

## Distribution and Flowering Ecology of Bromeliads along Two Climatically Contrasting Elevational Transects in the Bolivian Andes<sup>1</sup>

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### ABSTRACT

We compared the diversity, taxonomic composition, and pollination syndromes of bromeliad assemblages and the diversity and abundance of hummingbirds along two climatically contrasting elevational gradients in Bolivia. Elevational patterns of bromeliad species richness differed noticeably between transects. Along the continuously wet Carrasco transect, species richness peaked at mid-elevations, whereas at Masicurí most species were found in the hot, semiarid lowlands. Bromeliad assemblages were dominated by large epiphytic tank bromeliads at Carrasco and by small epiphytic, atmospheric tillandsias at Masicurí. In contrast to the epiphytic taxa, terrestrial bromeliads showed similar distributions across both transects. At Carrasco, hummingbird-pollination was the most common pollination mode, whereas at Masicurí most species were entomophilous. The proportion of ornithophilous species increased with elevation on both transects, whereas entomophily showed the opposite pattern. At Carrasco, the percentage of ornithophilous bromeliad species was significantly correlated with hummingbird abundance but not with hummingbird species richness. Bat-pollination was linked to humid, tropical conditions in accordance with the high species richness of bats in tropical lowlands. At Carrasco, mixed hummingbird/bat-pollination was found especially at mid-elevations, *i.e.*, on the transition between preferential bat-pollination in the lowlands and preferential hummingbird-pollination in the highlands. In conclusion, both richness patterns and pollination syndromes of bromeliad assemblages varied in distinct and readily interpretable ways in relation to environmental humidity and temperature, and bromeliad pollination syndromes appear to follow the elevational gradients exhibited by their pollinators.

### RESUMEN

Comparamos la diversidad, composición taxonómica y síndromes de polinización de comunidades de bromeliáceas con la diversidad y abundancia de colibríes a lo largo de dos gradientes altitudinales climáticamente diferentes en Bolivia. Los patrones de elevación de riqueza de especies de bromeliáceas difirieron notoriamente entre los transectos. A lo largo del transecto permanentemente húmedo de Carrasco, la riqueza de las especies alcanzó su punto máximo a elevaciones intermedias, mientras que en Masicurí la mayoría de las especies se encontraron en tierras bajas, calientes y semiáridas. Las comunidades de bromeliáceas estuvieron dominadas por grandes bromeliáceas epifíticas tanque en Carrasco y por pequeñas tillandsias atmosféricas epifíticas en Masicurí. En contraste a los taxones epifíticos, la distribución de bromeliáceas terrestres fue bastante similar en ambos transectos. En Carrasco, la polinización por colibríes fue la manera de polinización más común, mientras que en Masicurí la mayoría de las especies fueron entomófilas. La proporción de especies ornitófilas aumentó con la elevación en ambos transectos, mientras que la entomófila mostró el patrón contrario. En Carrasco, el porcentaje de especies de bromeliáceas ornitófilas estuvo correlacionado significativamente con la abundancia de colibríes pero no con la riqueza de especies de colibríes. La polinización por murciélagos se relacionó con condiciones húmedas y tropicales, coincidiendo con la alta riqueza de especies de murciélagos en las tierras bajas tropicales. En Carrasco, polinización mixta de colibríes/murciélagos fue encontrada principalmente a elevaciones intermedias, es decir, en la transición entre polinización preferencial por murciélagos en tierras bajas y polinización preferencial por colibríes en las montañas. En conclusión, los patrones de riqueza y síndromes de polinización de comunidades de bromeliáceas varían de maneras distintas y fácilmente interpretables en relación a condiciones de humedad y temperatura. Los síndromes de polinización de bromeliáceas parecen seguir los patrones exhibidos por sus polinizadores preferenciales.

*Key words:* bats; Bolivia; *Bromeliaceae*; diversity; hummingbirds; pollination; tropical montane forest.

THE TROPICAL ANDES ARE AMONG THE BOTANICALLY MOST DIVERSE regions worldwide (Barthlott *et al.* 1996). Due to the difficulties of studying species-rich tropical plant communities, however, our knowledge of the magnitude and distribution of this diversity is still fragmentary (Gentry 1995). The most conspicuous changes of community composition and richness in tropical mountains perhaps are

related to differences in elevation, but few studies have covered entire elevational gradients in enough detail to describe with precision how tropical forest characteristics change with elevation (Lieberman *et al.* 1996). The majority of elevational studies have focused on species richness (*e.g.*, Gentry 1995, Lieberman *et al.* 1996, Vázquez & Givnish 1998, Krömer *et al.* 2005) and elevational zonation of vegetation types (see Frahm & Gradstein 1991). Also, most studies have been based on woody plants (*e.g.*, Gentry 1988, 1995; Kitayama 1992; Lieberman *et al.* 1996), even though the majority of plant species in humid tropical forests belong to nontree life forms (Gentry & Dodson 1987, Ibsch 1996, Balslev *et al.* 1998). As a result, it is not yet known whether a general relationship exists

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between species richness and elevation, or even whether a universal explanation or model exists (Colwell & Hurtt 1994; Rahbek 1995, 1997).

The family Bromeliaceae is almost exclusively restricted to the New World tropics. Nearly 50 percent of the estimated 3000 bromeliad species are epiphytic (Benzing 2000). These have leaf-trichomes of varied forms which function as moisture- and nutrient-absorptive appendages (Benzing 1990, 2000). Studies on the elevational distribution and ecology of bromeliads are rare: Pittendrigh (1948) examined the vertical distribution of epiphytic bromeliads in Trinidad, Gilmartin (1973) related the distribution of 17 species growing on both slopes of the Ecuadorian Andes to meteorological data, and García-Franco and Peters (1987) and Castaño-Meneses *et al.* (2003) analyzed the spatial distribution patterns of selected species of *Tillandsia* along an elevational gradient in Mexico. Bromeliads have a wide range of pollinators, including bats, birds, and insects, and also include autogamous taxa (Gardner 1986, Till 1992, Benzing 2000, Kessler & Krömer 2000). Furthermore, bromeliads are one of the most important food sources for hummingbirds in many Neotropical forest regions (Cruden 1972; Araujo *et al.* 1994; Sazima *et al.* 1995a, 1996; Dzedzioch *et al.* 2003).

In the present study, we compared the diversity, taxonomic composition, and pollination syndromes of bromeliad assemblages as well as the diversity and abundance of hummingbirds along two climatically contrasting elevational gradients in Bolivia. Our primary aim was to study qualitatively the relationship of bromeliad pollination syndromes and one pollinator group (hummingbirds) to temperature and rainfall. By using two transects differing strikingly in humidity, we hoped to be able to disentangle the relative effects of elevation as such from that of humidity, which often also varies with elevation (Kessler *et al.* 2001). We did not specifically study bats and insects as pollinators due to the difficulties of sampling them quantitatively.

