

Interaction network and the relationships between bromeliads and hummingbirds in an area of secondary Atlantic rain forest in southern Brazil

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(Accepted 14 August 2007)

Abstract: The reciprocal importance of bromeliads and hummingbirds has been proposed for many years, even suggesting coevolution between these two groups. Nevertheless, data are lacking that allow a better test of the relationships involved. Here we investigate the relationship between bromeliads and hummingbirds in an area of secondary Atlantic rain forest in southern Brazil. The study examined the interactions among 12 species of bromeliad and 10 of hummingbird at Reserva Natural Salto Morato, Paraná state. The number of flowering species of bromeliad and the species richness and abundance of hummingbirds were quantified monthly between November 2004 and October 2005. Focal observations on each bromeliad species were made to determine the hummingbird visitors. Neither species richness nor abundance of hummingbirds were related to bromeliad phenology. Together with the monthly variation in visit frequency by a given pollinator to a given plant, these factors indicate a generalization in the use of bromeliads by hummingbirds and argue against tight coevolution. *Ramphodon naevius* and *Thalurania glaucopis* were the main pollinators in the community. *Aechmea nudicaulis* was the most generalist bromeliad species. The generalist species interacted with other generalists or with asymmetric specialists and there was no specialist–specialist interaction. This produced a strongly organized and nested matrix of interactions. This nestedness is similar to other plant–pollinators networks, supporting the hypothesis that the evolutionary relationship between bromeliads and hummingbirds is no stronger than that of other pollination networks.

Key Words: Bromeliaceae, coevolution, hummingbirds, interactions, nestedness, phenology, pollination systems

INTRODUCTION

Bats, butterflies and bees are known pollinators of bromeliads (Araújo *et al.* 2004, Machado & Semir 2006, Varassin 2002), but hummingbirds play the leading role: 61% of the bromeliad species in the Bolivian Andes (Kessler & Krömer 2000) and *c.* 85% of the species in the Atlantic forest are pollinated primarily or exclusively by hummingbirds (Araújo *et al.* 2004, Varassin 2002). On the other hand, in some areas of the Atlantic rain forest, bromeliad species represent more than 30% of the flowers used as a food resource by hummingbirds (Buzato *et al.* 2000). In montane forests, bromeliads are an important source of food, being represented by a large number of individuals (Dziedzioch *et al.* 2003).

Despite the importance of one group for the other, only in the last decade have more detailed studies about the relationship between bromeliads and hummingbirds been conducted (Araújo *et al.* 2004, Buzato *et al.* 2000, Machado & Semir 2006, Sazima *et al.* 1996, Varassin 2002, Varassin & Sazima 2000). Nevertheless, little is known about the response of hummingbird communities to the flowering phenology of bromeliads, or the nature of the plant–pollinator interactions that involve both bromeliads and hummingbirds.

Bromeliads have aggregated flowering in some locations (Kaehler *et al.* 2005), while flowering is distributed throughout the year in other places (Araújo *et al.* 2004). As birds respond to variation in resource availability (Poulin *et al.* 1992), it is possible that the timing of bromeliad flowering may influence the abundance or the presence of migrant and resident species of hummingbird. Hummingbird abundance was related to the presence of ornithophilous bromeliads along an altitudinal gradient in the Bolivian rain forest (Krömer *et al.* 2006).

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The idea of pair-wise coevolution – the extreme of specialization – is well known, especially in plant-pollinator interactions. Not surprisingly, coevolution between hummingbirds and some of their flowers, such as heliconias, has been suggested (Snow & Teixeira 1982, Stiles 1978). Bromeliads (Benzing 1980, Reitz 1983) and hummingbirds (Grantsau 1988, Sick 1997) overlap greatly in their overall distributions and centres of speciation (in the northern Andes) and a parallel evolution of both groups has been proposed (Sick 1997). On the other hand, hummingbirds have a life span longer than the blooming period of any bromeliad, so an extreme coevolution is physiologically unfeasible (Waser *et al.* 1996). According to Feisinger (1983), the interactions presently observed between plants and hummingbirds are derived at best from a diffuse coevolution, i.e. a group of pollinator species applying a reciprocal selection to a group of plant species.

Specialization should not be viewed as the rule in plant-pollinator relationships. As an alternative, generalist pollination systems and asymmetric specialization (i.e. specialized species interacting primarily with generalists) have been presented as common situations in nature (Vázquez & Aizen 2003, 2004; Waser *et al.* 1996). A lack of reciprocal specialized relationships and an eventual trend to generalization do not necessarily imply 'disorganisation' or randomness in plant-pollinator interactions. It may reflect a 'nested' organisation in a plant-pollinator matrix, which can be quantified (Bascompte *et al.* 2003). This nested matrix is the result of a core of generalist pollinators interacting with plants that are also generalists, along with cases of asymmetric specialization in both plants and pollinators (Bascompte *et al.* 2003, Jordano *et al.* 2006).

