



## Original article

## Spatial heterogeneity and the distribution of bromeliad pollinators in the Atlantic Forest

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## ABSTRACT

Interactions between plants and their pollinators are influenced by environmental heterogeneity, resulting in small-scale variations in interactions. This may influence pollinator co-existence and plant reproductive success. This study, conducted at the Estação Biológica de Santa Lúcia (EBSL), a remnant of the Atlantic Forest in southeastern Brazil, investigated the effect of small-scale spatial variations on the interactions between bromeliads and their pollinators. Overall, hummingbirds pollinated 19 of 23 bromeliad species, of which 11 were also pollinated by bees and/or butterflies. However, spatial heterogeneity unrelated to the spatial location of plots or bromeliad species abundance influenced the presence of pollinators. Hummingbirds were the most ubiquitous pollinators at the high-elevation transect, with insect participation clearly declining as transect elevation increased. In the redundancy analysis, the presence of the hummingbird species *Phaethornis eurynome*, *Phaethornis squalidus*, *Ramphodon naevius*, and *Thalurania glaucopis*, and the butterfly species *Heliconius erato* and *Heliconius nattereri* in each plot was correlated with environmental factors such as bromeliad and tree abundance, and was also correlated with horizontal diversity. Since plant-pollinator interactions varied within the environmental mosaics at the study site, this small-scale environmental heterogeneity may relax competition among pollinators, and may explain the high diversity of bromeliads and pollinators generally found in the Atlantic Forest.

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## 1. Introduction

Plant-pollinator interactions are limited by the spatial distribution of plants and the environmental constraints faced by their pollinators. The resulting temporal and/or spatial heterogeneity favors diversification of interactions, and is likely to be a contributing factor in the generation of diversity (Huston, 1994). Spatial resource partitioning (Feinsinger, 1976) and environmental factors are probably equally important (Lara, 2006; Graham et al., 2009; Dalsgaard et al., 2009; Abrahamczyk and Kessler, 2010).

Large environmental changes, such as those related to altitude, may affect the occurrence of insects and hummingbirds (Cruden, 1972; Arroyo et al., 1982). Regional hummingbird assemblages are apparently affected by environmental factors such as mean annual rainfall, minimum annual temperature (Aizen and Ezcurra, 1998; Abrahamczyk and Kessler, 2010), and altitude and habitat changes (Graham et al., 2009). These changes are thought to be associated

with a gradient of increasing specialization in hummingbird pollination as rainfall increases, and at higher altitudes and the associated lower temperatures (Aizen, 2003; Dalsgaard et al., 2009).

Many plant reproductive aspects may change on microspatial scales associated with changes in resource availability (Lechowicz and Bell, 1991). These changes may be expressed as the number and density of flowers (Grindeland et al., 2005; Scrok and Varassin, 2011), or the position of a plant in relation to the foraging area of a pollinator (Makino et al., 2007), and this can in turn affect plant-pollinator interactions (Grindeland et al., 2005). This spatial heterogeneity may locally facilitate pollinator co-existence, reducing interspecific interactions between hummingbirds (Lara, 2006). This spatial variation seems to be especially important in warm lowland habitats, where competition among hummingbirds seems to be an important factor structuring hummingbird communities (Graham et al., 2009). At a local scale, the number of flowers affects the number of hummingbird species (Abrahamczyk and Kessler, 2010).

Interactions between bromeliads and their pollinators tend to vary locally, and environmental variation can influence reproductive success within and among populations of Bromeliaceae (Paggi et al., 2007). Although these interactions have been extensively studied (Sazima et al., 1995a, 1996; Martinelli, 1997; Buzato et al., 2000; Walther and Brieschke, 2001; Dziedzioch et al., 2003;

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Kaehler et al., 2005; Krömer et al., 2006; Piacentini and Varassin, 2007), no previous community-level research has focused on the effects of small-scale spatial variation on bromeliad pollination.

Bromeliads are widely represented in the tropical rain forests of southeastern Brazil (Fontoura et al., 1991). In the Atlantic Forest, bromeliads are the main food resource used by hummingbirds, the most important bromeliad pollinator (Araújo et al., 1994; Sazima et al., 1995a, 1996; Martinelli, 1997), followed by bats (Sazima et al., 1995b, 1999; Martinelli, 1997) and bees (Benzing, 1980). Additionally, temporal variation in bromeliad resource availability provides food for pollinators during the year, and favors partitioning of pollinators (Araújo et al., 1994). Therefore, given the importance of bromeliads as a food source for animals, especially hummingbirds (Sazima et al., 1999; Buzato et al., 2000; Walther and Brieschke, 2001; Dziedzic et al., 2003), mapping the spatial availability of bromeliad flowers may help to understand hummingbird species diversity.

The present study aimed to answer the following questions regarding the interactions between bromeliads at the Estação Biológica de Santa Lúcia (EBSL) in southeastern Brazil, and their pollinators along an elevational gradient, taking spatial heterogeneity into consideration: (1) Do small-scale altitudinal changes, characteristic for the Brazilian Atlantic Forest, influence pollinator assemblages associated with transect distribution? (2) Do spatial variations in environmental factors (altitude, tree richness, size and abundance, bromeliad richness and abundance, number of treelets and herbs, canopy cover, and horizontal diversity, see Methods: 2.4 spatial pollinator fluctuations) affect the distribution of pollinators?

