

Chapter 1

Flowering Phenology in a *Restinga* Community: 7 Years of Study



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Abstract Since changes in climate can generate phenological shifts and temporal mismatches between plants and their pollinators, long-term studies of flowering phenology have become more common in the scenario of global climate change. Although in tropical environments, flowering cycles are diverse, irregular, and complex, the existing phenology studies have evaluated mainly tree species over short periods. We characterized, over 7 years, flowering events of a restinga (sandy coastal plain) plant community in southeastern Brazil, including 829 individuals, 78 species, and 36 families, with diverse life forms. In restinga, the general flowering strategy is annual, regular, with intermediate duration, although some species show continuous, sub-annual, or supra-annual strategies. Plants of various life forms flower continuously or sub-annually, whereas only trees flower annually. We recorded flowers throughout all the study years, but the highest rates of flowering activity and intensity occurred in the warmer and wetter season (October to March). Nectar, oil, pollen, and resin were available to pollinators throughout the year. We found significant positive correlations between the indexes of activity and intensity and the mean temperature and day length, but not precipitation. Our results suggest a high predictability of flowering periods and availability of floral resources for pollinators throughout the year.

Keywords Atlantic Forest · Climatic change · Floral resource

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1.1 Introduction

Phenological studies on flowering in plant communities are important for understanding plant reproduction and the spatiotemporal organization of floral resources available to animals (Newstrom et al. 1994a). The distribution of flowering events of the plant species in a community is selected over time by abiotic and biotic factors (van Schaik et al. 1993). Tropical environments are highly challenging for phenological studies because of the wide range of interactions and the environmental heterogeneity in these regions (Ramírez 2002). In temperate ecosystems and dry tropical forests, climatic seasonality directly influences plant phenology (Morellato et al. 2013; van Schaik et al. 1993). In contrast, most tropical forests have less pronounced climatic seasons; the highly diverse plant species with different life forms can provide blooms at any time of the year, with varying frequencies, regularities, and synchronisms, resulting in diverse and complex phenological patterns (Morellato et al. 2013; van Schaik et al. 1993). Therefore, tropical areas provide reliably and continuously available plant resources that support a rich spectrum of forage animals (Morellato et al. 2016).

Phenological studies in tropical environments focus mainly on tree species of forest vegetation and over short periods of time, mainly 1 or 3 years (Morellato 2008; Morellato et al. 2016), making it difficult to understand the factors that shape flowering patterns in plants with different life forms (Newstrom et al. 1994b). Long-term phenological data are rare but are beginning to gain significance in light of the importance of understanding phenological patterns in communities and, more recently, as a tool for understanding plant sensitivity to global climate change (Morellato 2008; Morellato et al. 2016; Dunham et al. 2018). Changes in period, duration, and amplitude of flowering events caused by climate changes have been reported (Primack et al. 2004; Morellato et al. 2016; Dunham et al. 2018) and may result in imbalances in the interactions between plants and their pollinators (Morellato et al. 2016).

The *restingas* are part of the Atlantic vegetation complex. They are distributed along the coastal plain formed by marine sediments of Quaternary origin. *Restinga* flora arose mainly from the Atlantic Forest (Scarano 2002, 2008). This environment is stressful due to the sandy soil with low water retention, low air humidity, and strong sea wind action (Rizzini 1979; Scarano 2002). Scarano (2002) proposed that epiphyte and hemi-epiphyte plants of the Atlantic Forest would have been mainly responsible for the colonization and diversification of Atlantic Forest marginal environments. Canopy plants are undemanding of resources from the substrate and, once migrating, would have been able to settle as terrestrial plants on sandy soils, creating conditions for the establishment of other species (Scarano 2002, 2008). This facilitation process would be the main explanation for the high diversity found in an environment with such low environmental potential (Scarano 2002, 2008). *Restinga* vegetation has been considered stable and little sensitive to climate fluctuations (Scheel-Ybert 2000, 2002). Paleoenvironmental studies have shown that the *restinga* vegetation of the southeastern coast of Rio de Janeiro state (RJ) did not vary in diversity through the second half of the Holocene (5500–1400 years BP)

(Scheel-Ybert 1999, 2000, 2001). The *restinga* at Maricá, RJ, does not have well-defined climatic seasons and did not have a dry season during the years 1989–2000 (Mantovani and Iglesias 2001); however, there are relatively frequent records of water deficit in the last 10 years, in July and August (INMET/RJ). In general, the mean monthly rainfall decreases significantly during the winter, but months with high rainfall in the winter and low rainfall in the summer are often recorded, characterizing an irregular rainfall distribution pattern (Mantovani and Iglesias 2001).

This study characterized the flowering phenophase of the species occurring in a *restinga* vegetation community at Maricá over 7 years. We analyzed the frequency, duration, regularity, and the percentages of activity (Bencke and Morellato 2002b) and intensity (Fournier 1974) of the flowering period of the species, relating them to the possible influences of climate variables. The following questions guided our work: (1) What are the flowering phenological strategies in this community? (2) Are there abiotic variables with significant potential to trigger flowering in the area? (3) Do flowering phenophases follow seasonal rhythms in this community? (4) Is the distribution of floral resources such as pollen, nectar, oil, and resin predictable through the year?

1.2 Material and Methods

1.2.1 Study Site

We conducted the study in the Maricá *restinga*, an environmentally protected area located on the border of the districts of Barra de Maricá and Itaipuaçu, municipality of Maricá, Rio de Janeiro state, Brazil (22°57'45"S to 42°53'33"W and 22°57'52"S to 42°53'48"W) (Fig. 1.1a).

The Maricá *restinga* is composed of two sandy ridges (inner and outer) formed between 3500 and 5500 years ago, respectively, in episodes of the last marine transgressions (Perrin 1984) (Fig. 1.1b). The study site contains a shrubby-arboreal formation that encompasses three typical *restinga* physiognomies: (1) flooded open shrubby area, located in periodically flooded places (Fig. 1.1b); (2) non-flooded open shrubby area, with thickets interspersed with bare spaces (Fig. 1.1b–d); and (3) non-flooded closed arboreal area, with dense vegetation (Fig. 1.1b, d).

1.2.2 Climate

The climate is Aw tropical humid (Köppen 1948), with rainy summers and dry winters (Mendonça and Danni-Oliveira 2007). Climatic data for the Maricá *restinga* from 2004 to 2010 were provided by the *Instituto Nacional de Meteorologia* for Maricá Station, located inside the protected area (22°055"S to 42°049"W). We calculated day length according to Pereira et al. (2001) and Varejão-Silva (2000)