In this context, the relationship between bromeliad phenology and the hummingbird community in the Atlantic rain forest of southern Brazil was examined. We tested the following hypotheses: (1) both groups are strongly linked and the number of bromeliad species flowering per month does relate to species richness or abundance of hummingbirds; (2) Conversely, both groups are very weakly influenced by each other and the visiting rate by hummingbirds is a result of random choice, i.e. the most abundant hummingbirds in each month are those who visit bromeliads the most; (3) The guilds of pollinators are similar between bromeliad species, without any trend to specialization; (4) The hummingbird species forage on the same bromeliad species, without any trend to specialization; (5) The hummingbird–bromeliad relationship is not structured and results in a random mutualistic network.

STUDY SITE

The Reserva Natural Salto Morato (RNSM) is located in Guaraqueçaba, on the northern coast of the

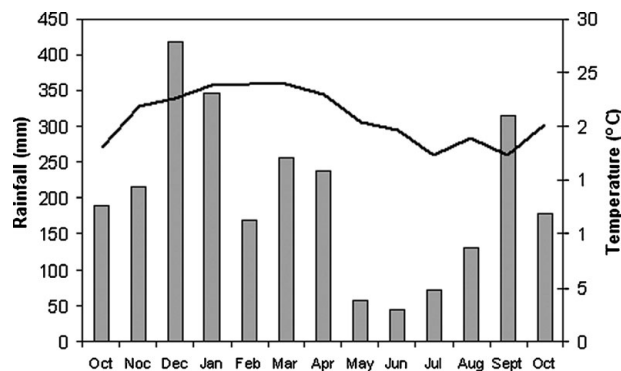


Figure 1. Rainfall (bars) and monthly mean temperature (line) in Guaraqueçaba, Paraná state. Historical means from 1978–2005 (IAPAR).

state of Paraná (25°09'–25°11'S, 48°16'–48°20'W). Recognized as a Natural Heritage Site by UNESCO in 1999, the reserve has an area of 2340 ha and ranges from 15 m to 918 m asl. Following the Koeppen classification (McKnight & Hess 2005), the climate of the region is Af – tropical wet, no dry season – with a mean annual temperature of 21 °C and monthly means ranging between 25 °C and 17 °C. From October to March high temperatures and rainfall prevail at RNSM, while from April to September the climate is colder and drier (Figure 1). RNSM is covered by Atlantic rain forest of different successional stages.

For data collection, we selected 6.35 km of trails from an already established network in RNSM. The majority of these trails lies in mature secondary forest (> 60 y old) and early secondary forest (up to 35 y old), but also pass through some more open areas of abandoned pasture in the beginning stages of regeneration (12 y old). Elevations in our study site were below 160 m asl.

There are 28 species of epiphytic bromeliad in the RNSM, the majority of which fall into one of two genera, *Vriesea* (12 species) or *Aechmea* (6 species; Gatti 2000), and there are 17 hummingbird species (Straube & Urben-Filho 2005).

METHODS

Data collection

We investigated bromeliad and hummingbird interactions during monthly field trips to the study site between November 2004 and October 2005. We quantified flowering bromeliad species by walking each trail and recording all bromeliads within view that had active inflorescences. We identified most bromeliads in the field, using published guides (Reitz 1983), but collected samples and/or consulted experts when necessary.

We performed two censuses per monthly field trip to estimate hummingbird abundance. Each census lasted about 4 h; during this time we observed hummingbird activity along our 6.35-km trail system, identifying species visually or acoustically (adapted from Bibby *et al.* 2000). We always carried out one census in the morning, starting about 30 min after sunrise, and the other in the afternoon, starting 4–5 h before sunset. Each month, we estimated the species richness of the hummingbird community based on the censuses, observations at flowering bromeliads, and opportunistic records. Taxonomy follows the Brazilian Ornithological Records Committee (<http://www.cbro.org.br>).

The frequency of visits of the hummingbirds to the bromeliads (number of visits per unit time) was obtained by direct observation of bromeliads in flower, using the method of focal observation (Dafni 1992). Flowering individuals of each bromeliad species were observed in the morning, starting about 30 min after sunrise, as well as in the afternoon, ending close to sunset. Individuals of each bromeliad species were observed altogether for at least 8 h per month, with a few exceptions due to adverse climatic conditions or the absence of flowers in the days following the first observation.

We opportunistically noted data on visits to bromeliads by other pollinators (e.g. bees), as well as hummingbird visits to other plants.

Statistical analyses

To test if monthly hummingbird abundance or species richness was influenced by bromeliad flowering phenology, we used Pearson correlations to compare the number of flowering bromeliad species per month to both the number of hummingbird species and overall hummingbird abundance, as well as to the monthly abundance of the hummingbird species that were recorded in every field trip.

We used a G-test of independence to examine whether visit frequencies of each hummingbird species to each bromeliad species reflected the relative abundance of those species in the study site, but only when the bromeliad species were visited by at least two hummingbird species in the same month.

We used the Jaccard index (Magurran 1988) to calculate the similarity of the bromeliad species according to their guild of hummingbird visitors and then we generated a dendrogram of similarity using the unweighted pair-group method with arithmetic averages (UPGMA) as the grouping method and the Fitopac software package (Shepherd 1987). The same procedure was used to calculate the similarity of the hummingbird species according to the bromeliads used by each species.

