

# Phenotypic variation of *Wittrockia cyathiformis* (Bromeliaceae) across life forms and forest types in the Atlantic Rainforest

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Academic editor: Luiza Teixeira-Costa ♦ Received 30 October 2024 ♦ Accepted 20 February 2025 ♦ Published 7 April 2025

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## Abstract

**Background and aims** – This study investigates the phenotypic plasticity of *Wittrockia cyathiformis* (Bromeliaceae), an endemic species of the Atlantic Rainforest, with the aim of evaluating its morphological variation in relation to different life forms and forest types, specifically Dense Ombrophilous Forest and Mixed Ombrophilous Forest.

**Material and methods** – Field collections were conducted in State Conservation Units and Campos Gerais National Park in Paraná during 2022 and 2023. We measured vegetative morphometric parameters of six to eight bromeliads for each life form (epiphytic, saxicolous, and terrestrial) in each forest type, totalling 43 specimens, with 22 from Dense Ombrophilous Forest and 21 from Mixed Ombrophilous Forest. Additionally, we assessed the national conservation status of the species in Brazil.

**Key results** – The different forest types of the Atlantic Forest exert a greater influence on the phenotypic variation of *W. cyathiformis* than life forms, with only leaf sheath length being greater in epiphytes and smaller in terrestrials. On the other hand, significant variations in leaf morphometry, such as leaf width and spine size, were strongly associated with the bioclimatic conditions of each forest type. Specimens from Dense Ombrophilous Forest exhibit characteristics typical of species adapted to warm and humid environments, with broader leaves, whereas those from Mixed Ombrophilous Forest have narrower leaves and smaller spines.

**Conclusion** – The different life forms of this species do not result in significant morphometric changes. However, its phenotypic plasticity is strongly influenced by the different forest types, which may favour adaptation to variable environmental conditions. Despite this adaptive capacity, *W. cyathiformis* is classified as endangered (EN) in its area of occupancy in Brazil. The ongoing habitat loss highlights the need for conservation measures to ensure the long-term persistence of its populations.

## Keywords

adaptive plasticity, bromeliad adaptation, climate-driven traits, leaf morphometrics, morphological variation

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## INTRODUCTION

Phenotypic plasticity (PP) refers to an organism's capacity to undergo morphological, physiological, or behavioural adjustments in response to environmental stimuli. In bromeliads, as well as in many other angiosperms, PP is expressed through variations in the shape, size, and number of vegetative and reproductive structures,

servicing as a critical adaptive mechanism. This plasticity allows these plants to thrive in diverse and often challenging environments, meeting the physiological demands imposed by their habitats (Givnish 1979; Neves et al. 2019).

While extensive research has explored the effects of environmental factors such as temperature, precipitation, and geographical distance on PP across various plant

species globally (e.g. Royer et al. 2009 (Aceraceae); Peppe et al. 2011 (multiple angiosperm families); Moles et al. 2014 (angiosperms, gymnosperms, ferns and fern allies, and bryophytes); Wright et al. 2017 (multiple families); Liu et al. 2021 (Pottiaceae)), studies focusing specifically on PP within the Bromeliaceae family, particularly in relation to bioclimatic and phytogeographical variations, remain limited (Chaves et al. 2018; Neves et al. 2019). This gap in literature underscores the need for further research, which our study aims to address by investigating the PP of Bromeliaceae, thereby contributing to a deeper understanding of adaptive strategies in this diverse plant family.

The Brazilian Atlantic Forest is renowned for its remarkable biodiversity and high levels of endemism, making it a global hotspot for conservation efforts (Myers et al. 2000). Unfortunately, more than 75% of its original extent has been lost due to human activities (Myers et al. 2000; Ribeiro et al. 2009). Among the unique endemic species found in this region is *Wittrockia cyathiformis* (Vell.) Leme, a tank bromeliad that occupies a variety of habitats, including rocky outcrops, terrestrial substrates, and epiphytic environments. This species is primarily distributed across the south-eastern and southern regions of Brazil, particularly within Dense Ombrophilous Forests (DOF) and Mixed Ombrophilous Forests (MOF) (Wanderley and Martins 2007; Tardivo 2023). The distinct forest typologies of the Atlantic Forest, such as MOF and DOF, provide an ideal context for studying the PP of *W. cyathiformis*, as each forest type presents unique phytogeoclimatic and climatic conditions (Struminski 2001; Maack 2012; Nitsche et al. 2019).

In the southern region of Brazil, MOF experiences a distinct seasonal pattern with a rainy season from October to March and a dry season for the remainder of the year, along with severe frosts and temperatures ranging from below 10°C in winter to over 20°C in summer (Maack 2012; Nitsche et al. 2019). Conversely, DOF in the same region is characterized by maritime influence and a warm coastal climate, featuring high humidity and precipitation levels averaging 3,700 mm annually (Struminski 2001; Maack 2012). This diverse array of environmental conditions offers a unique opportunity to investigate how *W. cyathiformis* adapts to its surroundings and exhibits PP in response to varying ecological factors.

As noted by Peppe et al. (2011), regions with higher annual mean temperatures tend to host angiosperms with elongated leaves relative to their width. Givnish (1984) further emphasizes that plants in warmer climates with limited water availability often develop leaves adapted to minimize water loss through evaporation, resulting in smaller leaf sizes compared to those in more humid environments. However, observations specific to Bromeliaceae, particularly in the genus *Vriesea* Lindl., highlight the prevalence of narrow-leaved species in regions characterized by hot climates and high rainfall (Neves et al. 2019). Consequently, the influence of climate on leaf size determination in bromeliads

remains ambiguous, and whether this corresponds to patterns observed in other angiosperms requires further investigation (Givnish 1984; Peppe et al. 2011; Wright et al. 2017; Neves et al. 2019).

Considering the ecophysiology of Bromelioideae, the subfamily to which *W. cyathiformis* belongs, water and nutrient absorption is primarily facilitated by peltate trichomes (scales) covering the leaf sheath portion in contact with the phytotelm, present on both the adaxial and abaxial surfaces, while the roots mainly serve absorptive and anchoring functions (Benzing 2000). Epiphytic bromeliads rely on these scales, and tank species also use their leaves to accumulate water, ensuring their survival on phorophytes, as they lack direct access to nutrients and water in forest soil (Benzing 2000; Oliveira 2004). In tank bromeliad species, trichome density is generally higher in the leaf sheath area. Accordingly, water and nutrient absorption through the leaf is influenced by the presence, shape, and distribution of scales on the surface of the sheath in contact with the phytotelm (Benzing 2000; Stefano et al. 2008).

The primary objective of this study was to explore the PP of *W. cyathiformis* across the diverse environments of the Brazilian Atlantic Rainforest in the state of Paraná. We aimed to investigate how variations in environmental conditions, particularly differences in life forms (terrestrial, epiphytic, and saxicolous) and forest types (DOF and MOF), influence the morphometric patterns of this species. Specifically, we examined whether the same life form (e.g. epiphytes) displays different morphometric traits in DOF versus MOF, and how these patterns compare across three life forms.

Our hypotheses predict that terrestrial bromeliads may present smaller leaf sheaths and lower density of peltate trichomes due to their possible reliance on roots for nutrition and hydration, while epiphytic and saxicolous species may exhibit the opposite pattern. Furthermore, we anticipate that *W. cyathiformis* in MOF may exhibit morphological patterns adapted to water scarcity, developing more elongated leaves. In contrast, those in DOF are likely to display wider leaf blades, favoured by the high-water availability combined with elevated temperatures. Ultimately, this research aims to expand our understanding of how PP enables *W. cyathiformis* to adapt to the diverse environmental conditions of the Atlantic Rainforest, while also filling part of the gap in knowledge regarding phenotypic plasticity in Bromeliaceae, and contributing to broader discussions in ecology and evolutionary biology.

## MATERIAL AND METHODS

### Study areas

Populations of *W. cyathiformis* were sampled in six fragments of MOF and four fragments of DOF in Paraná (Fig. 1) during the years 2022 and 2023. The locations

were selected based on herbarium data available on speciesLink (<https://specieslink.net/>).

### Sampling design

The sampling effort to locate populations of *W. cyathiformis* totalled 60 hours of searches at each of the ten sampling sites during 2022 and early 2023, with greater emphasis on visits during the flowering period (November to April), amounting to approximately 90 sampling days. Due to the scarcity of reproductive specimens, even during the flowering period, the largest specimens were selected at each site based on criteria such as the number of leaves, external diameter, and height. To avoid collecting specimens too close to each other, a minimum distance of 20 m was maintained between them.