## 2. Material and methods

### 2.1. Study area

The Santa Lúcia Biological Station – EBSL (19°57'10" and 19°59'00"S, 40°31'30" and 40°32'25"W) is located in the town of Santa Teresa, state of Espírito Santo (ES), southeastern Brazil. The EBSL has a total area of about 440 ha, covered by Tropical rain Forest (the Atlantic Forest) with altitudes ranging from 600 to 900 m (Mendes and Padovan, 2000). The annual mean temperature is 19.9 °C, with minimum and maximum temperatures averaging 14.3 °C and 26.2 °C, respectively (Thomaz and Monteiro, 1997). The warmest months are January and February, and the lowest temperatures occur in June and July. Mean rainfall is 1868 mm per year, with highest rainfall in November and lowest in June, when the mean rainfall is less than 60 mm. The climate is humid subtropical (Mendes and Padovan, 2000).

Our survey was conducted on three transects (340 m × 10 m), each subdivided into 34 plots of 10 × 10 m, delimited at each of the following elevations: low-elevation (650–660 m), mid-elevation (675–700 m), and high-elevation (820–855 m). The topography along the transects varies from almost flat to strongly undulating. There is low floristic similarity among tree species occurring at these different elevations, with only 12% of tree species shared among transects (Thomaz and Monteiro, 1997). Most terrestrial and epiphytic bromeliads were located with the help of binoculars, and a few through closer inspection by climbing the trees. All bromeliads with flowers, including those with up to half of their foliage inside the transects, were recorded, regardless of whether their host tree was located inside or outside the plot. Voucher specimens of the 39 species of bromeliads were identified by specialists (Appendix) and deposited in the MBML herbarium.

### 2.2. Pollination guilds

Focal observations (Dafni, 1992) were conducted from December 1997 through June 1999, monthly, with additional observations in October 2000 and April and June 2001. We focused observations on

23 of the 39 bromeliad species recorded at the EBSL, due to a small number of plants or to a lack of overlap between the flowering period and observation periods. Because observations were only possible when both flowers and pollinators were directly visible, the number of individual bromeliads recorded differed among species. All flower visitors were recorded. No record was made for the only species with nocturnal anthesis, *Vriesea* aff. *bituminosa* (see Appendix), since no focal observations were conducted at night. Animals visiting the flowers were documented, either after direct observation, with binoculars, or through photographs. Observations were made at a minimum distance of 3 m from the plant, except for bees, which were observed from a shorter distance to allow observation of their behavior. Focal observation efforts were generally conducted in the morning, and lasted three to five hours per day. The same plant species was observed in different plots, on different days. Floral visitors were classified as pollinators or robbers/thieves (Faegri and van der Pijl, 1971). Pollinators carry pollen and contact stigmas, whereas robbers/thieves visit the flowers without touching the reproductive structures. A total of 280 h 30 min of focal observations resulted in 554 records of flower visits. Additionally, we recorded 38 flower visits between the focal observation periods. Hummingbirds were identified with the help of taxonomic literature (Ruschi, 1982; Grantsau, 1988) and comparisons with specimens deposited in the zoological collection of the MBML. Bees were collected and identified by Gabriel A. R. Melo, Universidade Federal do Paraná; and butterflies were identified by Prof. Keith S. Brown Jr., Universidade Estadual de Campinas, using photographs.

The pollinator visitation rate was calculated by dividing the total number of visits recorded for a given pollinator species to a bromeliad species in each plot, by the total number of hours spent observing the given bromeliad species at that plot, and then the mean visitation rate was calculated for that species across all plots. For butterflies, when many flowers of an inflorescence were visited many times, usually more than 10 visits, we were unable to count all the visits, so the number of visits was recorded as 10.

### 2.3. Environmental heterogeneity

We measured the following variables: altitude (m), tree richness, tree size (mean DBH, cm), mean tree height (m), tree abundance, bromeliad richness, and bromeliad abundance. We also counted, in a subplot of 1 m<sup>2</sup> at the central point of each plot, the canopy cover (cm<sup>2</sup>; more details of data collection may be found in Varassin, 2002) and the number of treelets and herbs. In this subplot we estimated the horizontal diversity, considering the proportion of cover area occupied by bamboos, rocks, lianas, and fallen trees. We calculated the Horizontal Diversity Index, using the Shannon–Wiener Index (Magurran, 1988) as follows:

$$DH = - \sum_{i=1}^k p_i \ln p_i$$

where

$k$  = number of the different groups (bamboos, rocks, lianas, and fallen trees) covering the area in each subplot

$p_i$  = proportion of cover area occupied by bamboos, rocks, lianas, and fallen trees.

### 2.4. Spatial pollinator fluctuations

In order to test the presence of spatial autocorrelation in our data, we used a Mantel test (Mantel, 1967; Legendre and Fortin, 1989) with the R Software Version 2.14.1 (R Development Core

Team, 2011). Since in some plots there was no record of a flowering bromeliad and/or a pollinator, this analysis considered only the plots where there was an interaction record. Although the area surveyed at each elevation was identical, an uneven occurrence of interactions among bromeliads and pollinators resulted in a different number of plots at each elevation; that is, five plots in the low-elevation transect, 11 plots in the mid-elevation transect, and 16 plots in the high-elevation transect.

The latitude and longitude of plots were converted to geodesic distances and constituted the spatial matrix. The environmental variables were standardized using data conversion to mean zero and standard deviation one, and constituted the environmental matrix. Pollinator composition matrix (visitation rate of pollinators) and bromeliad composition matrix (species abundance) were log-transformed. The matrices were converted to distance matrices using Euclidean distance in the spatial and environmental matrices, and Bray–Curtis in the pollinator and bromeliad species-abundance matrices.