The nestedness (N) of the bromeliad–hummingbird network, as well as its connectivity, was calculated using the software ANINHADO (Guimarães & Guimarães 2006). We compared the bromeliad–hummingbird network with the null model ‘CE’ offered by the software: in this model, the probability of a cell a_{ij} showing a presence is $(P_i/C + P_j/R)/2$, in which P_i is the number of presences in the row i , P_j is the number of presences in the column j , C is the number of columns and R is the number of rows. That means that the probability of drawing an interaction is proportional to the observed number of interactions of both the animal and the plant species (Bascompte *et al.* 2003, Guimarães *et al.* 2007). This is a more conservative inference about the significance of nestedness than using a null model in which each cell in the matrix has the same probability of being occupied (Bascompte *et al.* 2003). Since the bromeliad–hummingbird network belongs to a wider network that encompasses the whole community of plants and their pollinators, we also calculated, for comparisons, the nestedness of a more comprehensive matrix that included all the other plants besides the bromeliads that were recorded to receive visits of hummingbirds.

For all analyses, we considered results significant if $P \leq 0.05$.

RESULTS

Hummingbird community composition and bromeliad phenology

We found 13 bromeliad species flowering at our study site during the study period and quantified hummingbird visitation for 12 of them (Table 1). There are at least seven other bromeliad species that occur in the study area (pers. obs.). *Vriesea erythrodactylum* was not included due to observer difficulty in viewing flowers.

Bromeliads in the RNSM flower throughout the year. In each month there were at least two bromeliad species in flower, except for October 2005, when only one species bloomed (Table 1). The months with the greatest number of blooming species were January (five species) and December, February and April (four species).

We found nine hummingbird species in our study site during the study period (Table 2), although a tenth species (*Calliphlox amethystina*) was observed during a field trip in September 2004. *Ramphodon naevius* and *Thalurania glaucopsis* were recorded at least once during each month of our study and were considered resident species. *Phaethornis squalidus* was also considered a resident, even though it was not recorded in four of the months. *Amazilia versicolor*, *Anthracothorax nigricollis*, *Florisuga fusca*, *Aphantochroa cirrochloris* and *Lophornis chalybeus* were considered summer migrants, i.e. they

Table 1. Monthly flowering of bromeliad species at Reserva Natural Salto Morato between November 2004 and October 2005. Species are listed according to their flowering sequence.

	N	D	J	F	M	A	M	J	J	A	S	O
<i>Aechmea nudicaulis</i> (L.) Grisebach	x											
<i>Nidularium innocentii</i> Lemaire	x	x	x									
<i>Vriesea erythrodactylon</i> Morren ex Mez	x	x	x	x								
<i>Aechmea pectinata</i> Baker		x	x	x								
<i>Nidularium procerum</i> Lindman		x					x					
<i>Vriesea ensiformis</i> (Vellozo) Beer			x	x	x	x						
<i>Vriesea incurvata</i> Gaudichaud			x	x	x	x						
<i>Vriesea rodigasiana</i> Morren					x	x	x					
<i>Aechmea ornata</i> Baker							x	x				
<i>Vriesea carinata</i> Wawra								x	x			x
<i>Aechmea organensis</i> Wawra									x	x		
<i>Vriesea</i> cf. <i>friburgensis</i> Mez										x	x	
<i>Ananas bracteatus</i> (Lindley) Schultes f.												x
Number of species	3	4	5	4	3	4	3	2	2	2	2	1

were present at RNSM only during the (austral) summer. Despite being recorded once in the surroundings of the reserve in May, *Amazilia fimbriata* was recorded inside RNSM only in September and October.

We also observed the bromeliad *Aechmea nudicaulis* being visited by three species of bee and a bird, the bananaquit *Coereba flaveola* (Linnaeus), and *Vriesea rodigasiana*, *Aechmea ornata* and *Ananas bracteatus* being visited by bees, the latter bromeliad also visited by two species of Lepidoptera. Hummingbirds were seen visiting plants of various other families, including: *Ramphodon naevius* and *Florisuga fusca* visiting *Costus spiralis* Rosc.; *R. naevius* and *Thalurania glaucopsis* visiting *Psychotria nuda* Wawra, *Erythrina speciosa* Andrews and *Heliconia velloziana* Emygdio; *R. naevius*, *T. glaucopsis*, *Anthracothorax nigricollis* and *Aphantochroa cirrochloris* visiting *Musa rosacea* Jacq.; *T. glaucopsis* and *F. fusca* visiting *Hedychium coronarium* Koenig; and *T. glaucopsis* visiting *Rubus* sp. and an unidentified Marantaceae (aff. *Calathea*). Note that *Musa rosacea* and *Hedychium coronarium* are not native species.

Bromeliad–hummingbird interactions

Aechmea nudicaulis was visited most frequently and by the largest number of species (Table 3). *Vriesea rodigasiana* was visited by the second largest number of species and *Ananas bracteatus* had the second highest frequency of hummingbird visits. Four bromeliad species were visited by two or more hummingbird species in the same month. When we determined the relative abundance of hummingbird species using the frequency of their visits to bromeliads, it was not equal to relative abundances derived from census data (*Aechmea nudicaulis*: $G = 56.2$, $df = 4$, $P < 0.05$; *Aechmea pectinata*: $G = 17.4$, $df = 3$, $P < 0.05$; *Vriesea rodigasiana*: $G = 18.2$, $df = 2$, $P < 0.05$; *Aechmea ornata*: $G = 24.9$, $df = 1$, $P < 0.05$).

