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Patterns and Ecological Correlates of Pollination Modes Among Bromeliad Communities of Andean Forests in Bolivia

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Abstract: We studied the distribution of five pollination modes (ornithophily, chiropterophily, entomophily, mixed/unspecific, autogamy) among the bromeliad communities of 74 forest sites in the Bolivian Andes and adjacent lowlands. We recorded a total of 188 bromeliad species belonging to 16 genera, including 115 (61%) ornithophilous, 14 (7%) chiropterophilous, 45 (24%) entomophilous, 8 (4%) autogamous, and 6 (3%) species with mixed pollination mode. Ornithophily was the dominant pollination mode at high elevations and in wet regions, while entomophily dominated in arid regions. Chiropterophily was most common in wet lowland regions, autogamy in arid sites, and mixed pollination in the lowlands. Pollination modes were rather evenly distributed among life-forms and ecophysiological types, with a few exceptions: terrestrial forest bromeliads, mostly belonging to unarmed, soft-leaved taxa, had a prevalence of entomophily and few ornithophilous species; large, spiny terrestrial bromeliads of *Puya* and Bromelioideae showed a prevalence of ornithophily; and autogamy was restricted to the neotenous subgenus *Diaphoranthema* of *Tillandsia*. The restriction of unspecific pollination modes to the lowlands is hypothesized to be related to the abundance of pollinators, eliminating the need for specialized co-evolution, or to the overall rarity of bromeliads in this environment, precluding the development of specialized relationships. The low representation of entomophilous species in small dry forest regions compared to extensive areas is assumed to be due to the seasonal influx of hummingbirds and/or bats. Overall, the frequency of individual pollination modes was related to the availability of pollinators as determined by temperatures and humidity.

Key words: Bats, bromeliads, diversity, hummingbirds, insects, montane forest, pollination.

Introduction

Pollination modes of plant communities vary geographically and with respect to ecological conditions (Endress, 1994[13]). In the tropics, pollination by hummingbirds, various insects, bats, and wind as well as self-pollination are all commonly observed (Janzen, 1975[31]; Bawa, 1990[7]; Endress, 1994[13]; Gentry, 1995[22]). Most studies of pollination in tropical forests have focussed on individual study sites and frequently on specific taxonomic groups or pollination modes (e.g., Stiles, 1975[61], 1977[62]; Beach, 1982[8]; Feinsinger et al., 1986[16]; Seres and Ramírez, 1995[58]; Sazima et al., 1996[54]). Thus, little is known on the geographical distribution of the frequency of pollination modes and its dependence on ecological factors, such as temperature, humidity or habitat heterogeneity.

With about 2800 described species, Bromeliaceae is among the most species-rich non-woody plant families in the Neotropics and has undergone one of the most remarkable adaptive radiations in the plant world (Benzing, 2000[9]). Most of the research on this family has focussed on morphological and ecophysiological aspects, while pollination ecology has been studied in much less detail. However, bromeliads have a wide range of pollinators, including birds, bats, and a variety of insects, and also include autogamous taxa (Gardner, 1986[21]; Till, 1992[67]). Furthermore, bromeliads are one of the most important food sources for hummingbirds in many neotropical forest regions (Cruden, 1972[12]; Araujo et al., 1994[2]; Sazima et al., 1995[53]). Bromeliad pollination modes frequently vary between closely related species and even geographically within some species and thus appear to be subject to direct adaptive selection, independently of ecophysiological adaptations (Utley, 1983[69]; Gardner, 1986[21]; Varadarajan and Brown, 1988[71]). Unlike plant families with tight evolutionary constraints on flower ecology (Baker and Baker, 1990[6]), Bromeliaceae is therefore a suitable family to study the geographical and ecological distribution of different pollination modes. In the present paper we analysed the distribution of pollination modes among the bromeliads of 74 forest sites, ranging from Amazonian and drought-deciduous Chaco forests in the lowlands to mossy elfin forests at the timberline. Our aim was to find ecological correlates of pollination mode, i.e., ecological parameters, such as elevation or humidity, that co-vary with the representation of different pollination modes. While the disclosure of such patterns does not directly imply causal relationships, this approach helps to formulate hypotheses about causal relationships and allows the evaluation of hypotheses predicting specific patterns.

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Materials and Methods

Study sites

In total, the analysis was based on 74 sites, including 68 sites surveyed by ourselves and six further localities with reliable species lists that were included in order to achieve a more complete geographical and ecological coverage (Table **1**, App. **1**). Field work was conducted at 69 sites in the Bolivian Andes and adjacent lowlands for 1 – 12 days per site between 1995 and 2000. For details of sampling regime, which included 1097 vegetation plots of 400 m^2 each, with 732 plots located in zonal forest habitats and 311 in azonal habitats with rock-faces, see Kessler (in press d[36]). Study sites were chosen to include the widest possible range of environmental conditions between them, while being ecologically homogeneous within. Thus, no site covered noticeably different geological substrates, an elevational range of more than 500 m or a horizontal distance greater than 10 km. Study sites in close geographical proximity of each other were treated as independent samples if separated by at least 500 m elevation or by at least 200 m elevation plus different geological substrates and/or strikingly different humidity conditions. These differences generally caused a turnover in species composition by at least 40%. An exception were sites 37 a, 38 a and 39 a (App. **1**) that were located along a continuously sampled elevational transect between sites 35 and 37, 37 and 38, and 38 and 39. These sites were included in analyses aimed at detecting general patterns that did not involve statistical analysis, but were excluded from analyses requiring statistical independence of samples.

Except for a few unmistakeable species (e.g., *Tillandsia usneoides*), all species encountered at every study site (but not in every single plot) were collected at least in triplicate, if possible, and have been deposited at the Herbario Nacional de Bolivia, La Paz (LPB) (including all unicates), at the Herbarium Göttingen, Germany (GOET), and at the Marie Selby Botanical Gardens, Sarasota, Florida (SELB). Identifications were mainly made by specialists (see acknowledgements). Collections that could not be identified to species level, in most cases because they were in a sterile condition, were excluded. Though recorded at three sites, the genus *Ananas* was also excluded from the entire study, since we do not known if the encountered sterile specimens were native or adventive. Similarly, *Greigia* was excluded because its pollination mode is unknown and cannot be inferred with certainty from morphology.

Pollination mode and other species attributes

All recorded species were grouped into five broad categories according to their main pollination mode as ornithophilous, chiropterophilous, entomophilous, mixed or unspecific (two or all of the first three categories) or autogamous. Classification was based on information from published sources (Gardner, 1986[21]; Bernardello et al., 1991[10]; Till, 1992[67]; Araujo et al., 1994[2]; Sazima et al., 1995[53], 1996[54]; Seres and Ramírez, 1995[58]; Benzing, 2000[9]), on personal field observations of flower visitors (assuming that regular flower visitors with appropiate 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 (HPLC) (T. Krömer, unpubl. data) which allows inferences to pollinators (Baker and Baker, 1983[5]; Bernardello et al., 1991[10]; Schwerdtfeger, 1996[56]). Species for which no such information was available were classified based on deductions from morphology and flower colouration (Gardner, 1986[21]; Baker and Baker, 1990[6]). 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 clearcut pollination syndromes often have more than one pollinator (Sazima et al., 1994[55]).