### Morphometric measurements

Vegetative morphometric parameters were measured for six to eight bromeliads of each life form in each forest type: epiphytes up to 2 m in height, saxicolous individuals occurring on rocks with little substrate, and terrestrial individuals, all the specimens under low light intensity, in the understory. In total, 43 specimens of *W. cyathiformis* were analysed, distributed as follows: 22 specimens from Dense Ombrophilous Forest (eight epiphytic, seven saxicolous, and seven terrestrial) and 21 specimens from Mixed Ombrophilous Forest (six epiphytic, seven saxicolous, and eight terrestrial).

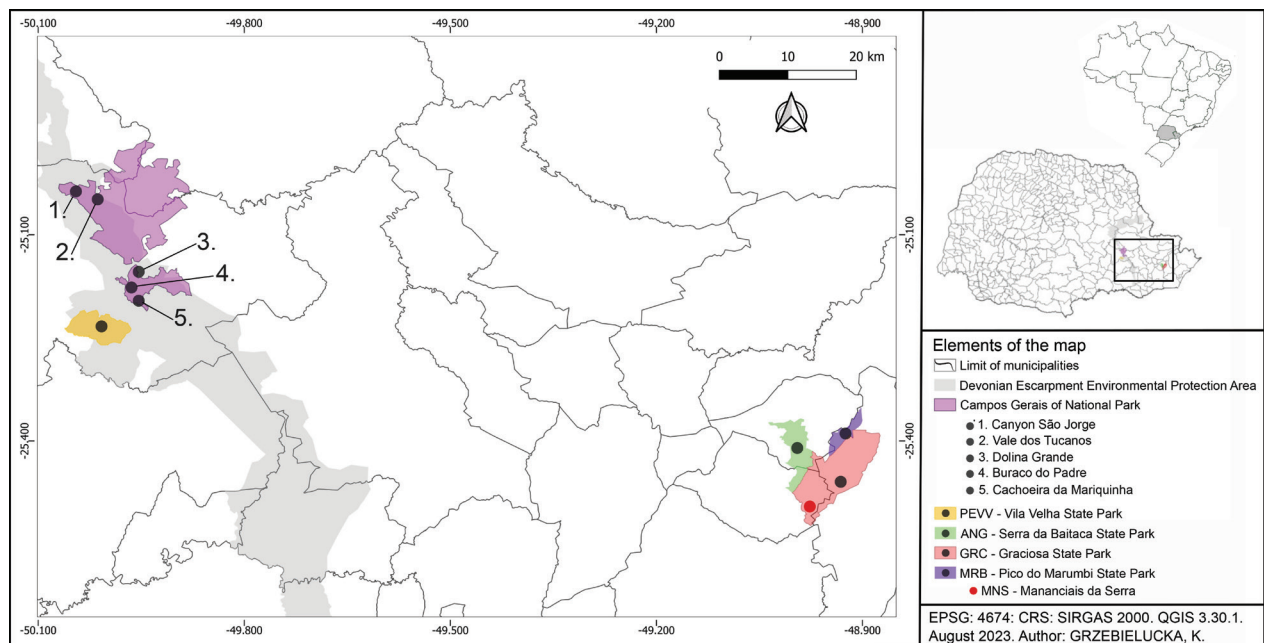
In the field, we conducted morphometric assessments using a metric tape measure (mm) to measure various parameters (Fig. 2): A: total leaf count; B: external diameter of the bromeliad, defined as the distance between opposing leaves; C: internal diameter, measured

as the width at the rosette's beginning; D: plant height, measured from the base to the apex of the tallest leaf. In the laboratory, we selected fully expanded mid-portion leaves and used callipers (precision: 0.02 mm) to measure: E: width of fully extended leaf sheaths; F: length of leaf sheaths; G: length of leaf blades; H: width of leaf blade apex (distal portion); I: width of middle leaf blade; J: length of the 4<sup>th</sup> spine at the leaf base; K: length of the 4<sup>th</sup> spine at the leaf apex (H–K based on Cogliatti-Carvalho et al. 1998; Lenzi et al. 2006; Voltolini and Santos 2011; Neves et al. 2019). The abbreviations of the morphometric parameters used and their respective descriptions are shown in Table 1.

### Trichome frequency analysis

We evaluated the frequency of trichomes in specimens using the same detached leaves, collected from at least three different locations for each forest type. In the DOF, the specimens included: two terrestrial, one epiphytic, and three saxicolous specimens from the Serra da Baitaca State Park; two terrestrial and two epiphytic specimens from the Pico do Marumbi State Park; and one epiphytic specimen from the Graciosa State Park. In the MOF, the specimens included: one epiphytic, one rupicolous, and one terrestrial specimen from Vila Velha State Park; one terrestrial and one saxicolous specimen from the Vale dos Tucanos; one terrestrial and one epiphytic specimen from the Cachoeira da Mariquinha; one saxicolous specimen from the São Jorge Canyon; one saxicolous specimen from the Buraco do Padre; and one epiphytic specimen from the Dolina Grande. In total, 21 specimens of *W. cyathiformis* were analysed for their trichome frequency.

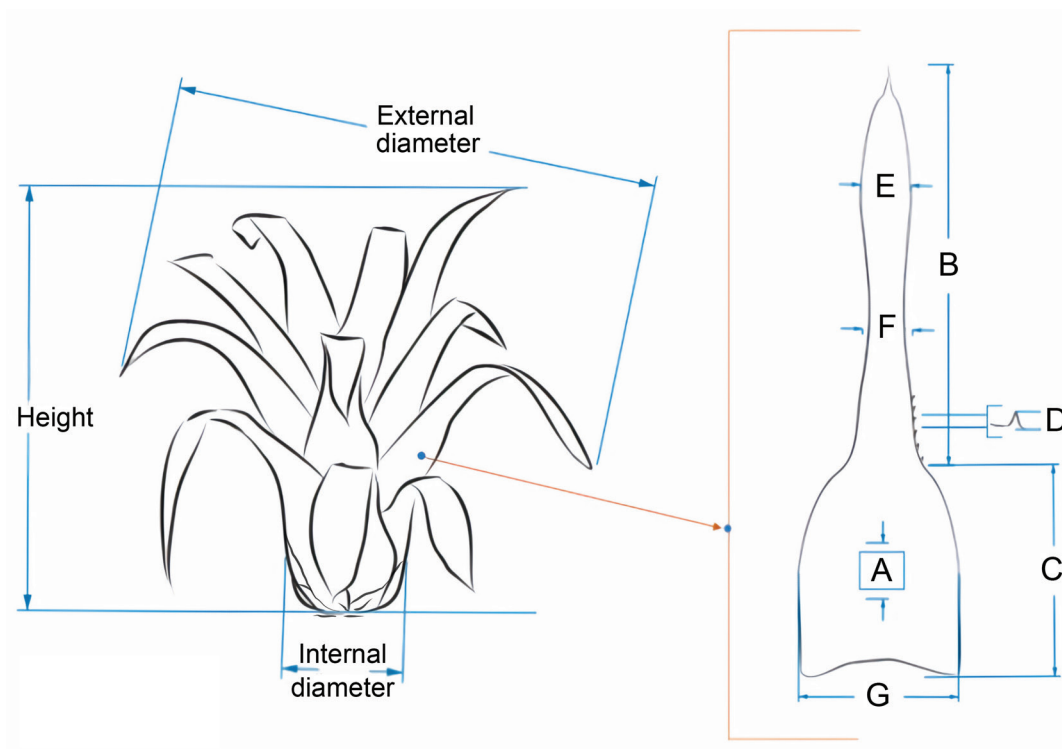
Using freehand cuts, leaf sheath sections of approximately 3 cm<sup>2</sup> were excised with a steel blade. To



**Figure 1.** Study areas in the Atlantic Forest fragments of Paraná. Collection points in Mixed Ombrophilous Forest are located on the left, and sampling sites in Dense Ombrophilous Forest are shown on the right.

