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VELLOZIACEAE FROM THE *INSELBERGS* OF THE SUGARLOAF LAND, SOUTHEASTERN BRAZIL: SPECIES DISTRIBUTION OVERVIEW

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Abstract: *Inselbergs*, composed of granite or gneissic rocks, rise abruptly from the landscape, forming island habitats. In southeast Brazil, these dome-shaped lowland *Inselbergs*, located in the Atlantic Forest Domain, are known as sugar loaves, and the area encompassing these outcrops is called "Sugarloaf Land" (SL). Due to adverse conditions such as lack of soil and water and high UV radiation, plant communities in *Inselbergs* exhibit specific adaptations, forming distinct habitats such as vegetation mats, mainly from monocot families. Notably, *Velloziac*eae, well adapted to drought, form mats in these *Inselbergs* but do not occur in the surrounding matrix. This study provides detailed maps of the distribution of *Vellozia* species in the SL region, highlighting endemic and widely distributed species. *Vellozia* species in these outcrops present taxonomic challenges, so we examined the relationship between geographic distribution and morphological plasticity. We identified seven species: *Vellozia albiflora, V. bahiana, V. candida, V. inselbergae, V. plicata, V. pulchra and V. variegata*. Despite having similar attributes, such as adventitious roots and desiccation tolerance, *Vellozia* species show different distribution patterns, with widely distributed species exhibiting greater morphological plasticity. By comparing distribution patterns and environmental conditions, researchers can better understand the evolutionary relationships and adaptive responses of these plants.

Keywords: morphological plasticity, rocky outcrops, Sugarloaf Land, *Velloziac*eae

INTRODUCTION

Southeastern Brazil is one of three global hotspots of plant diversity in *Inselbergs*, rich in species and endemism, alongside Madagascar and southwestern Australia (Porembski 2007). *Inselbergs* are composed of granite and/or gneissic rocks with sparse soil, rising abruptly from their surroundings and forming isolated habitats with unique microclimates (Porembski 2007). The dome-shaped lowland *Inselbergs* in the Atlantic Forest domain of southeastern Brazil are known as sugarloaves, with Rio de Janeiro's famous "Sugarloaf" being one of the best-known peaks (de Paula et al. 2016). The region along the eastern Atlantic margin, which comprises numerous granite outcrops, has been named " Sugarloaf Land" (SL) (de Paula et al. 2016,2020). These rocky outcrops occur in different climatic zones and are geologically old, presenting adverse environmental conditions such as lack of soil and water, high UV radiation and intense sunlight. Consequently, they harbor highly specialized vegetation. The main habitat types in *Inselbergs* include shallow depressions, epilithic vegetation, crevices, monocot mats, rock pools, and moist and ephemeral vegetation (Barthlott et al. 1993; Porembski 2007).

*Velloziac*eae, Bromeliaceae, and Cyperaceae are the major families of mat-forming vascular monocotyledonous plants on open rocky slopes, often forming nearly circular or ellipsoidal patches (Porembski et al. 1998). Other important mat-formers in rock outcrops include Cactaceae and Selaginellaceae (Porembski et al. 1998). The *Velloziac*eae (Pandanales) family is ancient and comprises approximately 250 species of perennial herbs and shrubs (Mello-Silva et al. 2011). Many species of *Velloziac*eae, adapted specifically to drought, occur exclusively in *Inselbergs* and not in the surrounding matrix. For these species, rock outcrops form islands of terrestrial

habitat characterized by varying degrees of geographic isolation, making them excellent models for studying species evolution.

In the Neotropics, *Velloziac*eae is very diverse, with many species belonging to the genera *Barbacenia*, *Barbaceniopsis* and *Vellozia* (Mello-Silva et al. 2011), while in the Paleotropics (Africa and Madagascar), all species belong to the genus *Xerophyta* (Behnke et al. 2013).

Interestingly, there is also a monospecific genus, *Acanthochlamys*, in China (Mello-Silva et al. 2011). Generic delimitation within *Velloziac*eae has been controversial, mainly due to the characters used to delimit groups (Smith & Ayensu 1974). Conflicting results were also obtained regarding intrafamily relationships based on morphological and molecular data (Menezes et al. 1994; Behnke et al. 2000).