Species were additionally classified according to life-form as epiphytes, terrestrials inside forest habitats, or saxicolous species, and according to ecophysiological type after Benzing (2000[9]). The latter classification groups species after their root and shoot architecture, adaptations of foliar trichomes, and photosynthetic syndromes (see also Pittendrigh, 1948[50]). Ecophysiological type I of Benzing (2000[9]) was further separated into two categories, corresponding (a) to species with herbaceous, mostly unarmed leaves, and (b) to species with succulent or chartaceous, spiny leaves.

Environmental variables

The following environmental variables were measured or estimated for each study site (for further details see Kessler, in press d[36]).

- **Elevation:** mean elevation at a given site.
- **Latitude:** given to the centre of each site.
- **Mean annual precipitation:** since there are no reliable precipitation maps or models for the Bolivian Andes, precipitation values had to be interpolated in many cases. Climatic data of 131 stations within or close to the study region were provided by E. Jordan (Geographical Institute, Univ. of Düsseldorf, Germany), with additional data taken from Morales (1990[44]). Ten of the study sites were situated close enough to climatic stations that the respective station data could be used without modification. Thirteen additional sites could be clearly linked to a climatic station at no more than 10 km linear distance, but due to slight differences in elevation and topographically modified precipitation levels, the respective values had to be corrected somewhat. The remaining 51 study sites were distant from any climatic station and their values were interpolated from nearby stations with similar vegetation types.
- **Number of humid months:** calculated based on the station data. Following Walter and Lieth (1967[73]), humid months were defined as having a value of mean monthly precipitation (in mm) at least twice as high as that of mean monthly temperature. Additionally, localities with > 100 mm mean monthly precipitation in every month were classified as perhumid (Lauer et al., 1996[42]).
- **Mean annual temperature:** based on the same 131 climatic stations mentioned above. To correct for elevational differences between stations and study sites we used a lapse rate of $0.54\,^{\circ}\mathrm{C} \times 100\,\mathrm{m}^{-1}$, calculated on the basis of all 131 stations.
- **Number of frost days per year:** estimated after Eriksen (1986[14]) and Jordan (1991[32]). This parameter is not linearly related to temperature.
- **Variability of NDVI and T_s:** these variables were included as indices of the interannual climatic variability. NDVI (Normalized Difference Vegetation Index) is highly correlated to

Table 1 Study sites (numbering follows App. 1) in relation to elevation and number of humid months. 12 p refers to perhumid sites with > 100 mm mean monthly precipitation in every month. Sites in southern Bolivia are in bold

Elevation (m)	Number of humid months 3–4	 5–6	 7–8	 9–10	 11–12	 12 p
3500–4000	–	II	18	16	39	–
3000–3500	24	–	–	8, 29, 31, 34	21	39 a
2500–3000	–	**45, 49**	32	–	20, 27, **43**	38
2000–2500	**47, 61**	14, **50, 57, 58**	26, 30, **65**	9, 25, **56, 60**	**44,** III	38 a
1500–2000	–	22, **63**	23, 28, **55**	**51, 59, V**	I	37
1000–1500	**54**	**46**	2, 11, 12, 17	10, **48, 52, 62**	5, 16	37 a
500–1000	–	**VI**	**64**	13, 19, **53**	4, 7	35
-500	–	–	**VI**	3, **42, 41**	1, 6, 40	33, 36

Table 2 Pearson correlation coefficients describing the bivariate relationships between abiotic attributes of 68 sites sampled in this study, i.e., excluding sites I–VI whose inclusion did not significantly alter the relationships reflected in this table

	Latitude	Precipitation	Temperature	No. frost days	Variability NDVI	Variability T_s	Distance to wetter habitats	Distance to dryer habitats	Canopy height	Bryophyte cover
Elevation	0.11	-0.42**	-0.96***	0.90***	0.01	0.07	-0.02	-0.46**	-0.70***	0.35
Latitude		-0.40*	-0.07	0.31	-0.03	-0.20	0.14	-0.06	-0.24	-0.08
Precipitation			0.32	-0.47**	0.25	0.04	0.41*	-0.07	0.67***	0.43*
Temperature				-0.85***	-0.10	-0.05	0.01	0.48**	0.63***	-0.42*
No. frost days					-0.11	0.06	0.13	-0.36*	-0.59***	0.30
Variability NDVI						0.00	-0.07	-0.06	-0.04	0.17
Variability T_s							-0.03	0.15	-0.13	-0.02
Distance to wetter habitats								0.00	0.32	0.48**
Distance to dryer habitats									0.13	-0.51***
Canopy height										0.16

* $p<0.05$, ** $p<0.01$, *** $p<0.001$, probabilities subjected to Bonferroni correction

vegetation parameters, such as green leaf biomass, absorbed photosynthetically active radiation, and biomass green vegetation (Holben et al., 1980[26]; Tucker et al., 1985[68]). T_s (land surface "skin" brightness temperature) is related, through the surface energy balance equation, to surface moisture availability and evapotranspiration, as a function of latent heat flux (Planet, 1988[51]). To quantify erratic and anomalous climatic events that may be biologically critical (e.g., droughts, cold spells, exceptional rains) (Stiles, 1992[64]), coefficients of variation in NDVI and T_s values were calculated by E. Lambin and co-workers (Dept de Géographie et de Géologie, Univ. Catolique de Louvain, Belgium) on a month-by-month basis based on 10 years (1983–1992) of the Global Area Coverage (GAC) remote sensing data provided by the National Aeronautics and Space Administration (NASA) for global change research. This is the same dataset employed by Fjeldså et al. (1999 b[18]) for a study of the relationships of avian endemism to ecoclimatic variability.

- **Distance to wetter habitats:** the linear distance to the closest site with at least 30% higher precipitation and not more than 1000 elevational meters difference from the study area was estimated as a measure of the environmental heterogeneity of a given study site.
- **Distance to dryer habitats:** as above, but with at least 30% lower precipitation.
- **Canopy height:** average natural forest canopy height was estimated to the closest 3 m (1 m at < 10 m canopy height) as a proxy for ecosystem productivity (Lieth, 1975[42]) and structural forest complexity (Terborgh, 1977[66]).
- **Bryophyte cover:** cover of epiphytic bryophytes on forest canopy branches was estimated to the closest 10% as an index of air humidity (Frahm and Gradstein, 1991[20]; Wolf, 1993[74]).