**Table 1.** Abbreviations of the morphometric parameters analysed in *Wittrockia cyathiformis*.

Abbrev.	Description
BH	Bromeliad height
ED	External diameter
ID	Internal diameter
NL	Number of leaves
LSL	Leaf sheath length
LSW	Leaf sheath width
LBL	Leaf blade length
WLBA	Width of the leaf blade apex
WLMB	Width at the midpoint of the leaf blade
LSBLB	Length of spines at the base of the leaf blade
LSALB	Length of spines at the apex of the leaf blade
NTAB10	Number of absorptive peltate trichomes on the abaxial side of the leaf sheath, 10× objective lens on optical microscope
NTAB4	Number of absorptive peltate trichomes on the abaxial side of the leaf sheath, 4× objective lens on optical microscope
NTAD10	Number of absorptive peltate trichomes on the adaxial side of the leaf sheath, 10× objective lens on optical microscope
NTAD4	Number of absorptive peltate trichomes on the adaxial side of the leaf sheath, 4× objective lens on optical microscope



**Figure 2.** Morphometric parameters analysed in *Wittrockia cyathiformis*. A. Area of the leaf sheath for making 3 cm<sup>2</sup> sections to evaluate absorptive peltate trichomes. B. Leaf blade length. C. Leaf sheath length. D. Length of the fourth spine at the base of the leaf blade. E. Width of the apex of the leaf blade. F. Width at the midpoint of the leaf blade. G. Width of the fully extended leaf sheath. The highlighted leaf in the figure shows its removal from the median region of the leaf rosette, which was detached from the bromeliad for evaluation of the morphometric parameters illustrated on the right.

ensure consistency, the cuts were made from the same region of the sheath for all specimens, dividing the width and length of the sheath in half (Fig. 2A). Subsequently, paradermal cuts were made on both the abaxial and adaxial surfaces of these samples to prepare semi-permanent slides mounted in glycerin-gelatin (Stefano et al. 2008). The scales were then examined under an Olympus® BX 41 epifluorescence microscope with 4×, 10×, and 40× objectives lenses and quantified using ImageJ v.1.53 with java 8.

For the analysis using Scanning Electron Microscopy (SEM), the sheath sections were fixed in FAA (Johansen 1940). Subsequently, the material was dehydrated in increasing ethanol concentrations (70%, 80%, 95%) for one hour at each concentration. After this step, the samples were placed on absorbent paper for 30 minutes to remove excess alcohol and immediately taken to the SEM (Mira 3/Tescan model) at the Multiuser Laboratory Complex (C-LABMU) of the State University of Ponta Grossa. In the SEM, the samples were subjected to the CO<sub>2</sub> critical point method and coated with gold in a vacuum for visualization and photography.

### Conservation status assessment

The national classification (Brazil) of *W. cyathiformis* aligns with the criteria established by the IUCN Standards and Petitions Committee (IUCN 2012). A survey of species collection records was conducted using data available on the speciesLink virtual herbarium (<https://specieslink.net/>), in addition to our own collections. Geographic coordinates were used to calculate the Extent of Occurrence (EOO) and Area of Occupancy (AOO) according to IUCN criterion B (IUCN 2012) using GeoCAT (Bachman et al. 2011). For *W. cyathiformis*, the Extent of Occurrence (EOO) was calculated as 189,660 km<sup>2</sup>, resulting in its classification as Least Concern (LC), while the Area of Occupancy (AOO) was calculated as 236,000 km<sup>2</sup>, classifying it as Endangered (EN).

### Statistical analysis

All analyses were performed in R v.4.1.2 (R Core Team 2021) using RStudio v.2021.9.1.372 (RStudio Team 2021). To ensure the dataset's suitability for parametric statistical analysis, we first conducted an exploratory analysis. Normality was assessed using the Shapiro-Wilk test, which yielded  $p > 0.05$ , indicating a parametric distribution. Additionally, homoscedasticity was evaluated using the Fligner-Killeen test from the R package "stats", with results showing  $p > 0.05$ , confirming the homogeneity of variances.

To explore differences in bromeliad phenotypic variables among life forms, we employed ANOVA followed by Tukey's Test (at a significance level of 5%). We applied the t test to evaluate the distinctions between forest types and to compare life forms across different forest environments (e.g. epiphytes from MOF compared to epiphytes from DOF, and so forth). The clustering of

bromeliad morphometry for each life form and studied forest types was examined through principal component analysis (PCA) using the R package stats in R v.4.1.2 (R Core Team 2021).

To compare the morphological attributes of bromeliads among different forest types and life forms, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations. The distance matrix was constructed using morphological trait data, with continuous variables previously standardized by Hellinger transformation. Dissimilarity was calculated using the Bray-Curtis index. PERMANOVA was then applied to test the influence of forest types and life forms on bromeliad morphological variation. The analysis was conducted in R using the vegdist() and adonis2() functions from the R package vegan v.2.6-4 (Oksanen et al. 2022).

To investigate the impact of climate on the phenotype of *W. cyathiformis* specimens, we obtained data on 19 bioclimatic variables considering the geographic coordinates of the specimens ( $n = 43$ ) from the WorldClim database (<https://www.worldclim.org/>) with a spatial resolution of 30 arc-seconds, utilizing the R package raster v.3.6-20 (Hijmans et al. 2022). We then compared bioclimatic variables between different forest types using the t test to identify any significant mean disparities. Subsequently, PCA was employed to assess the formation of bromeliad clusters by type and life form, with the most explanatory bioclimatic and morphometric variables selected for each axis using the R package FactoMineR v.2.8 (Lê et al. 2008). Finally, a correlation analysis was conducted between these variables using the R package corrplot v.0.92 (Wei and Simko 2021), considering explanatory values ranging from positive to negative ( $r < 0$  or  $r > 0$ ), while also accounting for  $p < 0.05$ .

## RESULTS

### Phenotypic variation

Minimal morphometric variation was observed among *W. cyathiformis* individuals when comparing different life forms studied, except for the leaf sheath length (LSL), which was notably higher in epiphytic specimens compared to terrestrial ones ( $p = 0.03$ ; Table 2), and the saxicolous ones did not differ from the epiphytes or the terrestrial ones. However, significant variations emerged when comparing *W. cyathiformis* across forest types, particularly evident in bromeliad height (BH), external diameter (ED), number of leaves (NL), leaf sheath width (LSW), and parameters related to leaf blade length (LBL) and width (WLBA and WLMB), sheath width (LSW), and as well as spine dimensions (LSBLB and LSALB) ( $p < 0.05$ ; Table 2).

When comparing life forms separately between forest types, we observed that specimens differed in

**Table 2.** Comparison of morphometric parameters of *Wittrockia cyathiformis* between Dense Ombrophilous Forest (DOF) and Mixed Ombrophilous Forest (MOF), and among its epiphytic, saxicolous, and terrestrial life forms. Morphometric parameter values are in millimetres, except for NTAB10, NTAB4, NTAD10, and NTAD4, which are in decimal numbers. Explanatory factors are marked according to significance level (\*0.05, \*\*0.005, \*\*\*0). The letters a, ab, b mean that the values with the same letter do not differ significantly from each other. Abbreviations of parameters are explained in Table 1.

Parameters	DOF (Mean ± SE)	MOF (Mean ± SE)	t test	p value	Life forms (Mean ± SE)			F value	p value
					Epiphytic	Saxicolous	Terrestrial		
BH	479.09 ± 111.31	683.33 ± 119.72	-5.79	0***	543.57 ± 159.45	599.29 ± 170.86	592.67 ± 135.99	0.54	0.59
ED	744.55 ± 143.65	1008.43 ± 186.31	-5.18	0***	888 ± 195.97	882.5 ± 248.74	851.33 ± 200.21	0.14	0.89
ID	194.55 ± 39.49	195.95 ± 46.09	-0.11	0.92	195.36 ± 42.17	201.43 ± 48.97	189.33 ± 37.7	0.29	0.75
NL	19.82 ± 2.82	21.67 ± 2.29	-2.36	0.02*	20.36 ± 3.69	20.93 ± 2.5	20.87 ± 1.85	0.18	0.84
LSL	141.5 ± 26.03	152.19 ± 20.71	-1.49	0.14	154.79 ± 17.88 <sup>a</sup>	152.21 ± 28.58 <sup>ab</sup>	134.07 ± 19.86 <sup>b</sup>	3.68	0.03*
LSW	110.36 ± 18.55	93.19 ± 15.28	3.32	0***	98.14 ± 20.38	110.36 ± 18.69	97.73 ± 16.18	2145.00	0.13
LBL	416.64 ± 113.53	665 ± 209.90	-4.68	0***	552.14 ± 249.40	552.71 ± 172.98	510.87 ± 194.05	0.18	0.83
WLBA	58.77 ± 7.96	47.81 ± 8.27	4.42	0***	51.14 ± 17.88	56.36 ± 8.7	52.8 ± 9.78	1.05	0.36
WLMB	63.77 ± 13.23	35.95 ± 7.37	8.57	0***	50.57 ± 18.94	50.86 ± 19.86	49.2 ± 15.27	0.04	0.97
LSBLB	1.03 ± 0.49	0.69 ± 0.31	2.72	0.01*	0.7 ± 0.3	0.93 ± 0.5	0.95 ± 0.46	0.22	0.80
LSALB	3.95 ± 1.18	1.7 ± 0.53	8.13	0***	2.06 ± 1.26	2.89 ± 1.53	3 ± 1.62	1458.00	0.25
NTAB10	13 ± 4.39	13.5 ± 2.15	0.61	0.55	14.71 ± 4.95	14 ± 2.20	13.28 ± 2.71	0.25	0.78
NTAB4	74.18 ± 15.34	71.1 ± 14.25	0.82	0.43	73 ± 15.35	69.86 ± 20.22	61.14 ± 11.93	0.21	0.81
NTAD10	14.45 ± 3.27	13 ± 1.67	0.00	1.00	13.43 ± 2.06	13.84 ± 3.81	12.14 ± 0.98	0.50	0.61
NTAD4	76.64 ± 18.25	61.2 ± 12.21	1.84	0.08	73 ± 15.35	69.86 ± 20.22	61.14 ± 11.93	1.16	0.35

