microclimates, but may also constrain its distribution to restrict environments, representing a trade-off between environmental tolerance and ecological flexibility.

This supports the notion that tank-less bromeliads like *Pitcairnia carinata* often occupy stress-tolerant niches, marked by slow growth and high resistance to extreme conditions (Schulte et al. 2009; Silvestro et al. 2014).

In contrast, *A. vanhoutteana*, which occurs in epiphytic, rupicolous and terrestrial habitats, exhibited anatomical and biochemical stability, suggesting low phenotypic sensitivity and a generalist ecological strategy. The lack of significant metabolic variation across environments reinforces its ecological resilience, potentially allowing persistence under both moderate stress and resource-rich conditions without requiring specialized traits. For *Q. kautskyi*, though more widely distributed, showed greater plasticity, particularly in terrestrial individuals. This may result from higher humidity and light intensity in terrestrial collection sites. These individuals exhibited a reduction in aquiferous parenchyma under high humidity and an increase in chlorenchyma under intense light. Such anatomical shifts may reflect adaptation to near-soil conditions, where organic matter enhances water retention (Geroy et al. 2011). Additionally, increased chlorenchyma thickness is often linked to CAM photosynthesis, a strategy that improves water-use efficiency under fluctuating environmental conditions (Males and Griffiths 2018).

Although no physiological measurements were performed to confirm CAM metabolism in *Quesnelia kautskyi*, anatomical traits such as chlorenchyma thickening and a well-developed aquiferous parenchyma suggest the possibility of a CAM photosynthetic pathway. However, this should be interpreted as a functional hypothesis based on anatomical evidence rather than as direct confirmation of the photosynthetic metabolism. Overall, our results support the hypothesis that species with more restricted distributions, such as *Pitcairnia carinata*, tend to exhibit greater functional specialization, particularly in anatomical and biochemical traits associated with tolerance to harsh environments. While such specializations may confer survival advantages, they can also reduce ecological flexibility and constrain distributional range. In contrast, more widely distributed species such as *Aechmea vanhoutteana* and *Quesnelia kautskyi* show comparatively stable trait expression, which may contribute to persistence across broader environmental gradients.

The variability and specialization of traits in the studied species is reinforced by PCA analysis. Such analysis indicates how ecological habit influences functional strategies in the studied species. In *Q. kautskyi*, clear functional divergence was observed between terrestrial and epiphytic individuals, reflecting contrasting strategies in response to water availability. Epiphytes, which are exposed to higher evaporative demand and irregular moisture supply, exhibited traits associated with water conservation (Zhang et al. 2016), such as thicker aquiferous parenchyma and lower stomatal density, indicating reliance on atmospheric humidity and rainwater. In contrast, terrestrial individuals showed greater variation in stomatal density, leaf area, and pigment composition, suggesting higher plasticity in resource-use traits and a broader tolerance to fluctuating environmental conditions. Nevertheless, in *Aechmea vanhoutteana* such divergence was not observed, with individuals from different habits (terrestrial, epiphytic, and rupicolous) maintained remarkably stable morphoanatomical and physiological profiles. This consistency suggests a generalist strategy, characterized by low phenotypic sensitivity and the ability to persist across structurally distinct habitats without major trait adjustments (Reich et al. 2003). Functional stability of this kind may represent a cost-effective strategy for niche expansion, particularly in heterogeneous environments such as rocky montane fields (Negreiros et al. 2014). It enables occupation of multiple niches without the energetic investment required for plastic or specialized responses. In contrast, *Pitcairnia carinata*, restricted to exposed rupicolous habitats, exhibited a markedly specialized strategy. Its trait profile was closely aligned with high light availability, thermal stress, and limited water access, conditions typical of rocky outcrops. Traits such as increased stomatal density, thick scale coverage, and phenolic accumulation point to fine-tuned adaptations for photoprotection, temperature buffering, and

conservative water use, reducing ecological amplitude but enhance performance within a narrow microclimatic range (Silvertown 2004; Grime 2006).

