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SEX-MEDIATED SPATIAL SEGREGATION AND HERBIVORY IN *Cecropia pachystachya*, A NEWCOMER TO THE XERIC CAMPO RUPESTRE

Geraldo Wilson Fernandes[1,2], *Jeruza Campos Araújo Ribeiro*[1] & *Letícia Fernanda Ramos Leite*[1]*

[1] Ecologia Evolutiva & Biodiversidade/DGEE, ICB/Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil.

[2] Centro de Conhecimento em Biodiversidade, 31270-901, Belo Horizonte, MG, Brazil.

E-mails: gw.fernandes@gmail.com, jeruzaecologia86@gmail.com, leticiaramos.bio@gmail.com (*Corresponding author)

Abstract: The spatial distribution and ecological interactions of *Cecropia pachystachya*, a newcomer and invasive species in the xeric campo rupestre were investigated. This species is dioecious and a frequent colonizer widely distributed in the Atlantic rainforest domain in southeastern Brazil. The aim of this study was to explore the ecological dynamics of this newly established species in an arid environment characterized by rich biodiversity and high environmental stress. The results showed that female individuals were predominantly located closer to watercourses. Herbivory rates were significantly higher in male plants, while females showed stronger physical defenses, which included thicker leaves and a higher density of trichomes. These findings highlight the complex interaction between resource availability, herbivory, and sex-based traits that influence the distribution and survival strategies of dioecious plants. The study also highlights the possible ecological impacts of the expansion of *C. pachystachya* in the Campo Rupestre, a fragile ecosystem rich in biodiversity that is under high pressure caused by human and climate disturbances. Understanding how this species interacts with its new environment is fundamental for predicting its long-term ecological dynamics and for devising strategies to mitigate biological invasion.

Keywords: Invasive species, mountain ecosystems, plant defense, spatial distribution, rupestrian grassland.

INTRODUCTION

Several factors act synergistically to shape the distribution of plants within the environment, consequently impacting interactions with their associated organisms (Fernandes et al. 1988, Ramos et al. 2019, Robinson et al. 2023). Habitat characteristics, including soil water and nutrient availability, radiation intensity, and temperature, are strong mediators of the rates of plant tissue consumption by herbivores (e.g., Fernandes & Price 1992, Ribeiro et al. 2021, Ramos et al. 2022). Additionally, factors such as plant ontogenetic development (e.g., Obeso 2002, Ochoa-López et al. 2015), types of defense mechanisms (including physical and chemical, as well as constitutive and induced defenses) (e.g., Vega-Frutis et al. 2012, Silva et al. 2021), species resistance or tolerance (e.g., Fernandes 1990, Campbell et al. 2014, Johnson et al. 2015), and even the sex of the host plant (Ashman 2002, Cornelissen & Stiling 2005, Vega-Frutis et al. 2012, Campbell et al. 2014, Johnson et al. 2015) are important traits that affect the success and development of a host plant within its environment.

The spatial distribution of dioecious plants is influenced by habitat quality (Barrett & Hough 2013, Fernandes et al. 2014, Liu & Korpelainen 2021), with female individuals predominating in wetter and more nutrient-rich environments, while male individuals are more common in arid and less fertile environments (Bierzychudek & Eckhart 1988, Barrett & Hough 2013, Liu & Korpelainen 2021). The allocation of resources for reproduction often differs between the sexes, with female plants typically requiring more water and nutrients for the production and maturation of fruits and seeds (Boecklen & Hoffman 1993, Obeso 2002, Charnov 2020). This leads to spatial segregation of the sexes, which is mediated by these resource requirements (Bierzychudek & Eckhart 1988, Barrett & Hough 2013). This greater need for resources by female plants leads to selective pressure between the genders, resulting in the distribution of female plants being concentrated in habitats with greater resource availability (Bierzychudek & Eckhart 1988, Barrett & Hough 2013, Liu & Korpelainen 2021).

Environmental limitations restrict the metabolic functions of plants, such as growth, defense, and reproduction (Herms & Mattson 1992), leading to trade-offs in resource allocation between these functions (e.g., Herms & Mattson 1992, Obeso 2002, Juvany & Munné-Bosch 2015). In dioecious plants, differences in morphology, physiology, and life history characteristics between the sexes (Barrett & Hough 2013, Juvany & Munné-Bosch 2015) are reflected in sexually dimorphic patterns of resource allocation for reproduction and defense (Obeso 2002, Cornelissen & Stiling 2005, Barrett & Hough 2013). Several studies have shown that herbivory rates differ between male and female plants, lending support to the 'sex-biased herbivory hypothesis', which posits that herbivorous insects preferentially target male plants, which usually have fewer defense mechanisms than female plants (e.g., Cornelissen & Stiling 2005, Vega-Frutis et al. 2012). Higher herbivory rates on male individuals have been documented for various dioecious plant species, such as *Ephedra trifurca* (Boecklen & Hoffman 1993), the shrub *Salix lasiolepis* (Boecklen et al. 1990), *Baccharis concinna* (Carneiro et al. 2005), *Salix cinerea* (Alliende & Harper 1989), and *Populus deltoides* (He et al. 2022).