## METHODS

**STUDY AREA AND THE ENVIRONMENT.**—Carrasco National Park covers an area of 6226 km<sup>2</sup> on the eastern slope in the department of Cochabamba, Bolivia (Ergueta & Gómez 1997; Fig. 1). Ranging from 300 to 4500 m, the park contains a complete set of elevational vegetation belts, many of which are in almost pristine state, especially at 1000–3000 m. The topography is extremely steep, with a horizontal distance of only 35–45 km from the highest peaks to the level lowlands of the Chapare region. The present study was conducted from 450 m near the cave “Cuevas del Repechón” to 3950 m along the old, now unused gravel road from Cochabamba to Villa Tunari (17°03′–09′S, 65°27′–37′W). Lowland forests were studied at 300–400 m in Parque Ecoturístico Machía and on the grounds of Hotel El Puente in the vicinity of the town of Villa Tunari (16°58′S, 65°26′W). These two sites, which are among the few forest areas remaining in a region largely devoted to coca cultivation (Henkel 1995), are hereafter referred to as Villa Tunari.

Mean annual precipitation at Villa Tunari, the only reliable climatic station in the region, is 5676 mm (10 yr data, Ibsch 1996).

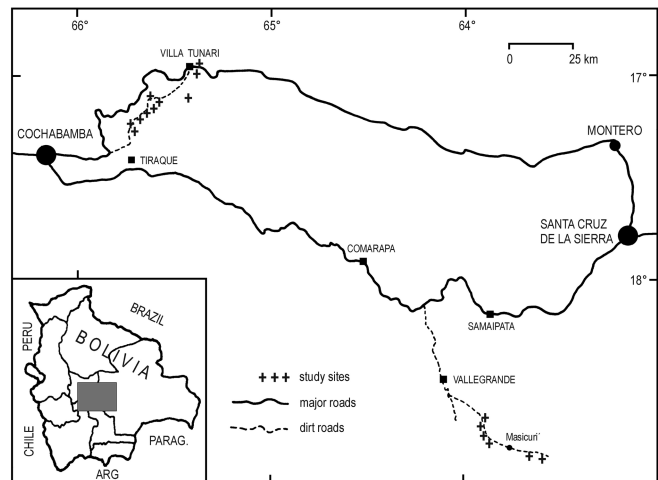


FIGURE 1. Map of Bolivia showing the location of the study sites.

Most precipitation falls between November and May, but even in the “dry” season from June to October every month receives >100 mm, thus creating a perhumid climate (*sensu* Lauer *et al.* 1996). There are no climatic stations at higher elevations, but since the steep topography concentrates the convective precipitation on a narrow belt, precipitation is undoubtedly higher than in the lowlands. Ibsch (1996) estimated >3500 mm mean annual precipitation at 2200 m elevation in the somewhat sheltered valley of Sehuencas, but it is likely that slopes directly exposed to incoming clouds at mid-elevations (1000–3000 m) in the NW of the park receive annual precipitation in excess of 8000 mm (J. Böhner, pers. comm.). Additional humidity is contributed by dew and fog condensation (Ibsch 1996). Mean annual temperature is 24.6°C at Villa Tunari and 12–15°C at 2200 m at Sehuencas (Ibsch 1996), with an annual variability of about 5°C. Nocturnal frosts occur down to 2000 m (Ibsch 1996, T. Krömer & M. Kessler, pers. obs.), especially during periodic influxes of southern polar winds during austral winter.

The natural vegetation of the entire study area consists of evergreen forest. Navarro (1997) proposed a preliminary delimitation of seven vegetation belts in Carrasco National Park defined by characteristic tree species, but in-depth studies of the forest vegetation are lacking. Tree community composition probably corresponds to that generally observed along humid east-Andean slopes (Gentry 1988, 1995; Ibsch 1996; Navarro 1997). Because of the steep topography and high rainfall, landslides are common and a considerable portion of the vegetation consists of varying stages of natural forest succession (Ibsch 1996, Kessler 1999). Above about 3500 m forests are dominated by *Pohlylepis racemosa* (Rosaceae; 3500–3800 m) and *P. pepeii* (3800–4200 m). These *Pohlylepis* forests have largely been destroyed through centuries of human-induced burning and today are restricted to relict patches, mostly in ravines or on boulder slopes (Kessler 1995, FjeldsÅ & Kessler 1996).

The second transect was located in the Masicuri valley from the confluence of the Masicuri and Grande rivers (19°02′S, 63°42′W; 500 m) to the highest accessible peaks at San Lorenzo (18°41′S, 63°55′W; 2500 m) on the west side of the valley along the road

from Vallegrande to Masicurí in western Departamento de Santa Cruz, Bolivia (Fig. 1). Mean annual precipitation at the village of Masicurí (800 m) is 1792 mm. Precipitation declines toward lower elevations, with values between 1000 and 1200 mm reported from various climatic stations along the Andean foothill base to the east of the study area. At higher elevations, precipitation and fog intensity increase noticeably (see Bianchi 1981, for data from Argentina), especially at about 1000–1200 m elevation (T. Krömer & M. Kessler, pers. obs.), but no quantitative measurements are available. Mean annual temperature is about 25°C at 500 m and declines by about 0.6°C per 100 m elevational increase (Eriksen 1986, Gerold 1987). Climate is seasonal, with about 75 percent of the precipitation falling in the austral summer (November to April), and a lower frost limit in the austral winter at 800 m (Eriksen 1986). Of particular importance is the regular influx of cold polar fronts along the Andean base in austral winter, locally known as *surazos*, which reduce temperatures considerably for several days and represent the main source of precipitation in this season (Fjeldså *et al.* 1999).

In accordance with climatic changes, three main elevational vegetation zones were discernible at Masicurí which are typical for this biogeographic region as a whole (Cabrera 1976, Ribera *et al.* 1992, Navarro 1997, Schulenberg & Awbrey 1997). Up to 850–1000 m, forests were deciduous to semideciduous and composed primarily of Leguminosae such as *Anadenanthera macrocarpa* (Benth.) Brenan, *Enterolobium contortisiliquum* (Well) Morong., and *Parapiptadenia excelsa* (Griseb.) Baker. Between 850–1000 m and about 1800 m, forests were evergreen and contained *Cedrela lilloi* C. DC (Meliaceae), *Chrysophyllum gonocarpum* (Mart. & Eichl.) Engl. (Sapotaceae), *Crinodendron tucumanum* Lillo (Elaeocarpaceae), *Ficus* spp. (Moraceae), *Miconia* spp. (Melastomataceae), as well as numerous naturalized orange trees (*Citrus aurantium* L.). Above 1800 m, the evergreen forest was dominated by *Podocarpus parlatoresi* Pilger (Podocarpaceae) and numerous Myrtaceae such as *Blepharocalyx salicifolius* (H.B.K.) O. Berg, *Myrcianthes callicoma* McVaugh, *M. pseudomato* (Legrand) McVaugh, and *Siphoneugenia occidentalis* Legrand.

Human activity varied according to climatic and topographic conditions. The alluvial plain of the Masicurí valley was completely deforested and used for intensive agriculture. Agricultural areas on slopes were located primarily at 900–1200 m and at 1700–2000 m, corresponding to the elevations with the most benign climate and least steeply inclined slopes. Forests on hillsides and slopes throughout the entire transect experienced selective timber extraction (especially *Cedrela*, *Podocarpus*, *Tabebuia* spp., depending on vegetation zone) and extensive cattle grazing. Many higher mountain areas had been burnt to establish cattle pastures.