Overall, pairwise correlations between the environmental variables revealed a rather well-balanced data matrix with few spurious correlations and reflecting all the known or expected causal relationships, e.g., between elevation and mean annual temperature (Table 2).

Data analysis

The calculations were generally conducted using all relevant information available in the dataset. In some cases, this included all species at all 74 sites, in other cases some sites or some species had to be excluded in order to obtain independent sample points (excluding sites 37 a, 38 a, 39 a) or because specific environmental factors or species attributes were not known. For this reason, sample size varied somewhat between analyses. In some analyses and figures, sites from tropical northern Bolivia were separated from those of southern Bolivia, which shows a strong subtropical influence. The boundary for this classification was the "Andean knee" at *ca.* 17°30'S, corresponding to a marked geomorphologic, climatic, and biogeographic transition zone (Ibisch, 1996[27]).

The representation of the pollination modes at a given site was calculated as the percentage relative to the total number of species recorded. For the present analyses, we used the bromeliad species lists of each site, without taking abundance into account. For Table **4**, data from sites within the same elevational and humidity class (Table **1**) were averaged.

Bivariate regressions of the representation of pollination modes to all environmental variables were calculated individually. Additionally, multivariate regressions, involving all environmental attributes, were calculated in order to obtain a measure of the overall variability captured by the factors included in the analysis. Where necessary, values were log or square root-transformed to approximate normality to fit the requirements of parametric statistics. To test for the nonrandomness of the distribution of pollination modes among different ecophysiological types or life forms, χ^2-Tests were performed. To control for type I error, significancy levels were subjected to a Bonferroni correction (Sokal and Rohlf, 1995[60]). Statistics were carried out with SYSTAT version 7.0 for Windows (SYSTAT, 1997[65]).

Table 3 Genera of Bromeliaceae recorded in this study, indicating the total number of species and the number of species per pollination mode (tro = ornithophilous, chi = chiropterophilous, ent = entomophilous, mi = mixed or unspecific, aut = autogamous)

	Species number	Pollination mode				
		orn	chi	ent	mi	aut
Aechmea	8	4		1	3	
Billbergia	6	5	1			
Bromelia	3	2			1	
Catopsis	1			1		
Deuterocohnia	4	2		2		
Dyckia	2	2				
Fosterella	16	1		15		
Guzmania	14	7	5	1	1	
Mezobromelia	2	2				
Pitcairnia	15	10	5			
Pseudananas	1				1	
Puya	33	32	1			
Racinaea	10	2		8		
Tillandsia	62	37		17		8
Vriesea	8	8				
Werauhia	3	1	2			
Totals	188	115	14	45	6	8

Results

In the 74 study sites we recorded a total of 188 species of Bromeliaceae, belonging to 16 genera (Table **3**). Eleven (69%) of 16 genera had two or more different pollination modes. Except for *Vriesea* with eight species, the genera with a single pollination mode only had one or two recorded species and may well contain species with other pollination syndromes in the study region or elsewhere.

The regression analysis revealed that 65% to 74% of the variation in the representation of pollination types could be explained by the environmental variables included in the analysis (Table **4**). Most of the captured variation could, in turn, be related to a distinct factor complex. The frequency of ornithophily was significantly related to elevation, mean annual temperature (negatively) and especially to number of frost days, in addition to bryophyte cover. All these factors co-vary closely (Table **2**) and especially point to a predominance of hummingbird pollination at high elevations. Chiropterophily was closely related to precipitation and canopy height, i.e., was most common in tall, wet forests. Entomophily was significantly negatively related to number of frost days and bryophyte cover, i.e., it was most common in warm, dry regions. Additionally, there was a significant negative relationship to distance to wetter habitats. The frequency of species with

Table 4 Bivariate linear regression coefficients between the representation of five pollination modes in Bolivian bromeliad communities and 11 environmental variables, and multivariate linear regression coefficients with all environmental variables

	Ornithophilous	Chiropterophilous	Entomophilous	Mixed/unspecific	Autogamous
Elevation	0.44**	-0.38	-0.32	-0.57***	0.25
Latitude	-0.18	-0.28	0.06	-0.17	0.34
Precipitation	0.09	0.62***	-0.24	0.05	-0.58***
Temperature	-0.48***	0.31	0.37	0.52***	-0.12
No. frost days	0.49***	-0.34	-0.45**	-0.47***	0.26
Variability NDVI	0.21	0.22	0.04	0.00	-0.25
Variability T_s	0.05	0.07	0.00	0.13	0.00
Distance to wetter habitats	0.16	0.22	-0.41*	0.10	-0.16
Distance to dryer habitats	-0.32	0.08	0.33	0.36	0.04
Canopy height	-0.01	0.59***	-0.18	0.33	-0.50***
Bryophyte cover	0.44**	0.06	-0.43**	-0.26	-0.52***
All variables	0.69***	0.69***	0.74***	0.65**	0.68***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, probabilities subjected to Bonferroni correction

Table 5 Percentage of the total bromeliad flora at individual study sites with different pollination modes in relation to humidity and elevation, based on 74 study sites. Perhumid sites, i.e., areas with > 100 mm mean annual precipitation in every month, were placed in a separate class (12 p). Where a direct comparison of values in northern and southern Bolivia was possible, bold numbers indicate the higher values

	North						South				
	3–4	5–6	7–8	9–10	11–12	12p	3–4	5–6	7–8	9–10	11–12
A Ornithophilous											
3500–4000	–	33	–	100	67	–	–	–	–	–	–
3000–3500	50	–	–	89	67	71	–	–	–	–	–
2500–3000	–	–	64	–	**63**	45	–	34	–	–	50
2000–2500	–	39	40	41	**59**	55	30	39	**50**	**45**	38
1500–2000	–	23	**37**	–	47	44	–	**50**	36	63	–
1000–1500	–	–	32	35	51	50	30	31	–	**40**	–
500–1000	–	–	–	**48**	48	44	–	45	38	19	–
–500	–	–	–	33	50	47	–	–	50	**38**	–
B Chiropterophilous											
3500–4000	–	33	–	0	0	–	–	–	–	–	–
3000–3500	0	–	–	0	0	0	–	–	–	–	–
2500–3000	–	–	0	–	**8**	20	–	0	–	–	0
2000–2500	–	0	0	0	12	25	0	0	0	0	**25**
1500–2000	–	0	0	–	13	24	–	0	0	0	–
1000–1500	–	–	5	**15**	9	18	0	8	–	7	–
500–1000	–	–	–	**14**	15	22	–	0	0	0	–
–500	–	–	–	**0**	25	47	–	–	0	0	–
C Entomophilous											
3500–4000	–	0	–	0	0	–	–	–	–	–	–
3000–3500	0	–	–	0	22	14	–	–	–	–	–
2500–3000	–	–	21	–	**19**	15	–	28	–	–	0
2000–2500	–	**39**	**27**	**37**	12	10	45	36	17	0	**13**
1500–2000	–	**54**	**41**	–	40	16	–	25	27	16	–
1000–1500	–	–	37	**35**	32	32	50	23	–	26	–
500–1000	–	–	–	23	24	22	–	36	42	**44**	–
–500	–	–	–	**33**	11	7	–	–	13	31	–
D Mixed/unspecific											
3500–4000	–	0	–	0	0	–	–	–	–	–	–
3000–3500	0	–	–	0	0	0	–	–	–	–	–
2500–3000	–	–	0	–	0	0	–	0	–	–	0
2000–2500	–	**8**	0	0	0	0	0	0	0	0	0
1500–2000	–	**8**	**4**	–	0	0	–	0	0	5	–
1000–1500	–	–	6	5	0	0	0	15	–	5	–
500–1000	–	–	–	**11**	6	6	–	9	8	6	–
–500	–	–	–	**33**	8	0	–	–	25	24	–
E Autogamous											
3500–4000	–	33	–	0	0	–	–	–	–	–	–
3000–3500	50	–	–	11	0	0	–	–	–	–	–
2500–3000	–	–	14	–	**4**	0	–	27	–	–	0
2000–2500	–	15	**23**	20	0	0	25	**25**	17	**35**	0
1500–2000	–	15	15	–	0	0	–	**25**	**27**	8	–
1000–1500	–	–	14	10	0	0	20	23	–	**13**	–
500–1000	–	–	–	3	0	0	–	9	10	**19**	–
–500	–	–	–	0	0	0	–	–	13	**7**	–