Plants exhibit different response mechanisms depending on the selective pressures exerted by herbivores and environmental conditions (Mauricio 2000, Campbell et al. 2014, Johnson et al. 2015, Fernandes et al. 2024). Plants possess a synergistic combination of defensive traits, known as defense syndromes, which are shaped by interactions with biotic factors (top-down), such as herbivory, and abiotic factors (bottom-up), such as resource availability (Whitman et al. 1983, Price 1990, 2000, Agrawal & Fishbein 2006, Ramos et al. 2023). Abiotic factors, in particular, influence plant traits such as leaf morphoanatomy, which serve multiple roles, including defense against herbivores (e.g., Woodman & Fernandes 1991, Hanley et al. 2007, Dourado et al. 2016). For instance, leaf sclerophylly (leaf hardness) is a key mechanical anti-herbivory defense shaped by resource availability (Lucas et al. 2000, Mello & Silva-Filho 2002, Hanley et al. 2007, Ramos et al. 2022). Beyond defense, these mechanisms also help prevent excessive heat gain and water loss (Woodman & Fernandes 1991, Agrawal & Fishbein 2006, Hanley et al. 2007, Carmona et al. 2011). Thus, the spatial distribution and sex of plants can act synergistically to shape defense strategies, influencing the extent of herbivorous insect attacks.

Cecropia pachystachya is a dioecious tree native to the tropical forests of Central and South America (Del Val & Dirzo 2003). Recently, however, a significant recruitment of *C. pachystachya* has been observed in the open ecosystem of Campo Rupestre (rupestrian grassland) in Serra do Cipó (G.W.F, personal communication). The forest habitats originally occupied by this species (see Berg & Rosselli 2005) contrast greatly with the open, rocky physiognomies of the campo rupestre (Fernandes et al. 2016). Previously, *C. pachystachya* was found only at the edges of riparian and forest patches and within the semi-deciduous forests of the region (Martins & Pirani 2010). Its colonization of Campo Rupestre may have begun following the paving of the MG-010 highway between 2003 and 2004, which altered soil chemistry in ways known to facilitate the establishment of invasive species (Barbosa et al. 2010). The spread of *C. pachystachya* poses a serious threat to the plant communities forming the habitat mosaic of Campo Rupestre (Fernandes et al. 2016, 2024, Silveira et al. 2016), as this fast-growing species produces substantial leaf biomass that contributes to soil fertilization (Berg & Rosselli 2005, Martins 2013). Its presence can alter

the naturally nutrient-poor soils characteristic of this unique ecosystem and strongly influence the evolution of this vegetation.

With the expansion of *C. pachystachya* into xeric areas, it is essential to understand the mechanisms driving its distribution and ecological interactions in the campo rupestre to develop effective management strategies for this already threatened ecosystem (Fernandes et al. 2018, 2020). The main goal of this study was to investigate the spatial distribution of *C. pachystachya* in a newly colonized campo rupestre area and to analyze its interactions with the local herbivorous insect community. Specifically, this research examines the distribution patterns of male and female individuals of *C. pachystachya* within the habitat, sex-based differences in leaf herbivory rates, the presence of physical anti-herbivory defenses on leaves, and variations in herbivory rates by distance from the watercourse. To achieve this, three hypotheses were tested: i) the *differential sex distribution hypothesis*, which predicts a higher concentration of female individuals in moist environments; ii) the *sex-biased herbivory hypothesis*, which anticipates higher herbivory rates in male individuals and stronger structural defenses (trichomes and leaf thickness) in females; and iii) the *stress hypothesis*, which predicts a positive correlation between herbivory rates and distance from water.

MATERIAL AND METHODS

Study system

Cecropia pachystachya Trécul (Urticaceae) is a pioneer species, commonly found in the early stages of succession, especially in areas of secondary regeneration, where clearings form in forest environments (Berg & Rosselli 2005). These trees typically reach 5–20 meters in height and 15–25 cm in trunk diameter (Berg & Rosselli 2005). In Brazil, *C. pachystachya* is widely distributed and plays an important ecological role, growing rapidly and contributing to soil fertilization through the high production of leaf biomass (Carvalho 2006, Martins 2013). *C. pachystachya* is dioecious, flowering between December and February and fruiting between May and June in Minas Gerais (Brandão & Gavilanes 1990). The species has expanded its distribution area into the Campo Rupestre (personal communication), generating concern about its potentially damaging effect on this ecosystem, which is known to be adapted to the low availability of nutrients in the soil (e.g., Negreiros et al. 2014, Fernandes 2016, Cunha-Blum et al. 2020).