**Table 3.** Comparison of the morphometric parameters of *Wittrockia cyathiformis* across its life forms (epiphytic, saxicolous, and terrestrial) separated by forest types: Dense Ombrophilous Forest and Mixed Ombrophilous Forest. Only significant values (p < 0.05) from the comparisons of morphometric parameters are presented in this table. For the full results of all comparisons, including non-significant ones, refer to Supplementary material 1. Abbreviations of parameters are explained in Table 1.

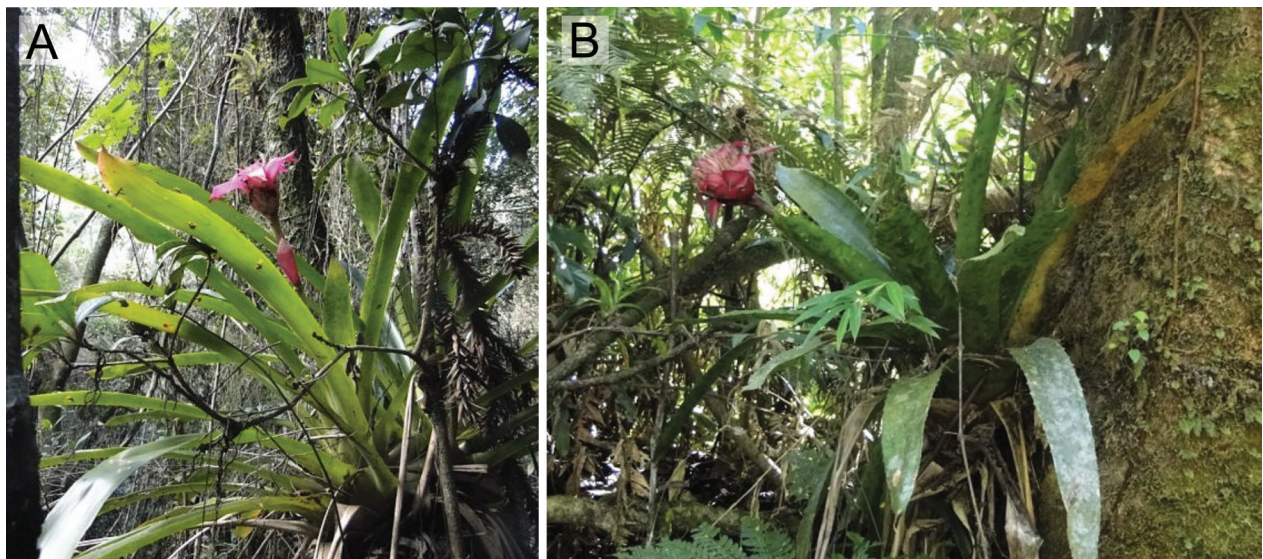
Parameters	Mean ± SE		t test	p value
	Epiphytic (DOF)	Epiphytic (MOF)		
BH	452.50 ± 122.32	665.00 ± 119.12	-3.30	0***
ED	763.75 ± 163.43	1053.66 ± 68.70	-4.51	0***
NL	18.62 ± 3.62	22.66 ± 2.42	-2.50	0.02*
LSW	109.62 ± 18.60	82.83 ± 10.18	3.43	0***
WLBA	56.87 ± 8.07	43.5 ± 8.93	2.88	0.01*
WLMB	63.37 ± 14.65	33.5 ± 4.41	5.43	0***
LSBLB	3.46 ± 0.94	1.54 ± 0.55	4.75	0***
	Saxicolous (DOF)	Saxicolous (MOF)		
BH	480.00 ± 143.06	718.57 ± 97.88	-3.64	0***
ED	711.42 ± 55.59	1053.35 ± 45.82	-3.53	0***
LBL	434.71 ± 153.34	670.71 ± 117.54	-3.23	0***
WLBA	60.85 ± 6.09	51.85 ± 8.91	2.20	0.05*
WLMB	67.42 ± 11.95	34.28 ± 8.44	5.99	0***
LSBLB	4.00 ± 1.32	1.78 ± 0.68	3.93	0***
LSALB	1.28 ± 0.39	0.57 ± 0.31	3.76	0***
	Terrestrial (DOF)	Terrestrial (MOF)		
BH	508.57 ± 58.99	666.25 ± 144.01	-2.84	0.01*
LBL	361.42 ± 73.86	641.62 ± 184.76	-3.93	0***
WLBA	58.85 ± 9.92	47.5 ± 6.16	2.62	0.02*
WLMB	60.57 ± 13.84	39.25 ± 7.74	3.60	0***
LSBLB	4.43 ± 1.20	1.75 ± 0.37	5.67	0***

morphometric parameters even when they shared the same life forms (Table 3). The morphometric parameters that varied across all three life forms included bromeliad height (BH), which was more pronounced in MOF, the length of spines at the base of the leaf blade (LSBLB), width of the leaf blade apex (WLBA) and width at the midpoint of the leaf blade (WLMB), which were larger in DOF (Table 3, Fig. 3). For epiphytes, the leaf sheath width (LSW) was greater in DOF, while the leaf blade length (LBL) was larger in MOF specimens in both terrestrial and saxicolous life forms (Table 3).

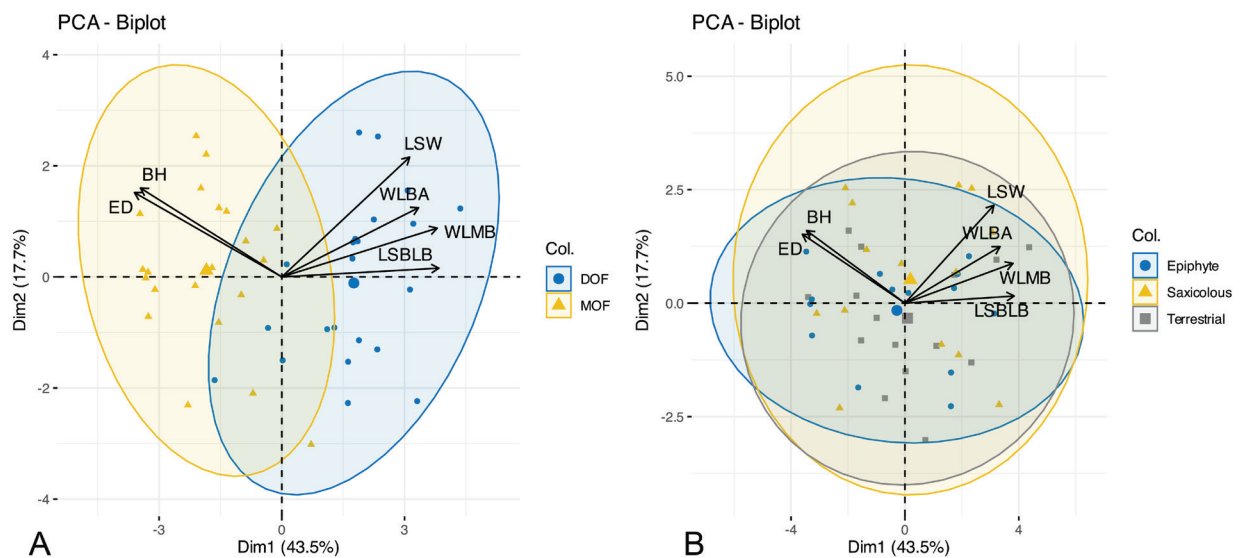
In MOF environments, *W. cyathiformis* specimens exhibited greater height, larger external diameter, and

longer leaf blades, which were narrower and featured smaller spines (Fig. 3A). Conversely, specimens from DOF areas were characterized by wider and broader leaf sheaths and blades, with larger spines both at the base and apex of the leaf blade, albeit with smaller external diameter and height (Fig. 3B).