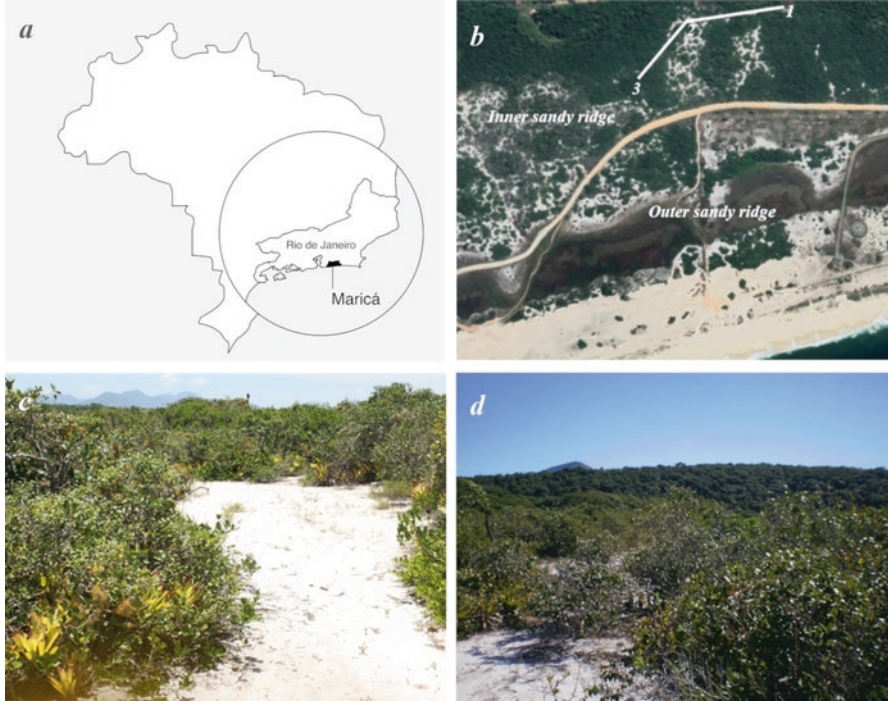


Fig. 1.1 The Maricá *restinga*. (a) Location of Maricá, Rio de Janeiro state, Brazil. (b) Aerial view of the study area, showing the transect across the inner sandy ridge and the three physiognomies (1, 2, and 3) sampled. (c) View of area 2 (non-flooded open shrubby area). (d) View of area 2 (non-flooded open shrubby area) in foreground and of area 3 (non-flooded and closed arboreal area) in background

(Fig. 1.2a). We considered two seasons: warmer/wetter (October to March) and colder/drier (April to September) (Figs. 1.2 and 1.3). The mean annual temperature ranged from 22.9 °C (2004) to 24.6 °C (2005). July was the coldest month in all years (Fig. 1.2b), with mean temperatures ranging from 19.5 °C (2010) to 21.8 °C (2005). In the warmer/wetter months (October to March), the mean temperature ranged from 25.6 °C (January 2004) to 28.5 °C (February 2010).

Total annual rainfall ranged from 1197.8 mm (2007) to 1435.8 mm (2005) (Fig. 1.2c). We recorded water deficits in the years 2004 (August, 15.1 mm; September, 31.2 mm; October, 38.2 mm), 2005 (August, 5.7 mm), 2007 (March, 33 mm; June, 33.8 mm; August, 30.6 mm; September, 16.6 mm), 2008 (August, 32 mm), and 2010 (August, 36.3 mm; September, 33.3 mm) (Fig. 1.3). Higher rainfall volumes were recorded from October to March of 2007–2008 and 2009–2010. Atypical rain peaks occurred in June 2004 and 2010 (Fig. 1.3). Although we have considered these two seasons (warmer/wetter and colder/drier), the temperature varied much less than the rainfall, which varied widely from year to year (Fig. 1.2b, c).

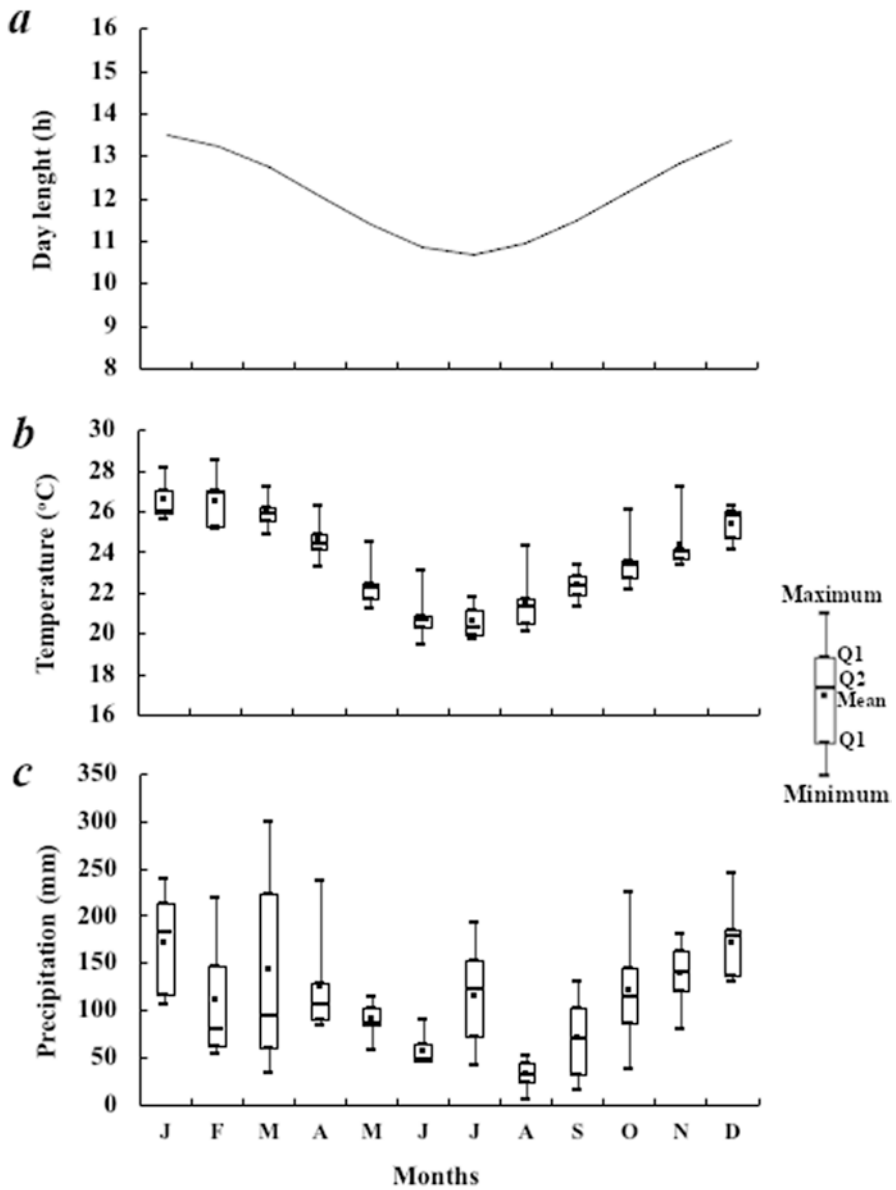


Fig. 1.2 (a) Day length (h), (b) box plots of monthly temperature (°C), (c) precipitation (mm) data for 2004–2010 in the Maricá *restinga*, Rio de Janeiro state, southeastern Brazil. (Source: INMET/RJ)

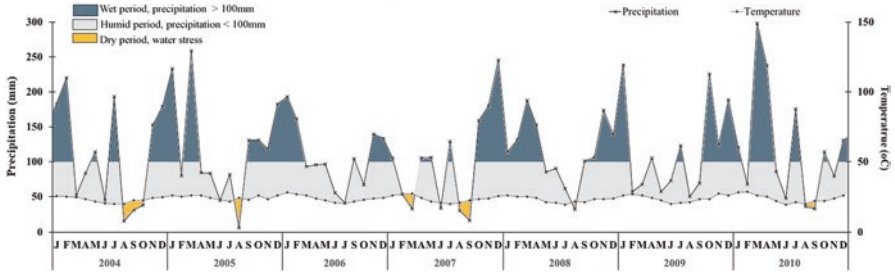


Fig. 1.3 Climatic diagram showing wet, humid, and dry periods during the study years (2004–2010) in the Maricá *restinga*, Rio de Janeiro state, Brazil. (Source: INMET/RJ)

1.2.3 Flowering Phenology

To conduct the phenological study, we marked 829 individuals from 78 species and 36 families. These individuals were inspected weekly from 2004 to 2010. We made these observations along a transect covering 5000 m² (500 m long × 10 m wide) on the inner sandy ridge, oriented east-west parallel to the coast and between coordinates 22°057'45"S to 42°053'33"W and 22°057'52"S to 42°053'48"W (Fig. 1.1b). This transect covered the following physiognomies: (1) flooded open shrubby area (1600 m²), (2) non-flooded open shrubby area (1300 m²), and (3) non-flooded closed arboreal area (2100 m²) (Fig. 1.1b). For species more than 1 m tall (here termed upper stratum), we marked up to 15 individuals with aluminum plates. Species with fewer than five individuals were disregarded (Fournier and Charpentier 1975). For species less than 1 m tall (here termed lower stratum), the sampling unit was 1 m² ($n = 150$ squares). Three 1 m² square frames were used to cover the vegetation at every 10 m along the transect. Where possible, we counted the number of individuals within the squares. For Poaceae and Cyperaceae, we estimated the number of individuals by the occupied proportion of the square, considering 100% of the occupied area as 50 individuals. Voucher specimens are housed in the herbarium of the Museu Nacional (R).