Study area

This study was conducted in the Vellozia Nature Reserve (19º17'46'S, 43º35'28'W), at approximately 1200 m elevation in the Serra do Cipó, southern Espinhaço Mountain Range, Minas Gerais, Brazil. The regional climate is classified as mesothermal (Cwb) under the Köppen system, characterized by pronounced seasonality. Two distinct seasons prevail: hot, rainy summers (November-April) and dry, cold winters (May-October), with an average annual rainfall of 1500 mm (Madeira & Fernandes 1999). The Reserve lies within the campo rupestre ecosystem, marked by high habitat heterogeneity and quartzite rock outcrops, shaping the predominantly herbaceous/shrubby and highly diverse vegetation (Fernandes 2016). The campo rupestre vegetation complex holds significant conservation value, harboring exceptional biodiversity and numerous endemic species (Carvalho et al. 2012, Resende et al. 2013, Silveira et al. 2016, Fernandes et al. 2020). The region's soils, primarily quartzite-derived, are highly infertile and aluminum-rich, favoring specialized plant species adapted to scarce edaphic resources (Negreiros et al. 2009, Carvalho et al. 2012, see reviews in Fernandes 2016).

Data collection

To test for differential sex distribution, the geographic coordinates of all adult *C. pachystachya* individuals present in the Vellozia Reserve were recorded based on field sampling carried out in 2023. A total of 48 reproductively mature individuals were identified, comprising 20 male and 28 female plants. All individuals were mapped, and the distance from each plant to the nearest watercourse (Córrego do Geraldinho) was measured (Figure 1). The map and individual plant distances to the wetland area were generated using QGIS software

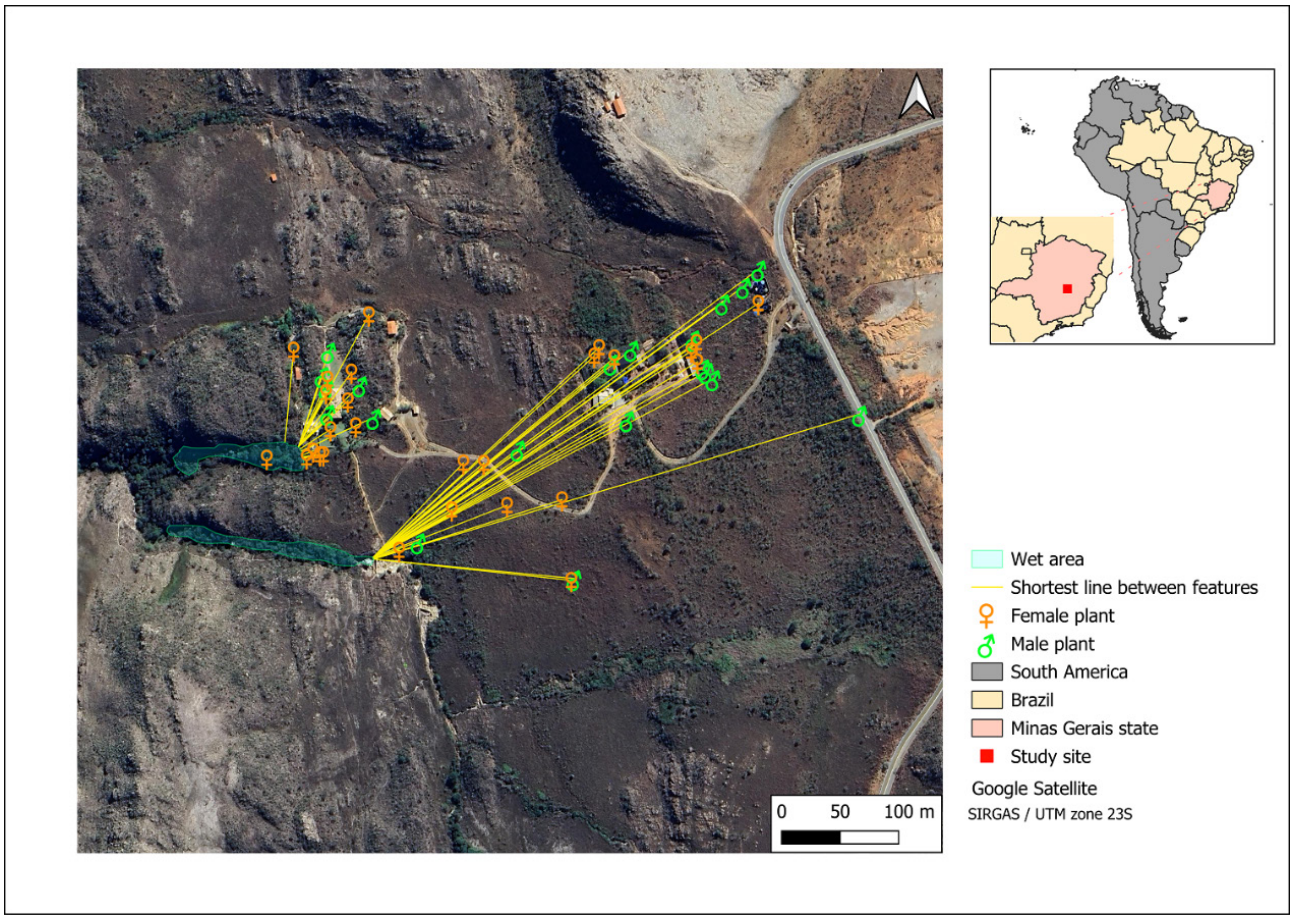

Figure 1. Spatial distribution of female (orange) and male (green) *Cecropia pachystachya* individuals in the Vellozia Reserve, state Minas Gerais, Brazil. Wet areas are highlighted in light green. Yellow lines represent the shortest distance from each individual to the nearest wet area (riparian zone), used as a proxy for distance to watercourse.

version 3.28.12. The coordinate reference system (CRS) used was SIRGAS 2000/UTM zone 23S, with meters as the unit of measurement.