We first tested the spatial autocorrelation in the environmental data and in pollinator species abundance, and we tested autocorrelation among pollinator species abundance and environmental data. To test for a relationship between pollinator species abundance and bromeliad species abundance, we first tested for spatial autocorrelation in bromeliad abundance, and autocorrelation among bromeliad abundance and environmental data. Then we tested for autocorrelation among pollinator and bromeliad abundance.

In order to test which environmental factors affected pollinator presence, we used direct gradient analysis to measure the fluctuation patterns of pollinator species in relation to environmental variables. As before, this analysis considered only the plots where there was an interaction record.

The matrix of environmental variables was transformed by ranging, using the program Fitopac (Shepherd, 1987), which employs the following formula:  $y = x - x_{\min}/(x_{\max} - x_{\min})$ . Based on the transformed matrix, the magnitude of the gradient around the axes, in units of standard deviation, was measured by Detrended Correspondence Analysis (DCA) (ter Braak, 1995) using the program DECORANA (Oksanen and Minchin, 1997). Because the gradient magnitude was lower than the standard deviations, we performed Redundancy Analysis (RDA), which is the canonical form of the PCA (Principal Components Analysis).

A matrix with the spatial distribution of the pollinators was coded with the presence and absence of species in each plot. Pollinators which occurred in at least five plots were selected (the hummingbirds *Phaethornis eurynome*, *Phaethornis squalidus*, *Ramphodon naevius*, and *Thalurania glaucopis*, and the butterflies *Heliconius erato* and *Heliconius nattereri*). For three plots, no data were obtained regarding number of individuals, number of species, or perimeter and height of trees. These missing values were replaced by the general mean estimated from the other 92 plots, so as to include the records of those plots which had a high record of flowering bromeliads. The environmental variables that showed high correlations in the RDA analysis were excluded (ter Braak, 1995). The selection of environmental variables was based on the marginal importance of the environmental variable and the conditional importance of the variable to explain the species-matrix variance (ter Braak and Verdonschot, 1995) during a step-by-step RDA. The association between the environmental variables and bromeliad distribution was tested using the RDA. The significance level of the RDA variables was established with a Monte Carlo permutation test (Verdonschot and ter Braak, 1994). Analyses were performed with the program CANOCO 4.02 for Windows (ter Braak and Smilauer, 1998) using the default selections, with the exceptions mentioned above.

### 3. Results

#### 3.1. Pollination guilds

A total of nine species of hummingbird pollinators were documented, on 19 species of bromeliads (Table 1) (this includes all bromeliad genera known at the EBSL, with the exception of *Acanthostachys*). Within the subfamily Phaethornithinae, *P. eurynome*, *P. squalidus*, and *R. naevius* visited the most bromeliad species; whereas *Glaucis hirsuta* visited only one species (Table 1). The hummingbird genus *Phaethornis* participated in 61% of the interactions, and of the subfamily Phaethornithinae, in 77% (Table 1). The bromeliad species *Aechmea araneosa* had the highest number of hummingbird pollinators (six), followed by *Aechmea bromeliifolia*, *Aechmea victoriana*, *Neoregelia magdalaena*, and *Quesnelia strobilispica* with five hummingbird pollinators (Table 1). Focal observations did not record any floral visitors on *Nidularium longiflorum*.

Nine species of butterflies, including five in the genus *Heliconius*, were documented on members of the bromeliad genera *Acanthostachys*, *Aechmea*, *Billbergia*, *Tillandsia*, and *Vriesea* (Table 2). Three species of bees, and one unidentified species of *Euglossa*, were recorded on species of the following bromeliad genera: *Aechmea*, *Billbergia*, *Neoregelia*, *Nidularium*, and *Quesnelia* (Table 2). A total of 56% (96/170 interactions) of the insect records and 95% (96/101 interactions) of the butterfly records were for the genus *Heliconius* (Table 2). Species of *Heliconius* were most often recorded on *A. araneosa*, the bromeliad with the highest rate of visits by insects (Table 2).

Most species of bromeliads were pollinated by hummingbirds (19 of 23 species) (Tables 1 and 2). Eleven species pollinated by hummingbirds were also pollinated by butterflies or bees (Tables 1 and 2). Specifically, six species of bromeliads were visited exclusively by hummingbirds and butterflies, three species exclusively by hummingbirds and bees, and two species by hummingbirds, butterflies, and bees. Only eight species of bromeliads were pollinated solely by hummingbirds, two species solely by bees, and one species solely by butterflies. With the exception of the genus *Tillandsia*, which was visited by both hummingbirds and butterflies (Tables 1 and 2), all bromeliad genera were visited preferentially by hummingbirds (Table 1). The genera *Neoregelia*, *Nidularium*, and *Quesnelia* were visited by bees (Table 2), in addition to hummingbirds. No butterfly visits were recorded for these genera (Table 2).

#### 3.2. Spatial pollinator fluctuations

Three species of hummingbirds, *P. eurynome*, *P. squalidus*, and *R. naevius* were considered resident species, because they were recorded in the three elevation areas sampled and in most months of the year (Table 3). Six other hummingbird species that were observed with high frequency, *T. glaucopis*, *Amazilia fimbriata*, *Aphantochroa cirrochloris*, *Clytolaema rubricauda*, *Leucochloris albicollis*, and *G. hirsuta* (Table 3) were ubiquitous during only a few months, and were therefore not considered resident species.