The frequency of visits by hummingbird species varied from month to month. With the same observation effort on *Vriesea ensiformis*, *Ramphodon naevius* made 16 visits in January, one in February and six in March. Similarly, in May *Ramphodon naevius* visited *Aechmea ornata* eight times, whereas in the following month it visited only

Table 2. Monthly occurrence of hummingbird species at Reserva Natural Salto Morato (RNSM) between November 2004 and October 2005. Numbers refer to the abundance observed during the censuses. An 'x' means that the species was observed in RNSM that month, but was not recorded during the censuses.

	N	D	J	F	M	A	M	J	J	A	S	O
<i>Ramphodon naevius</i> (Dumont)	12	4	19	18	15	15	15	17	15	29	28	9
<i>Thalurania glaucopsis</i> (Gmelin)	3	6	7	2	7	x	5	6	9	6	6	3
<i>Phaethornis squalidus</i> (Temminck)	1	2	2	1		x	x	x		x		
<i>Florisuga fusca</i> (Vieillot)	10	5	2	5	3							
<i>Anthracothorax nigricollis</i> (Vieillot)	2	1	2	x	1							x
<i>Amazilia versicolor</i> (Vieillot)	3	12	5	1	2							x
<i>Lophornis chalybeus</i> (Vieillot)	x		1								1	
<i>Aphantochroa cirrochloris</i> (Vieillot)		1		x								x
<i>Amazilia fimbriata</i> (Gmelin)											1	x
Number of species	7	7	7	7	5	3	3	3	2	3	4	6

Table 3. Total observation effort, rate of hummingbird visits and number of visiting species to each bromeliad species at Reserva Natural Salto Morato between November 2004 and October 2005. Rn = *Ramphodon naevius*, Tg = *Thalurania glaucopsis*, Ps = *Phaethornis squalidus*, Ff = *Florisuga fusca*, Av = *Amazilia versicolor*, Af = *Amazilia fimbriata*, Lc = *Lophornis chalybeus* and Ca = *Callyphlox amethystina* (Boddaert).

	Observ. effort (h)	Hummingbird visits (records h ⁻¹)								Number of species
		Rn	Tg	Ps	Ff	Av	Af	Lc	Ca	
<i>Aechmea nudicaulis</i>	9	0.11	3.22		0.11	1.22		0.55		5
<i>Nidularium innocentii</i>	13.8	0.51								1
<i>Nidularium procerum</i>	10	0.7								1
<i>Aechmea pectinata</i>	14	0.86	0.57							2
<i>Vriesea ensiformis</i>	26	0.84								1
<i>Vriesea incurvata</i>	33	0.33								1
<i>Vriesea rodigasiana</i>	16	0.31	0.5	0.12					*	4
<i>Aechmea ornata</i>	16	0.62	1.5							2
<i>Vriesea carinata</i>	18	0.17								1
<i>Aechmea organensis</i>	12	0.83	0.08							2
<i>Vriesea cf. friburgensis</i>	12		0.25				0.08			2
<i>Ananas bracteatus</i>	8	0.12	2.75							2

*A single opportunistic record from September 2004.

twice, and *Thalurania glaucopsis*, absent in May, visited the same bromeliad 24 times.

The number of flowering bromeliad species in each month was not related to either monthly species richness (Pearson, $r = 0.47$; $P = 0.12$; $n = 12$) or abundance of hummingbirds ($r = 0.42$; $P = 0.17$; $n = 12$). Nor did we find a relationship between the number of flowering bromeliad species and the abundance of the two hummingbird species that were recorded every month in our study site (*Ramphodon naevius*: $r = -0.18$; $P = 0.59$; $n = 12$; *Thalurania glaucopsis*: $r = -0.19$; $P = 0.56$; $n = 12$).

The dendrogram of similarity grouped the bromeliads according to the visitors/pollinators of each species, ranging from the most specialized species (those visited only by *Ramphodon naevius*) to the more generalist, such as *Aechmea nudicaulis*, which was visited by five hummingbird species (Figure 2).

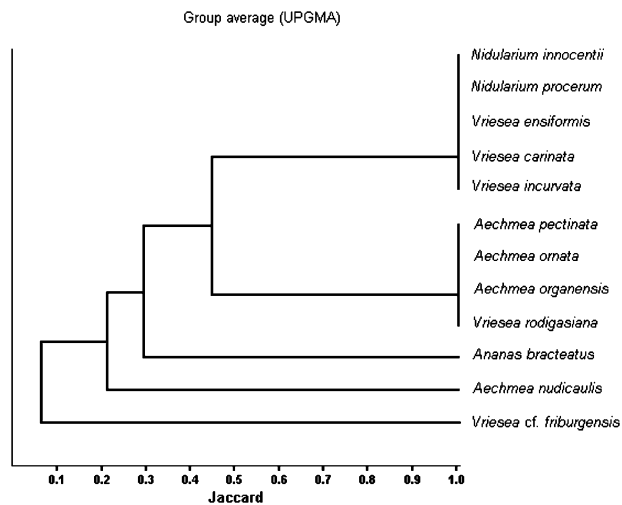


Figure 2. Dendrogram of similarity of bromeliad species at Reserva Natural Salto Morato in relation to their hummingbird visitors (cophenetic correlation = 0.96).