Most *Velloziac*eae are considered desiccation tolerant, meaning they can lose up to 95% of their cellular water, depending on the water balance in the environment, without dying (poikilohydric) (Porembski et al. 2021). They often degrade their chloroplasts (poikilochlorophilic), enter a dormant state and recover photosynthetic activity a few days after rain (Porembski & Barthlott 2000). This allows them to survive dry spells lasting from days to years, earning them the name "resurrection plants." Due to seasonal periods, these plants grow very slowly, with some species being hundreds of years old. For example, an individual of *Vellozia subscabra* was estimated to be 551 years old and 3.03 meters tall (at the time described as *Vellozia kolbekii*; Alves 1994).

A common phenomenon in the *Inselbergs* of southeastern Brazil is the widespread occurrence of species exhibiting a wide morphological variation, causing major taxonomic challenges (Mello-Silva 2004). Highly variable (polymorphic) species, whose variation is partially correlated with ecology and geography, are called *ochlospecies* (Cronk 1998). Extensive intraspecific variation was observed in certain taxa in sugarloaves, especially in populations of monocot taxa such as *Anthurium, Philodendron* (Araceae), *Alcantarea, Encholirium, Pitcairnia* (Bromeliaceae), *Barbacenia* and *Vellozia* (*Velloziac*eae), making their identification difficult (de Paula et al. al. 2017a). Considering these species complexes is crucial not only for resolving taxonomic questions but also for understanding species evolution on terrestrial islands like *Inselbergs*.

Notably, many floristic, taxonomic and ecological aspects of the *inselberg* vegetation in the SL within the Atlantic Forest have not yet been satisfactorily explored. It is clear that desiccation-tolerant mat-forming species play a significant role in this area, particularly the *Velloziac*eae.

Better understanding how these species cope with the harsh conditions of *Inselbergs* could provide insights for biotechnology, such as identifying genes related to desiccation tolerance for use in agricultural crops (Vicré et al. 2004). Furthermore, studying the evolutionary origins of this strategy could help identify plants that are most likely to successfully adapt to arid conditions. By comparing distribution patterns and environmental conditions, researchers can learn more about the evolutionary relationships and adaptive responses of these plants, helping to predict changes in their distribution areas under climate change scenarios.

This study aims to provide detailed maps of the distribution of *Vellozia* species in the SL, offering an overview of endemic and widely distributed species in the *Inselbergs* of the Atlantic Forest in southeastern Brazil. Given the taxonomic complexity of *Vellozia* species in these rock outcrops, we examined the relationship between geographic distribution

and morphological plasticity to support future studies on species distinction.

MATERIAL AND METHODS

The study area covers lowland *Inselbergs*, in the Atlantic Forest domain, in the states of Rio de Janeiro, Espírito Santo, southern Bahia and eastern Minas Gerais, that is, present in the SL region (de Paula et al. 2016,2020).

The data for preparing the list of *Vellozia* species occurring in the SL were obtained mainly from databases available online (INCT, 2023; Jabot-JBRJ, 2023; Flora and Funga of Brazil, 2023). The first step was the selection of all *Vellozia*ceae occurring in rocky outcrops in Brazil, which is possible with the online tools in the databases mentioned above. The second step was to look for species that form vegetation mats in the SL.

We used previously published floristic lists, taxonomic reviews, original species descriptions, herbarium data available online (INCT 2023; ``*Reflora*`` – Herbario Virtual 2023), the Herbarium collection of the Rio de Janeiro Botanical Garden (RB) and our own field observations for detailed information on *Vellozia* in rock outcrops and to define which species form mats in *Inselbergs*. We checked the identification of all selected samples. Information on life forms, geographic distribution and domains of occurrence was also acquired from the same sources. To assign conservation status, information from the National Flora Conservation Center was used (http://www.cncflora.jbrj.gov.br/portal), which provides a continually updated list of threatened plant species in the country (MMA 2022).

To produce distribution maps, we used species occurrence data (coordinates) available in online databases (INCT 2023; Jabot-JBRJ, 2023), referring to the previously mentioned target states. We checked all coordinates to confirm whether the species was occurring in the sugar loaves. To prepare the maps, we used *shapefiles* of Brazil as models to plot the species' occurrence points. The maps were generated using ArcGIS for Desktop software.