The marks left by free-living chewing insects on fully expanded leaves were evaluated. The main insect orders in this feeding guild are Orthoptera, Lepidoptera, and Coleoptera (Novotny et al. 2010). To assess whether there were differences in leaf herbivory rates between sexes, ten fully expanded leaves were randomly collected from each *C. pachystachya* individual (n=48), totaling 480 leaves. The leaves were then photographed with a Canon T6I camera, and measurements of total leaf area and area consumed by herbivores were taken using ImageJ software version 1.6.0 (Rasband, 1997). Herbivory was calculated as the percentage of area removed using the formula: Herbivory = (consumed area / total leaf area) * 100.

To evaluate whether mechanical defenses vary between sexes, data on leaf thickness and trichome density were collected. Leaf thickness was measured with a Mitutoyo digital micrometer (mm), with four measurements taken per leaf, always on the central lobe, on five randomly chosen leaves per plant. Trichome density was measured following a modified version of the method proposed by Gomes et al. (2021), where trichomes were counted within five 10 mm² grids per leaf, totaling an area of 50 mm² per leaf. Leaf sections were prepared for slide mounting, with one slide per leaf and three leaves per plant, always focusing on the central lobe of the leaf blade. The leaf epidermis slides were then photographed, and trichomes on the adaxial surface were counted using ImageJ. Trichome density was estimated as the average number of trichomes across the five 10 mm² areas, with an overall mean calculated per plant.

Data analysis

To evaluate the differential distribution of male and female plants across the landscape, a Generalized Linear Model (GLM) with a normal distribution was applied, using plant sex as the explanatory variable and distance from the watercourse as the response variable. To determine whether the proportion of leaf area removed by insects differed between plant sexes and across distances from the watercourse, GLMs were constructed with the interaction between distance and plant sex as explanatory variables, and average herbivory as the response variable. A GLM with a normal distribution was also used to examine whether leaf thickness (a proxy for sclerophily) varied between male and female individuals, with sex as the explanatory variable and leaf thickness as the response variable. Finally, to assess differences in trichome density between male and female plants, another GLM with a normal distribution was created, using plant sex as the explanatory variable and trichome density as the response variable. All analyses were performed using generalized linear models (GLMs). The significance of predictors was assessed using analysis of variance applied to the fitted models (likelihood ratio tests), adopting a significance level of $p < 0.05$. GLMs were fitted using the 'lme4' package in R (R Core Team, 2023).

RESULTS

The distance from the watercourse significantly influenced the distribution of male and female plants in the landscape ($F = 5.92$, $DF = 45$, $p = 0.018$). The mean distance of plants from the watercourse was 170 m. However, 51% of the female individuals were located less than 100 m from the watercourse, while 65% of the male plants were distributed at a distance greater than 100 m (Figure 1, 2).

In contrast, herbivory patterns were not influenced by distance from the watercourse ($p > 0.05$). The proportion of leaf area removed by herbivorous insects varied between the sexes of *C. pachystachya* ($F = 9.802$, $DF = 38$, $p < 0.0001$), with greater removal of leaf tissue in male individuals than in female individuals. The average herbivory rate on male plants was 0.015%, while on female plants, it was 0.004% (Figure 3). The other evaluated variables did not affect the proportion of leaf area