Altogether, these findings highlight how ecological habit is strongly associated with both inter- and intraspecific functional variation. They also emphasize the different roles that morphoanatomical and biochemical traits can play in resource use strategies and niche occupation. Functional specialization, as seen in *Pitcairnia carinata*, can enhance survival in extreme conditions but often limits distribution. Conversely, functional generalism or plasticity, as in *Quesnelia kautskyi* and *A. vanhoutteana*, supports broader niche occupancy and resilience to microhabitat variation. These contrasting strategies reflect a fundamental ecological trade-off between specialization and adaptability (Richards et al. 2006; Violle et al. 2007).

4.3 How do morphological, anatomical and biochemical traits differ in their response to abiotic factors and microclimatic variation?

From a functional perspective, traits can be categorized as either “effect” traits, which shape environmental interactions, or “response” traits, which vary according to environmental conditions (Violle et al. 2007). Morphological and anatomical traits play distinct roles in defining the functional niche species occupy, offering insight into which features actively shape the environment and which respond to it, influencing ecological specialization and differentiation (Violle et al. 2007; Vamosi et al. 2018).

Our findings highlight differences in trait responsiveness to environmental factors. Morphological traits, particularly those related to overall leaf architecture, showed limited variation across conditions, supporting their classification as “effect traits”, traits that influence species performance but remain relatively stable across environmental gradients (Violle et al. 2007; Vamosi et al. 2018). For instance, variation in leaf sheath area was modest and primarily associated with temperature and humidity, without clear trends in response to light or wind. However, in environments with higher temperatures, slight expansion of the leaf sheath resulted in more tapered, imbricated leaves, which in turn facilitate tank formation. In this context, morphological adjustments linked to tank development may reflect not only responses to abiotic stress but also strategies for niche differentiation, allowing species to exploit distinct microhabitats and reduce competition (Benzing 2000; Silvestro et al. 2014). Supporting this, tank-less bromeliads are typically associated with stress-tolerant niches, marked by slow growth, drought resistance, and a high capacity to endure extreme environmental conditions, often close to the limits of physiological tolerance (Schulte et al. 2009; Silvestro et al. 2014).

In contrast, anatomical and biochemical traits acted more clearly as “response traits,” which are more fine-tuned and varying sensitively with environmental stimuli. Anatomical features such as chlorenchyma thickness, scale and stomatal density, and aquiferous parenchyma responded dynamically to humidity, light, and temperature. Similarly, biochemical traits like chlorophyll, carotenoid, and phenolic content adjusted rapidly under thermal and light stress. These traits showed higher variability, potentially leading to distinct structural specializations tailored to the specific microclimates where species occur. These “response traits”, when accumulated and fixed over evolutionary timescales, may represent key innovations driving the emergence of new species and contributing to biodiversity (Silvestro et al. 2014; Vamosi et al. 2018).

Overall, the combined trait-based and PCA analyses here obtained highlight how key abiotic factors, mainly light, humidity, wind and temperature, act as environmental filters potentially shaping functional differentiation among Bromeliaceae species. Differences in trait variability, specialization and generalism reflect distinct ecological strategies and support niche partitioning in heterogeneous montane environments.

The study highlights the intricate interaction between abiotic factors and the morphoanatomical and biochemical traits of Bromeliaceae species across high-elevation habitats. Our results demonstrate that abiotic factors, particularly temperature, relative humidity and light intensity, play a potential role in shaping morphoanatomical trait expression and niche occupation in Bromeliaceae species. The integration of trait-based analyses and PCA revealed that *Pitcairnia carinata* showed specialized traits aligned with a resource-acquisition strategy, tightly adapted to open, rocky habitats. In contrast, *Aechmea vanhoutteana* exhibited a functionally stable, generalist profile across different habits, while *Quesnelia kautskyi* displayed marked plasticity, especially between epiphytic and terrestrial individuals.

Morphological traits tended to remain stable across environments, acting as “effect traits,” while anatomical and biochemical traits behaved as “response traits,” showing higher plasticity. These data highlight that differences in trait variability, specialization and generalism reflect distinct ecological strategies, what are critical for bromeliad species coexistence in the diverse and environmentally variable landscapes of tropical montane forests.

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Data availability All data generated or analysed during this study are included in this manuscript.

Declarations

Competing interests The authors declare that they have no competing interests.

Ethical approval The authors guarantee compliance with ethical standards.

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