**BOTANICAL SAMPLING.**—Fieldwork was conducted in 1996 from 23 June to 11 September along the Carrasco transect, from 12 to 19 September at Villa Tunari, and from 9 to 15 July 1995 and 20 May to 14 June 1996 in the Masicurí area. Bromeliads were studied on 283 plots of 400 m<sup>2</sup>, mostly of square shape but occasionally in other shapes to minimize habit heterogeneity. At Carrasco, we studied 183 plots (24 at 300–500 m, 24 at 500–1000

m, 24 at 1000–1500 m, 23 at 1500–2000 m, 26 at 2000–2500 m, 25 at 2500–3000 m, 20 at 3000–3500 m, and 17 at 3500–4000 m), and 100 plots at Masicurí (27 at 450–1000 m, 21 at 1000–1500 m, 26 at 1500–2000 m, 26 at 2000–2400 m). Plot size corresponds to the minimum area required for representative surveys of bromeliads in the vegetation types sampled and is small enough to keep environmental factors more or less uniform throughout the plots (Kessler & Bach 1999). Elevation was measured with a handheld Eschenbach altimeter to the nearest 50 m, correcting for weather-related inaccuracies by repeated measures and through reference to 1:250,000 topographic maps. Presence/absence of all species was registered in each plot, treating terrestrial and epiphytic plants separately. All species encountered in the survey area (but not in every single plot) were collected in triplicate and have been deposited at the Herbario Nacional de Bolivia (LPB, including all unicates), with the specialist H. Luther at Sarasota (SAR), and at the Herbarium Göttingen (GOET).

**POLLINATION MODES.**—All recorded species (except for two *Greigia* species where no information was available) were grouped into four broad categories according to their main pollination mode as ornithophilous, chiropterophilous, entomophilous, mixed or unspecific (two or all of the first three categories). Classification was based on information from published sources (Gardner 1986; Bernardello *et al.* 1991; Till 1992; Stiles & Freeman 1993; Sazima *et al.* 1995a, 1996; Benzing 2000; Dzedzioch *et al.* 2003), personal field observations of flower visitors (assuming that regular flower visitors with appropriate morphology to come into contact with anthers and styles are pollinators), and on nectar contents analysis of 79 bromeliad species by High Performance Liquid Chromatography (Krömer 2005), which allows inferences to pollinators (Baker & Baker 1983, Bernardello *et al.* 1991, Schwerdtfeger 1996). Species for which no such information was available were classified based on deductions from morphology and flower coloration (Gardner 1986, Baker & Baker 1990). A more detailed classification, especially of the entomophilous taxa, was not possible since many bromeliad species are little known with respect to their pollinators and because even species with apparently clear-cut pollination syndromes often have more than one pollinator (Sazima *et al.* 1994).

**HUMMINGBIRD DATA.**—Hummingbird communities were surveyed by S. K. Herzog in exactly the same areas as the botanical sampling with two exceptions on the Masicurí transect. At the lower end of that transect, surveys were restricted to the confluence of the Masicurí and Grande rivers (*ca* 500 m), with a survey gap extending up to an elevation of 1100 m. The accessible habitat in the intervening area was too degraded by human activities for a meaningful, comparable bird survey. At the upper end of the Masicurí transect (>2000 m), bird observations were concentrated on forest habitats, whereas bromeliads were sampled in all available habitats, including degraded shrubby areas. Fieldwork on the Carrasco transect was conducted between 22 June and 19 September 1996 (Herzog *et al.* 2005). The Masicurí transect was surveyed from 20 May to 13 June 1996, with a second visit to the confluence of the Masicurí

and Grande rivers from 10 to 14 August 1999 (Herzog & Kessler 2002).

Surveys followed the field procedures outlined in Herzog *et al.* (2002), which are only briefly summarized here. While walking slowly and quietly from dawn to midday and often again in late afternoon along roads, trails, and through the habitat where feasible, S. K. Herzog continuously recorded all visual and acoustical observations of all birds including hummingbirds (including numbers of individuals per species) within 50 m of the observer. The observer's movement rate largely depended on the level of bird activity. When spending longer periods in one spot and during occasional re-sampling of an area (the latter occurred to approximately the same degree in all elevational belts and thus did not introduce a systematic error), repeated counts of obviously territorial individuals were avoided. Tape recordings were made extensively to supplement observations and to identify unknown voices. Observation time exceeded 22 h in every belt.

**DATA ANALYSIS.**—Transects were divided into steps of 500 m, pooling all data within each step. Bromeliad richness was expressed as the total number of species recorded in each elevational belt, while the frequency of pollination modes was expressed as the percentage of species with a specific mode within a given belt. Hummingbird species richness was expressed as the total number of species recorded (*i.e.*, raw species counts) in each elevational belt, and the number of species observed divided by the number of hours of observation time in that belt. Hummingbird abundance in each belt was expressed as the number of individuals (regardless of species identity) observed divided by the number of hours of observation time in that belt. Concordance of the richness and abundance patterns of hummingbird-pollinated bromeliads and hummingbirds was calculated via correlation analyses.

## RESULTS

**SPECIES RICHNESS AND DISTRIBUTION OF BROMELIADS.**—On the Carrasco transect, a total of 49 bromeliad species in 10 genera was found (Appendix 1). Nearly 50 percent of these species belonged to the genera *Guzmania* and *Tillandsia*, which together included 23 species. Divided into life forms, there were 15 terrestrial species in 4 genera (*Fosterella*, *Greigia*, *Pitcairnia*, *Puya*) and 34 species of epiphytic tank bromeliads in 6 genera (*Aechmea*, *Billbergia*, *Guzmania*, *Racinaea*, *Tillandsia*, *Werauhia*). Highest species numbers were found in the elevational belts 1000–1500 m (23 species) and 1500–2500 m (19 species in each) (Fig. 2). Among the terrestrial genera, *Pitcairnia* had by far the widest elevational amplitude and was found in the lower and middle parts of the transect up to 2500 m. *Fosterella* was found only at mid-elevations (1100–1550 m), whereas *Greigia* and *Puya* were limited to the upper half of the transect. Epiphytic *Guzmania*, *Tillandsia*, and *Racinaea* covered a broad elevational range, extending from the lowlands to at least 3000 m. In contrast, *Aechmea*, *Billbergia*, and *Werauhia* were limited to the lower parts of the transect.