We also investigated the intraspecific morphological variation of two *Vellozia species* (*V. candida and V. plicata*) that occur in the SL, based on taxonomic reviews, online species descriptions and photographs of species in the field. The types of pollination and dispersal of species were also evaluated, based on online databases and published articles.

RESULTS

GENERAL INFORMATION ABOUT SPECIES OF *VELLOZIA* STUDIED IN SOUTHEAST BRAZIL

We found seven species of *Vellozia* occurring on sugar loaves in southeastern Brazil, in the Atlantic Forest domain: *Vellozia albiflora, V. bahiana, V. candida, V. inselbergae, V. plicata, V. pulchra* and *V. variegata* (Table 1, Figure 1)

All species are described as subshrubs, of which two species can also have a shrub life form and two are classified as herbs. Three species are endemic to rocky outcrops and none of the species occurs in forest formations (Table 2). *V. bahiana, V. pulchra* and *V. inselbergae* are the species that occur only on rupicolous substrates, while the others also appear on terrestrial substrates. Four of the species are restricted to the Southeast region of Brazil, but *V. albiflora, V. candida, V. inselbergae, V. plicata and V. variegata* also exist in the Northeast region (Table 3). Regarding conservation status, *V. pulchra* is the only species described as "endangered" (EN), *Vellozia albiflora* is described as "near threatened" (NT), the other species have not been evaluated. Four species are considered endemic to *Inselbergs* (Table 3).

Figure 1: Species of *Vellozia*ceae in the Land of Sugarloaf Mountains, present in the Atlantic Forest domain in Southeastern Brazil. From left to right, in line 1: *Vellozia albiflora, V. candida, V. plicata*; in line 2: *V. inselbergae, V. variegata, V. pulchra*. Photos by: L. de Paula, except *V. inselbergae* by Mello-Silva.

Species	Author	Synonyms
Vellozia albiflora	Pohl	*Vellozia circinans*Goethart & Henrard, *Vellozia* crassicaulis Mart. ex Schult. & Schult.f., *Vellozia macrantha* Lem.
Vellozia bahiana	LB Smith & Ayensu	No synonyms
Vellozia candida	JC Mikan	*Vellozia maritima*Vell., *Vellozia tertia* Spreng.
Vellozia inselbergae	Mello-Silva ex Andr.Cabral	No synonyms
Vellozia plicata	Mart.	*Nanuza plicata*LB Sm. & Ayensu, *Vellozia triquetra* Pohl, *Xerophyta plicata* (Mart.) Spreng., *Xerophyta triquetra* (Pohl) Baker
Vellozia pulchra	L. B. Smith	*Xerophyta pulchra* (LB Sm.) NL Menezes
Vellozia variegata	Goethart & Henriard	No synonyms

Table 1: List of *Vellozia* species occurring in sugar loaves in the Atlantic Forest, southeastern Brazil. Synonyms and authors are provided according to Flora and Funga of Brazil (2024).

Species	Life forms	Substrates	Phytogeographical Domains	Type of Vegetation
Vellozia albiflora	Herb; Subshrub	Rupicolous; Terrestrial	Caatinga, Central Brazilian savannah, Atlantic Forest	Campos de Altitude, Campo Rupestre de Altitude, Rock outcrop vegetation
Vellozia bahiana	Subshrub	Rupicolous	Atlantic Forest	Rock outcrop vegetation
Vellozia candida	Bush; Herb; Subshrub	Rupicolous; Terrestrial	Caatinga, Atlantic Forest	Altitude Fields, Rock Outcrop Vegetation
Vellozia inselbergae	Subshrub	Rupicolous	Atlantic Forest	Rock outcrop vegetation
Vellozia plicata	Bush; Subshrub	Rupicolous; Terrestrial	Caatinga, Central Brazilian savannah, Atlantic Forest	Campos de Altitude, Campo Rupestre de Altitude, Rock outcrop vegetation
Vellozia pulchra	Subshrub	Rupicolous	Atlantic Forest	Rock outcrop vegetation
Vellozia variegata	Subshrub	Rupicolous; Terrestrial	Caatinga, Atlantic Forest	Altitude Fields, Rock Outcrop Vegetation

Table 2: Summary of life forms, substrates, phytogeographic domains and vegetation types of *Vellozia* species occurring in sugar loaves in the Atlantic Forest, southeastern Brazil, according to Flora and Funga of Brazil (2024).