Regarding butterflies, *H. erato phyllis* and *H. nattereri* were the most frequent species, being recorded for five and six months of the year, respectively (Table 3). With respect to bees, the genus *Euglossa* was the most prevalent, being recorded from April through July, and in October (Table 3). With respect to the three elevations, bromeliad species pollinated exclusively by hummingbirds tended to occur at the high-elevation transect, decreasing in number as altitude decreased (Fig. 1). At the low-elevation transect, species pollinated by bees and butterflies, besides hummingbirds, became more prevalent (Fig. 1). While the hummingbird species *P. eurynome*, *P. squalidus*, and *R. naevius* were found at all three elevations, other hummingbird species occurred only at the high-elevation transect (*A. cirrochloris*, *C. rubricauda*), the high-

**Table 1**

Number and visitation rate (visits per hour of observation, in parenthesis) of hummingbirds on bromeliads at the Estação Biológica de Santa Lúcia, southeastern Brazil.

Bromeliad species	Trochilinae					Phaethornithinae				# of visiting species
	<i>Amazilia fimbriata</i>	<i>Aphantochroa cirrochloris</i>	<i>Clytolaema rubricauda</i>	<i>Leucochloris albigollis</i>	<i>Thalurania glaucopis</i>	<i>Glaucis hirsuta</i>	<i>Phaethornis eurynome</i>	<i>Phaethornis squalidus</i>	<i>Ramphodon naevius</i>	
<i>A. araneosa</i>	1 (0.3)			2(0.6)	8 (2.0)		8 (1.3)	8 (1.1)	3 (0.5)	6
<i>A. bromeliifolia</i>					6 (1.7)	1 (0.3)	1 (0.6)	1 (0.8)	11 (1.5)	5
<i>A. mutica</i>					2 (0.9)		35 (2.5)	14 (1.2)		3
<i>A. nudicaulis</i>							2 (0.5)			1
<i>A. pineliana</i>		1 (0.5)			11 (1.5)			1 (0.3)	5 (0.9)	4
<i>A. triangularis</i>	8 (1.8)			1(0.2)	6 (0.9)				4 (0.9)	4
<i>A. victoriana</i>	1 (1.0)				3 (0.9)		2 (0.9)	2 <sup>a</sup>	2 (0.4)	5
<i>B. amoena</i>							40 (3.7)	11 (0.9)		2
<i>C. triangulare</i>		2 (0.7)			1 (0.3)				4 (1.1)	3
<i>N. magdalaenae</i>	6 (2.3)				2 (2.2)		1 (0.2)	2 (0.41)	9 (1.3)	5
<i>Neoregelia</i> sp.								1 (0.4)		1
<i>Ni. cariacicaense</i>							18 (1.1)	13 (0.8)	2 (0.7)	3
<i>Ni. procerum</i>							7 (1.1)		2 (0.3)	2
<i>P. petropolitana</i>			1 <sup>a</sup>							1
<i>Q. strobilispica</i>	1 (1.0)				1 (0.6)		6 (0.8)	1 (0.6)	1 (0.3)	5
<i>T. geminiflora</i>	1 (1.0)				1 (1.0)		2 (0.7)			3
<i>V. gracilior</i>							9 (0.7)	3 (0.8)	2 (0.3)	3
<i>V. psittacina</i>				3 (2.0)			8 (1.2)	1 (0.3)	5 (1.2)	4
<i>V. simplex</i>							8 (0.9)			1
<b># of species visited</b>	<b>6</b>	<b>2</b>	<b>1</b>	<b>3</b>	<b>10</b>	<b>1</b>	<b>14</b>	<b>12</b>	<b>12</b>	
<b>Total interactions recorded</b>	<b>18</b>	<b>3</b>	<b>1</b>	<b>6</b>	<b>51</b>	<b>1</b>	<b>147</b>	<b>60</b>	<b>50</b>	—
<b>% of interactions recorded</b>	<b>5.3</b>	<b>0.9</b>	<b>0.3</b>	<b>1.8</b>	<b>15.1</b>	<b>0.3</b>	<b>43.6</b>	<b>17.8</b>	<b>14.8</b>	
<b>Total interactions recorded per subfamily (%)</b>	<b>79 (23.4)</b>					<b>258 (76.6)</b>				

A. = *Aechmea*, B. = *Billbergia*, C. = *Canistrum*, N. = *Neoregelia*, Ni. = *Nidularium*, P. = *Portea*, Q. = *Quesnelia*, T. = *Tillandsia*, V. = *Vriesea*.<sup>a</sup> Records outside systematic observation periods.

elevation transect and the mid-elevation transect (*A. fimbriata* and *T. glaucopis*), or the low-elevation transect (*G. hirsuta* and *L. albicollis*). With one exception, *Saliana triangularis*, which occurred at the high-elevation transect, all species of butterflies were recorded at the mid-elevation transect. Regarding the bees, *Bombus morio* was recorded only at the low-elevation transect, the genus *Euglossa* predominated at the mid-elevation transect and was not recorded at the high-elevation transect, and the robber/thief *Trigona fulviventris* was very common at all three transects.

Mantel tests indicated that the environmental data showed spatial autocorrelation ( $r = 0.2266$ ,  $P = 0.0057$ ). Pollinator species abundance responded to environmental variations, so that more similar environments had more similar pollinators ( $r = 0.191$ ,  $P = 0.0127$ ); but this was not spatially limited, since pollinator abundance showed no spatial correlation ( $r = 0.0863$ ,  $P = 0.1248$ ). Mantel tests indicated that the bromeliad species abundance showed spatial autocorrelation, that is, bromeliads are dispersal-limited ( $r = 0.3955$ ,  $P < 0.0001$ ). More similar environments showed a more similar bromeliad abundance ( $r = 0.2295$ ,  $P = 0.0071$ ), but pollinators were not related to bromeliad species abundance ( $r = 0.0856$ ,  $P = 0.1540$ ). These patterns indicate that some environmental restrictions on pollinators were unrelated to the spatial location of plots or to bromeliad species abundance.

