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Diversity and Ecology of Epiphytic Bromeliads Along an Elevational Gradient in the Bolivian Andes

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Photographs by the Author

The number of bromeliad species known from Bolivia has increased in recent years from 281 (Krömer et al. 1999) to ca. 310 due to many new species discoveries (e.g., Krömer & Gross 2001, Ibisch et al. 2002, Vásquez & Ibisch 2003). The total number of 400 estimated species (Ibisch et al. 2001) still ranks below the published numbers for Ecuador (440; Jørgensen & Léon-Yánez 1999), Peru (410), Colombia (391), and Venezuela (364) (all Holst 1994). Nevertheless, the number of genera (21) is second only to Venezuela reflecting the unique biogeographical position of Bolivia at the meeting point of the humid northern and central Andes, the dry southern Andes, Amazonia, the Gran Chaco, and the Brazilian Shield.

About 45% of Bolivia's bromeliad species are endemic to the country. This high percentage is largely due to the high number of endemic terrestrial taxa in the genera *Fosterella* and *Puya*, which have their centers of diversity in Bolivia (Ibisch et al. 2001, 2002) and can be found mostly in azonal habitats such as steep ravines, rock faces, and roadsides (Kessler 2002). Only *Tillandsia* has a similar high percentage of endemic species, which is mainly represented by atmospheric species adapted to the dry conditions of the Chiquitano and inter-Andean forests. Overall, diversity of bromeliads is highest in the humid montane forests ("Yungas") of the Andes (Ibisch et al. 2001), where mainly epiphytic tank bromeliads in the subfamily Tillandsioideae (e.g., *Guzmania*, *Racinaea*, *Tillandsia*) and Bromelioideae (e.g., *Aechmea*, *Billbergia*) abound.

Diversity

A study of the diversity of epiphytic bromeliads along an elevational gradient in the Yungas of La Paz (Prov. Nor Yungas, Sud Yungas) based on data of Krömer et al. (1999), Krömer (2003a), and Bach (2004) yielded a total of 54 species in 10 genera and showed great differences in species numbers and composition within three vegetation belts (TABLE 1). The lower montane forest (500-1500 m elevation) harbors the highest number of species (29) and genera (10) with *Aechmea, Billbergia, Catopsis,* and *Werauhia* occurring only in this belt. The upper montane forest (1500-2500 m) follows with 25 species in 6 genera, with especially high species numbers in *Guzmania*, *Racinaea*, and *Tillandsia*. Species richness in the cloud forest belt (2500-3500 m) decreases drastically to 14 species in 4 genera.

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When the altitudinal belts are divided into intervals of 500 m, however, the diversity of epiphytic bromeliads does not decrease linearly with increasing height. Instead, the species number in the lower and upper montane forest is relatively constant (FIGURE 36). Between 2000-2500 m there is a small peak, while above this level the epiphyte diversity strongly decreases due to occasional night frosts. On the other hand, the large genera *Guzmania*, *Racinaea*, and *Tillandsia* clearly show hump-shaped curves with maximum species numbers in the very humid mid-elevations. With a total of nine species *Tillandsia* contributes considerably to the high diversity between 2000-2500 m. The high total species richness in the warmer and less humid lower montane forest is due to the occurrence of many different genera, though relatively few species.

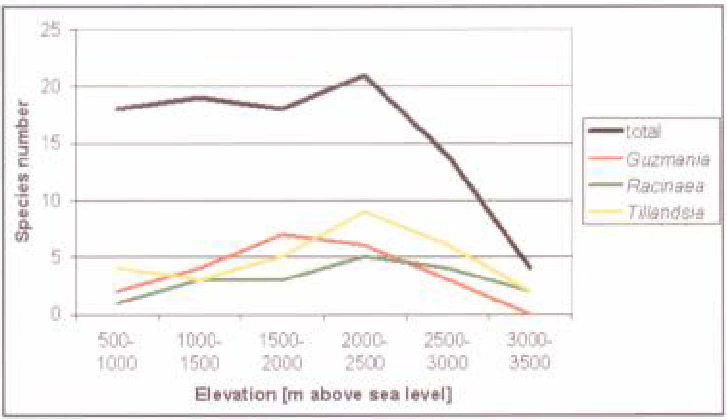

Figure 36. Elevational patterns of species richness of epiphytic bromeliads in the Yungas of La Paz.

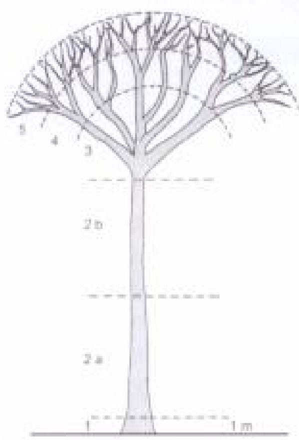

Figure 37. Subdivision of the tree into vertical zones after Johansson (1974).

Figure 38. Big tank bromeliad *Mezobromelia pleiosticha* and other epiphytes (e.g., ferns, orchids, peperomias) on a large vertical branch of a canopy tree.

Figure 39. Small night blooming flowers of *Guzmania calothyrsus*.

Figure 40. Bell-shaped night blooming flowers of *Werauhia gladioliflora*.

Figure 41. Bell-shaped night blooming flowers of *Werauhia sanguinolenta*.