Species	Geographic distribution	Threat status	Endemic to *inselberg*
Vellozia albiflora	Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro)	NT	
Vellozia bahiana	Southeast (Espírito Santo, Minas Gerais)	HUH	X
Vellozia candida	Northeast (Bahia), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro)	HUH	X
Vellozia inselbergae	Northeast (Bahia)	HUH	X
Vellozia plicata	Northeast (Bahia, Paraíba, Pernambuco, Piauí), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro)	HUH	
Vellozia pulchra	Southeast (Minas Gerais)	EN	X
Vellozia variegata	Northeast (Bahia), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro)	HUH	

Table 3: Endemism status and geographic distribution of *Vellozia* species occurring in sugar loaves in the Atlantic Forest, southeastern Brazil, according to Flora and Funga of Brazil 2024. The conservation status of the species is provided according to CNCFlora. EN = "in danger"; NT = "near threatened"; "NE" = "not evaluated".

Species	Type of Pollination	Dispersion Type	Type of Fruit	Desiccation Tolerance	*Radicum Canopy*
Vellozia albiflora	entomophilia (mainly bees), ornithophily**	(gravity assisted) autoquoria**	loculicidal capsule***	Yes	Yes
Vellozia bahiana	-	-	-	Yes	Yes
Vellozia inselbergae	-	-	-	Yes	Yes
Vellozia candida	entomophilia*	(gravity assisted) autoquoria**	loculicidal capsule***	Yes	Yes
Vellozia plicata	-	anemochory (Caatinga)°°	seed capsule°	Yes	Yes
Vellozia pulchra	-	-	-	Yes	Yes
Vellozia variegata	entomophilia*	(gravity assisted) autoquoria**	-	Yes	Yes

Table 4: List of some ecological aspects of the *Vellozia* species studied: pollination, dispersal and type of fruit. Information on desiccation tolerance and the presence of *velame radicum* is also provided (S. Porembski, personal communication). Entomophily = pollination by insects; Ornithophily = pollination by birds; Autoquoria = dispersal of seeds (or spores or fruits) by the plant itself, mainly in physical form; Anemochory = dispersion by wind.

The "-" symbol means that no information was found in the literature. *Porembski et al. 1998; **Jacobi & do Carmo 2011; ***Mello-Silva 2005; °Ayensu 1973; °°Quirino 2006.

The most common type of pollination in *Vellozia* is entomophily (Table 4). Regarding the type of fruit, the loculicidal capsule with numerous seeds is the most cited for *Vellozia* (Table 4). Regarding types of dispersal, gravity-assisted autoquory is the best known for *Vellozia* species. All *Velloziac*eae are known to be desiccation tolerant and possess a *radicum canopy* as special adaptations to drought (Table 4).

VELLOZIA DISTRIBUTION MAPS IN *INSELBERGS* IN SOUTHEAST BRAZIL

Regarding species distribution patterns, distinct distributions were found for *Vellozia* species in the SL region (Figure 2). *V. bahiana, V. candida, V. pulchra* and *V. inselbergae* are endemic to *Inselbergs* (granite rocks), while the other species also occur on other types of rock outcrops.

The map of *V. albiflora* (Figure 3A) shows records of the species in the central and southern areas of Espírito Santo. Most of the records are on the border with Minas Gerais, so most of them are found in the interior and not in the coastal area. Furthermore, the distances between rock outcrops are remarkably short.

Vellozia bahiana (Figure 3B) does not yet have many records; one is located on the border between Espírito Santo and Minas Gerais. The other is located far from the previous record, in the northeastern part of Minas Gerais. Although this species is called "bahiana", no records of it were found in Bahia.

For *V. candida* (Figure 3C), many records were found, revealing the widespread occurrence of this species. The samples were found in *Inselbergs* in the southeast of the state of Rio de Janeiro and also in the city of Rio de Janeiro. Furthermore, the species occurs in the coastal part of Espírito Santo, in the interior of northern Minas Gerais and on the border with Bahia.