On the Masicurí transect, we collected a total of 30 species in 8 genera (Appendix 1). The genus *Tillandsia* with 12 species

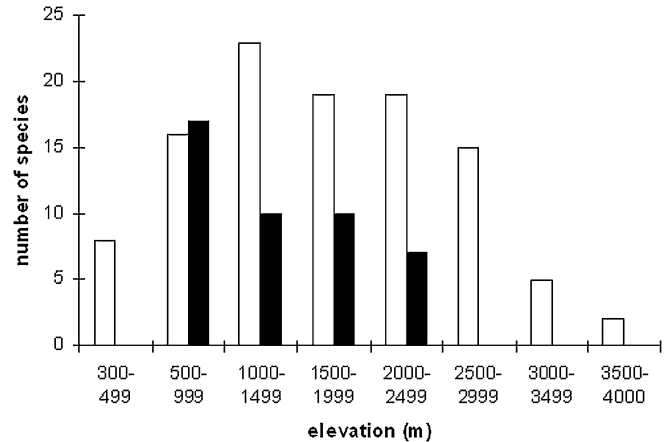


FIGURE 2. Number of bromeliad species along the elevational transect in Carrasco (white columns) and Masicurí (black columns).

was by far the most important, followed by *Fosterella* and *Puya* with 5 species each. The 16 terrestrial bromeliads belonged to 5 genera (*Bromelia*, *Dyckia*, *Fosterella*, *Pitcairnia*, *Puya*), whereas the 14 epiphytic species included 12 atmospheric tillandsias and 2 tank bromeliads (*Aechmea*, *Vriesea*). The highest number of species was found at 500–1000 m with 17 species (Fig. 2). The terrestrial genera *Fosterella* and *Pitcairnia* covered a wide elevational range of 500–1750 and 750–1950 m, respectively. *Bromelia* and *Dyckia* were limited to the lowlands, whereas *Puya* mostly occurred at high elevations but was also found down to 600 m. Among the epiphytic genera, *Tillandsia* covered the entire transect, whereas *Aechmea* and *Vriesea* were found only at mid-elevations.

**POLLINATION MODES.**—On the Carrasco transect, 51 percent of all recorded species were ornithophilous (Table 1), especially in the epiphytic genera *Tillandsia* (8 species) and *Guzmania* (5) and the terrestrial genera *Pitcairnia* (4) and *Puya* (4) (Appendix 1). Among the five chiropterophilous species, three were *Guzmania*, whereas all eight entomophilous species belonged to the genera *Fosterella* and *Racinaea*. Species with unspecialized pollination modes belonged mainly to the genera *Aechmea* and *Tillandsia*. The special case of species with mixed pollination by both bats and birds was dominated by *Guzmania*.

On the Masicurí transect, 40 percent of all species were ornithophilous (Table 1), including all species of the terrestrial genera *Dyckia* (1 species), *Pitcairnia* (4), and *Puya* (5) (Appendix 1). None of the species were chiropterophilous. The entomophilous species (47%) belonged to the genera *Fosterella* and *Tillandsia*, and the unspecialized species belonged to *Aechmea* and *Bromelia*.

Analyzing the frequency of pollination modes via the number of records within all plots revealed that on both transects ornithophilous species were less frequent than expected by their species numbers, whereas chiropterophilous species and species with mixed pollination by both bats and birds were more frequent in Carrasco (Table 1).

TABLE 1. Species numbers and frequency (number of plot-records relative to total number of plot-records; % are given relative to total species numbers and numbers of records, respectively) of different pollination modes (orn = ornithophilous, chi = chiropterophilous, ent = entomophilous, mi = mixed or unspecific, mi (chi/orn) = mixed ornithophilous/chiropterophilous) among bromeliads along the elevational transects at Carrasco and Masicurí.

	Carrasco				Masicurí			
	Species number	%	Records	%	Species number	%	Records	%
orn	24	51	216	40	12	40	63	35
chi	5	11	101	19	0			
ent	8	17	65	12	14	47	72	40
mi	6	13	40	7	4	13	44	25
mi (chi/orn)	4	8	118	22	0			
Total	47	100	540	100	30	100	179	100

Looking at the elevational distribution of pollination modes, on the Carrasco transect the relative contribution of ornithophilous species increased from 20 percent at 300 m to 100 percent above 3000 m, whereas the values for chiropterophilous species declined from 54 percent at 300 m to <10 percent above 2000 m (Fig. 3). Species with mixed bat/hummingbird-pollination showed a mixed pattern and reached their highest value of 47 percent at 2000–2500 m. Entomophilous species reached their highest contributions (14–17%) at 1000–3000 m, whereas unspecialized species declined from 25 percent in the lowlands to 0 percent at high elevations.

On the Masicurí transect, the relative contribution of ornithophilous species increased from 10 percent at 500 m to around 70 percent at 1500–2450 m (Fig. 3). Entomophilous species declined from 62 percent at 500 m to 8 percent at 1500–2000 m, and increased again to 31 percent above 2000 m. The unspecialized species showed a decline from 28 percent in the lowlands to 0 percent at high elevations.

HUMMINGBIRD RICHNESS AND ABUNDANCE.—We recorded a total of 28 hummingbird species in 22 genera along the Carrasco transect (Appendix 2). Hummingbird richness reached a maximum of 10 species at 1000–2000 m, but when standardizing values for observa-

tion time, richness peaked at 3000–3500 m (0.36 species/h), with a minor peak at 1500–2000 m (0.28 species/h; Fig. 4). Abundance of hummingbirds, however, showed an overall increase with elevation and peaked above 3000 m (4.3 individuals/h). On the Masicurí transect, a total of only 12 hummingbird species in 10 genera were recorded, including 7 species and 4 genera not observed on the Carrasco transect (Appendix 2). Species richness (7), number of species per hour (0.23), and abundance (1.3 individuals/h) all peaked at 1500–2000 m (Fig. 4).

At Carrasco, there was no significant correlation between species richness of hummingbird-pollinated bromeliads and hummingbirds, but highly significant correlations to the number of hummingbird species recorded per hour ( $r = 0.9$ ,  $P < 0.01$ ), and the number of hummingbird individuals recorded per hour ( $r = 0.98$ ,  $P < 0.01$ ) (Fig. 5). At Masicurí, there were no significant correlations between the richness and abundance values of bromeliads and hummingbirds.

## DISCUSSION

SPECIES RICHNESS AND DISTRIBUTION.—Elevational patterns of species richness differed noticeably between the transects (Fig. 2).

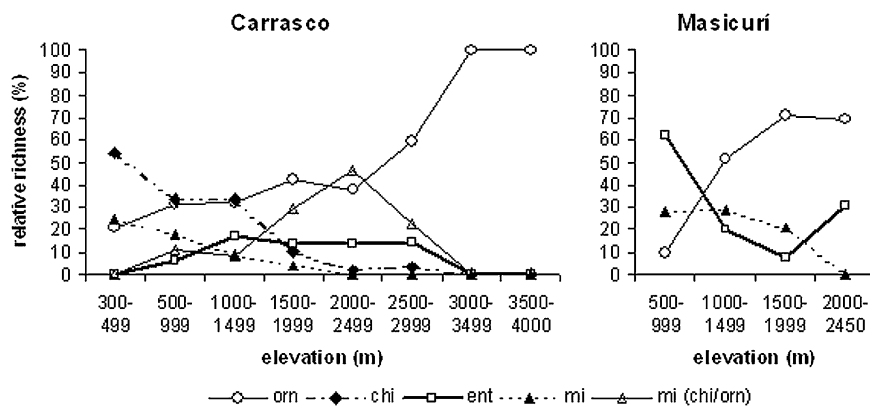


FIGURE 3. Relative representation of different pollination modes among bromeliads along the elevational transect in Carrasco and Masicurí.