The PERMANOVA analysis did not reveal significant differences among life forms within each forest type ( $R^2 = 0.049$ ;  $F = 0.491$ ;  $p = 0.83$ ) (Supplementary material 2). However, significant differences were observed between DOF and MOF ( $R^2 = 0.385$ ;  $F = 25.745$ ;  $p = 0.001$ ). The PCA analysis again highlighted that the forest environment exerted a pronounced influence on the



**Figure 3.** *Wittrockia cyathiformis*. **A.** Epiphytic specimen in Mixed Ombrophilous Forest with narrow leaf blades, displaying an inflorescence and bracts forming a cup shape. **B.** Epiphytic specimen in Dense Ombrophilous Forest exhibiting wide and marbled leaf blades with dark green spots throughout the extension.



**Figure 4.** Principal Component Analysis (PCA) of morphometric parameter data for *Wittrockia cyathiformis* ( $n = 43$ ). **A.** Ordination of morphometric variables based on different forest types (Mixed Ombrophilous Forest (MOF) and Dense Ombrophilous Forest (DOF)). **B.** Ordination of morphometric variables based on different life forms (epiphytic, saxicolous, and terrestrial).

specimens' phenotype, resulting in distinct clusters (Fig. 4A). In contrast, the life form of bromeliad specimens had a negligible impact on their morphometric conformation (Fig. 4B), as evidenced by the complete overlap of clusters considering the two evaluated principal components. Notably, external diameter (ED) and bromeliad height (BH) exhibited stronger associations with MOF, whereas DOF showed associations with leaf blade (WLBA and WLMB) and sheath width (LSW), as well as spine length (LSBLB).

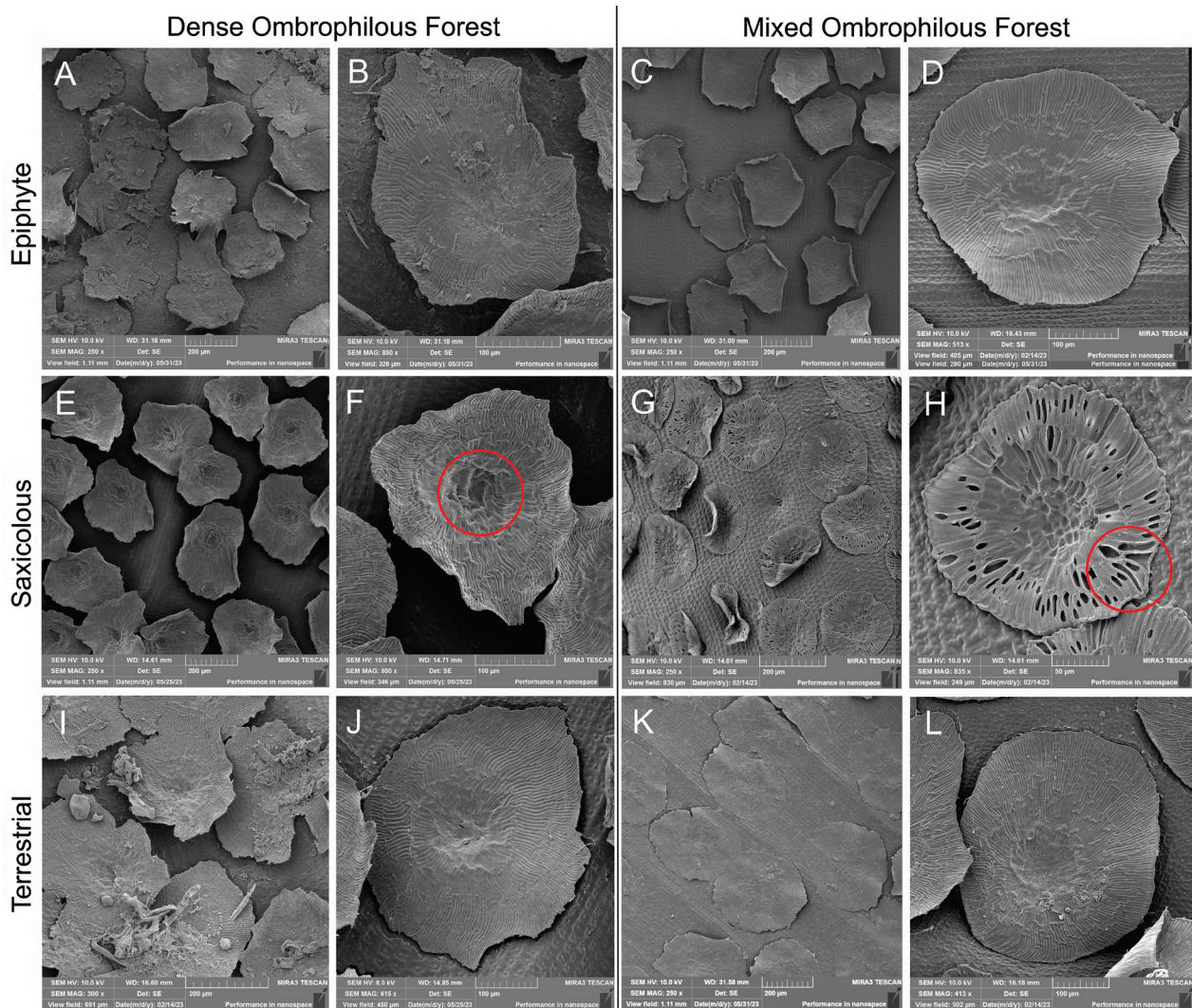
**Peltate absorbing trichomes**

The peltate absorbing trichomes exhibited the typical pattern of Bromelioideae, often asymmetrically occurring unequally along the leaf, with one or two outer series of shield cells, sometimes forming a discernible wing relative to the central disc cells (Fig. 5F). Greater spacing

between trichomes was observed in MOF, resulting in a more exposed epidermis (Fig. 5C, G, K). Some MOF specimens showed signs of dehydration in the wing (Fig. 5H). Despite variations in trichome arrangement and spacing, the average number of peltate trichomes (NTAB10, NTAB4, NTAD10, NTAD4) did not vary according to life form or environmental type ( $p > 0.05$ ; Table 2).

**Climate influence**

The average annual temperature (DOF:  $20.01 \pm 2.549$ ; MOF:  $17.40 \pm 32.124$ ;  $t = 36.056$ ;  $p < 0.001$ ) and annual precipitation (DOF:  $2,049.9 \pm 389.835$ ; MOF:  $1,567.4 \pm 35.978$ ;  $t = -6.244$ ;  $p < 0.001$ ) peaked in DOF. The highest temperature recorded in DOF was  $31.2^{\circ}\text{C}$ , whereas in MOF, it reached  $26.7^{\circ}\text{C}$ . The only variable that exhibited no variance between forest types was



**Figure 5.** Absorptive peltate trichomes on the adaxial side (NTDA4 and NTDA10) of the leaf sheaths of *Wittrockia cyathiformis* in epiphytic, saxicolous, and terrestrial life forms between Dense and Mixed Ombrophilous Forests in Paraná, Brazil, photographed under a scanning electron microscope (SEM). A, B. Graciosa State Park. C. Vila Velha State Park. D. Cachoeira da Mariquinha. E, F. Serra da Baitaca State Park, with central cells of the disc highlighted in red, distinguishable from the wing. G, H. Vale dos Tucanos (PARNA), with signs of dehydration in the wing highlighted in red. I. Pico do Marumbi State Park. J. Serra da Baitaca State Park. K. Vila Velha State Park. L. Cachoeira da Mariquinha.



**Table 4.** Correlation between bioclimatic variables and morphometric parameters of *Wittrockia cyathiformis* in Paraná. The table presents the  $r$  values, with those indicating  $p < 0.05$  shown in bold. BH = bromeliad height, LSW = leaf sheath width, LBL = leaf blade length, WLMB = width at the midpoint of the leaf blade. Abbreviations of parameters are explained in Table 1.

Bioclimatic variables	Parameters			
	BH	LSW	LBL	WLMB
Annual Mean Temperature	-0.59	-0.18	-0.27	-0.41
Temperature Seasonality	-0.23	0.45	-0.14	-0.01
Maximum Temperature of Warmest Month	0.43	-0.17	0.15	0.02
Minimum Temperature of Coldest Month	0.58	0.18	0.21	0.43
Mean Temperature of Wettest Quarter	0.17	0.06	0.31	0.7
Mean Temperature of Warmest Quarter	-0.45	0.14	-0.14	-0.2

the precipitation of the driest quarter (Supplementary material 3). However, concerning the correlation model, bioclimatic variables primarily associated with temperature demonstrated the greatest explanatory capacity, with DOF showcasing the highest mean bioclimatic variables in the correlation model.