The distribution of *V. plicata* (Figure 3D) is similar to that of *V. candida*, but does not reach the city of Rio de Janeiro. However, there are records in the southeast region of Minas Gerais and even further inland, around 160 km near Belo Horizonte. The largest concentration of records is located in Espírito Santo, around 80 km from the coast, in the northwest part of the state, on the border with Minas Gerais. Some plants were found directly in or near Vitória. *V. plicata* spreads to *Inselbergs* in northeastern Minas Gerais and a sample was found in southern Bahia, close to the borders with Minas Gerais and Espírito Santo. Here we evaluated the records only in the SL region. It is worth mentioning that this species has records in other states that have not been evaluated, such as Paraíba, Pernambuco, Piauí.

Vellozia pulchra (Figure 3E) is a species that occurs in the central part of Espírito Santo and also in the northeast region of Minas Gerais, as well as *V. candida* and *V. plicata*, but the distribution of this species is more restricted when compared to the other two.

The records of *V. variegata* (Figure 3F) show a different pattern than the other species. The southernmost individual was found in the north of Rio de Janeiro, two records are located near the border of Minas Gerais and Espírito Santo, but in general this species is widely distributed throughout the territory of Espírito Santo.

Vellozia inselbergae was recently discovered and added to the database, but is only known from its type locality so far (Figure 3G), which is located in a private area in the south of the state of Bahia.

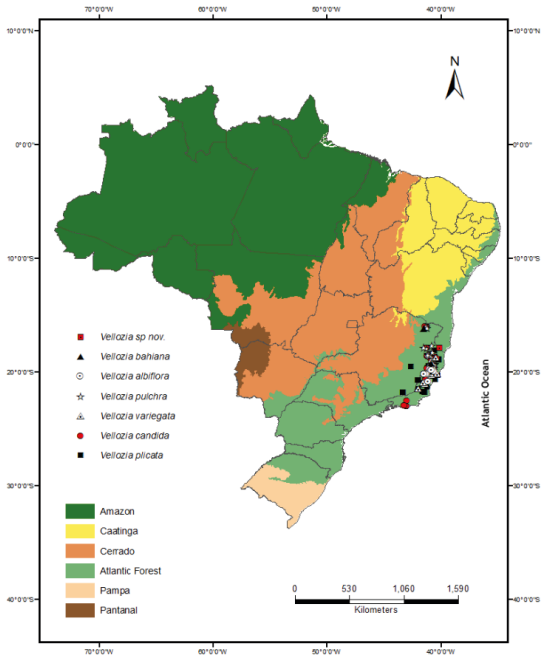

Figure 2: Map of Brazil highlighting the biomes (Amazon, Caatinga, savannah, Atlantic Forest, Pampa, Pantanal) in different colors, showing the distribution of the seven species of *Vellozia* in the *Inselbergs* of the Sugarloaf Land, in the Atlantic Forest, southeastern Brazil.