mixed or unspecific pollination modes was negatively related to elevation and number of frost days, and positively to mean annual temperature, i.e., was highest at low elevations. Finally, autogamy was negatively related to precipitation, canopy height, and bryophyte cover and was thus most common in open, arid habitats. There were no significant relationships of the frequency of specific pollination modes to latitude, variability of NDVI and T_s, or distance to drier habitats (Table **4**).

The close relationship of the occurrence of pollination modes to elevation and humidity is also evidenced in Table **5**. In regions with seven or more humid months, ornithophily was the dominant pollination mode (Table **5 A**). In more arid regions, entomophily took over as the dominant mode (Table **5 C**). With respect to elevation, ornithophily showed a slight increase with elevation while entomophily was conspicuously absent at highest elevations. Looking at the less frequent polli-

Table 6 Percentual representation of different pollination modes among bromeliad species with epiphytic, terrestrial, and saxicolous life-forms. Pollination modes are significantly non-randomly distributed among entomophilous taxa ($\chi^2_2 = 16.8$, $p < 0.01$) and almost so among ornithophilous taxa ($\chi^2_2 = 6.8$, $p = 0.07$) (probabilities subjected to Bonferroni correction)

	Ornithophilous	Chiropterophilous	Entomophilous	Mixed/unspecific	Autogamous	Total
Epiphytes	56.6	7.5	25.5	4.7	5.7	106
Terrestrials	41.7	8.3	43.8	6.2	0	48
Saxicoles	57.7	7.7	26.0	2.9	5.8	104

Table 7 Percentual representation of different pollination modes among the bromeliad species recorded in this study with respect to ecophysiological type. In all cases, ecophysiological types are distributed non-randomly among the different pollination modes ($\chi^2_5 = 23.7$ to 56.5, $p < 0.05$ in all cases; probabilities subjected to Bonferroni correction)

Ecophysiological types	Ornithophilous	Chiropterophilous	Entomophilous	Mixed/unspecific	Autogamous	Total
Ia[1]	27.5	12.5	60.0	0	0	40
Ib[2]	87.9	3.0	9.1	0	0	33
II[3]	50	0	0	50	0	4
III[4]	64.3	7.1	7.1	21.4	0	14
IV[5]	65.6	11.5	21.3	1.6	0	61
V[6]	47.1	0	35.3	0	17.7	34

[1] Terrestrials with absorptive soil roots, no phytotelma, nonabsorptive foliar trichomes, C_3 photosynthetic pathway, and herbaceous, non-armed leaves.

[2] Terrestrials with absorptive soil roots, no phytotelma, nonabsorptive foliar trichomes, CAM, and thick, spiny leaves.

[3] Terrestrials with absorptive soil and apogeotropic roots, weakly developed phytotelma, foliar trichomes absorptive on leaf bases, and CAM.

[4] Epiphytes, saxicoles or terrestrials with mechanical or conditionally absorptive roots, well-developed phytotelma, foliar trichomes absorptive on leaf bases, and mostly CAM.

[5] Mostly epiphytes with mechanical or conditionally absorptive roots, well-developed phytotelma, foliar trichomes absorptive on leaf bases, and mostly C_3.

[6] Mostly saxicoles or epiphytes with mechanical or missing roots, no phytotelma, foliar trichomes absorptive over entire shoot, and CAM ("grey atmospheric bromeliads").

nation modes, chiropterophilous species occurred primarily in wet regions at low to mid-elevations (Table **5 B**), species with mixed or unspecific pollination were clustered at low elevations (Table **5 D**), and autogamous species were best represented in arid to semihumid regions, avoiding low elevations (Table **5 E**). Ornithophily was about as common in northern as in southern Bolivia, while chiropterophily, entomophily, and mixed modes were somewhat better represented in northern Bolivia (Table **5**). Autogamy, by contrast, was more common in southern Bolivia.

With respect to life-form and ecophysiological type, ornithophily was significantly underrepresented among terrestrial taxa and species with ecophysiological type I a and was overrepresented among species with type I b (Tables **6, 7**). Entomophily, in contrast, was overrepresented among terrestrials and species with ecophysiological types I a and V, and was underrepresented with respect to ecophysiological type II. Because of the low number of species exhibiting the other three pollination modes, differences were rarely statistically significant here, even though autogamy was overrepresented for ecophysiological type V.

Discussion

The present study confirms the view that specific pollination modes are most advantageous under different ecological conditions (Bawa, 1990[7]; Gentry, 1995[22]). While wind pollination, a common mode in arid habitats, does not occur within the Bromeliaceae (Benzing, 2000[9]), the different modes of animal pollination show distinct patterns.

Ornithophily is the prevalent pollination mode at high elevations and showed a stronger correlation to number of frost days than to elevation or mean temperature as such in our study. A prominence of hummingbird pollination in montane forest areas has repeatedly been documented (Cruden, 1972[12]; Feinsinger, 1983[15]; Bawa, 1990[7]) and most likely relates to the limited activity and scarcity of insects under cold conditions. This is supported by the strong negative relationship of entomophily to number of frost days observed by us. At high elevations, bromeliads can be the most important food sources for hummingbirds (Kraemer et al., 1993[40]).