The analysis of similarity on the use of bromeliads by the hummingbirds grouped *Ramphodon naevius* and *Thalurania glaucopsis* as the two most differentiated in the community. Not surprisingly, these were also the most generalist hummingbirds. The remaining hummingbirds visited only one bromeliad species and thus were grouped according to the species visited (Figure 3).

The matrix of interactions between bromeliad and hummingbird species had a nestedness value of $N = 0.922$ ($P = 0.01$; Figure 4a), with 25% connectivity. Amplifying the matrix to include the other plants observed to be food resources for the hummingbirds, the nestedness value remained similar, $N = 0.918$ ($P = 0.01$; Figure 4b), but with a slightly lower connectivity: 19%, as expected from the well-known negative relationship between connectivity and number of species.

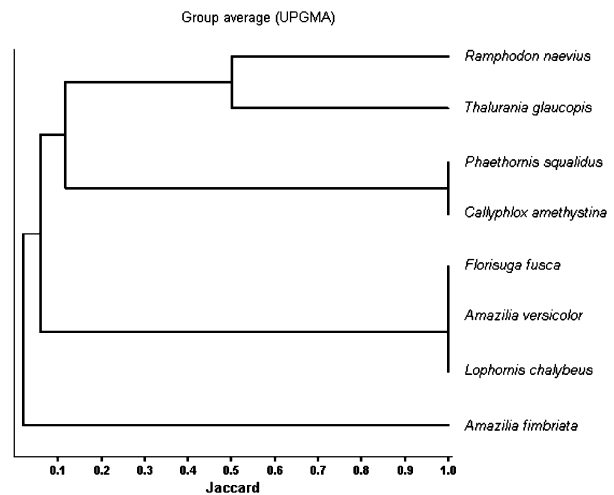


Figure 3. Dendrogram of similarity of hummingbird species at Reserva Natural Salto Morato according to the bromeliads used by each species (cophenetic correlation = 0.99).

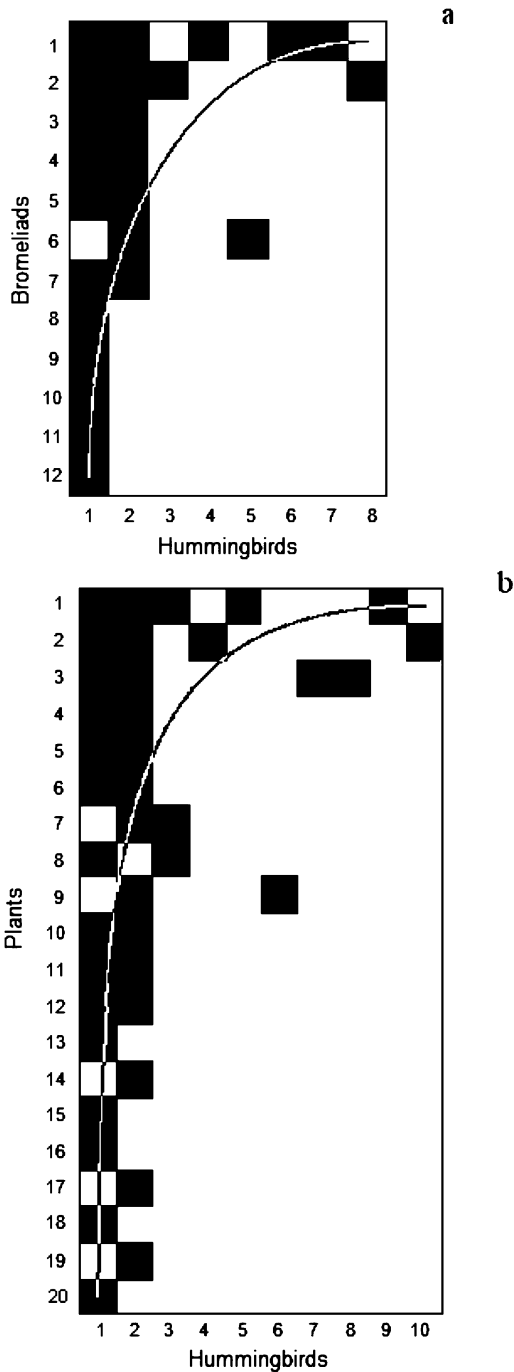


Figure 4. Mutualistic networks at Reserva Natural Salto Morato. The network between hummingbirds and bromeliads only (a); between hummingbirds and all plants observed receiving hummingbird visits (b). Each black square represents an interaction between the plant species in that row and the hummingbird species in that column. The solid line is the isocline of perfect nestedness and all interactions should be above the line in a perfect nested matrix. The numbers refer to the species according to the total number of interactions. (Figures plotted with Nestedness Temperature Calculator, AICS Research, University Park, NM, and The Field Museum, Chicago).

DISCUSSION

Community composition

The total number of bromeliad species we observed in flower represents *c.* 50% of the bromeliad richness in the RNSM (Gatti 2000). The occurrence of no flowering individuals in other bromeliad species that occur in the study area is probably due to a 2-y interval between their blooming seasons (e.g. *Vriesea philippocoburgii* Wawra; Araújo *et al.* 2004).