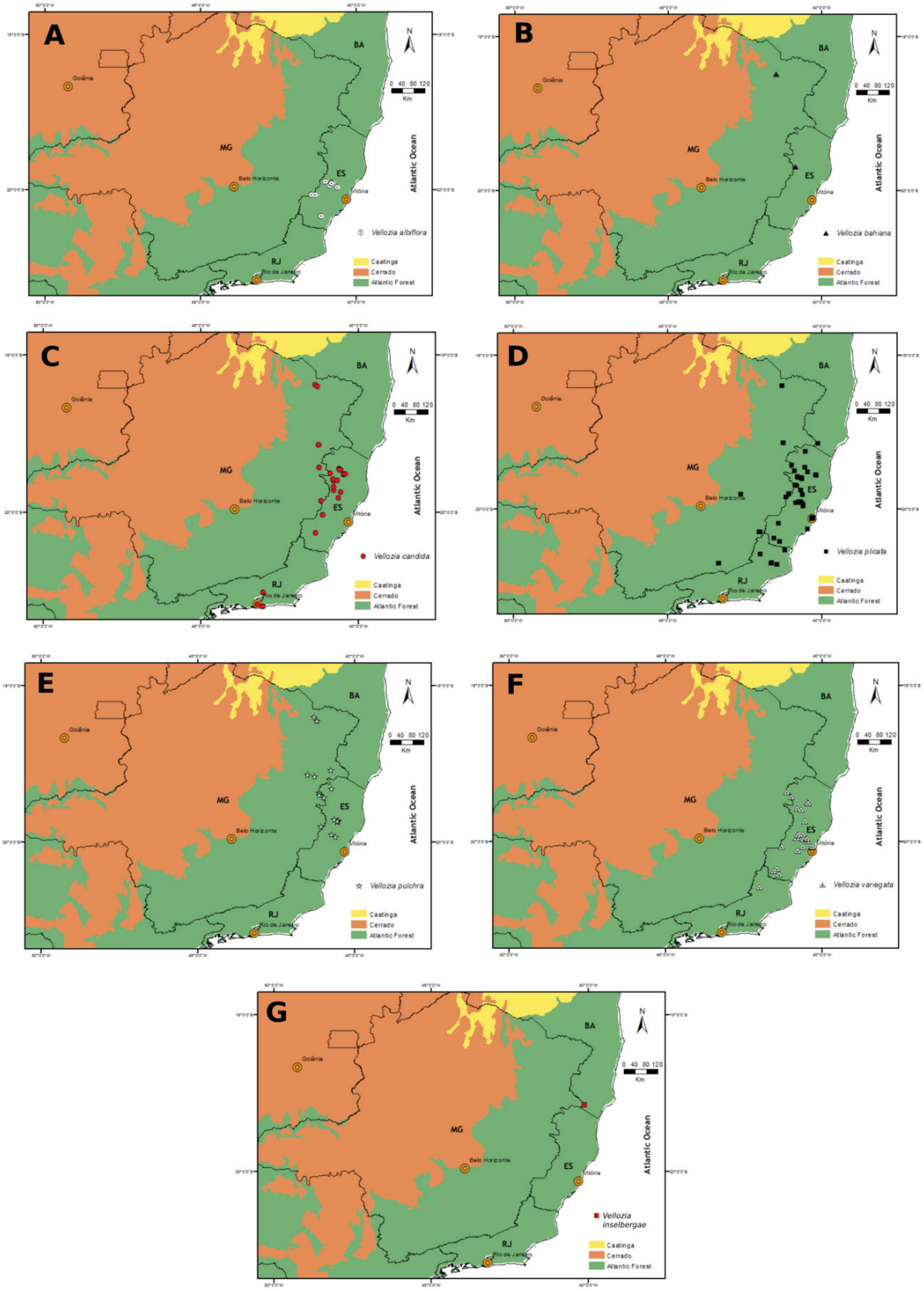

Figure 3: Distribution of *Vellozia* species in *inselbergs* in the Land of Sugarloaf Mountains, in the Atlantic Forest domain, southeastern Brazil. State abbreviations: MG = Minas Gerais, BA = Bahia, ES = Espírito Santo, RJ = Rio de Janeiro.

MORPHOLOGICAL PLASTICITY OF SPECIES: *VELLOZIA*

Vellozia candida and *V. plicata* are the most widely distributed species and both show high morphological plasticity in relation to height, fruit size and flowers (Table 5). The other species are more restricted to certain areas and do not exhibit as much variability (as far as we know), with the exception of *V. albiflora*, which also shows high intraspecific variability in rupestrian fields and other areas of Brazil. However, the typical habitat of this species is not *Inselbergs*, and for this reason we will not include detailed information about *V. albiflora* in the present study.

As for *V. candida*, individuals can reach up to 2 m in height or can flower at 60 cm in height (Table 5). In the city of Parati, individuals reach 1.7 m in height and in the city of Rio de Janeiro some grow up to 1.8 m. In general, plants are smaller and reach a height of 60 cm, but individuals from the north in ``*Itabirinha de Mantena*`` (Minas Gerais) reach 1 m in height and up to 2 m in ``*Pedra Azul*`` (Minas Gerais) (Mello-Silva 2004). Another example of their morphological variability is the number of stamens that individuals can have, which can vary from 5 to 24 (Table 6).

In relation to *V. plicata*, the height can vary between ~80 cm and 1.5 m (Table 5). The length of the leaf sheath can fluctuate over a wide range from 2 to 25 cm, as well as the number of stamens and the size of seed capsules can also differ in this species (Table 6). Furthermore, the size of the flower is also very variable, consequently the size of the capsule can also be different.