The analysis of the bioclimatic and morphometric variables of *W. cyathiformis* revealed several significant correlations (Table 4). Negative values indicated that with increases in the annual mean temperature and the mean temperature of the warmest quarter, the size of the specimens tends to decrease, affecting parameters such as height (BH), leaf sheath length (LSL), and width at the midpoint of the leaf blade (WLMB) (Table 4).

On the other hand, positive correlations emerged between the maximum temperature of the warmest month and the minimum temperature of the coldest month. *Wittrockia cyathiformis* also tends to present greater height (BH) and width at the midpoint of the leaf blade (WLMB) (Table 4). Interestingly, leaf sheath width (LSW) emerged as the only morphometric characteristic positively correlated with seasonality without any other negative result (Table 4;  $r = 0.45$ ). This suggests that increased temperature seasonality, particularly in DOE, may contribute to an increase in the LSW observed in the specimens (Tables 2, 3).

## DISCUSSION

Our results demonstrate that the different forest types of the Atlantic Forest exert a greater influence on the phenotypic variation of *W. cyathiformis* than life forms (epiphytic, saxicolous, and terrestrial). Significant variations in leaf morphology, such as leaf width, bromeliad height, and spine size, were strongly associated with the bioclimatic conditions of each forest type. In contrast, the analysis of *W. cyathiformis* specimens without considering forest type revealed that only leaf sheath length varied among different life forms. This suggests that life form alone has a limited influence on the PP of this species.

However, when analysing life forms between different forest types, we observed significant differences in several morphometric parameters, highlighting the importance

of environmental conditions in shaping the morphology of *W. cyathiformis*. Although microenvironmental differences occur among epiphytic, saxicolous, and terrestrial forms, these conditions did not result in significant morphometric differences within the same forest type, reinforcing that broader environmental factors play a more decisive role in phenotypic variation.

Considering broadly the comparison between life forms, *W. cyathiformis* exhibits phenotypic variation only in leaf sheath length, which is greater in epiphytic specimens and smaller in terrestrial ones, while the number of trichomes showed no significant differences. These results differ from the literature (Stefano et al. 2008; Zorger et al. 2019) and do not fully support our initial hypothesis, which predicted that terrestrial bromeliads would have smaller leaf sheaths and a lower number of trichomes, possibly due to the use of roots for nutrient and water absorption from the soil. The absence of variation in trichome number may be associated with the ecophysiological and genetic characteristics of *W. cyathiformis*, which make its life forms less dependent on root absorption for survival (Smith and Downs 1979).

The absence of differences in the number of trichomes in *W. cyathiformis* highlights the plant's ecophysiological plasticity, enabling its survival in different life forms without significant changes in trichome density, also suggesting a reduced reliance on nutrient and water absorption through roots in its terrestrial form. The discrepancy compared to other studies (Stefano et al. 2008; Zorger et al. 2019) that identified differences in trichome numbers between epiphytic and terrestrial forms suggests that adaptive responses may vary among species due to genetic and ecophysiological differences.

According to the Classification of Ecophysiological Types of Bromeliaceae (Benzing 2000), species in the subfamily Bromelioideae, such as *W. cyathiformis*, have terrestrial, saxicolous, or epiphytic life forms with well-developed leaf tanks. In these plants, the leaves function in absorption through the leaf sheath, while the roots primarily provide mechanical support and are conditionally absorptive. Based on morphometric parameters, terrestrial specimens do not appear to rely on distinct root-provided nutrition compared to other life forms. However, epiphytic specimens invest more in leaf

sheath length, possibly to ensure greater accumulation and retention of water and debris in the leaf rosette, which are essential for their nutrition and hydration (Voltolini and Santos 2011).

However, Zorger et al. (2019), while studying epiphytic and terrestrial forms of *Billbergia euphemiae* É.Morren (Bromelioideae - Bromeliaceae), observed that epiphytic bromeliads exhibited a higher density of absorptive peltate trichomes on the abaxial surface. Given the scarcity of evidence and the contrast with other authors (Stefano et al. 2008; Zorger et al. 2019). Therefore, considering the scarcity of evidence and the contrast with other studies (Stefano et al. 2008, Zorger et al. 2019), we emphasize the need for research that integrates physiology, morpho-anatomy, and genetics of Bromelioideae, including multiple species and broad sampling, to elucidate the relationship between trichomes and ecophysiological adaptations in this group.

In the context of different forest types, our results support the initial hypothesis that specimens in the DOF have broader leaf blades, influenced by higher water availability and elevated temperatures. Distinct phenotypic patterns were observed between forest types: in DOF, bromeliads exhibit broad leaf blades and sheaths with large spines, whereas in MOF, the leaf blades are long but narrow, with smaller spines, a larger external diameter, and a higher number of leaves.

The sampled forest fragments exhibit distinct climatic characteristics typical of their respective forest types. According to climatic data from DOF in Paraná (Struminski 2001), temperatures range from approximately 18°C in the coldest months to 22°C in the warmest months. However, we observed notable seasonality and increased temperatures in the sampled areas of DOF, with this bioclimatic particularity being the main factor associated with the greater sheath width across the three life forms of the specimens in this forest type.

In the DOF areas of the Serra do Mar in Paraná, high temperatures and substantial rainfall predominate. According to Wright et al. (2017), it is common to find angiosperms with large leaves in environments where high temperatures and significant humidity coexist. The authors conducted a global analysis of 7,670 angiosperm species across various climatic zones and highlighted that species with broad leaves prevail in warm and humid environments due to their greater efficiency in thermal regulation through transpiration. These climatic conditions influence plant morphology, demonstrating species adaptation to the local climate (Wright et al. 2017).

All plants perform evaporative cooling to reduce leaf temperature, which results in water loss through transpiration (Givnish 1984). For this mechanism to be efficient without leading to dehydration, it is essential that the plant has access to an adequate amount of water (Givnish 1984; Wright et al. 2017). In the DOF, where temperatures are high and precipitation is

abundant, bromeliads have broad and large leaves, possibly as an adaptation to the high-water availability that allows greater efficiency in thermal regulation through transpiration. In contrast, in water-restricted environments such as the MOF, plants tend to develop narrower leaves, an adaptation that minimizes water loss (Givnish 1984; Wright et al. 2017).

Our results differ from those found by Neves et al. (2019), who studied the morphometry of *Vriesea* (Tillandsioideae - Bromeliaceae) in the Serra do Mar (DOF). While Neves et al. (2019) observed a predominance of specimens with narrow leaf blades and sheaths in regions with warm climates and high rainfall, our study focused on a different species, whose morphology exhibits distinct patterns under similar conditions. In another type of habitat, Lenzi et al. (2006) observed that the leaves of *Aechmea lindenii* (É.Morren) Baker var. *lindenii* (Bromelioideae - Bromeliaceae) are shorter, broader, and more coriaceous in herbaceous restinga environments, where they are fully exposed to solar radiation. On the other hand, individuals of the same species exhibit longer, narrower, and more membranous leaves in arboreal restinga areas, which provide more shade. These contrasts suggest that different bromeliad species or genera respond differently to phytological and bioclimatic variables, reflecting specific adaptations to each habitat.

The distribution of trichomes on the leaf sheaths is another phenotypic variation in *W. cyathiformis* that may have been influenced by the climatic variables of each forest typology. Smaller and asymmetrical trichomes do not cover the entire leaf surface in drier locations, as trichomes structured in this way, as observed in bromeliads in MOF, help promote water condensation on the leaves, allowing better circulation of droplets (Pierce 2007). Another interesting point regarding trichomes was the presence of scales showing signs of dehydration in the saxicolous specimen in MOF, a characteristic that occurs when the epidermis is not sufficiently moist in its habitat (Benzing 1976; Strehl 1983), corroborating the bioclimatic conditions observed in MOF.

The spines of *W. cyathiformis* varied greatly in size according to forest typology, both at the base of the leaf blade and at its apex, with bromeliads in DOF presenting more robust spines. According to Benzing (2000), the presence of spines on the leaf margins is a predominant characteristic in most Bromelioideae and many Pitcairnioideae. Specifically, ground-level plants in these subfamilies invest more in mechanical defences, such as spines, due to the significant predation they are subjected to, reducing physical damage to the plant (Benzing 2000). These relationships highlight how various ecological pressures shape morphological traits in bromeliads, allowing their adaptation to different habitats.