The environmental variables excluded from the RDA analysis due to their high correlation were bromeliad richness (correlated with bromeliad abundance), tree height (correlated with tree DBH), and tree richness and altitude (correlated with tree abundance). The environmental variables selected significantly explained pollinator presence in the RDA analysis ( $P = 0.001$  in the Monte Carlo permutation test). The variance in pollinator presence that could be explained in relation to the total variance was 30% for all three axes, and the variance relative to the relationship species-environmental variables was 60% for the first axis and 87% for the first two axes combined. The inflation factors ranged from 1.0 to 1.2.

The first ordination axis,  $\lambda = 0.156$ , was defined by bromeliad abundance, and was highly significant ( $P = 0.005$  in the Monte Carlo permutation test). The correlation between pollinator species

and environmental variables was 0.687. The second axis,  $\lambda = 0.069$ , was defined by the Horizontal Diversity Index and tree abundance (Fig. 2). The correlation between pollinator species and environmental variables was 0.627.

Among the environmental variables analyzed, the presence of some pollinator species was correlated with the abundance of bromeliads, abundance of trees, and the horizontal diversity in each plot (Fig. 2). *R. naevius*, *T. glaucopis*, and *H. nattereri* correlated positively with high bromeliad abundance and low horizontal diversity in the habitat (Fig. 2). *P. eurynome* occurred in plots with higher tree abundance, whereas *P. squalidus* and *H. erato* occurred in plots with fewer trees (Fig. 2).

## 4. Discussion

### 4.1. Pollination guilds

The proportion of bromeliads visited by hummingbirds at the ESBL was high (19 of 23 species), even considering that several previous studies have reported hummingbirds foraging on bromeliads (Martinelli, 1997; Buzato et al., 2000; Dziedzioch et al., 2003; Kaehler et al., 2005; Machado and Semir, 2006; Piacentini and Varassin, 2007). The high representation of hummingbirds may be partly due to the high local hummingbird species richness (Simon, 2000), but local heterogeneity may explain different species records in different situations (see 4.2. Spatial variations in pollinator composition). *P. eurynome*, *P. squalidus*, *T. glaucopis*, and *R. naevius* were responsible for 92% of the hummingbird visits to bromeliads, and can be considered keystone pollinator species (*sensu* Sazima et al., 1995a).

The abundance of Phaethornithinae on bromeliads may be explained by the stratified use of the forest by these hummingbirds (Sazima et al., 1995a, 1996; Buzato et al., 2000; Varassin and Sazima, 2000; Rocca-de-Andrade, 2006) and their preference for forests and understory microhabitats (Bleiweiss, 1998). The low evolutionary flexibility of the subfamily Phaethornithinae compared with the Trochilinae (Fleming and Muchhala, 2008), and the restriction of



**Table 2**

Number and visitation rate (visits per hour of observation, in parenthesis) of bees and butterflies on bromeliads at the Estação Biológica de Santa Lúcia, southeastern Brazil.

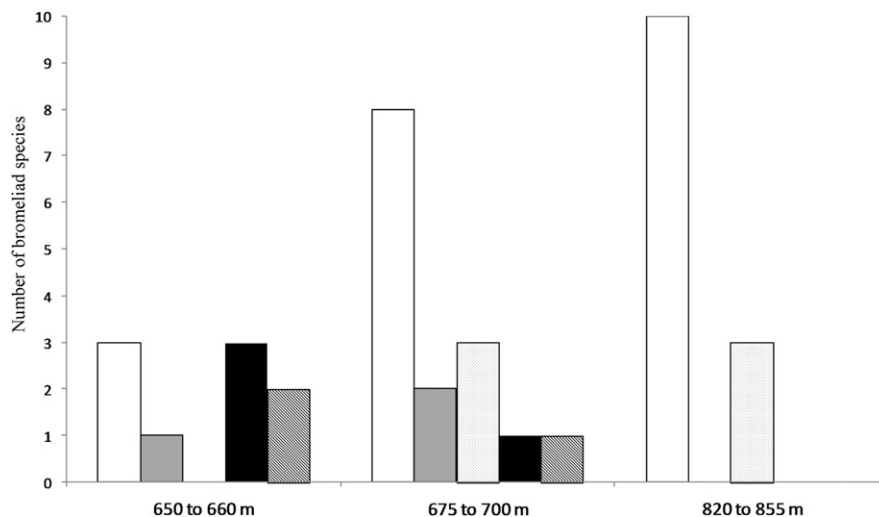
Bromeliad species	Butterflies									Bees					# of visiting species
	<i>Heliconius erato</i>	<i>H. ethilla</i>	<i>H. nattereri</i>	<i>H. numato</i>	<i>H. sara</i>	<i>Oleria aquata</i>	<i>Paracalystos</i> sp	<i>Saliana triangularis</i>	<i>Strymon oreala</i>	<i>Bombus morio</i>	<i>Epicharis obscura</i>	<i>Euglossa chalybeata</i>	<i>Euglossa</i> sp.	<i>Trigona fulviventris</i>	
<i>Ac. strobilacea</i>			1 (0.3)	2 (0.7)											2
<i>A. araneosa</i>	11 (1.9)	20 (4.2)	30 (3.9)	14 (2.2)									15(1.1)	11 (1.9)	7
<i>A. lingulata</i>											3 <sup>a</sup>				1
<i>A. mutica</i>								2 (0.7)						2 (1.0)	2
<i>A. nudicaulis</i>	2 (0.5)		3 (0.8)		3 (0.8)										3
<i>A. pineliana</i>		1 <sup>a</sup>													1
<i>A. triangularis</i>			1 (0.3)			1 (0.3)			1 (0.2)					1 (0.2)	4
<i>A. victoriana</i>														1 (0.2)	1
<i>B. amoena</i>		1 (0.3)					1 (0.2)						1 (0.2)		3
<i>N. magdalaenae</i>										1 (0.2)			3 (0.7)		2
<i>Neoregelia</i> sp												7 (0.9)	5 (0.6)		2
<i>Ni. cariacicaense</i>										1 (<0.1) +1 <sup>a</sup>					1
<i>Q. strobilispica</i>										1 (0.3)				1 (0.6)	2
<i>T. tenuifolia</i>	4 (0.4)		1 (0.4)	1 (0.3)										11 (2.0)	4
<i>V. gracilior</i>			1 (0.3)											1 (0.3)	2
<b># of species recorded</b>	<b>3</b>	<b>3</b>	<b>6</b>	<b>3</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>3</b>	<b>1</b>	<b>1</b>	<b>4</b>	<b>7</b>	
<b>Total interactions recorded</b>	<b>17</b>	<b>22</b>	<b>37</b>	<b>17</b>	<b>3</b>	<b>1</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>4</b>	<b>3</b>	<b>7</b>	<b>27</b>	<b>28</b>	
<b>% of interactions recorded</b>	<b>10.0</b>	<b>12.9</b>	<b>21.8</b>	<b>10.0</b>	<b>1.8</b>	<b>0.6</b>	<b>0.6</b>	<b>1.2</b>	<b>0.6</b>	<b>2.4</b>	<b>1.8</b>	<b>4.1</b>	<b>15.9</b>	<b>16.5</b>	
<b>Total of interactions recorded per order (%)</b>	<b>101 (59.4)</b>									<b>69 (40.6)</b>					