Species	Height	Leaf blade	Sheet width	Leaf sheath length	Flower
Vellozia candida	60 - 200cm	up to 1.4 cm	-	-	white*
Vellozia plicata	~80 – 150 cm**	≥ 8cm***	~0.3-0.9 cm**	2 - 25 cm**	white**

Table 5: Morphological aspects of *Vellozia candida* and *V. plicata* collected from scientific articles (Ayensu 1973; ***Smith et al. 1968; **Alves 2002; *Mello-Silva 2004) as an example of their plasticity. The "–" symbol means that no information was found in the literature.

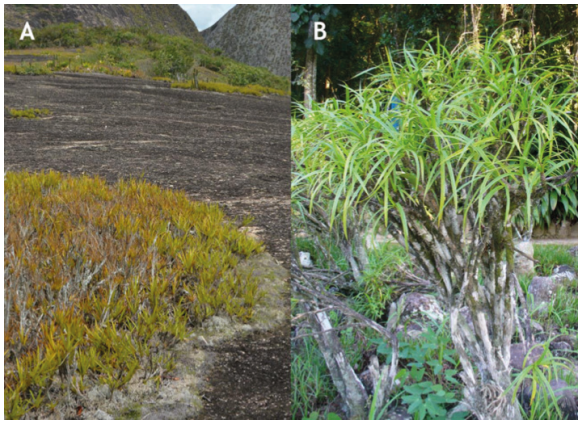

Figure 4: Morphological plasticity demonstrated in the height of *Vellozia candida* in southeastern Brazil, A – *V. candida* forming a carpet in the state of Minas Gerais, B – shrubby habit in the state of Rio de Janeiro. Photos by: L. de Paula and L. Azevedo.

Figure 5: Morphological plasticity demonstrated in the height of *Vellozia plicata* in southeastern Brazil, A – *V. plicata* forming a carpet in the state of Minas Gerais, B – shrubby habit of *V. plicata* in the state of Espírito Santo. Photos by: L. de Paula.

Species	Flower Width	Flower Length	Stamens	Capsule Length	Capsule Diameter	Capsule Width
Vellozia candida	~3cm*	-	15 - 24	~3cm*	-	1.9 cm*
Vellozia plicata	~0.15-0.7cm**	~2.7-8.0 cm**	6 or more**	~3-7 cm**	0.2-0.9cm**	0.7cm*

Table 6: Size spectrum of the reproductive parts of *Vellozia candida* and *V. plicata* collected from scientific articles (Ayensu 1973; **Alves 2002; *Mello-Silva 2004) as an example of their morphological plasticity. The "–" symbol means that no information was found in the literature.

DISCUSSION

This study reveals the distribution of *Velloziac*eae species in the Land of Sugarloaf Mountains (SL). The areas of Rio de Janeiro, Espírito Santo and northern Minas Gerais stand out as diversity *hotspots* for *Vellozia* species that occur in sugar loaves in the Atlantic Forest, in southeastern Brazil.

Regarding species distribution, we assessed that *Velloziac*eae have both widely distributed species and restricted species in the SL region. It is important to mention that *V. albiflora* is not common in lowland *Inselbergs*, but has its center of diversity in rupestrian fields. Therefore, there are few records of this species in the distribution maps of the present study, which only consider records in SL *Inselbergs*. In general, rupestrian fields are the main center of diversity for *Vellozia* species (Smith & Ayensu 1976), but as lowland *Inselbergs* have similar environmental conditions, some species can colonize both types of rock outcrops. It is possible that more species of *Vellozia*, which currently occur only in the rupestrian fields, could colonize *Inselbergs* in the future.

The low number of records of *V. bahiana* on its distribution map can be attributed to the lack of research and the difficulty of finding this species in the field. In Smith and Ayensu (1976), which contains the first description of the species, the type did not have an exact locality and the distribution was unknown, but they stated that it was found in Bahia. Thus, only the type collection is known in Bahia.

In turn, *V. pulchra* is a species endemic to *Inselbergs* and is therefore not found in other types of rock outcrops. Its distribution is restricted to granitoids inserted in semi-deciduous forests in the states of Espírito Santo and Minas Gerais. On the other hand, *V. variegata* is not endemic to *Inselbergs*, but occurs mainly in Espírito Santo, showing a relatively restricted distribution.