To quantify the presence/absence of the flowering phenophase, we calculated the percentage of activity, which indicates the proportion of species that are manifesting a given phenological event in a given month (Bencke and Morellato 2002a). To quantify the flowering intensity of the individuals, we adopted the method proposed by Fournier (1974) and modified by Bianchini et al. (2006), which uses a semiquantitative scale, from 0 to 3, to express the intensity of flowers per plant: 0 (absence of flowers); 1 (low intensity), 1–33% flowering branches; 2 (moderate intensity), 34–66% flowering branches; and 3 (high intensity), more than 66% flowering branches. Each individual was evaluated weekly, assigned a score from 0 to 3, and the mode of the assigned values was used to estimate the intensity of the event in each species, over the various months of follow-up.

To evaluate the flowering intensity in the community, we used the percentage of intensity (Fournier 1974), given by the formula:

$$\%Intensity = (\sum \text{monthly Fournier categories of each species} / 3 \times N) / 100 \quad (1.1)$$

where N is the total number of species and 3 is the highest category.

We classified the flowering patterns according to Newstrom et al. (1994a, b) based on the frequency (*continuous*, flowering throughout the year; *annual*, one flowering event per year; *sub-annual*, more than one flowering event per year; and *supra-annual*, flowering events with an interval longer than 1 year), duration (*brief*, up to 1 flowering month; *intermediate*, 2–4 flowering months; *long*, more than 4 flowering months), and regularity (*regular*, flowering event always occurs in the same period; *irregular*, unpredictable flowering events).

For each species, we recorded the life form, sexual system, and floral resources available to pollinators. The life form was defined according to Flora do Brasil (2021), considering the prevalent life form of the species in the community. To determine the available floral resources, we used four classes: (1) pollen (species that offer only pollen), (2) nectar (species that offer nectar, even if together with other resources), (3) oil (species with elaiophores), (4) resin (resinous species), and (5) anemophilous (species with no resource). To assess the availability of resources over the years, we plotted the percentage of intensity of the species in flower in each month, according to the resource offered.

1.2.4 Statistical Analysis

We correlated the flowering of the species to climatic factors (total monthly precipitation, mean monthly temperature, and day length). Correlations were determined using the Spearman correlation index in StatSoft Inc (2005).

1.3 Results

1.3.1 The Study Community: General Characterization

In the delimited area of the community, the 78 plant species marked and analyzed belong to 71 genera and 36 families (Table 1.1). Bromeliaceae, with seven species, was the most important family in number of species, followed by Myrtaceae and Fabaceae (six species each); Rubiaceae, Euphorbiaceae, and Apocynaceae (four species each); and Orchidaceae and Malpighiaceae (three species each). The three sampled physiognomies had different species compositions, with different dominances. The flooded open shrubby physiognomy contained species as tall as 5 m; *Pleroma gaudichaudianum* (Fig. 1.4a), *Myrcia ilheosensis* (Fig. 1.4b), and *Tapirira guianensis* (Fig. 1.4c) were the most important species in the upper stratum, and species of Poaceae (Fig. 1.4d) and Cyperaceae were the most important in the lower

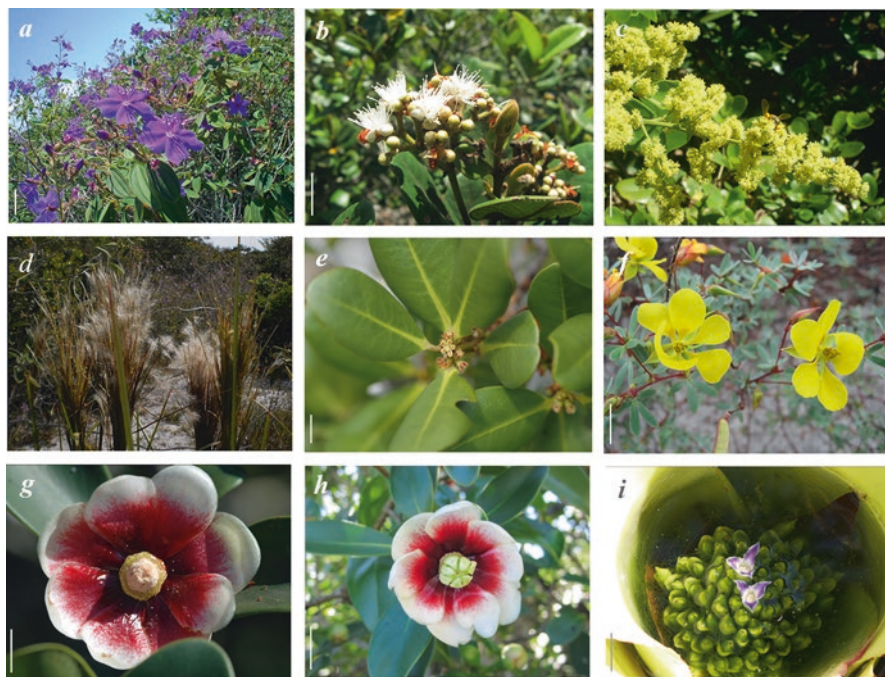


Fig. 1.4 Species from the inner sandy ridge of the Maricá *restinga*, Rio de Janeiro state, Brazil. (a) *Pleroma gaudichaudianum* (Melastomataceae), (b) *Myrcia ilheosensis* (Myrtaceae), (c) *Tapirira guianensis* (Anacardiaceae), (d) Poaceae, (e) *Myrsine parvifolia* (Primulaceae), (f) *Chamaecrista ramosa* (Fabaceae), (g) *Clusia lanceolata* (staminate flower), (h) *Clusia lanceolata* (pistillate flower), (i) *Neoregelia cruenta*. Scales: 2 cm (a), 1 cm (b–i)

stratum. In the non-flooded open shrubby physiognomy, *Neomitranthes obscura* and *Myrsine parvifolia* (Fig. 1.4e) were prominent in bush clumps, while *Chamaecrista ramosa* (Fig. 1.4f) and *Cuphea flava* predominated in bare spaces. In the non-flooded closed arboreal physiognomy, individuals from 1 m to 6 m tall occurred; *Clusia lanceolata* (Fig. 1.4g, h) and *Neomitranthes obscura* were the most important species in the upper stratum and *Neoregelia cruenta* (Fig. 1.4i) and *Aechmea nudicaulis* (Fig. 1.5b) in the lower stratum.