Ac. = Acanthostachys, A. = Aechmea, B. = Billbergia, N. = Neoregelia, Ni. = Nidularium, Q. = Quesnelia, T. = Tillandsia, V. = Vriesea.

<sup>a</sup> Records outside systematic observation periods.

Distribution of recorded bromeliad pollinators along the year at the Estação Biológica de Santa Lúcia, southeastern Brazil.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<b>Hummingbirds</b>												
<i>Amazilia fimbriata</i>							X	X	X	X	X	X
<i>Aphantochroa cirrochloris</i>				X	X		X	X		X	X	X
<i>Clytolaema rubricauda</i>		X	X							X	X	
<i>Glaucis hirsuta</i>									X	X		
<i>Leucochloris albicollis</i>	X	X							X			
<i>Phaethornis eurynome</i>	X	X	X	X	X	X	X	X	X	X	X	X
<i>P. squalidus</i>	X	X	X	X	X	X	X	X	X	X	X	X
<i>Ramphodon naevius</i>	X	X	X	X	X	X	X	X	X	X	X	X
<i>Thalurania glaucopis</i>				X	X		X	X	X	X	X	X
<b>Butterflies</b>												
<i>Heliconius erato</i>	X	X	X		X	X	X	X				
<i>H. ethilla narcaea</i>	X	X	X		X	X	X	X				
<i>H. nattereri</i>	X	X	X	X	X	X	X	X				X
<i>H. numato</i>	X	X	X		X	X	X	X		X		X
<i>H. sara</i>		X	X			X	X	X		X		
<i>Oleria aquata</i>										X	X	
<i>Paracalystos</i> sp.					X	X				X		
<i>Saliana triangularis</i>				X	X							
<i>Strymon oreala</i>				X	X					X	X	
<b>Bees</b>												
<i>Bombus morio</i>			X	X	X					X	X	
<i>Epicharis obscura</i>	X	X	X	X	X					X	X	
<i>Euglossa chalybeata</i>				X	X	X	X	X				
<i>Euglossa</i> sp.				X	X	X	X	X		X	X	



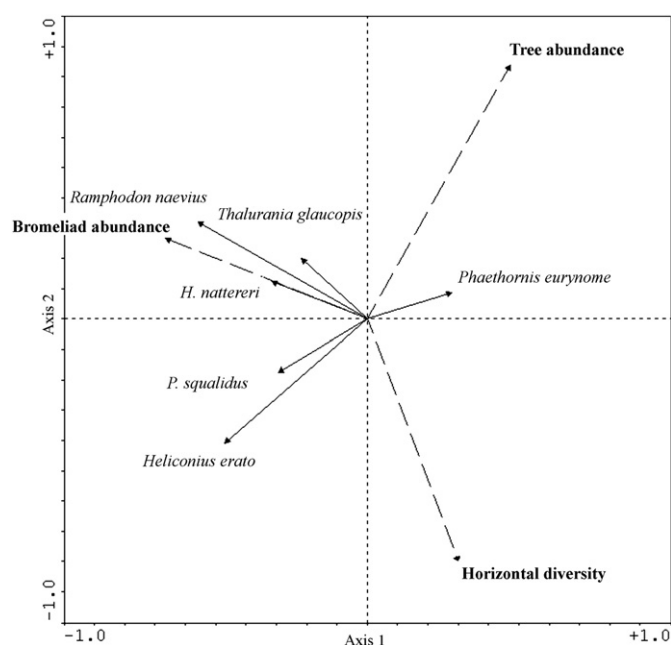
**Fig. 1.** Bromeliad species pollinated by hummingbirds (white bars); butterflies (gray); hummingbirds and butterflies (black dots), bees and hummingbirds (black), and bees, hummingbirds, and butterflies (dashed) in transects at different elevations in the Estação Biológica de Santa Lúcia, southeastern Brazil.