These patterns suggest that the distribution of *Vellozia* species may not only be related to the specificity of rock types, but also to the geographic location of *Inselbergs*. Regional climatic conditions may play a crucial role in the distribution of certain *Vellozia* taxa (de Paula et al. 2021), which could explain why some endemic and non-endemic species exhibit restricted distributions.

However, we emphasize that, as there are not many records of *Vellozia* species in online databases, distribution maps for certain species may be incomplete. Another cause may be that some records are misidentified as another species due to the 'species concept problem', which will be addressed later.

It can be said that the large number of synonyms of *V. candida* and *V. plicata*, more widely distributed species, may also reflect intraspecific variation, as many individuals appear different enough to be considered as a new species by many botanists. The long-term isolation of *Inselbergs* in the large distribution area of these species may be one of the reasons for the high morphological variability of *V. candida* and *V. plicata*. Furthermore, species with fragmented distributions often experience reduced gene flow, significant

genetic drift, and high levels of population divergence (Barbará et al. 2007). This helps explain the high morphological plasticity of certain *Vellozia* taxa and supports the view of *Inselbergs* as centers of species diversity and endemism (Barbará et al. 2007; de Paula et al. 2017b). Furthermore, *Vellozia plicata* has a very special position in the phylogeny of the genus: it is the sister clade of all other Brazilian species of *Vellozia* (Mello-Silva et al. 2011), being even considered in another genus in previous studies (*Nanuza plicata*: Smith and Ayensu 1976; Mello-Silva 2005). The high morphological plasticity, together with the interesting phylogenetic position of *V. plicata*, offers many opportunities for researchers to investigate evolutionary questions related to the speciation process.

It is important to emphasize that other *inselberg* specialists, belonging to different plant families, also have their center of diversity in the outcrops of southeastern Brazil, showing high morphological variability in their populations. Many members of Bromeliaceae are mat-formers and frequently co-occur with *Velloziac*eae on rocky outcrops in Brazil, exhibiting a wide range of phenotypes and high intraspecific and interspecific variation. However, the adaptation strategies of species from these two families to the adverse conditions of *Inselbergs* vary greatly. Bromeliaceae differ from *Velloziac*eae in their adaptations to low water availability, such as tank-shaped rosettes and leaf trichomes to store and absorb water, respectively (Benzing 2000), while *Velloziac*eae mainly display the desiccation tolerance strategy (Porembski et al., 2021).

Another drought adaptation in Velloziaceae is the fibrous stem composed of persistent leaf bases and adventitious roots, meaning that only a small apical part is actually the living plant, growing epiphytically on its dead parts. Its xeromorphic leaves can curl and shrink during desiccation to protect itself from high solar irradiation and temperature (Porembski & Barthlott 2000). Furthermore, adventitious roots possess a unilamellar to multilamellar *velame radicum*, a tissue specialized for rapid water absorption, also found in the roots of most epiphytic Orchidaceae (Porembski & Barthlott 2000).

The most common type of pollination in *Vellozia* is entomophily (Porembski et al. 1998), carried out especially by bees and wasps, but other insects are also possible pollinators. However, ornithophilia is also cited for the family, especially through hummingbirds (Jacobi & do Carmo 2011). Gravity-assisted autochory is known for some species of *Vellozia* (Jacobi & do Carmo 2011), anemochory appears to exist in *V. plicata*, but has only been proven in the Caatinga region (Quirino 2006). Generally, the loculicidal capsule with numerous seeds appears to be the most common fruit type in *Vellozia*, but poricidal capsules also occur (Mello-Silva 2005). For *V. plicata*, the only information about the type of fruit in the literature was "seed capsule". More pollination and dispersal studies are needed to better understand the reproductive dynamics and ecology of these species, especially in relation to the intraspecific variability and evolutionary adaptations that allowed the successful colonization of *Inselbergs* and other rock habitats. Understanding these interactions can provide valuable insights into the survival and reproduction strategies of *Vellozia*, contributing to the conservation and management of these species in their natural habitats.

Future studies must try to better understand the distribution patterns of *Vellozia* species both in the SL and in other regions of Brazil, for example in the Caatinga domain, which also comprises many *Inselbergs*. We believe that by comparing distribution patterns

and environmental conditions, researchers can learn more about the evolutionary relationships and adaptive responses of these desiccation-tolerant plants, helping to predict changes in distribution area under a climate change scenario.

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