Six species, all from the genera *Racinaea* and *Tillandsia*, display an especially wide elevational range (> 1000 m), but only *Racinaea schumanniana* occurs in all three altitudinal belts, while *Tillandsia fendleri* has the maximum range with 1400 m. However, the majority of the species with several records show an intermediate distribution range of 500-1000 m. Only one voucher each exists for ten species found within the relatively well sampled study area, with *Guzmania madisonii, Tillandsia platyrachis, T. wurdackii*, and *Vriesea tequendame* being the first records for Bolivia. This fact implies a need for further botanical collecting expeditions.

	Lower montane forest 500–1500m	Upper montane forest 1500–2500m	Cloud forest 2500–3500m
Aechmea	4	-	-
Billbergia	2	-	-
Catopsis	1	-	-
Guzmania	6	7	3
Mezobromelia	2	1	-
Pitcairnia	1	1	-
Racinaea	3	6	4
Tillandsia	5	9	6
Vriesea	3	1	1
Werauhia	2	-	-
Total	**29**	**25**	**14**

TABLE 1: Species numbers of different genera within three vegetation belts in the Yungas of La Paz.

Vertical distribution

Epiphytes do not occur randomly on the trees but often occupy very specific niches which can be divided into five zones (FIGURE 37) according to Johansson (1974). For example, the trunk base is zone 1, where mainly ferns and bryophytes occur. Lower branches of the canopy (zones 3-4) are "epiphyte paradise," with a high diversity and abundance of all epiphyte groups, including big tank bromeliads (FIGURE 38). Outer canopy twigs (zone 5) harbor small twig epiphytes, especially orchids. Because the epiphyte flora on shrubs and treelets in the forest understory is usually different from that on the large canopy trees (Gradstein & Krömer 2003), I recently proposed the understory as the additional zone U (Krömer 2003a).

Epiphytes can be classified into three ecological groups based on their vertical distribution on the tree (Acebey et al. 2003). **Generalists** occur in more or less all tree zones and also in the shady understory, while specialists can be divided into **sun** exposed and **shade** tolerant **epiphytes**, both occuring only in a limited number of zones. Most epiphytic bromeliads in the Yungas of La Paz show a wide ecological flexibility and are able to grow in shady as well as in sunny habitats such as, e.g., *Racinaea spiculosa* (FIGURE 42). Fewer species have a special habitat preference and occur mostly in the canopy like the sun epiphytes *Guzmania roezlii* and *Mezobromelia capituligera* (FIGURE 42), while shade-loving epiphytes are somewhat lacking.

Flower ecology

Bromeliads are known to have a wide rage of pollinators, including birds, bats, and a variety of insects, and also include autogamous taxa

(Benzing 2000). Most bromeliads in Bolivia are bird-pollinated and provide one of the most important food sources for hummingbirds (Kessler & Krömer 2000). Pollination by bats has been studied in much less detail, although it is an important pollination mode, especially in the genus *Guzmania* (Krömer 2003b). In the Yungas of La Paz, six out of 12 *Guzmania* species are very likely pollinated by small nectar-feeding bats (Phyllostomidae: Glossophaginae). Their floral syndrome includes small, night blooming flowers with brown or green bracts, greenish to whitish petals (FIGURE 39), and most have a specific smell (e.g., garlic-like odor in *Guzmania sphaeroidea*).

Other bat-pollinated (chiropterophilous) bromeliads are found in the genera *Billbergia* (*B. robert-readii*) and *Werauhia* (*W. gladioliflora, W. sanguinolenta*). Furthermore, two terrestrial species that occur in the study area (*Pitcairnia crassa, Puya ferruginea*) are bat-pollinated (Krömer 2000). All these, in contrast to *Guzmania*, show large and nectar-rich flowers which indicates bigger bat species as pollinators. Both species of *Werauhia* are characterized by bell-shaped (campanulate) flowers (FIGURES 40, 41, p. 219) that fit like a "head-mask" on the elongated rostrum of the nectar-feeding bat. *Werauhia gladioliflora*, a relatively frequent species in the lower montane forest, shows a vertical distribution focused in the understory and the trunk area, where its flowers are projected into the open air. This exposure, similar to cauliflory, provides space for wing movements of the bat during hovering.

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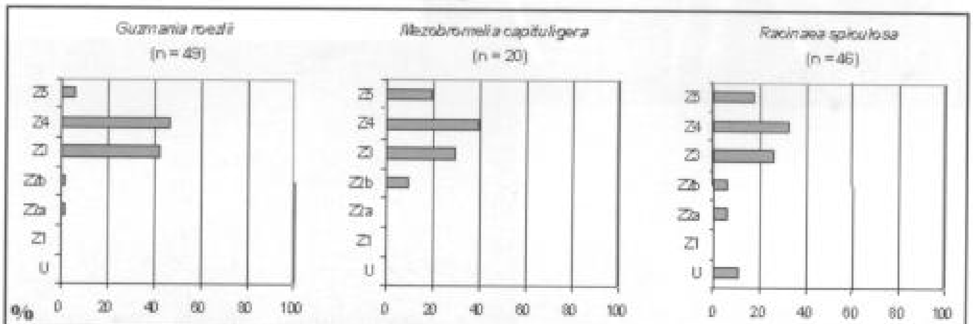

Figure 42. *Guzmania roezlii, Mezobromelia capituligera*, and *Racinaea spiculosa* shown as percent of the total number of records (n) within the vertical zones.

Krömer - Bolivia. Continued from p. 221

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