species of Phaethornithinae to low altitudes, forest environments, and the understory (Bleiweiss, 1998) may indicate a higher dependency on bromeliads, which are abundant in the understory of this type of forest. Hummingbirds at the EBSL are associated with the bromeliad genera *Aechmea*, *Billbergia*, *Nidularium*, and *Vriesea* (Varassin and Sazima, 2000), which tend to thrive in the understory (Varassin, 2002). While *Aechmea*, *Billbergia*, and *Vriesea* concentrate on lower portions of the host plants at EBSL, 98% of the specimens of *Nidularium* tend to concentrate from the ground level to about 2 m high (Varassin, 2002). *Tillandsia*, on the other hand, occupies the higher strata of the forest, especially treetops (Varassin, 2002), where they are visited by butterflies and hummingbirds. It is possible that vertical resource partition occurs among pollinators, with hummingbirds more restricted to understory levels.

#### 4.2. Spatial variations in pollinator composition

The altitudinal variation at the EBSL is a contributing factor to the increased environmental diversity. Hummingbird species richness was higher at the high-elevation transect, whereas insects were more diverse at the low-elevation transect. Although there was only one transect at each elevation, reducing the generality of our results, this is consistent with the hypothesis that pollination by invertebrates, particularly bees (Arroyo et al., 1982) decreases with increasing altitude (Cruden, 1972; Arroyo et al., 1982; Krömer et al., 2006). Contrary to reports for the Andean region, where the relationship between functional groups of pollinators and altitude is perceived only above 1000 m (Krömer et al., 2006), even the small altitudinal variation between our study areas was sufficient to detect these differences. The major participation of hummingbirds at high altitudes and the increased insect participation as altitude decreases were also reported for small altitudinal variations in plant-hummingbird communities in the West Indies (Dalsgaard et al., 2009).

Habitat characteristics, including bromeliad and tree abundance and horizontal habitat diversity, influenced pollinator visits to bromeliads. This heterogeneity in pollinator distribution may bias small-scale studies, especially those which consider few individuals in focal observations. In fact, pollinator species that occur concomitantly in a heterogeneous habitat may differ in the way they utilize the available resources. Interestingly, the spatial distribution of bromeliad species had no influence on pollinators, and neither did the spatial location of plots. This is in accordance with the observation that at a local scale, the local diversity of hummingbirds is affected by flower abundance (Abrahamczyk and Kessler, 2010), although in our study, flower abundance was correlated with the flower diversity. The absence of a dispersal limitation, observed through the absence of spatial autocorrelation, associated with the environmental influence on pollinator distribution may indicate some environmental preference in the use of space. For instance, the different species of Phaethornithinae were influenced by different environmental factors. While *R. naevius* preferred areas with more abundant resources (i.e., bromeliads), records of *P. eurynome* and *P. squalidus* were strongly correlated with tree abundance. *P. eurynome* occurred in areas with the highest abundance of trees, whereas *P. squalidus* was most often recorded in areas with the lowest tree abundance. The relationship between these hummingbirds and tree abundance was not



**Fig. 2.** Ordination diagram of the bromeliad pollinators recorded at the Estação Biológica de Santa Lúcia, southeastern Brazil, and the environmental variables, based on pollinators' RDA by the environmental variables (see variables in Spatial pollinator fluctuations in Material and methods). The figure shows 86.9% of the relative variance in relation to species/environmental variables.  $\lambda_1 = 0.156$ ,  $\lambda_2 = 0.069$ . Axes were re-scaled.

established. It is possible, however, that areas with fewer trees also have a more open understory. Considering the butterflies, the slow-moving butterfly *H. erato* (Brown, 1972) has a more flexible behavior compared with *H. nattereri*, and can survive in different habitats (Brown, 1972).

The relatively strong presence of the subfamily Heliconinae on the bromeliads of the EBSL may also be associated with habitat characteristics. Males of *H. nattereri* prefer sunny areas such as the upper strata of the forest, and *H. erato* is frequently found in open fields (Brown, 1972), both environments that are usually rich in bromeliads.

The hummingbird *T. glaucopsis*, which usually has a generalistic behavior (Buzato et al., 2000), tends to forage more frequently in areas with abundant resources, much like the butterfly *H. nattereri* at the EBSL. The bromeliad patches frequented by *R. naevius*, *T. glaucopsis*, and *H. nattereri* seem to be situated in more homogenous environments. This is the case of gaps dominated by bromeliads, the environments most likely to be chosen by these species, as described for males of *H. nattereri* (Brown, 1972).

The environmental heterogeneity is reflected in the different ways in which pollinators are distributed in the environment, for example the occurrence of different species in shaded areas of the understory than in sunny areas. In spite of this, there seems to be no clear-cut partition of resources when it comes to bromeliads, because there was a large foraging overlap by pollinators in bromeliad flowers. Interactions vary within the various environmental mosaics at the EBSL, likely with relaxed selective pressures, with specialization patterns and local adaptation/specialization

varying according to the landscape (Thompson, 2005). Since spatial heterogeneity may reduce interspecific interactions between hummingbirds (Lara, 2006) and competition seems to be an important factor structuring hummingbird communities in warm lowland habitats (Graham et al., 2009), the small-scale environmental heterogeneity found at the study site may relax competition among pollinators and may explain the high diversity of bromeliads and pollinators that is generally found in the Atlantic Forest.