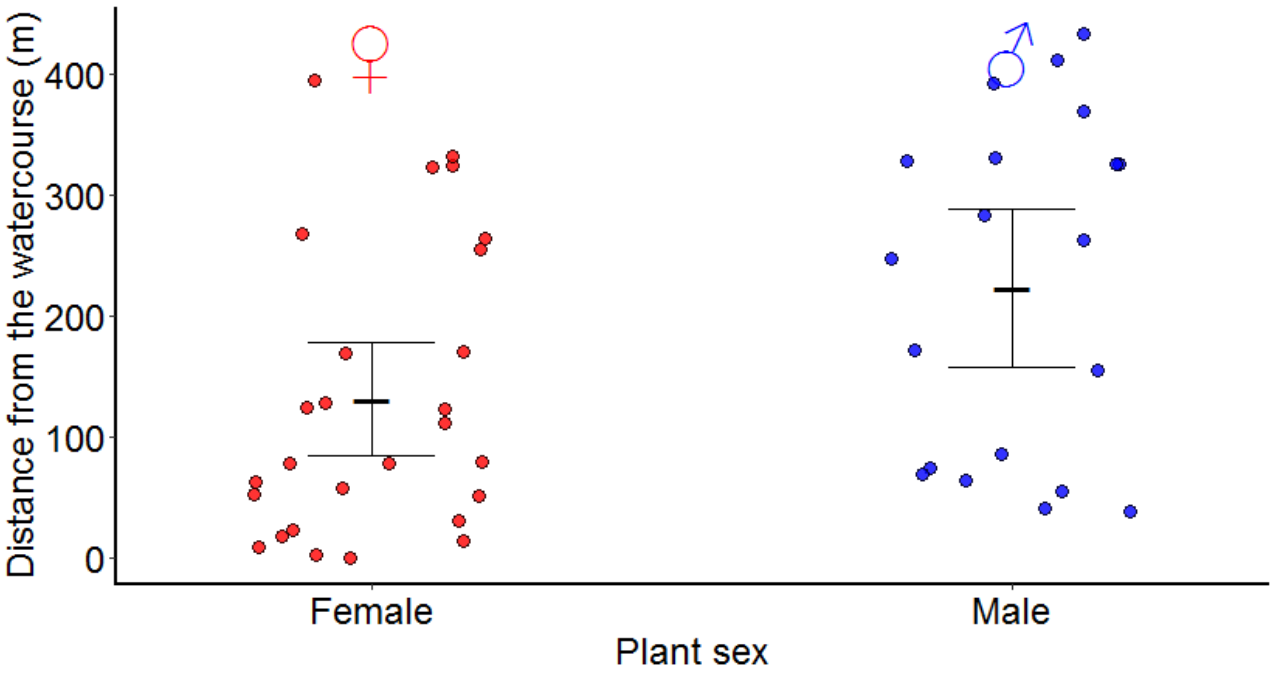

Figure 2. Variation in the distance (m) of female and male *Cecropia pachystachya* individuals from the watercourse in the Vellozia Reserve, state of Minas Gerais, Brazil. The error bars are standard errors (with maximum and minimum values) and the thick bar is the mean.

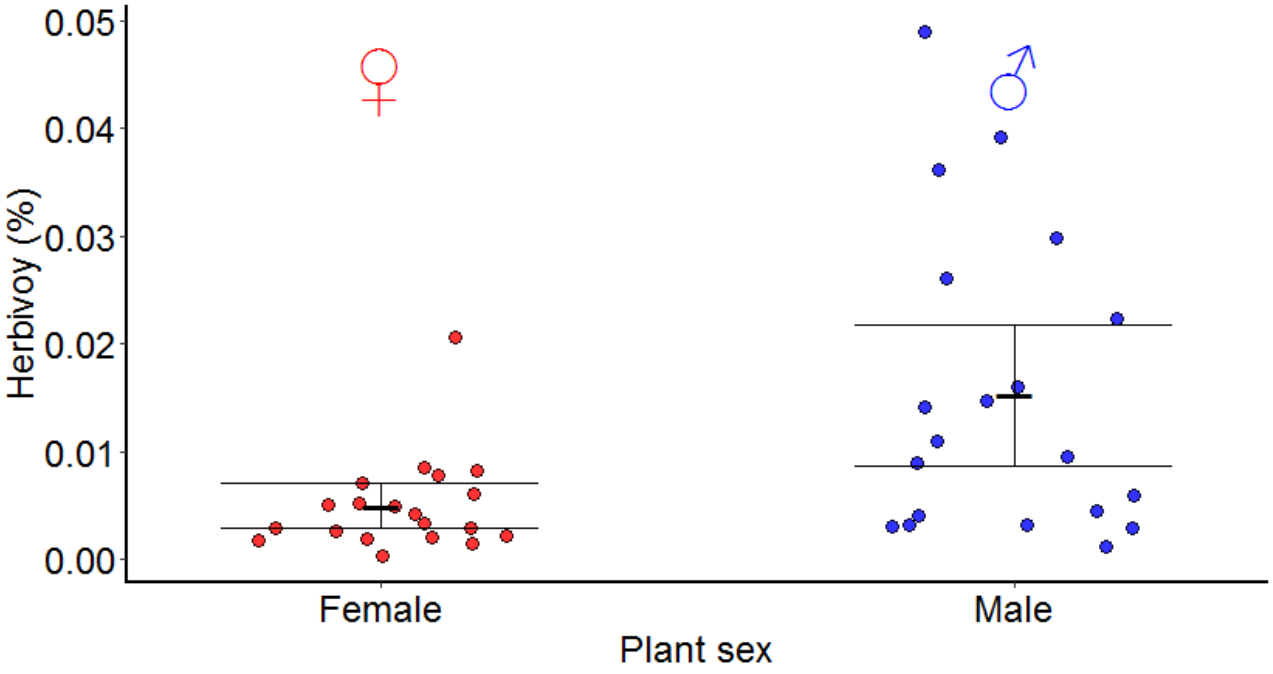

Figure 3. Variation in the percentage of herbivory in male and female *Cecropia pachystachya* plants in the Vellozia Reserve, state of Minas Gerais, Brazil. The error bars are standard errors (with maximum and minimum values) and the thick bar is the mean.