The high PP observed in our results may indicate a diverse gene pool in this species, allowing its local adaptation to variable environmental conditions (Ward et al. 2008; Townsend et al. 2010). However, climate change

and the conversion of natural habitats into anthropogenic landscapes pose significant threats to biodiversity (Lemes et al. 2013; Ferro et al. 2014). Habitat alterations caused by human activities occur at a pace incompatible with evolutionary adaptations. Thus, despite the considerable adaptation of *W. cyathiformis* across different forest types in the Atlantic Forest, it is likely that the species will be adversely affected by these anthropogenic factors and intensified climate changes (Sala et al. 2000; Thomas et al. 2004; Dirzo et al. 2014).

Although *W. cyathiformis* is classified as Least Concern (LC) based on the extent of its occurrence, the species is considered Endangered (EN) due to its restricted area of occupancy. The ongoing loss and fragmentation of the Atlantic Forest threaten the integrity of its populations. Between 2018 and 2019, Paraná was the third state in Brazil with the highest deforestation rates in this biome (Vieira and Mendonça 2021). Fire also represents a constant threat, with 11.6 million hectares burned in the Atlantic Forest between 1985 and 2023, 39% of which were native vegetation, especially forests, which are highly vulnerable to fire as they are not adapted to it, resulting in significant biodiversity loss (Pinto et al. 2025). It is possible that areas previously inhabited by *W. cyathiformis* populations have already disappeared, making this an important focus of investigation for future studies.

The preservation of protected areas and remaining forest fragments, along with ecological corridors and the strengthening of fire prevention and control programs, play a crucial role in species persistence and the maintenance of their genetic diversity (Araújo and Bastos 2019; Pinto et al. 2025). Therefore, understanding the plasticity and phenotypic variations in species such as *W. cyathiformis* is essential for elucidating its ecology and supporting conservation strategies, especially considering its vulnerability to extinction threats (Kunin and Gaston 1997).

## CONCLUSION

Our results demonstrate that the different life forms of *W. cyathiformis* have a limited influence on morphometric variation, with a significant difference only in leaf sheath length, which is greater in epiphytic specimens. The absence of variation in trichome number suggests that terrestrial specimens do not rely on differentiated root-based nutrition, reinforcing the importance of leaf sheaths in resource absorption. Additionally, distinct morphometric patterns were observed between the Atlantic Forest types, associated with the specific bioclimatic conditions of each ecosystem. The broad leaves in Dense Ombrophilous Forest (DOF) follow the typical pattern of angiosperms in warm and humid habitats but contrast with other bromeliads in similar environments, highlighting the uniqueness of the adaptive responses of *W. cyathiformis*.

We emphasize the need to expand studies on the PP, physiology, and genetics of Bromeliaceae, including multiple species and representative sampling. This effort is essential for understanding the interactions between morphology, ecology, and environmental factors, as well as providing a basis for effective conservation practices. The ongoing loss and fragmentation of the Atlantic Forest pose a critical threat to endemic species such as *W. cyathiformis*, whose area of occupancy is already considered endangered. We recommend future studies to assess the impact of these threats on the species' populations, using the observed morphological adaptations as a foundation for management and conservation strategies. The preservation of natural habitats and the implementation of ecological corridors are urgent measures to ensure the survival of this and other vulnerable species.

## ACKNOWLEDGEMENTS

This work was made possible by the financial support of the Coordination for the Improvement of Higher Education Personnel (CAPES). Thanks to research permit no. 46.21 granted by the Water and Land Institute (IAT) of Paraná. Special thanks to the State University of Ponta Grossa (UEPG) and its Herbarium (HUPG) for transportation and support in conducting field collections. We also thank the Laboratory of Genetics and Evolution (LAGEV) and the Multiuser Laboratory Complex at UEPG (C-LABMU) for all the infrastructure and support for the development of this research.

## REFERENCES

- Araújo TMS, Bastos FH (2019) Corredores ecológicos e conservação da biodiversidade: aportes teóricos e conceituais. *Revista da Casa da Geografia de Sobral* 21(2): 716–729. <https://doi.org/10.35701/rcgs.v21n2.575>
- Bachman S, Moat J, Hill AW, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *Zookeys* 150: 117–26. <https://doi.org/10.3897/zookeys.150.2109>
- Benzing DH (1976) Bromeliad trichomes: structure, function, and ecological significance. *Selbyana* 1: 331–348. <https://www.jstor.org/stable/41759602> [accessed 20.04.2023]
- Benzing DH (2000) Bromeliaceae: profile of an adaptive radiation. Cambridge University Press, 1–708.
- Chaves CJN, Leal BSS, Lemos-Filho JP (2018) How are endemic and widely distributed bromeliads responding to warming temperatures? A case study in a Brazilian hotspot. *Flora* 238: 110–118. <https://doi.org/10.1016/j.flora.2017.05.003>
- Cogliatti-Carvalho L, Almeida DR, Rocha CFD (1998) Phenotypic response of *Neoregelia johannis* (Bromeliaceae) dependent on light intensity reaching the plant microhabitat. *Selbyana* 19(2): 240–244. <https://www.jstor.org/stable/41759994> [accessed 14.05.2023]
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. *Science* 345(6195): 401–406. <https://doi.org/10.1126/science.1251817>
- Ferro VG, Lemes P, Melo AS, Loyola R (2014) The reduced effectiveness of protected areas under climate change