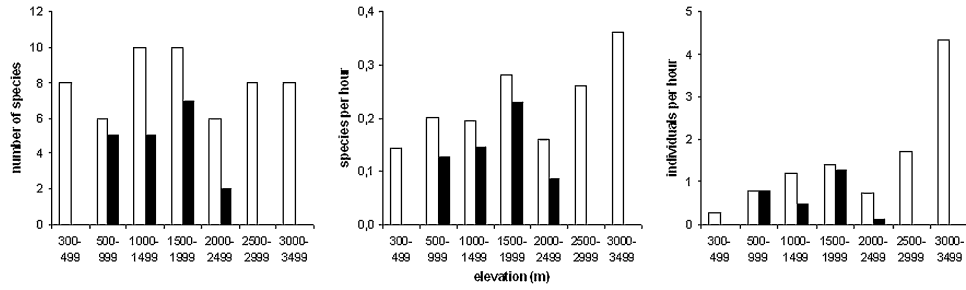


FIGURE 4. Number of hummingbird species, number of hummingbird species recorded per hour, and number of hummingbird individuals recorded per hour along the elevational transect at Carrasco (white columns) and Masicurí (black columns).

The perhumid Carrasco transect had its highest number of species at 1000–2500 m. This is the elevational range of the main cloud condensation level typically observed in the Bolivian Andes and is characterized by maximum humidity and moderate temperatures. Opposed to this, at Masicurí most species were found in the hot, semiarid lowlands, whereas the temperate, semihumid zone of the Tucumano-Boliviano forest at 1000–2000 m was relatively poor in species. These patterns correspond to those of previous studies both for Andean rain forests (Sugden & Robins 1979, Sugden 1981, Cleef *et al.* 1984) and for dry forests (Ibisch 1996).

These contrasting patterns likely reflect the climatic conditions of the transects. At Carrasco, with its perhumid climate, bromeliad assemblages are dominated by large epiphytic tank bromeliads, whereas in semihumid Masicurí they are characterized by small, epiphytic, atmospheric (“gray”) tillandsias. Tank bromeliads capture rain and humidity with dense rosettes formed by the bases of their leaves and cannot survive long periods of heat and dryness. In contrast, atmospheric tillandsias capture water from dew condensa-

tion and rain by leaves covered with specialized scales (Smith 1989; Benzing 1990, 2000). The paucity of tank bromeliads at higher elevations at Masicurí probably reflects the regular occurrence of frost in the area (Kessler 2002b).

In contrast to the epiphytic taxa, the distribution of terrestrial bromeliads was much more similar among transects. Although only one species (*Fosterella albicans*) was common to both transects, the main genera *Fosterella*, *Pitcairnia*, and *Puya* were the same and showed comparable richness patterns. Whereas *Fosterella* and *Pitcairnia* were found only at low and mid-elevations, *Puya* was almost limited to the upper parts of both transects, which are characterized by extreme climatic conditions with high solar radiation and night temperatures below freezing. These three genera are by far the most numerous and important terrestrial bromeliad genera in Bolivia (Krömer *et al.* 1999, Krömer 2000) and can be found in all biogeographic regions of the country. The remaining terrestrial genera are less common and were found only at one of the two transects: *Greigia* is a typical element in the understory of montane

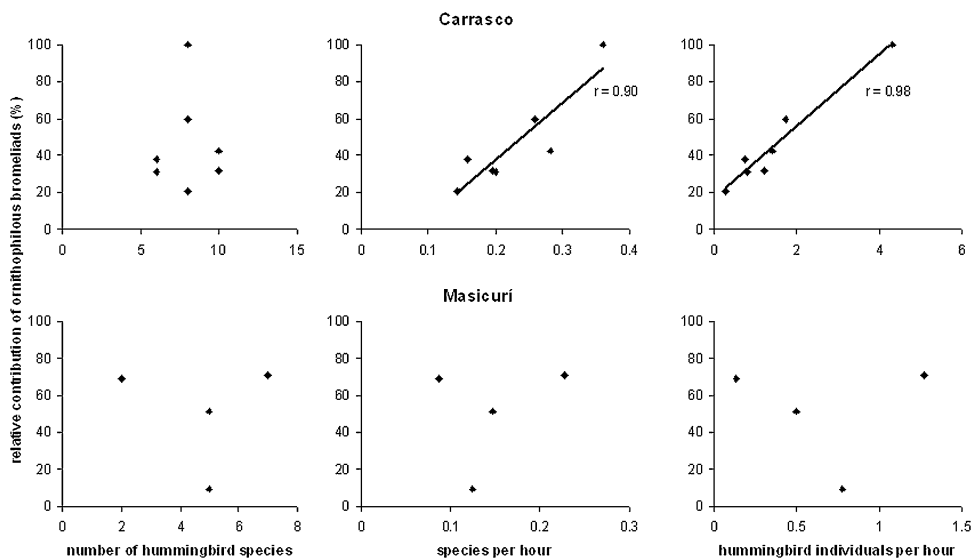


FIGURE 5. Correlation between number of hummingbird species/number of hummingbird species recorded per hour/number of hummingbird individuals recorded per hour, and the relative contribution of ornithophilous bromeliads in Carrasco and Masicurí.

and cloud forests, whereas *Bromelia* and *Dyckia* are common in dry lowland to mid-elevation areas where they colonize open and disturbed areas (Krömer *et al.* 1999, Vásquez & Ibsch 2003, Will *et al.* in press). In conclusion, the uptake of water and nutrients through the root system clearly renders terrestrial bromeliads less dependent on climatic conditions, in particular on humidity, than their epiphytic relatives.

**POLLINATION MODES.**—On the Carrasco transect, hummingbird-pollination was the most common pollination mode. This corresponds to the overall situation in Bolivia, where 61 percent of all species are ornithophilous, compared to 24 percent entomophilous, 7 percent chiropterophilous, 4 percent autogamous, and 3 percent with mixed pollination modes (Kessler & Krömer 2000). Ornithophily was also common at Masicurí, but even more species were entomophilous. On both transects, the percentage of ornithophilous species increased with elevation, although values were generally higher in perhumid Carrasco compared to semiarid Masicurí. Bromeliad richness correlated very well with the abundance of hummingbirds along the Carrasco transect but not with hummingbird species richness. At Masicurí, the low number of hummingbirds above 2000 m is striking, but may be partly due to a sampling bias. Whereas bromeliads were sampled in all available habitats, including degraded shrublands where most species were found, bird observations were concentrated on forest habitats, where hummingbirds and bird-pollinated bromeliads were rare (S. K. Herzog, pers. obs.). One caveat in this context is the seasonal elevational migratory movements of hummingbirds (Stiles 1977, 1978) that may lead to temporary shifts in their elevational distribution of richness and abundance. We do not believe that this would have severely affected our results because when we used the full known elevational range of each hummingbird species (based on Hennessey *et al.* 2003) to calculate the elevational pattern of species richness (data not shown), the resulting pattern closely corresponded to the richness pattern documented here. Nevertheless, it would certainly be interesting to study the seasonal variation of bromeliad flowering and hummingbird abundances and richness.