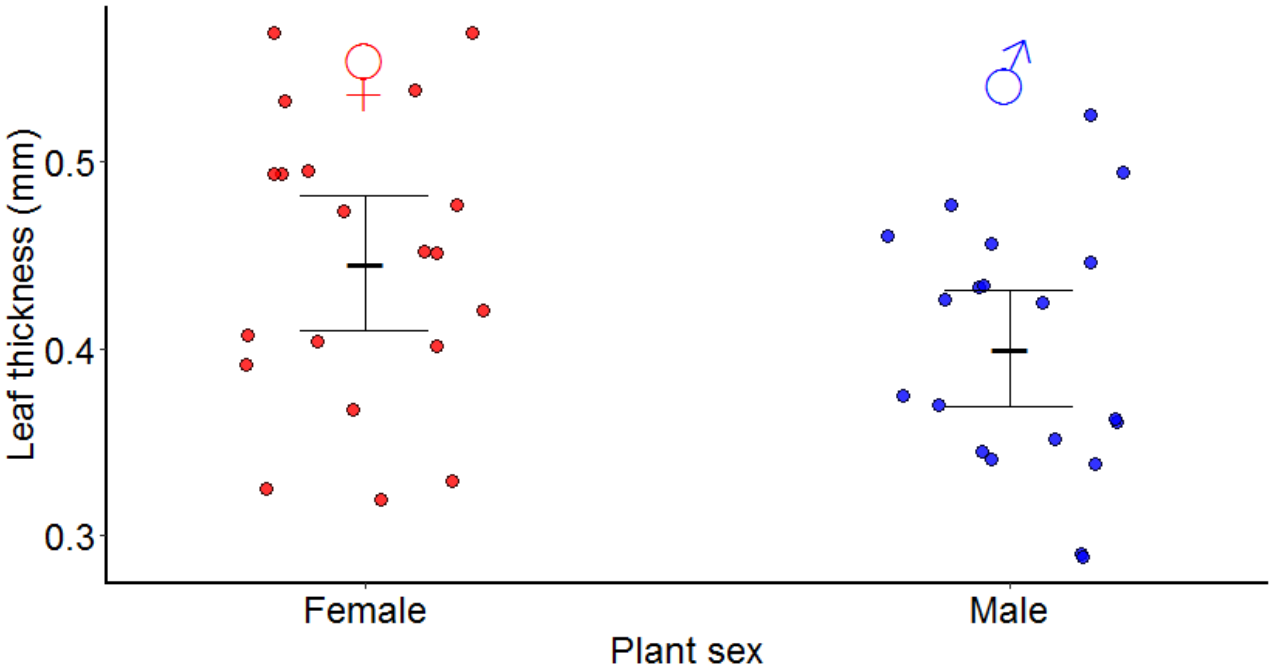

Figure 4. Variation in trichome density (mm²) in leaves of male and female *Cecropia pachystachya* plants in the Vellozia Reserve, state of Minas Gerais, Brazil. The error bars are standard errors (with maximum and minimum values) and the thick bar is the mean.

consumed, indicating that plant sex was the main mediator of herbivory on *C. pachystachya*.

Similarly, leaf thickness also varied between the host plant sexes (F = 3.98, *DF* = 38, p < 0.04), with female plants showing thicker (more sclerophyllous) leaves (0.45 mm ± se 0.005) than male plants (0.40± se 0.005) (Figure 4). The number of leaf trichomes varied between the sexes of *C. pachystachya* (F =