The 10 hummingbird species recorded equal about 60% of the total hummingbird richness at RNSM (Straube & Urben-Filho 2005). Most of the hummingbirds not recorded are typical of higher altitude areas of the reserve (> 400 m), not sampled in our study.

The extended flowering phenology observed agrees with those of other Atlantic forest sites (Buzato *et al.* 2000, Machado & Semir 2006, Varassin 2002), *Araucaria* forest (Buzato *et al.* 2000), and lowland sites in the state of Sao Paulo (Araújo *et al.* 2004), but differ from the pattern found in montane forest in the states of Rio de Janeiro and Paraná (Kaehler *et al.* 2005, Martinelli 1997), where it was aggregated. Although there are bromeliads flowering every month at RNSM, we found more bromeliad species blooming during the rainy season (October–March), as reported to other bromeliad communities (Araújo *et al.* 2004, Machado & Semir 2006) and considered common in ornithophilous plants (Arizmendi & Ornelas 1990, Sazima *et al.* 1995).

Relationships between bromeliads and hummingbirds

The peak in flowering during the rainy season could have an influence on the hummingbird species richness and abundance, which includes both migrant and resident species. Resident species, such as *Ramphodon naevius* and *Thalurania glaucopis*, may benefit from the continuous availability of food resources provided by the year-round flowering of bromeliads (Sazima *et al.* 1996), while the increase in flower availability during the rainy season may accommodate the addition of migrants to the hummingbird community. However, we found no relationship between the number of hummingbird species and the number of blooming bromeliad species recorded each month, suggesting that bromeliad phenology does not influence hummingbird richness. Also, the main bromeliad visitors, *Ramphodon naevius* and *Thalurania glaucopis*, showed no relationship between their monthly abundances and the number of bromeliad species in flower each month, suggesting that there is no direct dependence on bromeliads. This analysis must be viewed with caution, since comparing bromeliad richness does not consider abundance of plants and volume and sugar concentration

of the nectar produced by each species, i.e. differences on the resource supply provided by each bromeliad species. On the other hand, among the summer migrant hummingbirds (*Anthracothorax nigricollis*, *Aphantochroa cirrochloris*, *Florisuga fusca*, *Amazilia versicolor* and *Lophornis chalybeus*), two species were not recorded on bromeliads and *Florisuga fusca* was observed feeding on bromeliad nectar only once, so the presence of these species in the RNSM is little influenced by bromeliad phenology.

The species composition of hummingbird pollinators in RNSM is quite different to other areas in Atlantic forest (Canela & Sazima 2003, Sazima *et al.* 1995, Snow & Snow 1986). This may reflect regional differences or differences in methods (cf. Canela & Sazima 2003). On the other hand, all studies in Atlantic rain forest indicate a Phaethornithinae species as the main bromeliad pollinator, usually *Ramphodon naevius*, as at RSMN, or *Phaethornis eurynome* (Buzato *et al.* 2000, Kaehler *et al.* 2005, Machado & Semir 2006, Sazima *et al.* 1995, Snow & Snow 1986, Snow & Teixeira 1982, Varassin & Sazima 2000), and some studies indicate a Trochilinae species may also share this role (Buzato *et al.* 2000, Sazima *et al.* 1996), as *T. glaucopsis* at RSMN. The usual dominance of *Ramphodon* and *Phaethornis* – long-billed hummingbirds (Grantsau 1988) – is linked to the presence of bromeliads with long, tubular corollas that limit access to their nectar, such as those in genus *Nidularium* and many *Vriesea* species.

The *Nidularium* species, together with *Vriesea carinata*, *V. ensiformis* and *V. incurvata*, form a group of specialized bromeliads, i.e. those with a single pollinator. The remaining species have two or more pollinators. Among this group *Aechmea nudicaulis* had the greatest number of pollinators, as has been reported for other areas of Atlantic forest (Buzato *et al.* 2000, Sazima *et al.* 1996, but see Machado & Semir 2006, Varassin & Sazima 2000). Visitation by bees, bananaquits and butterflies seems to be associated with more generalistic bromeliads. These pollinators were recorded visiting only the bromeliad species with the highest diversity of hummingbird visitors, namely *Aechmea nudicaulis*, *Ananas bracteatus*, *Aechmea ornata* and *Vriesea rodigasiana*. Although bees were not observed visiting *Aechmea pectinata* in the RNSM, they are known pollinators of this bromeliad (Canela & Sazima 2003). This difference in specialization was expected since in a site in south-eastern Brazil, the genera *Nidularium* and *Vriesea* have been shown to specialize in hummingbird pollinators, while *Aechmea* was shown to be much more of a generalist (Varassin & Sazima 2000).

These data, as well as the variation in visitation rates of a given hummingbird to a given bromeliad species between months, imply a very general relationship between bromeliads and hummingbirds in the RNSM (Waser *et al.* 1996). But, the fact that the most frequent hummingbird visitors to bromeliads are not the most abundant hummingbirds in the study site

indicates that the assemblage of hummingbird visitors to each bromeliad species are not defined by chance. Therefore, there seems to be some level of organization in the relationship between the bromeliads and the hummingbirds.