Hummingbirds play a crucial role in the pollination of both epiphytic and terrestrial plants in Andean forests (Stiles 1978, Feinsinger 1983, Bawa 1990, Dziedzic *et al.* 2003). Many epiphytic bird-pollinated bromeliads are adapted to their pollinators by producing few flowers over relatively long time periods (Ackerman 1986; Benzing 1990, 2000), thereby assuring a constant food supply for hummingbirds for which bromeliads are among the most important food plants (Cruden 1972; Araujo *et al.* 1994; Sazima *et al.* 1995a, 1996). In contrast, ornithophilous terrestrial bromeliads often tend to produce many flowers over short time periods, attracting an abundance of hummingbirds (Kraemer *et al.* 1993). We are unaware of any published explanation for this striking contrast in pollination strategies between epiphytic and terrestrial bromeliads, but we hypothesize that limitations in water availability may force epiphytic bromeliads to limit nectar production and to offset this disadvantage by providing a long-term reliable nectar source. For example, the rosette plant *Lobelia rhynchopetalum* (Hochst. ex

A. Rich.) Hemsl. (Campanulaceae), which resembles large *Puya* species in habit and ecology, uses 0.3–0.6 liter of water per day vegetatively and up to 3.4 liter when flowering, mostly for the production of up to 2 liter of nectar (R. Zimmermann, pers. comm.). The only comparable study on epiphytic bromeliads (Ordano & Ornelas 2004) shows that nectar removal by pollinators induces higher nectar production through a dilution of the sugar contents, *i.e.*, through higher water secretion, but the overall limited amount of water (<20 ml) does not allow an inference on whether the pollination strategy is influenced by water availability. Ecophysiological studies of the water budget of epiphytic and terrestrial bromeliads during flowering and nonflowering periods may be used to test the hypothesis presented here.

Entomophily was of limited importance along the Carrasco transect and at middle elevations along the Masicurí transect, but was the most important pollination mode at low elevations at Masicurí, mainly due to the prevalence of species of *Tillandsia* and *Fosterella*. Contrasting hummingbird and insect pollination, we found thus that hummingbird-pollination among the bromeliad assemblages increased with decreasing temperatures and with increasing humidity, while entomophily showed the opposite pattern. This general pattern was paralleled by the hummingbird assemblages, especially considering abundance. A probable reason for the predominance of hummingbirds as pollinators in cold and humid habitats is that they are the best-adapted major biotic pollinator group under these conditions. As warm-blooded organisms, hummingbirds can function even at low temperatures, and their ability to fall into torpor at night is highly energy-efficient. Opposed to this, insects depend on warm and dry conditions for optimal activity. In seasonal climates, such as along the lower part of the Masicurí transect, the seasonal shortage of nectar is deleterious to hummingbirds and is favorable to insects, which, in the case of some Hymenoptera, can store nectar or pollen and therefore represent the dominant pollinator group under these conditions (Proctor *et al.* 1996, Kessler & Krömer 2000).

The importance of bat-pollination among bromeliads in tropical lowlands has been largely overlooked until very recently. Whereas many species of the genera *Vriesea* and *Werauhia* are known to be chiropterophilous (Grant 1995, Sazima *et al.* 1995b), there are few additional records of bat-pollinated bromeliads (Benzing 2000). However, recent observations have shown that about 35 percent (8 of 18) of the Bolivian species of the genus *Guzmania* are very likely pollinated by small nectar-feeding bats (Phyllostomidae: Glosophaginae) (Krömer 2003a). Their floral syndrome includes small, night-blooming flowers with brown or green bracts, greenish to whitish petals, and mostly a specific smell such as garlic-like odor in *Guzmania sphaeroidea*. Further chiropterophilous bromeliads are found in the genera *Billbergia* (*B. robert-readii*), *Pitcairnia* (*P. crassa*), and *Puya* (*P. ferruginea*; Krömer 2003a). All these, in contrast to *Guzmania*, have large and nectar-rich flowers, which suggests that they are pollinated by fairly large bat species. Both Bolivian species of *Werauhia* are characterized by bell-shaped (campanulate) flowers that fit like a “head-mask” on the elongated rostrum of the nectar-feeding bats. *Werauhia gladioliflora*, a relatively frequent species in lower montane forest, primarily grows in the understory and the

trunk area, where its flowers are projected into the open air (Krömer 2003b). This exposure, similar to cauliflory, provides space for wing movements of the bats during hovering. Generally speaking, bat-pollination is clearly linked to humid, tropical conditions (Kessler & Krömer 2000) in accordance with the high species richness of bats in tropical lowlands (Patterson *et al.* 1996).

Interestingly, at 1500–2500 m on the Carrasco transect, we found three *Guzmania* (*G. danielii*, *G. killipiana*, *G. morreniana*) and one *Pitcairnia* (*P. cf. trianae*) species that could not be readily assigned to any of the main pollination syndromes, but which contributed 23–49 percent of all bromeliad individuals. On the one hand, the inconspicuous, brownish flowering stands of the *Guzmania* species and their nocturnal anthesis (T. Krömer, pers. obs.) suggest bat-pollination. Further, they have hexose-rich nectar (T. Krömer, pers. comm.), corresponding to typical bat-pollinated species (Baker & Baker 1983). However, the flowers are also open during the day and are scentless (at least to human observers), which suggests that they are also pollinated by hummingbirds, as indeed observed in *G. killipiana* in Ecuador (Dziedziuch *et al.* 2003). Similar intermediate pollination syndromes have been found for three species of the genus *Abutilon* (Malvaceae) (Buzato *et al.* 1994) and for *Siphocampylus sulfureus* E. Wimm. (Lobeliaceae) (Sazima *et al.* 1994). Strikingly, on the Carrasco transect, mixed hummingbird/bat-pollination was found especially at mid-elevations, *i.e.*, in the transition zone between preferential bat-pollination in the lowlands and preferential hummingbird-pollination in the highlands.

Species with mixed pollination visited by hummingbirds and insects were found most frequently at low elevations along both transects. Such unspecific pollination has repeatedly been recorded among bromeliads and other tropical plants (Bernardello *et al.* 1991, Seres & Ramírez 1995, Benzing 2000). A possible explanation for the prevalence of this mode in the lowlands could be the absence of harsh environmental conditions limiting the availability of specific pollinators. Under harsh conditions with few available pollinators, it may be advantageous for plants to adapt to specific pollinators in order to ensure reliable pollination (Kessler & Krömer 2000).

In conclusion, we found that both the richness patterns and pollination syndromes of bromeliad assemblages varied in distinct and readily interpretable ways in relation to environmental humidity and temperature, as shown by the different patterns on the two climatically contrasting study transects. In all cases, the prevalence of certain pollination syndromes under specific climatic conditions was determined by the physiological adaptations and tolerances of the pollinator taxa, suggesting that in the studied plant–animal interactions the plants adapt mainly to the animals and not *vice versa*. This interpretation is further supported by the fact that bromeliad richness trailed hummingbird abundance at Carrasco, whereas hummingbird diversity was largely independent of bromeliad diversity. Naturally, the adaptive potential of bromeliads is limited by their ecophysiological growth adaptations to ecoclimatic conditions (Benzing 2000; Kessler 2002a,b). How the respective bromeliad genera realize the adaptation to a certain pollinator is apparently influenced by life form, and potentially by other life history attributes as well. Our study thus suggests that bromeliads strive toward an

optimization of their pollination success by pollinator shifts and different nectar reward strategies within the limitations of their evolutionary and ecophysiological bounds.