Regarding the life form, most species were shrubs (30.8%) or herbs (28.2%), followed by subshrubs (15.4%), vines (14.1%), and trees (11.5%). In relation to the sexual system, hermaphroditism (74%) prevailed, followed by dioecism (17%) and monoecism (9%). In general, the species have attractive flowers that provide a variety of floral resources for biotic pollen vectors (Figs. 1.5 and 1.6). Nectar is provided by 52 species from 27 families (67% of the species), the most important being Bromeliaceae, Apocynaceae, Fabaceae, and Rubiaceae (Fig. 1.5 and Table 1.1). Pollen is provided by 14 species from 7 families (18% of the species), the most important being Myrtaceae (Figs. 1.4b and 1.6a) (except *Myrrhinium atropurpureum*, whose petals are the main resource; Fig. 1.6b), Araceae, Fabaceae, and

Table 1.1 List of species, including the respective number of individuals analyzed, life form, sexual system, floral resource, frequency, regularity, duration, and flowering period (with Fournier scale) over 7 years (2004–2010) in the Maricá *restinga*, Rio de Janeiro state, Brazil

Family	Species	<i>n</i> individuals	Life form	Resource	Sexual system	Frequency	Regularity	Duration	Years	J	F	M	A	M	J	J	A	S	O	N	D										
Anacardiaceae	<i>Tapirira guitanensis</i> Aubl.	15	Tree	Nectar	D	Annual	Irregular	Inter	2004	1	1	1	1							1	2	2									
									2005	2	2	1	1																		
									2006																			1	2	1	
									2007	1	2																	1	2	1	
									2008																				2	3	
									2009	1																				1	
									2010																			1	2	3	
Apocynaceae	<i>Aspidosperma pyricollum</i> Müll.Arg.	15	Tree	Nectar	H	Annual	Regular	Inter	2004	1	1										1	3									
									2005	1																		1	1		
									2006	1																			2	3	
									2007	1																			2	3	
									2008	1																				1	
									2009																					1	
									2010																			1	3	2	
									2004																				2	3	
									2005	1																			2	3	3
									2006	2																			3	2	3
2007	1	1																		3	2	3									
2008	1																				3	1									
2009	2																					1									
2010	3																			1	3	2	1								

(continued)

Table 1.1 (continued)

Family	Species	n individuals	Life form	Resource	Sexual system	Frequency	Regularity	Duration	Years	J	F	M	A	M	J	J	A	S	O	N	D	
	<i>Mandevilla guanabaria</i> Casar. ex M.F.Sales et al.	15	Climber	Nectar	H	Continual	Regular	Long	2004	3	3	3	2	2	2	2	2	2	2	3	3	
									2005	3	3	3	2	2	2	2	1	2	2	3	2	
									2006	3	3	2	2	2	2	1	1	1	1	2	3	
									2007	3	2	2	2	2	1	1	1	2	2	3	2	
									2008	3	2	2	2	2	2	1	2	2	2	3	3	
									2009	3	3	3	3	3	2	1	2	2	2	3	3	
									2010	3	3	2	3	1	1	3	1	2	2	2	2	
	<i>Peplonia asteria</i> (Vell.) Fontella & E.A.Schwarz	15	Climber	Nectar	H	Continual	Irregular	Long	2004	2	3	2	3	2	2	2	3	3	3	2	2	
									2005	2	3	2	3	2	2	2	2	3	2	3	2	
									2006	2	3	2	2	2	2	2	2	1	3	2	2	
									2007	2					1	2	2	1	3	2	2	
									2008	2					1	2	2				3	
									2009						1	2	2				3	
									2010	2	2	3	2	2	1	1	1	2	1	2	2	
Araceae	<i>Anthurium harrisii</i> (Graham) G.Don	15	Herb	Pollen	M	Annual	Irregular	Inter	2004	3											2	
									2005	3												2
									2006	2	2							1	2			2
									2007	3												2
									2008	3												2
									2009	3												2
									2010	2	2	3	1	1	1	3	1					2

Table 1.1 (continued)

Family	Species	n individuals	Life form	Resource	Sexual system	Frequency	Regularity	Duration	Years	J	F	M	A	M	J	J	A	S	O	N	D
	<i>Vriesea neoglutinosa</i> Mez		Herb	Nectar	H	Annual	Regular	Long	2004						1	1	1				
									2005						2	2	3	3	2		
									2006							1	2	2	1		
									2007							1	2	2	1		
									2008							1	2	2	3		
									2009												
									2010						2				2		
	<i>Vriesea procera</i> (Mart. ex Schult. & Schultf.) Wittm.		Herb	Nectar	H	Annual	Regular	Long	2004	3	2	3	2	2	1						3
									2005	3	2	3	2	2	2						3
									2006	2	3	3	3	1	1						
									2007	2	3	2	2								
									2008	2	3	2	1								3
									2009	2	2										
									2010	3	3	3	2	1							2
Burseraceae	<i>Protium brasiliense</i> (Spreng.) Engl.	10	Shrub	Nectar	D	Annual	Regular	Inter	2004						3	2	3				
									2005							2	3	2			
									2006						3	3	3	2			
									2007						3	3	3	2			
									2008						3	3	3	2			
									2009											2	2
									2010						1	2	3	2			

Table 1.1 (continued)

Family	Species	<i>n</i> individuals	Life form	Resource	Sexual system	Frequency	Regularity	Duration	Years	J	F	M	A	M	J	J	A	S	O	N	D										
Clusiaceae	<i>Clusia lanceolata</i> Cambess.	15	Tree	Resin	D	Annual	Regular	Long	2004	2	2	3	2	2	2	2	2	2	1												
									2005	2	2	2	3	3	2	2	2	2	2	1											
									2006	1	2	3	3	2	2	3	2	2	3	2	2	2	2	2	2	1					
									2007	1	2	2	1	2	3	2	2	1	1												
									2008	1	2	2	1	2	3	2	1														
									2009	1	1	2	1	2	3	2	1														
									2010	1	1	2	3	3	2	1															
									2004							Inter	2004						2	3	3	1				1	
									2005	1							2005	1									3	2			
									2006								2006								3	2					
2007								2007																							
2008								2008									2														
2009								2009											2	2											
2010								2010	1										2	2	1										
Com-melinaceae	<i>Commelina erecta</i> L.	8	Herb	Nectar	H	Annual	Irregular	Long	2004	3	3	2	1							2	3	3									
									2005	3	3	2	1												2	3	3				
									2006	2	3	2	1														1	2	2		
									2007	1	2	2	2	2														1	2	2	
									2008	1	2	2	2	2														1	2	3	3
									2009	3							2009	3					2	3	2					3	
									2010	1	1	2	3	3	1		2010	1	1	2	3	3	1	1	1			1	2	2	