In the RNSM, *Ramphodon naevius* and *Thalurania glaucopsis* may be considered the core species of the hummingbird–bromeliad relationship. As such, these two hummingbirds may be driving the evolution of the community (Bascompte *et al.* 2003). Since the interaction network between bromeliads and hummingbirds (Araújo *et al.* 2004, Buzato *et al.* 2000, Kaehler *et al.* 2005, Machado & Semir 2006, Varassin & Sazima 2000) varies geographically, including some changes in the core species composition, the result of these selective pressures must be viewed in terms of the geographic mosaic of coevolution proposed by Thompson (2005). This theory proposes that reciprocal selection favours the emergence of a core set of mutualistic traits allowing a high geographic interchangeability in mutualistic participants.

Recently, Vázquez & Aizen (2004) proposed that, in a plant–pollinator network of a given community, asymmetric specialization predominates, i.e. the specialist species interact with the generalist species. This prediction was in some ways corroborated by our study, since specialist hummingbirds such as *Amazilia versicolor*, *Florisuga fusca*, *Lophornis chalybeus* and *Phaethornis squalidus* (considering only bromeliads as resources) depended on abundant generalist partners, such as *Aechmea nudicaulis* and *Vriesea rodigasiana*. From the bromeliad perspective, the specialist species (*Vriesea carinata*, *V. ensiformis*, *V. incurvata* and *Nidularium* spp.) interacted with the most generalist hummingbird, *Ramphodon naevius*. Given that the generalist species of both groups also interacted among themselves, the structure of the bromeliad–hummingbird matrix was nested (Bascompte *et al.* 2003, Jordano *et al.* 2006). Comparing the ‘subnetwork’ of bromeliad–hummingbird interactions with the expanded matrix that includes all observed plant–hummingbird interactions, there is almost no difference in the degree of nestedness. Connectivity was greater in the subnetwork than in the overall matrix, a characteristic also noted by Jordano *et al.* (2006). The nestedness value observed in our study is within the range of values reported for other plant–pollinator networks (Bascompte *et al.* 2003), thus reinforcing the idea that the evolutionary relationship between bromeliads and hummingbirds is no stronger than that of other pollination networks.

ACKNOWLEDGEMENTS

We are grateful to Andréa C. Araújo, Márcia Marques, James J. Roper and Gustavo S. Betini for their comments

and suggestions on earlier drafts. Two anonymous reviewers made useful comments on the manuscript. Fundação o Boticário de Proteção à Natureza provided financial and logistical support that allowed us to carry our study at RNSM. We also thank the staff of RNSM and A. P. Cordeiro, D. Peterson, M. Niedfeld, M. Sberze, L. L. Wedekin and A. P. Winter for their assistance and company in the field; and M. Kaehler (Mülleriana) and G. Martinelli (Jardim Botânico do Rio de Janeiro) for their help with the identification of a few bromeliads. VQP received a grant from CAPES during the second year of his master course.