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APPENDIX 1. *Bromeliad species observed on the Carrasco and Masicurí elevational transects in the Bolivian Andes. Pollination mode based on*<sup>1</sup> *published sources:*<sup>a</sup> *Sazima et al. (1995a),*<sup>b</sup> *Benzing (2000),*<sup>c</sup> *Dzedziuch et al. (2003);*<sup>2</sup> *personal observation;*<sup>3</sup> *nectar content:*<sup>a</sup> *Bernardello et al. (1991),*<sup>b</sup> *Stiles and Freeman (1993),*<sup>c</sup> *T. Krömer, pers. comm.;*<sup>4</sup> *deduction based on flower morphology.*

Species	Corolla length (mm)	Bract color	Petal color	Pollination mode	Elevational range	
					Carrasco	Masicurí
<i>Aechmea angustifolia</i> Poepp. & Endl.	12–16	Red	Yellow	mi <sup>4</sup>	300–1050	
<i>Aechmea distichantha</i> Lem.	18	Rose	White, purple or blue	mi <sup>1a,2,3a</sup>		1500–1950
<i>Aechmea longifolia</i> (Rudge) L. B. Sm. & M. A. Spencer	25–30	Pink or rose	White	mi <sup>3c</sup>	400–450	
<i>Billbergia jandrabanderi</i> R. Vásquez & P. L. Ibsch	85–100	Pink	Green	orn <sup>3c</sup>	850–1600	
<i>Bromelia serra</i> Griseb.	15	Red	Blue-purple	mi <sup>3a</sup>		500–800
<i>Dyckia</i> cf. <i>leptostachya</i> Baker			Red-orange	orn <sup>4</sup>		500–550
<i>Fosterella albicans</i> (Griseb.) L. B. Sm.	5.5	Green	White	ent <sup>1b</sup>	1300	1750
<i>Fosterella chaparensis</i> Ibsch, Vásquez & Gross	4–5	Green	White	ent <sup>1b</sup>	1550	
<i>Fosterella</i> cf. <i>schidosperma</i> (Baker) L. B. Sm.	5	Green	White	ent <sup>1b</sup>	1100–1300	
<i>Fosterella</i> spec. 1 MK 5284		Green	White	ent <sup>1b</sup>		500
<i>Fosterella</i> spec. 2 MK 5373		Green	White	ent <sup>1b</sup>		1000
<i>Fosterella</i> spec. 3 MK 5973		Green	White	ent <sup>1b</sup>		1250
<i>Greigia cochabambae</i> H. Luther	32	Castaneous	Pale purple	no data	1700–2200	
<i>Greigia</i> cf. <i>kessleri</i> H. Luther	20	Brown	Rosey purple	no data	2600–3500	
<i>Guzmania besseae</i> H. Luther	ca 25	Castaneous	White	orn <sup>1c</sup>	2000–2200	
<i>Guzmania calothyrsus</i> Mez	45	Green to brown	White	chi <sup>2</sup>	300–900	
<i>Guzmania danielii</i> L. B. Sm.	ca 25	Castaneous	White	mi (chi/orn) <sup>3c</sup>	1600–2700	
<i>Guzmania gloriosa</i> (André) André ex Mez	50	Red	Yellow	orn <sup>1c</sup>	1700–3000	
<i>Guzmania killipiana</i> L. B. Sm.	38	Castaneous	White	mi (chi/orn) <sup>1c,3c</sup>	650–2600	
<i>Guzmania marantoidea</i> (Rusby) H. Luther	ca 25	Red	Violet	orn <sup>4</sup>	1000–1300	
<i>Guzmania melinonis</i> Regel	28	Red	Yellow	orn <sup>3c</sup>	300–1050	
<i>Guzmania morreniana</i> (Linden Hortus) Mez	22	Castaneous	White	mi (chi/orn) <sup>3c</sup>	1300–2300	
<i>Guzmania retusa</i> L. B. Sm.	23	Green	White	chi <sup>2</sup>	1300–1600	
<i>Guzmania roetzlii</i> (E. Morren) Mez	23	Pale green	White	mi <sup>2</sup>	500–1050	
<i>Guzmania sphaeroidea</i> (André) André ex Mez	ca 25	Green or brown	Cream or green	chi <sup>3c</sup>	450–1550	
<i>Guzmania squarrosa</i> (Mez & Sodiro) L. B. Sm. & Pittendrigh	ca 50	Red to orange	Yellow	orn <sup>3c</sup>	1600	
<i>Mezobromelia capituligera</i> (Grisebach) J. R. Grant	28	Red or orange	White or yellow	orn <sup>4</sup>	500–2200	
<i>Pitcairnia amboroensis</i> Ibsch, Vásquez, Gross & Kessler	53	Red	Red	orn <sup>4</sup>	650–1300	
<i>Pitcairnia brittoniana</i> Mez	40	Red	Yellow or orange	orn <sup>3b</sup>	650–1750	
<i>Pitcairnia divaricata</i> Wittmack	50		Red	orn <sup>4</sup>		1750–1900
<i>Pitcairnia lanuginosa</i> Ruiz & Pavón	90		Green with purple lines	orn <sup>4</sup>	300–900	
<i>Pitcairnia paniculata</i> (Ruiz & Pavón) Ruiz & Pavón	45		Red	orn <sup>4</sup>	300–1300	1900–1950
<i>Pitcairnia</i> cf. <i> trianae</i> André	ca 45	Green	Greenish yellow	mi (chi/orn) <sup>3c</sup>	1900–2500	
<i>Pitcairnia</i> spec. 1 MK 5956				orn <sup>24</sup>		750–1200
<i>Pitcairnia</i> spec. 2 MK 6010				orn <sup>24</sup>		1150
<i>Puya atra</i> L. B. Sm.	60		White	orn <sup>4</sup>	2800–2950	
<i>Puya ferruginea</i> (Ruiz & Pavón) L. B. Sm.	140	Castaneous	Greenish white	chi <sup>1b,2</sup>	2200–2550	
<i>Puya herzogii</i> Wittmack	50		Yellow	orn <sup>3c</sup>	3450–3800	
<i>Puya leptostachya</i> L. B. Sm.	30		Blue	orn <sup>4</sup>	3650	
<i>Puya nana</i> Wittm.	40	Brown	Blue-green	orn <sup>3c</sup>		2100–2400
<i>Puya sanctae-crucis</i> (Baker) L. B. Sm.	40		Dark violet	orn <sup>4</sup>		1950–2150