- threatens Atlantic Forest tiger moths. *PLoS ONE* 9(9): e107792. <https://doi.org/10.1371/journal.pone.0107792>
- Givnish TJ (1979) On the adaptive significance of leaf form. In: Solbrig OT, Jain S, Johnson GB, Raven PH (Eds) *Topics in Plant Population Biology*. Palgrave, London, 375–407. [https://doi.org/10.1007/978-1-349-04627-0\\_17](https://doi.org/10.1007/978-1-349-04627-0_17)
- Givnish TJ (1984) Leaf and canopy adaptations in tropical forests. In: Medina E, Mooney HA, Vázquez-Yanes C (Eds) *Physiological Ecology of Plants of the Wet Tropics. Tasks for Vegetation Science, Vol. 12*. Springer, Dordrecht, 51–84. [https://doi.org/10.1007/978-94-009-7299-5\\_6](https://doi.org/10.1007/978-94-009-7299-5_6)
- Hijmans RJ, Van Etten J, Sumner M, Cheng J, Baston D, Bevan A, Bivand R, Busetto L, Canty M, Fasoli B, Forrest D, Ghosh A, Golicher D, Gray J, Greenberg JA, Hiemstra P, Hingee K, Ilich A, Institute for Mathematics Applied Geosciences, Karney C, Mattiuzzi M, Moshier S, Naimi B, Nowosad J, Pebesma E, Lamigueiro OP, Racine EB, Rowlingson B, Shortridge A, Venables B, Wueest R (2022) Raster: Geographic Data Analysis and Modeling. R Package Version 3.6-20. <https://doi.org/10.32614/CRAN.package.raster>
- IUCN (2012) Guidelines for Application of IUCN Red List Criteria at Regional and National Levels. Version 4.0. IUCN, Gland, Switzerland and Cambridge, UK, 1–41. <https://portals.iucn.org/library/sites/library/files/documents/RL-2012-002.pdf> [accessed 01.09.2023]
- Johansen D (1940) *Plant Microtechnique*. McGraw-Hill Book Company, New York, 1–523.
- Kunin WE, Gaston KJ (1997) *The Biology of Rarity. Causes and Consequences of Rare-Common Differences*. Chapman & Hall, London, 1–291. <https://doi.org/10.1007/978-94-011-5874-9>
- Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software* 25: 1–18. <https://doi.org/10.18637/jss.v025.i01>
- Lemes P, Melo AS, Loyola RD (2013) Climate change threatens protected areas of the Atlantic Forest. *Biodiversity and Conservation* 23: 357–368. <https://doi.org/10.1007/s10531-013-0605-2>
- Lenzi M, Matos JZ, Orth AI (2006) Variação morfológica e reprodutiva de *Aechmea lindenii* (E. Morren) Baker var. *lindenii* (Bromeliaceae). *Acta Botanica Brasílica* 20(2): 487–500. <https://doi.org/10.1590/S0102-33062006000200024>
- Liu L, Jiang Y, Song X, Tang J, Kou J, Fan Y, Shao X (2021) Temperature, not precipitation, drives the morphological traits of *Didymodon rigidulus* in Tibet. *Ecological Indicators* 133: 108401. <https://doi.org/10.1016/j.ecolind.2021.108401>
- Maack R (2012) *Geografia Física do Estado do Paraná*. UEPG Publishing, Ponta Grossa, 1–526.
- Moles AT, Perkins SE, Laffan SW, Flores-Moreno H, Awasthy M, Tindall ML, Sack L, Pitman A, Kattge J, Aarssen LW, Anand M, Bahn M, Blonder B, Cavender-Bares J, Cornelissen JHC, Cornwell WK, Díaz S, Dickie JB, Freschet GT, Griffiths JG, Gutierrez AG, Hemmings FA, Hickler T, Hitchcock TD, Keighery M, Kleyer M, Kurokawa H, Leishman MR, Liu K, Niinemets U, Onipchenko V, Onoda Y, Penuelas J, Pillar VD, Reich PB, Shiodera S, Siefert A, Sosinski Jr EE, Soudzilovskaia NA, Swaine EK, Swenson NG, Bodegom PMV, Warman L, Weiher E, Wright IJ, Zhang H, Zobel M, Bonser SP (2014) Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* 5(5): 1167–1180. <https://doi.org/10.1111/jvs.12190>
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. <https://doi.org/10.1038/35002501>
- Neves B, Zanella CM, Kessous IM, Fernando P, Uribe FP, Salgueiro F, Bered F, Antonelli A, Bacon CD, Costa AF (2019) Drivers of bromeliad leaf and floral bract variation across a latitudinal gradient in the Atlantic Forest. *Journal of Biogeography* 47: 261–274. <https://doi.org/10.1111/jbi.13746>
- Nitsche PR, Caramori PH, Ricce WS, Pinto LFD (2019) Atlas Climático do Estado do Paraná. Instituto Agronômico do Paraná – IAPAR, Londrina (PR), 1–210. <https://www.idrparana.pr.gov.br/Pagina/Atlas-Climatico> [accessed 17.02.2023]
- Oliveira RR (2004) Importância das bromélias epífitas na ciclagem de nutrientes da Floresta Atlântica. *Acta Botanica Brasílica* 18: 793–799. <https://doi.org/10.1590/S0102-33062004000400009>
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlenn D, Ouellette MH, Cunha ER, Smith, T, Stier A, Ter Braak CJF, Weedon J, Borman T (2022) *vegan: community ecology package, version 2.6–2*. <https://cran.r-project.org/web/packages/vegan/> [accessed 11.08.2023]
- Peppe DJ, Royer DL, Cariglino B, Oliver SY, Nwman S, Leight E, Enikolopov G, Burgos-Fernandez M, Herrera F, Adams JM, Correa E, Curran ED, Erickson JM, Hinojosa LF, Hoganson JW, Iglesias A, Jaramillo CA, Johnson KR, Jordan GJ, Kraft NJB, Lovelock EC, Lusk CH, Niinemets Ü, Peñuelas J, Rapson G, Wing SL, Wright IJ (2011) Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytologist* 190: 724–739. <https://doi.org/10.1111/j.1469-8137.2010.03615.x>
- Pierce S (2007) The jeweled armor of *Tillandsia* – Multifaceted or elongated trichomes provide photoprotection. *Aliso* 23: 44–52. <https://doi.org/10.5642/ALISO.20072301.06>
- Pinto LFG, Ribeiro M, Crusco N, Rosa M, Arruda VLS, Silva W, Alencar A (2025) Dinâmica do fogo na Mata Atlântica entre 1985 e 2023 e o caso de 2024. Technical report. <https://doi.org/10.13140/RG.2.2.10397.42721>
- R Core Team (2021) A language and environment for statistical Computing. Version 4.1.2. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> [accessed 20.03.2023]
- R Studio Team (2021) RStudio: integrated development for R. Version 2021.9.1.372. PBC, Boston, USA. <https://posit.co/products/open-source/rstudio/> [accessed 20.03.2023]
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142(6): 1141–1153. <https://doi.org/10.1016/j.biocon.2009.02.021>
- Royer DL, Meyerson LA, Robertson KM, Adams JM (2009) Phenotypic plasticity of leaf shape along a temperature gradient in *Acer rubrum*. *PLoS ONE* 4(10): e7653. <https://doi.org/10.1371/journal.pone.0007653>
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HÁ, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287(5459): 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>
- Smith LB, Downs RJ (1979) Bromelioideae (Bromeliaceae). *Flora Neotropica Monograph* 14(3): 1493–2142. <https://www.jstor.org/stable/4393700> [accessed 06.04.2023]
- Stefano M, Papini A, Brighigna L (2008) A new quantitative classification of ecological types in the bromeliad genus *Tillandsia* (Bromeliaceae) based on trichomes. *Revista de Biología Tropical* 56(1): 191–203.
- Strehl T (1983) Forma, distribuição e flexibilidade dos tricomas foliares usados na filogenia de Bromeliáceas. *Iheringia Série Botânica* 31: 105–119.

- Struminski E (2001) Parque Estadual do Pico do Marumbi. UFPR Publishing, Curitiba, 1–179.
- Tardivo RC (2023) *Wittrockia cyathiformis* (Vell.) Leme. Flora e Funga do Brasil. <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB6580> [accessed 05.04.2023]
- Thomas CD, Chris DT, Alison C, Rhys EG, Michel B, Linda JB, Yvonne CC, Barend FNE, Marinez FS, Alan G, Lee H, Lesley H, Brian H, Albert SVJ, Guy FM, Lera M, Miguel AOH, Townsend P, Oliver LP, Stephen EW (2004) Extinction risk from climate change. *Nature* 427(6970): 145–148. <https://doi.org/10.1038/nature02121>
- Townsend CR, Begon M, Harper JL (2010) Fundamentos em Ecologia. Artmed, Porto Alegre, 1–576.
- Vieira M, Mendonça YCM (2021) Desmatamento da Mata Atlântica paranaense: análise espacial para o período 2014 e 2019. *Revista Catarinense de Economia* 5(1): 46–57. <https://doi.org/10.54805/RCE.2527-1180.v5.n1.106>
- Voltoini CH, Santos M (2011) Variações na morfoanatomia foliar de *Aechmea lindenii* (E. Morren) Baker var. *lindenii* (Bromeliaceae) sob distintas condições ambientais. *Acta Botanica Brasílica* 25(1): 2–10. <https://doi.org/10.1590/S0102-33062011000100002>
- Wanderley MGL, Martins SE (2007) Bromeliaceae. In: Wanderley MGL, Shepherd GJ, Melhem TS, Giulietti AM (Eds) Flora Fanerogâmica do Estado de São Paulo. Instituto de Botânica, São Paulo, 39–162. <https://www.infraestruturameioambiente.sp.gov.br/institutodebotanica/wp-content/uploads/sites/235/2016/02/Bromeliaceae.pdf> [accessed 24.03.2025]
- Ward SM, Gaskin JF, Wilson LM (2008) Ecological genetics of plant invasion: what do we know? *Invasive Plant Science and Management* 1: 98–109. <https://doi.org/10.1614/ipsm-07-022.1>
- Wei T, Simko V (2021) R package ‘corrplot’: visualization of a correlation matrix (Version 0.92). <https://github.com/taiyun/corrplot> [accessed 25.07.2023]
- Wright IJ, Dong N, Maire V, Prentice C, Westoby M, Díaz S, Gallagher RV, Jacobs BF, Kooyman R, Law EA, Leishman MR, Niinemets Ü, Reich PB, Sack L, Villar R, Wang H, Wilf P (2017) Global climatic drivers of leaf size. *Science* 357(6354): 917–921. <https://doi.org/10.1126/science.aal4760>
- Zorger BB, Arrivabene HP, Milanez CRD (2019) Adaptive morphoanatomy and ecophysiology of *Billbergia euphemiae*, a hemiepiphyte Bromeliaceae. *Rodriguésia* 70: e00592018. <https://doi.org/10.1590/2175-7860201970091>

## SUPPLEMENTARY MATERIALS

### Supplementary material 1

Comparison of the morphometric parameters of *Wittrockia cyathiformis* across its life forms (epiphytic, saxicolous, and terrestrial) separated by forest types: Dense Ombrophilous Forest and Mixed Ombrophilous Forest.

<https://doi.org/10.5091/plecevo.140559.suppl1>

### Supplementary material 2

PCA of morphometric parameters considering the habitats of the specimens (epiphytic, saxicolous, and terrestrial) for each type of forest in the Atlantic Forest (A: Dense Ombrophilous Forests (DOF); B: Mixed Ombrophilous Forests (MOF)).

<https://doi.org/10.5091/plecevo.140559.suppl2>

### Supplementary material 3

Bioclimatic variables compared between forest types: Dense Ombrophilous Forest and Mixed Ombrophilous Forest.

<https://doi.org/10.5091/plecevo.140559.suppl3>