<i>Astraea klotzschii</i> Didr.	15	Subshrub	Nectar	M	Continual	Regular	Long	2004	3	2	3	1	1	1	1	1	1	1	2	3	1							
								2005	3	2	3	1	1	1	1	1	1	1	1	2	3	1						
								2006	2	2	1	1	2	3	2	1	2	2										
								2007	3	3	3	2	2	3	2	1	2	2										
								2008	3	2	3	1	1	1	1	1	2	3	1									
								2009	3	2	1	1	1	1	1	1	2	2	1									
								2010	3	2	2	2	2	1	2	2	3	2										
								2004	3	1	1	1	2						3	2	3							
								2005	3	1	1	1	2							3	2	3						
								2006	3	2	2	2	1						2	2	2	3	3					
2007	2	2	2	1							1	2	2	2	3	3												
2008	2	2	2	1							1	2	1	2	2	3												
2009	2	2	2	2																								
2010	2	2	2	1	1	1	1	1	1	1	1	1	1	2	1	2												
<i>Dalechampia micromeria</i> Baill.	7	Climber	Resin	M	Continual	Irregular	Long	2004	2	3	2	2	2	1	1	3	1	2	3	3								
								2005	2	3	2	2	2	1	1	3	1	3	3	3								
								2006	3	3	3	2	2	2	2	2	3	1	3	3	3							
								2007	3	3	3	2	2	2	2	2	3	1	3	3	3							
								2008	3	3	3	2	2	2	2	2	3	1	3	3	3							
								2009	3	2	2	1	1	1	1	1	1	1	1	1	2	2						
								2010	3	2	3	1	3	2	2	2	3	2	2	3	2	2						
								<i>Microstachys comiculata</i> (Vahl) Griseb.	15	Subshrub	Pollen	M	Continual	Regular	Long	2004	2	3	2	2	2	1	1	3	1	2	3	3
																2005	2	3	2	2	2	1	1	3	1	3	3	3
																2006	3	3	3	2	2	2	2	2	3	1	3	3
2007	3	3	3	2	2	2	2									2	3	1	3	3	3							
2008	3	3	3	2	2	2	2									2	3	1	3	3	3							
2009	3	2	2	1	1	1	1									1	1	1	1	1	2	2						
2010	3	2	3	1	3	2	2									2	3	2	2	3	2	2						

(continued)

Table 1.1 (continued)

Family	Species	n individuals	Life form	Resource	Sexual system	Frequency	Regularity	Duration	Years	J	F	M	A	M	J	J	A	S	O	N	D										
Fabaceae	<i>Andira legalis</i> (Vell.) Toledo	8	Tree	Nectar	H	Annual	Regular	Brief	2004									2													
									2005															3							
									2006																	3					
									2007																		3				
									2008																						
									2009																			3			
									2010																			1			
									2004																			3			
									2005																			3			
									2006																			3			
2007																			3												
2008																			3												
2009																			3												
2010																			1												
	<i>Chamaecrista ramosa</i> (Vogel) H.S.Irwin & Barneby	15	Subshrub	Pollen	H	Continual	Regular	Long	2004	3	3	3	2	2	2	2	2	2	2	2	3	3									
2005									3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3				
2006									3	3	3	2	1	2	3	2	2	2	3	2	2	2	2	2	2	2	3	3			
2007									3	3	2	2	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	3			
2008									3	3	2	2	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2			
2009									1	3	2	2	1	1	2	2	2	2	2	2	2	1	1	1	1	2	2	2			
2010									3	1	1	3	1	1	2	2	2	2	2	2	2	2	2	2	2	2	3	2			
2004									3	3	2	1															2	2	2		
2005									3	3	2	1															1	2	2		
2006									3	3	2																	1	2		
2007	3	3	2																	1	2										
2008	3	3	2																	1	2										
2009	2	2												1	2	3	1			2	2										
2010	1	2	1	3	2	1	1							3	2	1	1			2	3										
	<i>Clitoria laurifolia</i> Poir.	12	Climber	Nectar	H	Annual	Irregular	Long	2004	3	3	2	1								2	2									
2005									3	3	2	1															1	2			
2006									3	3	2																		1		
2007									3	3	2																		1		
2008									3	3	2																		1		
2009									2	2												1	2	3	1			2	2		
2010									1	2	1	3	2	1	1							3	2	1	1			2	3		

Lythraceae	<i>Struthanthus taubateensis</i> Eichler	10	Herb	Nectar	H	Annual	Regular	Inter	2004	1	1																
									2005	1	1																
									2006	2	1	1															
									2007	1	2	1	1														
									2008	1	2	1	1														
									2009	2	2																
									2010	1	2																
									2004	3	3	2	1	2	1	1	2	1	1	2	1	1	2	1	3	3	
									2005	3	3	2	1	2	1	1	2	1	1	2	1	1	2	3	2	3	
									2006	3	3	3	2	1	1	1	2	3	3	3	3						
2007	1	3	3	2	1	1	1	2	3	3	3	3															
2008	1	3	3	2	1	1	1	2	3	2	3	3															
2009	2	2	1																								
2010	2	1	2	1	1	1																					
Malpighiaceae	<i>Byrsonima sericea</i> DC.	15	Shrub	Oil	H	Annual	Regular	Long	2004	2	3	2	1														
									2005	1	1	1	1														
									2006	2	1	1	1														
									2007	1	3	1															
									2008	1	3	1															
									2009	1	1																
									2010	1																	
									2004	3	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2		
									2005	3	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2		
									2006	3	2	3	2	1	1	2	2	1	2	2	1	2	2	2	2		
2007	3	2	3	2																							
2008	3	2	3	2																							
2009	2	1	1																								
2010	3	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1										

(continued)

Table 1.1 (continued)

Family	Species	n individuals	Life form	Resource	Sexual system	Frequency	Regularity	Duration	Years	J	F	M	A	M	J	J	A	S	O	N	D	
	<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	15	Shrub	Pollen	H	Annual	Regular	Inter	2004	1	1									1	1	
									2005	2	3	3										
									2006													
									2007	2	1											
									2008	2	1											
									2009												1	
									2010	1	1	1									1	
	<i>Myrrhinium atropurpureum</i> Schott	15	Shrub	Petal	H	Annual	Regular	Long	2004						1	3	2	2	1			
									2005							2	3	3	2	1		
									2006						3	3	2	1				
									2007						3	3	2	1				
									2008						3	3						
									2009							1	1	1	1	1		
									2010						1	1	1	1	1	1	1	1
	<i>Neomitranthes obscura</i> (DC.) N.Silveira	15	Shrub	Pollen	H	Annual	Regular	Inter	2004					3	2	1						
									2005					3	1	1						
									2006													
									2007							3						
									2008							3						
									2009					1	2							
									2010					1	1							

Passifloraceae	<i>Passiflora silvestris</i> Vell.	15	Climber	Nectar	H	Subannual	Irregular	Long	2004	2	2	2	1	1					1	2	2										
									2005	2	2	2	1															1	2		
									2006	3	2	2	1					1	2										2	3	2
									2007	2	3								2										2	3	2
									2008	2	3								2												
									2009	2																					
									2010	3	3	2																			
									2004	2	2																				
									2005	2	2																				
									2006	3	1	1																			
2007	3	3	1																												
2008	3	3	1																												
2009																															
2010																															
Poaceae	<i>Paspalum maritimum</i> Trin.	Herb	Herb	AN	H	Annual	Irregular	Inter	2004	2	2																				
									2005	2	2																				
									2006	3	1	1																			
									2007	3	3	1																			
									2008	3	3	1																			
									2009																						
									2010																						
									2004	2	2																				
									2005	2	2																				
									2006	2	1																				
2007	3	3	1																												
2008	3	3	1																												
2009																															
2010																															
Polygonaceae	<i>Coccoloba arborescens</i> (Vell.) R.A.Howard	15	Climber	Nectar	D	Annual	Regular	Inter	2004																						
									2005																						
									2006																						
									2007																						
									2008																						
									2009																						
									2010																						
									2004																						
									2005																						
									2006																						
2007																															
2008																															
2009																															
2010																															

(continued)

<i>Denscanthia</i> <i>cymosa</i> (Spreng.) E.L.Cabral & Bacigalupo	10	Herb	Nectar	H	Annual	Irregular	Long	2004	3	2	2	1	2	2
								2005	3	2	2			1
								2006	3	2	2	1	2	3
								2007	3	2	2			1
								2008	3	2	2			1
								2009	2	2		2	3	1
								2010	2	2	2	2	1	2
						Annual	Regular	Inter	2004					
									2005	2				
									2006					
								2007	3	1				
								2008	3					
								2009	1					
								2010	1					
Sapindaceae					Annual	Regular	Inter	2004				1	3	2
								2005				1	2	1
								2006						
								2007						
								2008						
								2009						
								2010						