APPENDIX 1. *Continued.*

Species	Corolla length (mm)	Bract color	Petal color	Pollination mode	Elevational range	
					Carrasco	Masicurí
<i>Puya</i> cf. <i>secunda</i> L. B. Sm.	40	Red	Dark violet	orn <sup>3c</sup>	2200	
<i>Puya serranoensis</i> Rauh	60–70	Rose	Blue-green	orn <sup>3c</sup>		2100–2400
<i>Puya</i> spec.1 MK 5332				orn <sup>2d</sup>		750
<i>Puya</i> spec.2 MK 6516				orn <sup>2d</sup>		2400
<i>Racinaea kessleri</i> H. Luther	5–7	Brown	Yellow	ent <sup>4</sup>	2950	
<i>Racinaea schumanniana</i> (Wittmack) J. R. Grant	5	Green	White to yellowish	ent <sup>4</sup>	650–2550	
<i>Racinaea seemanii</i> (Baker) M. A. Spencer & L. B. Sm.	12–15	Red	White	orn <sup>1c,3c</sup>	2000–3150	
<i>Racinaea spiculosa</i> (Grisebach) M. A. Spencer & L. B. Sm.	5–10		Greenish white	ent <sup>4</sup>	650–1400	
<i>Racinaea tetrantha</i> (Ruiz & Pavón) M. A. Spencer & L. B. Sm.	14		Yellow	ent <sup>1c</sup>	2500–2950	
<i>Racinaea</i> spec. MK 6976	?			ent <sup>2d</sup>	1600–2550	
<i>Tillandsia asplundii</i> L. B. Sm.	20	Red	Yellow	orn <sup>4</sup>	1300–2500	
<i>Tillandsia australis</i> Mez	20–40		Violet	orn <sup>4</sup>	2200	
<i>Tillandsia bryoides</i> Griseb.	5–9		Sulphur-yellow	mi <sup>4</sup>		500
<i>Tillandsia capillaris</i> Ruiz & Pavón	5		White, yellow or brown	mi <sup>4</sup> , auto <sup>1</sup>		1250–2450
<i>Tillandsia complanata</i> Bentham	20–25	Red or purple	Rose, purple or blue	orn <sup>1c,3a</sup>	1800–2550	
<i>Tillandsia didisticha</i> (E. Morren) Baker	15–20	Red	White	mi <sup>2,3a</sup>		500–1800
<i>Tillandsia fendleri</i> Grisebach	25–45	Yellow or red	Blue-violet	orn <sup>4</sup>	650–1400	
<i>Tillandsia ionochroma</i> André ex Mez	20	Red	Blue or violet	orn <sup>4</sup>	2700–3400	
<i>Tillandsia kessleri</i> H. Luther	35	Yellow	Violet	orn <sup>4</sup>	2100–3000	
<i>Tillandsia</i> cf. <i>kuntzeana</i> Mez	20–25		Violet	orn <sup>3c</sup>	1700–3050	
<i>Tillandsia krukoffiana</i> L. B. Sm.	10		Blue	orn <sup>4</sup>	2200	
<i>Tillandsia loliacea</i> Martius ex Schultes f.	6–10		Pale violet to yellow	mi <sup>4</sup>		500–1000
<i>Tillandsia pohliana</i> Mez	18–25	Green to pale rose	White	mi <sup>4</sup>	1100	750–800
<i>Tillandsia recurvata</i> (L.) L.	10–13	Green	Pale violet or white	mi <sup>4</sup> , auto <sup>1</sup>		500–1000
<i>Tillandsia</i> cf. <i>reichenbachii</i> Baker	7		Blue-violet	mi <sup>4</sup>		500–600
<i>Tillandsia</i> cf. <i>rusbyi</i> Baker	30	Red	White	mi <sup>4</sup>	500–1050	
<i>Tillandsia spiralipetala</i> Gouda	12	Green	Yellow-brown	mi <sup>4</sup>		500–1250
<i>Tillandsia streptocarpa</i> Baker	18–25		Blue or purple	mi <sup>4</sup>		500–1550
<i>Tillandsia tenuifolia</i> L.	20	Pink to red	White, rose or blue	orn <sup>3a</sup>		800–2300
<i>Tillandsia tricholepis</i> Baker	7	Green	Yellow greenish	mi <sup>4</sup>		500–1000
<i>Tillandsia usneoides</i> (L.) L.	9–11		Pale green	mi <sup>4</sup>		1200–2450
<i>Tillandsia violascens</i> Mez	7		Violet	mi <sup>4</sup>	1300–1550	
<i>Vriesea maxoniana</i> (L.B. Sm.) L. B. Sm.	45	Greenish yellow	Yellow	orn <sup>4</sup>		1000–1900
<i>Werauhia gladioliflora</i> (Wendland) J. R. Grant	40–70	Green	Greenish white	chi <sup>1b</sup>	300–1500	

APPENDIX 2. Elevational distribution of hummingbird species observed along the study transects. Taxonomy and species sequence follow Remsen *et al.* (2005).

Species	Carrasco	Masicuri
<i>Phaethornis ruber</i> (Linnaeus)	300–500	
<i>P. stuarti</i> Hartert	500–1000	
<i>P. pretrei</i> (Lesson & DelLattre)		1100–1950
<i>P. malaris</i> (Nordmann)	300–2000	1100–1500
<i>Campylopterus largipennis</i> (Boddaert)	300–1500	
<i>Colibri delphinae</i> (Lesson)	1500–2000	
<i>C. thalassinus</i> (Swainson)	1000–3000	1500–1950
<i>Anthracothorax nigricollis</i> (Vieillot)	300–500	
<i>Klais guimeti</i> (Bourcier)	500–1500	
<i>Lophornis delattrei</i> (Lesson)	1500–2000	
<i>Chlorostilbon mellisugus</i> (Linnaeus)	2000–2500	1100–1950
<i>C. aureoventris</i> (d'Orbigny & Lafresnaye)		500
<i>Thalurania furcata</i> (J. F. Gmelin)	300–1000	500–2500
<i>Hylocharis chrysura</i> (Shaw)		500
<i>Chrysuronia oenone</i> (Lesson)	300–1000	
<i>Amazilia chionogaster</i> (Tschudi)	500–1950	
<i>A. fimbriata</i> (J. F. Gmelin)	300–500	
<i>Adelomyia melanogenys</i> (Fraser)	1100–3000	1100–1950
<i>Heliodoxa leadbeateri</i> (Bourcier)	1500–2000	
<i>Aglaeactis pamela</i> (d'Orbigny)	3000–3500	
<i>Coeligena coeligena</i> (Lesson)	1100–2000	
<i>C. torquata</i> (Boissonneau)	2000–3500	
<i>C. violifer</i> (Gould)	2500–3500	
<i>Pterophanes cyanopterus</i> (Fraser)	2500–3500	
<i>Patagona gigas</i> (Vieillot)	3000–3500	
<i>Helianthus amethysticollis</i> (d'Orbigny & Lafresnaye)	2000–3500	
<i>Eriocnemis glaucopoides</i> (d'Orbigny & Lafresnaye)		1500–1950
<i>Ocreatus underwoodii</i> (Lesson)	1100–2000	
<i>Sappho sparganura</i> (Shaw)		2000–2500
<i>Metallura tyrianthina</i> (Loddiges)	2000–3500	
<i>M. aeneocauda</i> (Gould)	2500–3500	
<i>Algaioercus kingi</i> (Lesson)	1100–2500	
<i>Schistes geoffroyi</i> (Bourcier)	300–2000	
<i>Heliomaster longirostris</i> (Audebert & Vieillot)	300–500	
<i>Microstilbon burmeisteri</i> (P. L. Sclater)	500	