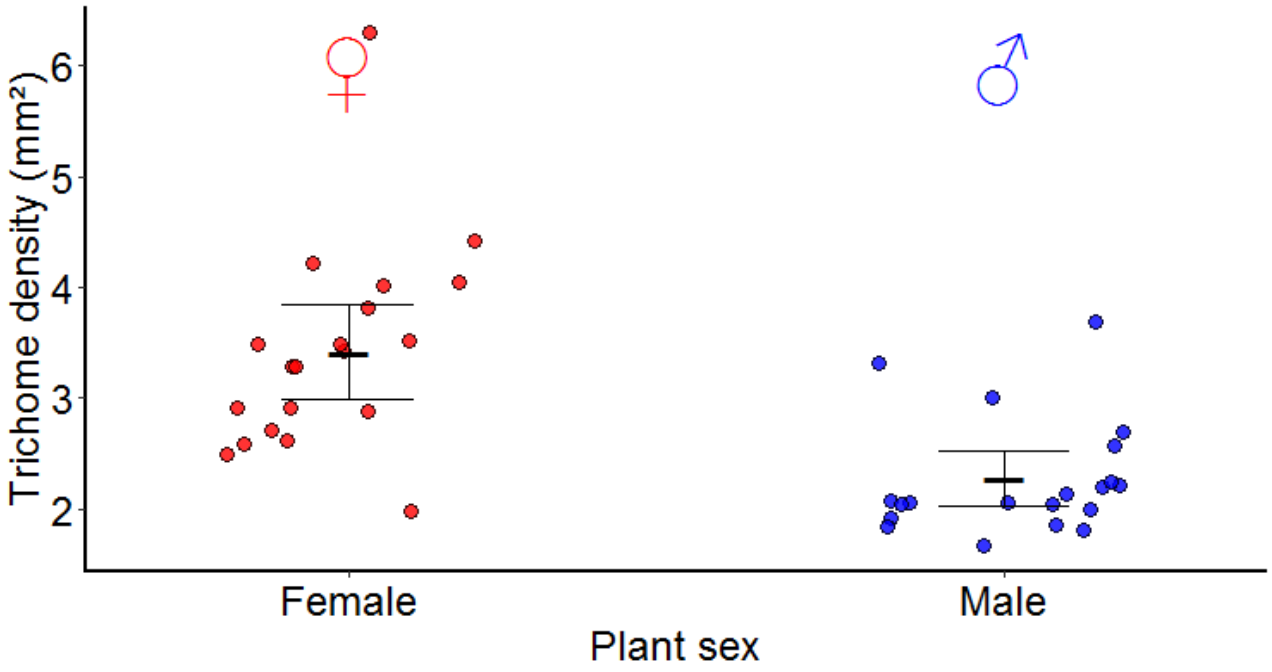

Figure 5. Variation in leaf thickness (mm) of male and female *Cecropia pachystachya* plants in the Vellozia Reserve, state of Minas Gerais, Brazil. The error bars are standard errors (with maximum and minimum values) and the thick bar is the mean.

22.9, $p < 0.001$), with female individuals showing a higher density of trichomes (Figure 5) than male individuals. The average density (mm²) of trichomes was higher in female plants (3.32± se 0.16) than in male plants (2.27± se 0.11).

DISCUSSION

Understanding the mechanisms driving the differential distribution of sexes, herbivory rates, and physical defenses in dioecious plants such as *C. pachystachya* has far-reaching implications. These mechanisms shed light on patterns of coexistence and interaction between species, revealing how selective pressures, such as herbivory and water availability, shape population structure and resource allocation in plants (Coley & Barone 1996). Identifying herbivory patterns across moisture gradients is crucial for understanding how environmental changes, including rainfall shifts, affect herbivore dynamics (Coley et al. 1985, Cornelissen & Stiling 2005). Moreover, as *C. pachystachya* is a newcomer to the campo rupestre, elucidating these mechanisms is vital for guiding conservation efforts aimed at preserving the diverse habitats of this rich and threatened ecosystem (Fernandes et al. 2016, 2024).

Several studies evaluating the spatial segregation of sexes in dioecious plants have reported that male individuals predominate in more arid conditions, whereas female plants are more frequent in areas with greater resource availability, such as water and nutrients, necessary for seed and fruit production and maturation (e.g., Bierzychudek & Eckhart 1988, Obeso 2002, Barrett & Hough 2013, Juvany & Munné-Bosch 2015). Similarly, our study found the same pattern in C. pachystachya, with female plants located closer to watercourses. This difference in spatial distribution reflects an adaptation to specific reproductive demands: female plants, which allocate more resources to reproduction, tend to dominate in resource-rich habitats, while male plants, requiring fewer resources, are more distributed in the environment (Hultine et al. 2016, Mesgaram et al. 2019). The physiological and morphological specialization of sexes in different microhabitats enhances spatial segregation, with male plants generally being less sensitive to increased aridity (Juvany & Munné-Bosch 2015, Hultine et al. 2016). Thus, the differential distribution of sexes in this dioecious species represents habitat-mediated natural selection, influenced by the life history particularities of sexual morphs (Barrett & Hough

2013). Similar sex-biased spatial patterns have been documented in other dioecious species across different ecosystems. In *Populus deltoides*, male plants show higher performance under moderate to severe drought conditions, indicating a dimorphic response to water stress (He et al. 2022). In the endemic Australian semi-arid shrub Maireana pyramidata, female plants allocate substantially more biomass to flowers and fruits, resulting in less conservative water use during reproduction (Leigh & Nicotra 2003). In the Brazilian Cerrado, sexual segregation shaped by habitat conditions has also been reported for *Amaioua guianensis* (Amorim & Oliveira 2006), reinforcing that sex-specific ecological strategies are widespread among dioecious plants (Liu & Korpelainen 2021).

C. pachystachya, a pioneer species typically found in forests, thrives in environments characterized by higher soil humidity and milder temperature habitats (Berg & Rosselli 2005). Its presence in the nutrient-poor and the xeric habitats of the campo rupestre represents a remarkable niche expansion, potentially disrupting the delicate balance of the ecosystem and impacting associated flora and fauna. As a pioneer species, *C. pachystachya* exhibits rapid growth and enhances soil fertility through its substantial leaf biomass production (Berg & Rosselli 2005, Martins 2013). Consequently, its presence in the campo rupestre can enrich naturally impoverished soils, contributing to ecosystem modification. Although the ecophysiological strategies and differential plasticity of male and female plants of *C. pachystachya* remain poorly understood, the observed spatial segregation suggests that higher reproductive resource demands in female plants may be a key driver of sex-specific habitat use (Obeso 2002, Barrett & Hough 2013, Charnov 2020). In the Cerrado, *C. pachystachya* flowers from December to February and fruits from May to June (Brandão & Gavilanes 1990); however, in the campo rupestre, fruiting coincides with the dry season, a period of pronounced water limitation (G.W.F., personal communication). Despite these harsh conditions, *C. pachystachya* has demonstrated remarkable adaptability, not only persisting but expanding its occurrence in the campo rupestre. This rapid adaptability highlights the species' invasive potential, which may impose additional pressure on an already threatened ecosystem, increasing risks to native habitats and endemic species.