(continued)

Table 1.1 (continued)

Family	Species	<i>n</i> individuals	Life form	Resource	Sexual system	Frequency	Regularity	Duration	Years	J	F	M	A	M	J	J	A	S	O	N	D									
	<i>Paullinia weinmanniifolia</i> Mart.	15	Climber	Nectar	M	Annual	Regular	Inter	2004			3	3	3	1															
									2005			3	3	3	1															
									2006	1		2	1																	
									2007	1		2	1																	
									2008	1		2	1																	
									2009						2															
									2010				3	2	3															
Verbenaceae	<i>Stachytarpheta canescens</i> Kunth	6	Subshrub	Nectar	H	Annual	Irregular	Long	2004	2	1	2	2	2	1	1				2	2	2								
									2005	2	1	2	2	2	1	1				2	2	2	2	2	2					
									2006	2	1	2	2	2	1										2	1	2	2		
									2007	2	1	2	2	1												2	1	2	2	
									2008	2	1	2	2	1													2	1	1	2
									2009	1	1																		2	2
									2010	1	2	2	1	2	2	1	2	2	1	2	2	1	2	2	1	1	2	2	1	2

AN anemophilous, H hermaphroditic, D dioecious, M monoecious, Inter intermediate

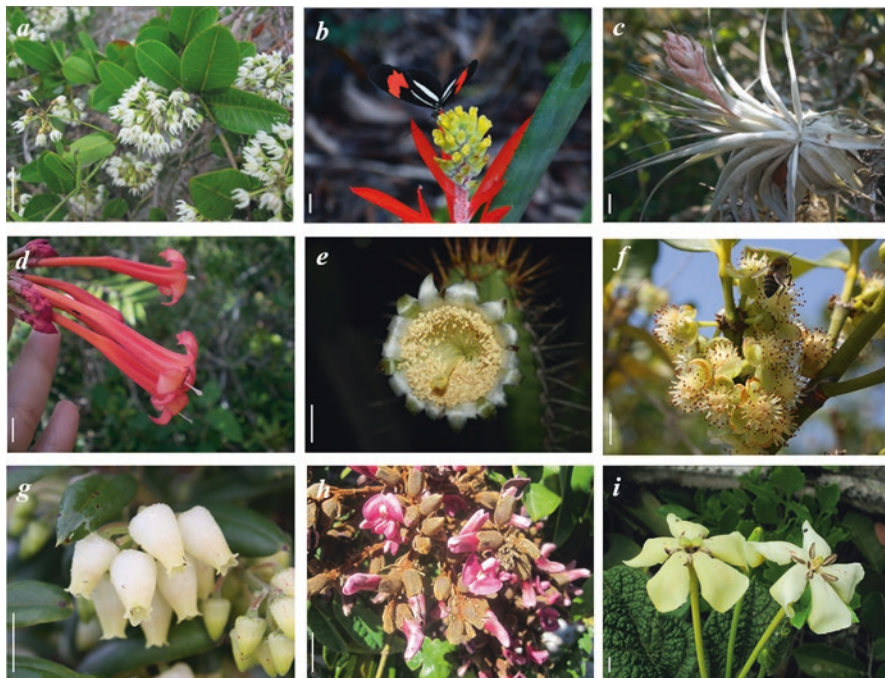


Fig. 1.5 Species from the inner sandy ridge of the Maricá *restinga*, Rio de Janeiro state, Brazil. (a) *Ditassa banksii* (Apocynaceae), (b) *Aechmea nudicaulis* (Bromeliaceae), (c) *Tillandsia gardneri* (Bromeliaceae), (d) *Lundia cordata* (Bignoniaceae), (e) *Pilosocereus arrabidaei* (Cactaceae), (f) *Garcinia brasiliensis* (Clusiaceae), (g) *Agarista revoluta* (Ericaceae), (h) *Tocoyena bullata*. Scales: 1 cm



Fig. 1.6 Species from the inner sandy ridge of the Maricá *restinga*, Rio de Janeiro state, Brazil, and their floral resources: pollen (a), petal (b), oil (c), resin (d). (a) *Myrciaria floribunda* (Myrtaceae), (b) *Myrrhinium atropurpureum* (Myrtaceae), (c) *Peixotoa hispida* (Malpighiaceae), (d) *Dalechampia micromeria* (Euphorbiaceae). Scales: 2 cm (a, b), 1 cm (c), 0.5 cm (d)

Melastomataceae (Fig. 1.4a and Table 1.1). Oil is provided by only three (4% of the species) members of Malpighiaceae (*Stigmaphyllon paralias*, *Byrsonima sericea*, and *Peixotoa hispidula*; Fig. 1.6c and Table 1.1), while resin is offered by only two species (3% of the species), *Dalechampia micromeria* (Euphorbiaceae) (Fig. 1.6d) and *Clusia lanceolata* (Clusiaceae) (Fig. 1.4g, h and Table 1.1). Six species (8% of the species) from four families (Cyperaceae, Euphorbiaceae, Primulaceae, and Poaceae) do not provide any resources, as they are anemophilous (Fig. 1.4d, e and Table 1.1).

1.3.2 Flowering Phenology

The plants of the Maricá *restinga* community bore flowers throughout the study period (Fig. 1.7b). We recorded cyclical and regular increases in the percentages of activity and intensity of the flowering phenophase in the warmer/wetter periods (October through March) and decreases in these percentages in the colder/drier periods (April through September) (Fig. 1.7a, b).

The maximum percentages of activity (between 45% and 65%) coincided with the maximum percentages of intensity (between 32% and 49%) and characterized the flowering peaks in the community (i.e., months with a large proportion of species exhibiting very intense flowering) (Fig. 1.7b, c). In general, the flowering peaks were repeated through the years, in January and/or February (Fig. 1.7b). However, in 2010, two flowering peaks occurred, one in January and the other in October through December (Fig. 1.7b). The minimum percentages of activity (between 19% and 38%) also coincided with the minimum percentages of intensity (between 11% and 19%) and characterized months with a small proportion of species showing mostly low flowering intensity in the area (Fig. 1.7b, c). In general, periods of low flowering were also repeated yearly, in June or July (Fig. 1.7b), although low flowering also occurred in April 2009.

In practically every year and month, species flowering in moderate intensity (2 on the Fournier scale) predominated (Fig. 1.7c). The highest intensities of flowering (scale 3) were observed in the warmer/wetter season (October to March), especially in January and February, from 2004 to 2008. Fewer species with high flowering intensity were observed in the colder/drier period (April to September) (Fig. 1.7c), when the number of species flowering at low intensity (Fournier scale 1) increased. Differently from previous years, in 2009 and 2010, more species flowered with low intensity, and the number of species flowering with high intensity was surprisingly small (Fig. 1.7c).

We recorded significant positive correlations between flowering (intensity and activity percentages) and the mean temperature and day length (Table 1.2). Flowering was positively and significantly correlated with total precipitation only in 2006 and 2008 (Table 1.2).