Entomophily is most common in arid regions with a pronounced dry season. Hummingbirds, which depend on a year-round supply of nectar, are less abundant in dry forests and frequently show seasonal movements (Stiles, 1981[63]; Arizmendi and Ornelas, 1990[3]). In this context, the negative relationship of entomophily to distance to wetter habitats is noteworthy, since it shows that entomophily is more common in extensive dry forest regions than in small pockets of dry forest. Isolated dry forest areas occur in several rain-shadowed valley bottoms of the Bolivian Andes, often as narrow bands only a few kilometers wide (Bach et al., 1999[4]; Kessler and Helme, 1999[38]; Kessler et al., 2000[37]). Under such conditions, hummingbirds, and perhaps also bats, may easily migrate seasonally or move on a daily basis from adjacent humid forests into the dry forest areas. Such movements have been observed for frugivorous birds in Bolivia (S. K. Herzog and M. Kessler, unpubl. data). Accordingly, ornithophily and chiropterophily may be more common, and entomophily less pronounced, in such valleys, despite their general aridity and seasonality. If this hypothesis is correct, then hummingbird and/or bat pollination would appear to be more advantageous or reliable to bromeliads under these conditions than insect pollination. Otherwise, there would be no reason for the observed shift in the pollination modes, since pollinating insects should not be in short supply in dry forest habitats.

Chiropterophily is clearly linked to humid, tropical conditions, in accordance with the diversity of bats in general and of nectarivorous bats in particular (Patterson et al., 1996[48]). A noteworthy exception is the occurrence of *Puya ferruginea* above 3500 m in the arid La Paz valley (site II), especially considering that no nectarivorous bats are known from the area (Mercado and Miralles, 1991[43]; Anderson, 1997[1]). However, while we have observed bat pollination of this species at other sites at lower elevations and have classified it accordingly, it is conceivable that in the La Paz valley *Puya ferruginea* shows self-pollination or is pollinated by other agents, e.g., sphingid moths.

Species with mixed animal pollination, i.e., visited by hummingbirds as well as various insects and/or bats, occur most frequently at low elevations. Such unspecific pollination has repeatedly been recorded among bromeliads and other tropical plants (Bernardello et al., 1991[10]; Buzato et al., 1994[11]; Sazima et al., 1994[55]; Seres and Ramírez, 1995[58]). A possible explanation for the prevalence of this mode in the humid 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. In the tropical lowlands, by contrast, there may be no shortage of pollinators, eliminating the need for such a specialization. Alternatively, the low overall abundance of bromeliads in tropical lowland forests (Benzing, 2000[9]) may preclude the development of specialized relationships which depend on a minimum abundance and reliability of the food source (Feinsinger, 1983[15]; Bawa, 1990[7]).

Species with autogamy are restricted in our data set to the subgenus *Diaphoranthema* of the genus *Tillandsia*. This subgenus is characterized by adaptations to extremely xeric conditions, involving neoteny, polyploidy, and autogamy (Till, 1992[67]). Thus, the ecological distribution of these species may be linked to their pollination mode or to their morphological and physiological adaptations. In this sense, autogamy is an exception to the statement made in the introduction emphasizing the evolutionary independence of pollination modes.

The occurrence of pollination modes with respect to life-form is surprisingly homogeneous. The only exception is the prevalence of entomophily and the rarity of ornithophily among terrestrial bromeliads occurring inside forest habitats. Understorey hummingbirds, mostly belonging to the distinct subfamily Phaethorninae, are primarily associated with large monocotyledoneous herbs, notably *Heliconia*, and are absent at higher elevations (Stiles, 1981[63]). Accordingly, terrestrial forest bromeliads show a predominance of entomophily. This is further documented by the frequency of this mode in species with ecophysiological type Ia, mostly corresponding to small, herbaceous, understorey bromeliads of the genera *Fosterella*.

Bromeliad taxa with ecophysiological types Ib and II, corresponding to large, tough, and spiny species of *Puya* and various Bromelioideae, while also growing on the ground, show a prevalence of ornithophily. This is in accordance with their abundance at high elevations and their occurrence in open habitats (Varadarajan, 1990[70]; Ibisch, 1998[28]).

In summary, the patterns shown by the different pollination modes among the Bromeliaceae can be convincingly interpreted in the light of the availability of pollinators in the large variety of habitats colonized by this family, even though a direct causal relationship is difficult to establish. The lack of correlation with ecoclimatic variability is noteworthy, since it could have been expected that the different pollinator groups vary in their susceptibility to extreme climatic events and thus in their reliability as pollinators. Overall, the regression coefficients of $R = 0.65$ to 0.74, corresponding to determination coefficients of $R^2 = 0.42$ to 0.55, are quite satisfactory for ecological studies of this type, even though the fact that some environmental variables had to be estimated implies that these values should be considered with caution. The unexplained variance is certainly partly due to sampling stochasticity. Additionally, the frequency of pollination modes in Bromeliaceae may be influenced by other plant families. However, for hummingbirds of the subfamily Trochilinae, comprising the majority of hummingbird taxa and those species frequenting open habitats and the canopy, the Bromeliaceae is one of the most important coevolved nectar sources (Stiles, 1981[63]; Sazima et al., 1995[54]) and is therefore likely to reflect the overall distribution of ornithophily.

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Appendix 1 Sites included in this study. For sites 1 – 65 plot-based data were available, while for sites I – VI only species lists were used. Forest types are deciduous (D), semideciduous (SD), and evergreen (E). References (Ref.) include site descriptions as well as species lists (see footnote)