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## Appendix

Bromeliad species from the Estação Biológica de Santa Lúcia (EBSL), southeastern Brazil. Habit: E = epiphytic, F = facultative, T = terricolous, N. R. = not recorded. HE = high-elevation transect, ME = Mid-elevation transect, LE = low-elevation transect. Authors follow Brumitt and Powell (1992) for species nomenclature.

Species	Habit	Number recorded			Identified by	Voucher
		HE	ME	LE		
1 <i>Acanthostachys strobilacea</i> (Schult. f.) Klotzsch	E	1	7	6	E. Leme	I. G. Varassin 64 and 65
2 <i>Aechmea araneosa</i> L. B. Sm.	F	0	2	0	T. Wendt	I. G. Varassin 35
3 <i>A. bromelifolia</i> (Rudge) Baker	F	9	6	5	I. G. Varassin	I. G. Varassin 41 and 45
4 <i>A. castanea</i> L. B. Sm.	E	5	6	6	I. G. Varassin	I. G. Varassin
5 <i>A. hostilis</i> E. Pereira	T	0	1	0	E. Leme	I. G. Varassin 12
6 <i>A. lingulata</i> (L.) Baker	E	1	1	0	T. Wendt	N. R.
7 <i>A. mutica</i> L.B.Sm.	T	10	0	0	T. Wendt	I. G. Varassin 33
8 <i>A. nudicaulis</i> (L.) Griseb.	E	1	8	0	T. Wendt	I. G. Varassin 25
9 <i>A. pineliana</i> (Brogn. ex. Planch.) Baker	E	8	2	0	T. Wendt	I. G. Varassin 24
10 <i>A. triangularis</i> L. B. Sm.	E	1	0	0	T. Wendt	I. G. Varassin 78
11 <i>A. victoriana</i> L. B. Sm.	F	0	0	0	T. Wendt	I. G. Varassin 39
12 <i>Billbergia amoena</i> (Lodd.) Lindl.	E	1	3	5	T. Fontoura	I. G. Varassin 73
13 <i>B. vittata</i> Brongn. ex Morel	E	5	1	5	T. Fontoura	I. G. Varassin 26
14 <i>Billbergia</i> sp.	F	3	8	0	T. Fontoura	I. G. Varassin 42 and 43
15 <i>Canistrum triangulare</i> L. B. Sm. & Reitz	E	1	0	1	I. G. Varassin	I. G. Varassin 55.
16 <i>Hohenbergia augusta</i> (Vell.) E. Morren	E	0	0	1	E. Leme	I. G. Varassin 75
17 <i>Neoregelia dungsiana</i> E. Pereira	N.R.	0	0	1	E. Leme	I. G. Varassin 17
18 <i>N. magdalaenae</i> L. B. Sm. & Reitz	F	6	3	9	E. Leme	I. G. Varassin 51
19 <i>N. pauciflora</i> L. B. Sm.	E	0	0	2	E. Leme	I. G. Varassin 47
20 <i>Neoregelia</i> sp.	E	3	8	5		I. G. Varassin 69 and 70
21 <i>Neoregelia</i> sp. 1	F	3	0	1		N. R.
22 <i>Neoregelia</i> sp. 2	F	1	1	0		N. R.
23 <i>Nidularium cariacicaense</i> (W. Weber) Leme	F	12	20	33	E. Leme	I. G. Varassin 14
24 <i>N. longiflorum</i> Ule	F	0	4	8	E. Leme	I. G. Varassin 15
25 <i>N. procerum</i> Lindm.	F	23	4	2	E. Leme	I. G. Varassin 5 and 71
26 <i>Portea petropolitana</i> (Wawra) Mez	E	2	0	0	E. Leme	I. G. Varassin 25
27 <i>Quesnelia quesneliana</i> (Brongn.) L. B. Sm	E	0	2	0	C. Vieira	I. G. Varassin 76
28 <i>Q. strobilispica</i> Wawra sensu lato.	F	14	0	0	C. Vieira	I. G. Varassin 36 and 77
29 <i>Racinea spiculosa</i> (Grisebach) M. A. Spencer & L. B. Sm.	E	0	0	1	I. G. Varassin	I. G. Varassin 61
30 <i>Tillandsia geminiflora</i> Brongn.	E	23	37	11	R. Tardivo	I. G. Varassin 38 and 44
31 <i>T. kautskyi</i> E. Pereira	E	25	7	4	R. Tardivo	I. G. Varassin 34
32 <i>T. tenuifolia</i> (Mez) L. B. Sm.	F	70	190	83	R. Tardivo	I. G. Varassin 27, 28, 30, 58, 67 and 68
33 <i>Vriesea</i> aff. <i>bituminosa</i> L. B. Sm	E	9	0	0	A. Costa	I. G. Varassin 60
34 <i>V. drepanocarpa</i> (Baker) Mez	F	0	0	3	A. Costa	I. G. Varassin 62
35 <i>V. gracilior</i> (L. B. Sm.) Leme	F	44	0	0	I. G. Varassin	I. G. Varassin 8
36 <i>V. longicaulis</i> (Baker) Mez	F	5	0	9	A. Costa	I. G. Varassin 29
37 <i>V. psittacina</i> (Hook. f.) Lindl.	F	45	5	19	A. Costa	I. G. Varassin 06
38 <i>V. simplex</i> (Vell.) Beer	F	107	41	57	A. Costa	I. G. Varassin 07
39 <i>Vriesea</i> sp.	E	0	0	1	I. G. Varassin	I. G. Varassin 72



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