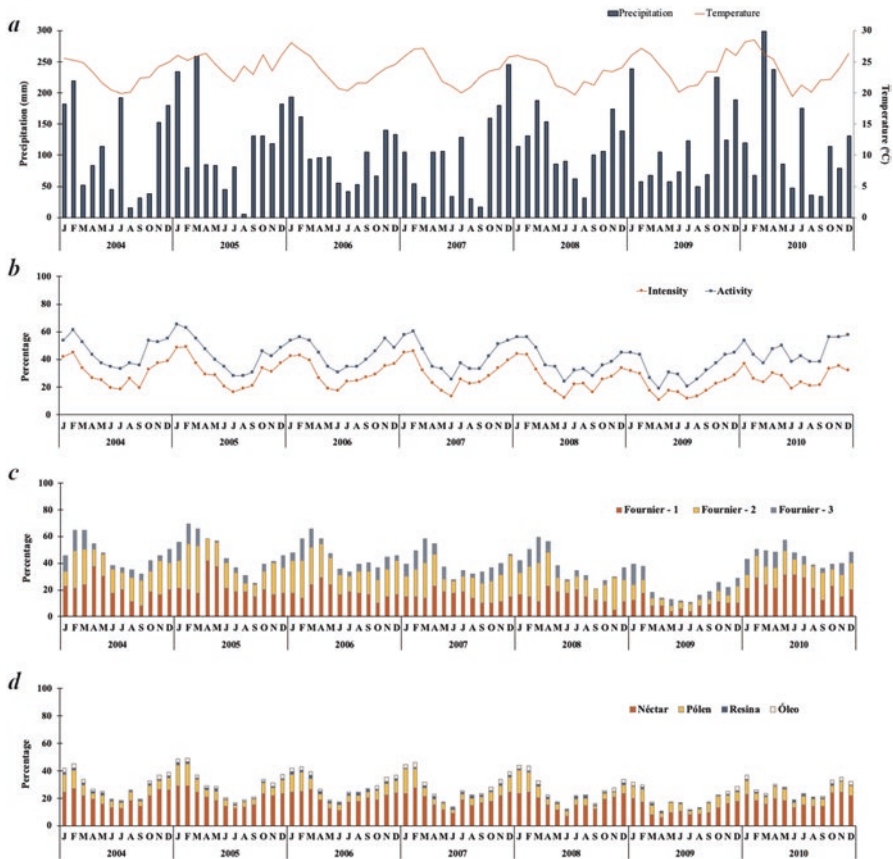


Fig. 1.7 Climatic data and flowering events during the study period (2004–2010) in the Maricá *restinga*, Rio de Janeiro state, Brazil. (a) Monthly data for mean temperature (°C) and total precipitation (mm) (Source: INMET/RJ). (b) Flowering intensity and activity percentages for the community. (c) Monthly proportion of species flowering, according to Fournier semiquantitative intensity scale: 0 (absence of flowers), 1 (low flowering intensity), 2 (moderate flowering intensity), 3 (high flowering intensity). (d) Monthly availability of floral resources, based on the proportion of flowering species with nectar, pollen, oil, and resin flowers

Although the community as a whole had some species in flower year-round, most individual species showed seasonal flowering events in an annual frequency (67%), followed by continuous (15%), sub-annual (13%), and supra-annual (5%) (Table 1.1).

The annual flowering pattern was recorded for all trees and for a large proportion of the shrubs, herbs, and climbing species. The continuous flowering pattern was observed in subshrubs, climbers, and herbaceous species, but rarely in shrubs (*Ouratea cuspidata*) and never in trees. Continuous emission of flowers predominated in species from open areas between bushes (*Chamaecrista ramosa* and

Table 1.2 Spearman correlation indices (rs) obtained in the correlation analysis between the climatic factors (mean temperature, total precipitation, and day length) and the percentages of Fournier and activity of flowering (78 species) of the Maricá *restinga*, Rio de Janeiro state

Year	Percentages	Temperature	Precipitation	Day length
2004	F	0.90*	0.45	0.91*
	A	0.81*	0.36	0.86*
2005	F	0.67*	0.53	0.93*
	A	0.70*	0.57	0.86*
2006	F	0.88*	0.71*	0.90*
	A	0.86*	0.73*	0.86*
2007	F	0.73*	0.35	0.87*
	A	0.77*	0.44	0.87*
2008	F	0.86*	0.62*	0.88*
	A	0.87*	0.67*	0.89*
2009	F	0.70*	0.35	0.87*
	A	0.61*	0.36	0.80*
2010	F	0.64*	0.42	0.73*
	A	0.46	0.26	0.58*
All years	F	0.90*	0.45	0.91*
	A	0.81*	0.36	0.86*

F percentages of Fournier, A percentages of activity of flowering

*Significant values for $p < 0.05$

Cuphea flava) and edges of bushes (*Epidendrum denticulatum*, *Mandevilla guanabaraica*, and *Peplonia asteria*) in the open, non-floodable shrub physiognomy. In some years, species that tended to flower continuously reduced or even stopped flowering for a few weeks or months, as occurred with *Ouratea cuspidata* (2008 and 2010), *Peplonia asteria* (2007–2009), *Dalechampia micromeria* (2004–2006 and 2009), *Cuphea flava* (2009–2010), *Stylosanthes guianensis* (2006 and 2008–2010), and *Peixotoa hispidula* (2007–2010). The sub-annual and supra-annual flowering patterns were least common, but occurred in species with varied life forms, except for trees. Among the species with sub-annual flowering, *Marcetia taxifolia* (Melastomataceae) had the largest number of floral episodes per year (four events) (Table 1.1).

The regular flowering pattern predominated (54%), and the irregular (45%) pattern occurred in all the species with sub-annual frequency of flowering. We did not classify regularity for *Vanilla chamissonis*, as this species flowered only once during the study (Table 1.1). Three species alternated between sub-annual and annual flowering over the 7 years (*Gaylussacia brasiliensis*, *Erythroxylum subsessile*, and *Chiococca alba*) (Table 1.1).

Restinga species tended to have a long (41%) or intermediate (56%) flowering duration. Brief flowerings occurred in only 3% of species (*Andira legalis*, *Neomarica candida*, and *Vanilla chamissonis*) (Table 1.1).

1.3.3 Availability of Floral Resources During the Year

Nectar, pollen, oil, and resin were available to anthophile visitors year-round (Fig. 1.7d). Nectar and pollen were abundant and continuously available (Fig. 1.7d), while oil and resin were less abundant and occasionally absent, mainly in the colder/drier periods (oil, May and June; resin, May, August, September, and November) (Fig. 1.7d).

Unlike nectar and pollen, which were offered by many different species flowering concomitantly, the annual supply of oil and resin was provided by a small number of species that alternated periods or peaks of flowering. For example, when *Clusia lanceolata* ceased flowering in the beginning and middle of the warmer/wetter season (October–December), floral resin was still supplied by continuous emission from *Dalechampia micromeria* inflorescences. Similarly, when *Byrsonima sericea* ceased flowering at the beginning of the colder/drier season, floral oil was still available from *Peixotoa hispidula* and *Stigmaphyllon paralias*, which tended to exhibit more extensive or continuous blooms over part of the colder/drier period. Differently from other years, in the 2009–2010 cold/wet season, *Peixotoa hispidula* underwent a sharp reduction in flowering activity, probably also reducing the amount of floral oil available.

1.4 Discussion

The phenological flowering pattern in the Maricá *restinga* shows a seasonal flowering rhythm at both the community and species level. This conclusion is supported by the occurrence of regular peaks (in warmer/wetter seasons) and depressions (in colder/drier seasons) in the activity and intensity curves over the 7 years of the study. We also observed a high proportion of species flowering in an annual (66.7%) and regular (55%) pattern. This flowering pattern has also been recorded in areas with less-pronounced seasonal climatic changes in other phytophysiognomies of the Atlantic Forest Domain in southeastern Brazil (Morellato et al. 2000; Talora and Morellato 2000; Straggemeier and Morellato 2011). Taken together, these studies reinforce the idea that the flowering phenophase in the Atlantic Forest follows a general pattern (Morellato et al. 2000; Talora and Morellato 2000; Straggemeier and Morellato 2011).