No.	Study site	Forest type	Coordinates	Elevation (m)	Ref.
1	Río San Antonio	E	13°35′S, 68°30′W	400	
2	Río Machariapo	SD	14°37′S, 68°27′W	1050 – 1350	1
3	Estación Biológica del Beni	SD	14°47′S, 66°19′W	200	2
4	Río Yuyo	E	15°02′S, 68°28′W	850 – 1000	
5	Cerro Asunta Pata	E	15°04′S, 68°28′W	1200 – 1500	
6	Río D'Artagnan	E	15°07′S, 67°05′W	400 – 500	
7	Serranía Pilón Lajas	E	15°09′S, 67°06′W	700 – 950	3
8	Chullina	E	15°09′S, 68°55′W	3300 – 3450	
9	Charazani	E	15°10′S, 68°55′W	2150 – 2400	
10	Río Camata	SD	15°13′S, 68°43′W	1150 – 1350	
11	Camata	D	15°14′S, 68°46′W	1400 – 1450	
12	Consata	D	15°25′S, 68°32′W	1000 – 1400	
13	Sapecho	E	15°32′S, 67°18′W	450 – 750	4
14	Tacacoma	D	15°32′S, 68°40′W	2000 – 2400	
15	Quiabaya	E	15°38′S, 68°35′W	3500	
16	Serranía Bellavista	E	15°40′S, 67°30′W	1150 – 1500	
17	Yolosillas	SD	16°12′S, 67°45′W	1100 – 1200	5
18	Zongo	E	16°12′S, 68°07′W	4050	
19	Las Mercedes	SD	16°15′S, 67°18′W	850 – 1000	5
20	Chuspipata	E	16°17′S, 67°42′W	2500 – 2800	6
21	Coscapa	E	16°18′S, 67°44′W	3000 – 3500	6
22	Miguillas	D	16°33′S, 67°22′W	1300 – 1800	5
23	Huara	D	16°35′S, 67°26′W	1550 – 1700	5
24	Huajchillas	D	16°37′S, 68°03′W	3100 – 3150	7
25	Lambate	SD	16°38′S, 67°34′W	2300 – 2350	
26	Cotacajes deciduous	D	16°46′S, 66°44′W	1600 – 1750	8
27	Pujyani	E	16°47′S, 66°42′W	2600 – 3100	8
28	Cotacajes semideciduous	SD	16°47′S, 66°44′W	2000 – 2150	8
29	Casay Vinto	D	16°52′S, 66°38′W	3350 – 3500	8
30	Inquisivi	D	16°54′S, 67°09′W	2250 – 2500	5
31	Saila Pata Podocarpus	E	16°55′S, 66°55′W	3000 – 3500	8
32	Saila Pata deciduous	D	16°55′S, 66°56′W	2550 – 2800	8
33	Villa Tunari	E	16°58′S, 65°25′W	300 – 450	9
34	Quime	E	17°01′S, 67°16′W	3350	
35	El Palmar	E	17°06′S, 65°30′W	500 – 1000	
36	Sajta	E	17°07′S, 67°05′W	220	
37a	Carrasco NP 1000 – 1500 m	E	17°08′S, 65°38′W	1000 – 1500	
37	Carrasco NP 1500 – 2000 m	E	17°08′S, 65°38′W	1500 – 2000	
38a	Carrasco NP 2000 – 2500 m	E	17°08′S, 65°38′W	2000 – 2500	
38	Carrasco NP 2500 – 3000 m	E	17°14′S, 65°43′W	2500 – 3000	
39a	Carrasco NP 3000 – 3500 m	E	17°16′S, 65°44′W	3000 – 3500	
39	Carrasco NP 3500 – 3950 m	E	17°19′S, 65°44′W	3500 – 3950	
40	Río Colomelín	E	17°23′S, 64°24′W	350 – 600	
41	Macuñucú	SD	17°44′S, 63°36′W	450 – 500	
42	Santa Cruz Botanical Garden	D	17°47′S, 63°04′W	450	9
43	Karahuasi	E	17°49′S, 64°42′W	2150 – 2400	
44	Siberia	E	17°50′S, 64°43′W	2600 – 3000	
45	Río Jaya Mayu	D	17°53′S, 65°55′W	2500 – 2800	5
46	San Juan del Potrero	D	17°59′S, 64°15′W	1350 – 1600	5
47	Río Caine	D	18°06′S, 65°46′W	2200 – 2300	5
48	Los Volcanes	SD	18°07′S, 63°35′W	1000 – 1300	
49	San Vicente	SD	18°13′S, 65°18′W	2550 – 2700	5
50	Novillero	D	18°18′S, 65°15′W	2300 – 2450	5
51	San Lorenzo	E	18°35′S, 63°54′W	1800 – 2300	10
52	Loma Larga	E	18°46′S, 63°50′W	1200 – 1500	10
53	Masicurí	D	18°49′S, 63°41′W	500 – 800	10
54	Río Grande	D	18°51′S, 64°18′W	900 – 1300	
55	Río La Haciendita	D	18°56′S, 64°17′W	1500 – 1750	

continued next page

Appendix 1 continued

No.	Study site	Forest type	Coordinates	Elevation (m)	Ref.
56	Nuevo Mundo	E	18°59′S, 64°18′W	2100–2450	
57	Sopachuy	D	19°20′S, 64°33′W	2100	
58	Icla	D	19°23′S, 64°48′W	2250–2500	
59	Padilla	D	19°30′S, 64°11′W	1700	
60	Tarvita	D	19°34′S, 64°27′W	2000	
61	Río Pilcomayo	D	19°34′S, 64°51′W	2000–2050	
62	Río Azero	D	19°40′S, 64°06′W	1150–1500	5
63	Villa Orias	E	19°50′S, 64°29′W	2150–2200	
64	Río Itacua	D	19°56′S, 63°32′W	850–1000	
65	Cordillera de Mandinga	SD	19°56′S, 64°34′W	2250–2550	
I	Tunquini	E	16°17′S, 67°48′W	1400–1900	
II	La Paz	SD	16°30′S, 68°08′W	3500–4000	7
III	Sehuencas	E	17°30′S, 65°16′W	2100–2300	11
IV	Las Bolsas	D	17°50′S, 62°50′W	300	12
V	Samaipata	SD	18°11′S, 63°54′W	2000	13
VI	Ivitiapi	D	20°10′S, 63°15′W	700	14

References: 1: Parker and Bailey, 1991[46]; Perry et al., 1997[49]; Kessler and Helme, 1999[38]*; 2: Hanagarth, 1993[23]; 3: Smith and Killeen, 1998[59]; Kessler, in press a[33]; 4: Seidel, 1995[57]; 5: Herzog et al., 1997[25]; 6: Morales, 1995[45]; 7: Forno and Baudoin, 1991[19]*; 8: Fjeldså et al., 1999 a[17]*; Herzog et al., 1999[24]; 9: Saldias, 1991[52]; Parker et al., 1993[47]; 10: Kessler et al., in press[39]*; Kessler, in press b[34]; 11: Ibisch, 1996[27]*; pers. comm.; 12: P. L. Ibisch, pers. comm.; 13: Ibisch et al., 1996[29]*, 1999[30]*; 14: Vásquez, 1994[72]*. References including Bromeliaceae species lists are marked with *.

References

[1] Anderson, S. (1997) Mammals of Bolivia. Taxonomy and Distribution. Bull. Am. Mus. Nat. Hist., 231.

[2] Araujo, A. C., Fischer, E., and Sazima, M. (1994) Floração sequencial e polinização de três expécies de *Vriesea* (Bromeliaceae) na região de Juréia, sudeste do Brasil. Revta brasil. Bot. 17, 113–118.

[3] Arizmendi, M. C. and Ornelas, J. F. (1990) Hummingbirds and their floras resources in a tropical dry forest in Mexico. Biotropica 22, 172–180.

[4] Bach, K., Kessler, M., and Gonzales, J. (1999) Caracterización preliminar de los bosques deciduos andinos de Bolivia en base a grupos indicadores botánicos. Ecología en Bolivia 32, 7–22.

[5] Baker, H. G. and Baker, I. (1983) Floral nectar sugar constituents in relation to pollinator type. In Handbook of experimental pollination biology (Jones, C. E. and Little, R. J., eds.), New York: Van Nostrand Reinhold, pp. 111–141.