Despite the relatively low amount of leaf material removed, the proportion of leaf area lost to herbivores differed between the sexes in *C. pachystachya*, with male plants showing higher levels of damage than female plants. This supports the hypothesis of sex-mediated herbivory (Ashman 2002, Cornelissen & Stiling 2005). The females showed more robust mechanical defenses, including a higher density of trichomes and thicker leaves, compared to the male individuals. In contrast, distance from the watercourse did not influence herbivory rates, regardless of plant sex. Instead, intrinsic plant characteristics associated with sex, such as investment in defense, appear to play a more important role in mediating herbivory than spatial position along the moisture gradient. Several studies have investigated variations in herbivory rates between plant sexes, generally finding that female plants are less susceptible to herbivory (Ashman 2002, Vega-Frutis et al. 2012, Campbell et al. 2014, Johnson et al. 2015). Several dioecious species, such as *Ephedra trifurca* (Boecklen & Hoffman 1993), Salix lasiolepis (Boecklen et al. 1990), *Baccharis concinna* (Carneiro et al. 2005), *Salix cinerea* (Alliende & Harper 1989) and *Populus deltoides* (He et al. 2022), show greater herbivory on male individuals. Reviews on the subject reveal a general pattern: herbivores generally prefer male plants, which tend to have less developed defenses compared to female plants (Ashman 2002, Vega-Frutis et al. 2012).

The detrimental effects of herbivory can be intensified in female plants (Barrett & Hough 2013), as the reduction in photosynthetic tissue can impair their ability to acquire resources necessary for reproduction, which may justify the development of sex-based defensive adaptations (Obeso 2002, Ashman 2002, Vega-Frutis et al. 2012). In *C. pachystachya*, we observed that female plants allocate more resources to defensive traits, such as a higher density of trichomes and thicker leaves, leading to lower herbivory rates compared to male individuals. While many studies have shown that female plants also produce higher levels of chemical defense compounds (Campbell et al. 2014, Johnson et al. 2015, He et al. 2022), this aspect was not addressed in the present study. Nonetheless, leaf morphological traits serve as important physical defenses against herbivores (e.g., Fernandes 1994,

Lucas et al. 2000, Mello & Silva-Filho 2002, Hanley et al. 2007, Carmona et al. 2011, Ramos et al. 2022).

In tropical environments, average herbivory rates range between 11% and 15% (Coley & Barone 1996, Mendes et al. 2021, Robinson et al. 2023). However, in this study, we observed very low herbivory rates, with less than 1% of the total leaf area consumed. Sampling was conducted on fully expanded, mature leaves prior to senescence, minimizing the influence of seasonal peaks in herbivory on our estimates. This suggests that herbivore consumption may not be the sole factor driving the expression of these defenses or that plant-herbivore interactions in the campo rupestre might differ. Plant phenotypic plasticity allows for responses to both habitat conditions and herbivore attacks, with the expression of mechanical defenses serving as an effective strategy in both situations (Hanley et al. 2007). Morphological traits, such as high trichome density and thicker leaves, function not only as mechanical barriers against herbivory but also as physical shields that reduce excessive heat gain and water loss (Woodman & Fernandes 1991, Agrawal & Fishbein 2006, Hanley et al. 2007). Thus, the observed morphological adaptations may reflect a strategy of female plants to avoid dehydration, indirectly contributing to the lower herbivory rates. Additional studies comparing herbivory rates, eco-physiology, and reproductive events of *C. pachystachya* in both its original habitats and in the campo rupestre could provide valuable insights into selective pressures and adaptability of native species with invasive potential.

This study reports, for the first time, the differential distribution of the sexes, herbivory rates and physical defenses of the species *C. pachystachya*, a newcomer to the campo rupestre. Female plants, which are more frequently located near water sources, invest more in defensive characteristics, such as a higher density of trichomes and thicker leaves, which results in lower rates of herbivory. These findings corroborate patterns observed in other dioecious species, where female plants tend to be less consumed due to more robust defenses (Ashman 2002, Cornelissen & Stiling 2005). In addition, the presence of *C. pachystachya* in the campo rupestre, a dry and nutrient-poor environment, raises concerns about its invasive potential, since the species can alter the composition and functionality of the ecosystem due to its rapid adaptation and the increase in soil fertility due to the high production of leaf biomass (Martins 2013). These results highlight the importance of future research into the selective pressures and adaptability of this species in environments with different conditions, providing valuable information for management and conservation strategies in tropical ecosystems.

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