The flowering events recorded in the Maricá *restinga* showed significant and positive correlations with mean temperature and day length, suggesting that these factors determine the seasonality of flowering at this site. In contrast to expectation for a harsh environment such as the *restinga* (characterized by high salinity, unstable sandy soil with low water retention, strong winds, direct sunlight, and high temperatures; Scarano 2002), we did not observe a strong relationship between phenological events and rainfall. For the Marambaia *restinga*, which is also located in Rio de Janeiro state, Carvalho et al. (2015) also found a low correlation between the

phenological flowering events of Sapindaceae species and rainfall. To explain this lack of correlation, the authors suggested that the Marambaia region does not have sufficiently low precipitation levels to induce water stress during the dry season (Mattos 2005) and that the summer rains replenish swamps, swampy forests, seasonal ponds, and seasonally flooded forests, regularly providing groundwater for non-flooded areas. The Maricá region has no regular prolonged dry season that might expose the vegetation to periods of water limitation (Mantovani and Iglesias 2001). In this *restinga*, dew and the shallow water table (Dau 1960) can also serve as water sources, which may contribute to the absence of a correlation between flowering events and rainfall (Gomes et al. 2008). Studies in other phytophysiognomies of the Atlantic Forest where the climate is less seasonal than in Maricá have also found no correlation between phenology and rainfall and have shown that day length is highly important for flowering periodicity (Morellato et al. 2000; Straggemeier and Morellato 2011). Therefore, our results reinforce the hypothesis that day length is important for the seasonal distribution of flowering events through the year in areas with an irregular rainfall regime and without a severe and well-defined dry season.

Among the species monitored in the Maricá *restinga*, 92% provided some floral resources during the flowering period, suggesting that these plants are highly dependent on biotic pollen vectors for sexual reproduction. Four types of floral resources (nectar, pollen, oil, and resin) occur. Notably, *Myrrhinium atropurpureum* offers sweet petals as a floral resource (Roitman et al. 1997). As in other assessments of the proportion and temporal distribution of floral resources in plant communities, in the Maricá *restinga*, nectar is the most frequent resource, followed by pollen, oil, and resin; however, resin was not found in some of these studies (Atlantic Forest, Silva et al. 1997; *restinga*, Viana 1999; Cerrado, Silberbauer-Gottsberger and Gottsberger 1988 and Oliveira and Gibbs 2000; Caatinga, Rodarte 2003 and Machado and Lopes 2004). This was expected since nectar is used by a wide variety of anthophilous visitors, both diurnal and nocturnal (Simpson and Neff 1983; Endress 1994; Agostini et al. 2014). Pollen is a rich source of proteins and amino acids together with numerous other compounds of potential nutritional value; it is used mainly by bees but also by beetles and mammals (Endress 1994; Agostini et al. 2014). Floral oil is collected by solitary female bees and together with pollen grains serves as food for the larvae (Endress 1994; Agostini et al. 2014). Resin is a non-nutritive resource, also collected only by female bees for coating and asepsis of the nests (Simpson and Neff 1983; Endress 1994; Agostini et al. 2014).

Although we observed a concentration of species blooming in the warmer/wetter period, the Maricá *restinga* has some species blooming throughout the year, and floral resources are always available for pollinators. Among the species with a flowering peak restricted to the colder/drier season are *Lundia corymbifera*, *Billbergia amoena* (both pollinated by hummingbirds), *Agarista revoluta* (pollinated mainly by nocturnal insects), and *Protium brasiliensis*, *Guapira opposita*, *Coccoloba arborescens*, and *Neomithrantes obscura* (all pollinated by various insects). These species are annual, regular, with intermediate to long and intense flowering, and attract diurnal (Rodarte 2008; Benevides 2011, 2015a; Moreira et al. 2017, 2019) and nocturnal visitors (Moreira et al. 2017, 2019).

The large number of continuously flowering species recorded here may be an effect of sampling plants with different life forms, as most phenology studies that have evaluated mainly tree species found a very small number of species with continuous flowering (Newstrom et al. 1994a, b; Engel and Martins 2005). Species with continuous flowering predominated among herbs, vines, and subshrubs, with a tendency for higher flowering intensity in the warmer/wetter season. Particularly important are *Dalechampia micromeria*, which supplies some Euglossini and Meliponini bees with floral resin when *Clusia lanceolata* stops flowering at the end of the year (Rodarte 2008), and *Peixotoa hispidula*, an important source of floral oil, used mainly by Centridini bees (Vieira 1995) when *Byrsonima sericea* is not flowering.

The temporal distribution and the intensity of the flowering periods in a community affect the quantity and quality of floral resources available to pollinators and are important community structural factors (Newstrom et al. 1994b; Olesen et al. 2008; Rosas-Guerrero et al. 2014). The regularity of events over the years provides predictability in the supply of resources for these pollen vectors (Morellato et al. 2016), promoting consistent, diversified, and often specialized plant-pollinator interactions, as observed in most species in this study, particularly for species pollinated by bees (Rodarte 2008).

The climate is one of the main factors involved in the control and regulation of plant phenological events (leaf emission and loss, flowering, and fruiting). In recent years, studies of phenology have gained in importance in the face of the threat of climate change, which is potentially capable of disrupting interactions such as those between plants and pollinators (Morellato et al. 2016). Anthracological studies using carbonized woody remains from *sambaquis* (prehistoric kitchen middens) on the southeast coast of Rio de Janeiro state found a high floristic diversity in the *restinga* areas, correspondence between the taxa recorded and currently existing plants, and virtually no vegetation variation during the entire second half of the Holocene, approximately 5500 to 1400 years BP (Scheel-Ybert 1999, 2000, 2001, 2004). Based on these results, Scheel-Ybert (2001, 2004) suggested that *restinga* vegetation appears to be stable and not exceptionally sensitive to climatic fluctuations. In parallel, the regular flowering rhythms and the consequent predictable availability of floral resources found here for *restinga* vegetation over 7 years also suggest that interactions between plants and pollinators in this environment can be quite stable and resilient. Certain phenological characteristics such as annual and long-lasting flowering (more than 4 months), together with diversified plant-pollinator interactions, from generalists to specialists (Rodarte 2008), reinforce the idea of resilient interactions, leading to sexual reproductive success. The high capacity for vegetative propagation that is commonly documented in *restinga* plants (Cirne and Scarano 2001; Faria et al. 2006; Benevides et al. 2015b) is also an important reproductive strategy and contributes to plant resilience in this ecosystem. The *restinga* vegetation comprises a pool of species with high ecological plasticity that migrated from the Atlantic Forest and colonized the geologically younger and resource-poor *restingas* (Scarano 2002). Despite the high ecological plasticity, the

colonization and succession in natural *restinga* areas characterizes this vegetation as unique and vulnerable (Scarano 2002).

Recent studies based on models that compared current climate conditions to future climate scenarios, projected to 2050 to assess potential changes in taxonomic and functional diversities of woody *restinga* species, revealed that climatic changes can critically alter the biodiversity in *restinga* communities, mainly through loss of species and homogenization of the vegetation (Inague et al. 2021). The present study of flowering phenology in a *restinga* area showed how the temporal distribution of flowering events, availability of floral resources, pollination, and reproductive success of plant species are interdependent events that can become mismatched, resulting in irreparable losses of ecosystem services. Therefore, anthropic actions and climate changes together would increase the vulnerability of these coastal communities and require urgent conservation measures such as restoration of degraded areas, increases in the number of *restinga* areas, and strengthening of legal protections of *restingas*, in order to mitigate the expected impacts.

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