[6] Baker, H. G. and Baker, I. (1990) The predictive value of nectar chemistry to the recognition of pollinator types. Israel. J. Bot. 39, 147–166.

[7] Bawa, K. S. (1990) Plant-pollinator interactions in tropical rain forests. Ann. Rev. Ecol. Syst. 21, 399–422.

[8] Beach, J. H. (1982) Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). Am. J. Bot. 69, 1074–1081.

[9] Benzing, D. H. (2000) Bromeliaceae. Profile of an adaptive radiation. Cambridge: Cambridge Univ. Press.

[10] Bernardello, L. M., Galetto, L., and Juliani, H. R. (1991) Floral nectar, nectary structure and pollinators in some Argentinian Bromeliaceae. Ann. Bot. 67, 401–411.

[11] Buzato, S., Sazima, M., and Sazima, I. (1994) Pollination of three species of *Abutilon* (Malvaceae) intermediate between bat and hummingbird flower syndromes. Flora 189, 327–334.

[12] Cruden, R. W. (1972) Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. Science 176, 1439–1440.

[13] Endress, P. K. (1994) Diversity and evolutionary biology of tropical flowers. Cambridge: Cambridge University Press, p. 511.

[14] Eriksen, W. (1986) Frostwechsel und hygrische Bedingungen in der Puna Boliviens. Ein Beitrag zur Ökoklimatologie der randtropischen Anden. Bolivien. In Beiträge zur physischen Geographie eines Andenstaates (ed. by Buchholz, H. J.), Hannover: Jahrb. Geogr. Ges. Hannover 1985, pp. 1–21.

[15] Feinsinger, P. (1983) Community organization among neotropical nectar-feeding birds. Am. Zool. 18, 779–795.

[16] Feinsinger, P., Murray, G., Kinsman, S., and Busby, W. H. (1986) Floral neighborhood and pollination success in four hummingbird-pollinated cloud forest plant species. Ecology 67, 449–464.

[17] Fjeldså, J., Kessler, M., and Swanson, G. (eds.) (1999 a) Cocapata and Saila Pata: People and biodiversity in a Bolivian montane valley. Rønde, Denmark: DIVA Technical Report, 7, p. 175.

[18] Fjeldså, J., Lambin, E., and Mertens, B. (1999 b) Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. Ecography 22, 63–78.

[19] Forno, E. and Baudoin, M. (1991) Historia natural de un valle de los Andes: La Paz. La Paz: Instituto de Ecología, UMSA.

[20] Frahm, J.-P. and Gradstein, S. R. (1991) An altitudinal zonation of tropical rain forests using bryophytes. J. Biogeogr. 18, 669–678.

[21] Gardner, C. S. (1986) Inferences about pollination in *Tillandsia* (Bromeliaceae). Selbyana 9, 76–87.

[22] Gentry, A. H. (1995) Diversity and composition of neotropical dry forests. In Seasonally dry tropical forests (Bullock, S. H., Mooney, H. A., and Medina, E., eds.), Cambridge, U. K.: Cambridge Univ. Press, pp. 146–194.

[23] Hanagarth, W. (1993) Acerca de la geoecología de las sabanas del Beni en el noreste de Bolivia. La Paz: Instituto de Ecología, UMSA.

[24] Herzog, S. K., Fjeldså, J., Kessler, M., and Balderrama, J. A. (1999) Ornithological surveys of the Cordillera Cocapata, depto. Cochabamba, Bolivia, a transition zone between humid and dry intermontane Andean habitats. Bull. Brit. Orn. Club 119, 162–177.

[25] Herzog, S. K., Kessler, M., Maijer, S., and Hohnwald, S. (1997) Distributional notes on birds of Andean dry forests in Bolivia. Bull. Brit. Orn. Club 117, 223–235.

[26] Holben, B. N., Tucker, C. J., and Fan, C. J. (1980) Spectral assessment for soybean leaf area and leaf biomass. Photogr. Engin. and Remote Sensing 46, 651–656.

[27] Ibisch, P. L. (1996) Neotropische Epiphytendiversität - das Beispiel Bolivien. Archiv naturwissenschaftlicher Dissertationen 1. Wiehl, Germany: Martina Galunder-Verlag.

[28] Ibisch, P. L. (1998) Estado de conservación de las especies bolivianas del género *Puya* (Bromeliaceae) aplicando un nuevo método de evaluación -Valor Nacional de Conservación. Rev. Soc. Boliviana Botánica 2, 89-99.

[29] Ibisch, P. L., Rojas, P., de la Barra, N., Fernández, E., Mercado, M., Ovando, L., and Vargas, G. (1996) Un "lugar de encuentro": Flora de la zona arqueológica "El Fuerte", Samaipata, (Prov. Florida, Dpto. Santa Cruz, Bolivia). Ecología en Bolivia 28, 1-28.

[30] Ibisch, P. L., Vásquez, R., and Gross, E. (1999) New species of *Puya* and *Pitcairnia* (Bromeliaceae) from the Amboró National Park and vicinities (Santa Cruz, Bolivia): a neglected center of diversity and endemism of Pitcairnioideae. J. Bromeliad Soc. 49, 124-135.

[31] Janzen, D. H. (1975) Ecology of plants in the tropics. London: Edward Arnold Publishers.

[32] Jordan, E. (1991) Die Gletscher der bolivianischen Anden. Stuttgart: Franz Steiner Verlag.

[33] Kessler, M. (in press a) Diversidad y endemismo de grupos selectos de plantas en la Serranía de Pilón Lajas, depto. Beni, Bolivia. Rev. Soc. Boliviana Botánica 3.

[34] Kessler, M. (in press b) Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. Plant Ecology.

[35] Kessler, M. (in press c) Environmental patterns and ecological correlates of range-size among bromeliad communities of Andean forests in Bolivia. In Andes and Tepuis: Plant evolution and endemism in the uplands of South America (Young, K., Ulloa, C., Luteyn, J., León, B., and Knapp, S., eds.), New York: New York Botanical Garden.

[36] Kessler, M. (in press d) Pteridophyte species richness in Andean forests in Bolivia. Biodiv. Conserv.

[37] Kessler, M., Bach, K., Helme, N., Beck, S. G., and Gonzales, J. (2000) Floristic diversity of Andean dry forests in Bolivia - an overview. In Ergebnisse weltweiter ökologischer Forschung. Beiträge des 1. Symposiums der A. F. W. Schimper-Stiftung von H. und E. Walter, Hohenheim, Oktober 1998 (Breckle, S.-W., Schweizer, B., and Arndt, U., eds.), Stuttgart: Günter Heimbach Verlag, pp. 219-234.

[38] Kessler, M. and Helme, N. (1999) Floristic diversity and phytogeography of the central Tuichi Valley, an isolated dry forest locality in the Bolivian Andes. Candollea 54, 341-366.

[39] Kessler, M., Krömer, T., and Jimenez, I. (in press) Inventario de grupos selectos de plantas en el valle de Masicurí (Santa Cruz - Bolivia). Rev. Boliviana Ecol. Conserv.