LITERATURE CITED

- ARAÚJO, A. C., FISCHER, E. & SAZIMA, M. 2004. As bromélias na região do Rio Verde. Pp. 162–171 in Marques, O. A. V. & Duleba, W. (eds.). *Estação Ecológica Juréia-Itatins. Ambiente físico, flora e fauna*. Holos Editora, Ribeirão Preto.
- ARIZMENDI, M. C. & ORNELAS, J. F. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. *Biotropica* 22:172–180.
- BASCOMPTE, J., JORDANO, P., MÉLIAN, C. J. & OLESEN, J. M. 2003. The nested assembly of plant-animal mutualistic network. *Proceedings of the National Academy of Science, USA* 100:9383–9387.
- BENZING, D. H. 1980. *The biology of bromeliads*. Mad River Press, Eureka. 305 pp.
- BIBBY, C., JONES, M. & MARSDEN, S. 2000. *Bird surveys (Expedition Field Techniques Series)*. BirdLife International, Cambridge. 134 pp.
- BUZATO, S., SAZIMA, M. & SAZIMA, I. 2000. Hummingbird-pollinated floras at three Atlantic Forest sites. *Biotropica* 32:824–841.
- CANELA, M. B. F. & SAZIMA, M. 2003. *Aechmea pectinata*: a hummingbird-dependent bromeliad with inconspicuous flowers from the rainforest in south-eastern Brazil. *Annals of Botany* 92:731–737.
- DAFNI, A. 1992. *Pollination ecology. A practical approach*. Oxford University Press, Oxford. 250 pp.
- DZIEDZIOCH, C., STEVENS, A.-D. & GOTTSBERGER, G. 2003. The hummingbird plant community of a tropical montane rain forest in southern Ecuador. *Plant Biology* 5:331–337.
- FEISINGER, P. 1983. Coevolution and pollination. Pp. 282–310 in Futuyma, D. & Slatkin, M. (eds.). *Coevolution*. Sinauer Associates Publishers, Sunderland.
- GATTI, A. L. S. 2000. *O componente epifítico vascular na Reserva Natural Salto Morato, Guaraqueçaba – PR*. Dissertação de mestrado, UFPR, Curitiba, 93 pp.
- GRANTSAU, R. 1988. *Os beija-flores do Brasil*. Expressão e Cultura, Rio de Janeiro. 233 pp.
- GUIMARÃES, P. R. & GUIMARÃES, P. 2006. Improving the analyses of nestedness for large sets of matrices. *Environmental Modelling and Software* 21:1512–1513.
- GUIMARÃES, P. R., SAZIMA, C., DOS REIS, S. F. & SAZIMA, I. 2007. The nested structure of marine cleaning symbiosis: is it like flowers and bees? *Biology Letters* 3:51–54.
- JORDANO, P., BASCOMPTE, J. & OLESEN, J. M. 2006. The ecological consequences of complex topology and nested structure in pollination webs. Pp. 173–199 in Waser, N. M. & Ollerton, J. (eds.). *Plant-pollinator interactions: from specialization to generalization*. University of Chicago Press, Chicago.
- KAEHLER, M., VARASSIN, I. G. & GOLDENBERG, R. 2005. Polinização em uma comunidade de bromélias em Floresta Atlântica Alto Montana no Estado do Paraná, Brasil. *Revista Brasileira de Botânica* 28:219–228.
- KESSLER, M. & KRÖMER, T. 2000. Patterns and ecological correlates of pollination modes among Bromeliad communities of Andean forests in Bolivia. *Plant Biology* 2:659–669.
- KRÖMER, T., KESSLER, M. & HERZOG, S. K. 2006. Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. *Biotropica* 38:183–195.
- MACHADO, C. G. & SEMIR, J. 2006. Fenologia da floração e biologia floral de bromélias ornitófilas de uma área de Mata Atlântica do Sudeste brasileiro. *Revista Brasileira de Botânica* 29:163–174.
- MAGURRAN, A. 1988. *Ecological diversity and its measurement*. Croom Helm, London. 179 pp.
- MARTINELLI, G. 1997. Biologia reprodutiva de Bromeliaceae na Reserva Ecológica de Macaé de Cima. Pp. 213–250 in Lima, H. C. & Guedes-Bruni, R. R. (eds.). *Serra de Macaé de Cima: diversidade florística e conservação em Mata Atlântica*. Jardim Botânico do Rio de Janeiro, Rio de Janeiro.
- MCKNIGHT, T. L. & HESS, D. 2005. *Physical geography: a landscape appreciation*. Prentice Hall, Upper Saddle River. 640 pp.
- POULIN, B., LEFEBVRE, G. & MCNEIL, R. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73:2295–2309.
- REITZ, R. 1983. *Bromeliáceas e a malária-bromélia endêmica*. Flora Ilustrada Catarinense, Itajaí. 559 pp.
- SAZIMA, I., BUZATO, S. & SAZIMA, M. 1995. The saw-billed hermit *Ramphodon naevius* and its flowers in southeastern Brazil. *Journal für Ornithologie* 136:195–206.
- SAZIMA, I., BUZATO, S. & SAZIMA, M. 1996. An assemblage of hummingbird-pollinated flowers in a montane forest of southeastern Brazil. *Botanica Acta* 109:149–160.
- SHEPHERD, G. J. 1987. *Manual do Fitopac*. Departamento de Botânica, IB/Unicamp, Campinas. 93 pp.
- SICK, H. 1997. *Ornitologia Brasileira*. Ed. Nova Fronteira, Rio de Janeiro. 862 pp.
- SNOW, D. W. & SNOW, B. K. 1986. Feeding ecology of hummingbirds in the Serra do Mar, southeastern Brazil. *Hornero* 12:286–296.
- SNOW, D. W. & TEIXEIRA, D. L. 1982. Hummingbirds and their flowers in the coastal mountains of southeastern Brazil. *Journal für Ornithologie* 123:446–450.
- STILES, F. G. 1978. Ecological and evolutionary implications of bird pollination. *American Zoologist* 18:715–727.
- STRAUBE, F. C. & URBEN-FILHO, A. 2005. Avifauna da Reserva Natural Salto Morato (Guaraqueçaba, Paraná). *Atualidades Ornitológicas* 124:12. [on-line supplement with full content list of species available at www.ao.com.br/download/morato]
- THOMPSON, J. N. 2005. *The geographic mosaic of coevolution*. University of Chicago Press, Chicago. 400 pp.

- VARASSIN, I. G. 2002. *Estrutura espacial e temporal de uma comunidade de Bromeliaceae e seus polinizadores em Floresta Atlântica no sudeste do Brasil*. Ph.D. thesis, Universidade Estadual de Campinas.
- VARASSIN, I. G. & SAZIMA, M. 2000. Recursos de Bromeliaceae utilizados por beija-flores e borboletas em Mata Atlântica no sudeste do Brasil. *Boletim do Museu de Biologia Mello Leitão (N. Sér.)* 11/12:57–70.
- VÁZQUEZ, D. P. & AIZEN, M. A. 2003. Null model analyses of specialization in plant-pollinator interactions. *Ecology* 84:2493–2501.
- VÁZQUEZ, D. P. & AIZEN, M. A. 2004. Asymmetric specialization: a pervasive feature of plant-pollinator interactions. *Ecology* 85:1251–1257.
- WASER, N. M., CHITTKA, L., PRICE, M. V., WILLIAMS, N. & OLLERTON, J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060.