[40] Kraemer, M., Schmidt, U., and Schuchmann, K. L. (1993) Notes on the organization of a neotropical high-altitude hummingbird-flower community. In Animal-plant interactions in tropical environments (Barthlott, W., Naumann, C. M., Schmidt-Loske, K., and Schuchmann, K. L., eds.), Bonn:, pp. 61-65.

[41] Lauer, W., Rafiqpoor, M. D., and Frankenberg, P. (1996) Die Klimate der Erde. Eine Klassifikation auf ökophysiologischer Grundlage der realen Vegetation. Erdkunde 50, 275-300.

[42] Lieth, H. (1975) Modeling the primary productive of the world. In Primary Productivity of the Biosphere (Lieth, H. and Whittaker, R. H., eds.), New York: Springer-Verlag, pp. 237-263.

[43] Mercado, T. I. D. and Miralles, G. J. (1991) Mamíferos. In Historia natural de un valle de los Andes: La Paz (Forno, E. and Baudoin, M., eds.), La Paz: Instituto de Ecología, UMSA, pp. 293-343.

[44] Morales, C. de (1990) Bolivia. Medio ambiente y ecología aplicada. La Paz: Instituto de Ecología, UMSA.

[45] Morales, C. de (1995) Caminos de Cotapata. La Paz: Instituto de Ecología - FUNDECO.

[46] Parker, T. A. and Bailey, B. (1991) A biological assessment of the Alto Madidi region and adjacent areas of Northwest Bolivia. RAP Working Papers 1. Washington, D. C.: Conservation International.

[47] Parker, T. A., Gentry, A. H., Foster, R. B., Emmons, L. H., and Remsen Jr., J. V., (1993) The lowland of dry forests of Santa Cruz, Bolivia: a global conservation priority. RAP Working Papers 4. Washington, D. C.: Conservation International.

[48] Patterson, B. D., Pacheco, V., and Solari, S. (1996) Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. J. Zool. Lond. 240, 637-658.

[49] Perry, A., Kessler, M., and Helme, N. (1997) Birds of the central Río Tuichi valley, with emphasis on dry forests, Parque Nacional Madidi, depto. La Paz, Bolivia. Ornithol. Monogr. 48, 557-576.

[50] Pittendrigh, C. S. (1948) The bromeliad-*Anopheles*-malaria complex in Trinidad. I. The bromeliad flora. Evolution 2, 58-89.

[51] Planet, W. G. (1988) Data extraction and calibration of TIROS-N-NOAA radiometers. NOAA Tech. Mem. NESS 101-Rev. 1. Washington, D. C.: U. S. Dept. of Commerce - Nat. Oceanic and Atmos. Adm.

[52] Saldias, P. M. (1991) Inventario de árboles en el bosque alto del Jardín Botánico de Santa Cruz, Bolivia. Ecología en Bolivia 17, 31-46.

[53] Sazima, I., Buzato, S., and Sazima, M. (1995) The saw-billed hermit *Ramphodon naevius* and its flowers in southeastern Brazil. J. Ornith. 136, 195-206.

[54] Sazima, I., Buzato, S., and Sazima, M. (1996) An assemblage of hummingbird-pollinated flowers in a montane forest in southeastern Brazil. Bot. Acta 109, 149-160.

[55] Sazima, M., Sazima, I., and Buzato, S. (1994) Nectar by day and night: *Siphocampylus sulfureus* (Lobeliaceae) pollinated by hummingbirds and bats. Pl. Syst. Evol. 191, 237-246.

[56] Schwerdtfeger, M. (1996) Die Nektarzusammensetzung der Asteridae und ihre Beziehung zu Blütenökologie und Systematik. Diss. Bot. 264 Berlin: J. Cramer.

[57] Seidel, R. (1995) Inventario de los árboles en tres parcelas de bosque primario en la Serranía de Marimonos, Alto Beni. Ecología en Bolivia 25, 1-35.

[58] Seres, A. and Ramírez, N. (1995) Biología floral y polinización de algunas monocotiledoneas de un bosque nublado venezulano. Ann. Missouri Bot. Gard. 82, 61-81.

[59] Smith, D. N. and Killeen, T. J. (1998) A comparison of the structure and composition of montane and lowland tropical forest in the Serrania Pilón Lajas, Beni, Bolivia. In Forest biodiversity in North, Central and South America, and the Caribbean. Research and Monitoring (Dallmeier, F. and Comiskey, J. A., eds.), Paris - New York: UNESCO - Parthenon Publishing Group, pp. 681-700.

[60] Sokal, R. R. and Rohlf, F. J. (1995) Biometry. New York: Freeman.

[61] Stiles, F. G. (1975) Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology 56, 285-301.

[62] Stiles, F. G. (1977) Coadapted competitors: flowering seasons of hummingbird food plants in a tropical forest. Science 198, 1177-1178.

[63] Stiles, F. G. (1981) Geographical aspects of bird-flower coevolution, with particular reference to Central América. Ann. Missouri Bot. Gard. 68, 323-351.

[64] Stiles, F. G. (1992) Effect of a severe drought on the population biology of a tropical hummingbird. Ecology 73, 1375-1390.

[65] SYSTAT, (1997) SYSTAT for Windows, statistics, version 7.0. Chicago: SPSS Inc.

[66] Terborgh, J. (1977) Bird species diversity on an Andean elevational gradient. J. Ecology 58, 1007-1019.

[67] Till, W. (1992) Systematics and evolution of the tropical-subtropical *Tillandsia* subgenus *Diaphoranthema* (Bromeliaceae). Selbyana 13, 88-94.

[68] Tucker, C. G. F., Townshend, J. R. G., and Goff, T. R. (1985) African land-cover classification using satellite data. Science 227, 369-375.

[69] Utley, J. F. (1983) A revision of the middle American thecophylloid *Vriesea* (Bromeliaceae). Tulane Stud. Zool. Bot. 24, 1-81.

[70] Varadarajan, G. S. (1990) Patterns of geographic distribution and their implications on the phylogeny of *Puya* (Bromeliaceae). J. Arnold Arbor. 71, 527 – 552.

[71] Varadarajan, G. S. and Brown, G. K. (1988) Morphological variation of some floral features of the subfamily Pitcairnioideae (Bromeliaceae) and their significance in pollination biology. Bot. Gaz. 149, 82 – 91.

[72] Vásquez, R. (1994) Un viaje de observación botánica a la región de Ivitiapi (Provincia Cordillera, Departamento de Santa Cruz). Rev. Soc. Estudios Botánicos 1, 61 – 69.

[73] Walter, H. and Lieth, H. (1967) Klimadiagramm-Weltatlas. Jena.

[74] Wolf, J. H. D. (1993) Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. Ann. Missouri Bot. Gard. 80, 928 – 960.

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