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Dynamics of Nectar Resources of Hummingbird-visited Plants in a Montane Forest of Southern Ecuador

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With 2 Figures

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Summary

PAULSCH C., STEVENS A.-D. & GOTTSBERGER G. 2012. Dynamics of nectar resources of hummingbird-visited plants in a montane forest of southern Ecuador – Phyton (Horn, Austria) 52 (1): 121–138, with 2 figures.

Changes of nectar resources offered by hummingbird-visited plants in the eastern Andes of southern Ecuador were studied in an area of 1 hectare over the course of a full year. A total of 3186 flowering plant individuals were visited by hummingbirds, belonging to 67 species, 29 genera and 12 families. The mean nectar volume per flower and day was 38.6 µl with a high interspecific variability (SD 153.5 µl) [calculated without the bat blossoms of *Ceiba*: 20.2 µl (SD 30.2 *l)]. Nectar sugars revealed an average concentration of 18.8% (SD 4.4%), with a preponderance of sucrose in a subset of species analysed by HPLC. This supports that the majority of the investigated plant species is in fact ornithophilous and regularly pollinated by hum-

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mingbirds. Short-term changes in the quantity and composition of the nectar resources were characteristic for the observed dynamics. Considered in terms of energy available, resource levels attained their maximum in a rainy month (April) and were at a minimum in a drier month (January). However, it was not possible to show significant correlations between measured precipitation and either the number of flowers or the amount of energy available. Only 27 of the 67 hummingbird-visited plant species could be verified to contribute substantially to the nectar resources; these species either flowered at least during one third of the year (contributing less than 10% of energy/day), or they contributed at least at one observation date more than 10% of the total energy available. The present study substantiated that the supply of resources provided by hummingbird-visited plants in the montane rainforests of Ecuador is subject to a high degree of temporal and spatial dynamics.

Resumen

PAULSCH C., STEVENS A.-D. & GOTTSBERGER G. 2012. Dynamics of nectar resources of hummingbird-visited plants in a montane forest of southern Ecuador. [La dinámica del recursos del nectar de plantas visitadas por colibríes en un bosque tropical montano en el sur del Ecuador] – Phyton (Horn, Austria) 52(1): 121–138, with 2 figures.

La dinámica del recursos del nectar de plantas visitadas por colibríes fue investigada en el sur del Ecuador en una parcela de una hectarea y comprendió un ciclo completo de un año. Se encontró un total de 3186 individuos en flor de plantas visitadas por colibríes, distribuidos en 12 familias, 29 géneros y 67 especies. La variabilidad entre especies del volumen de néctar fue muy alta, siendo 38.6 µl (SD 153.5 µl) por día y flor en promedio. El análisis del néctar resultó en una concentración de azucar de 18.8% (SD 4.4%), con una dominancia de sacarosa en un grupo de especies investigado por HPLC. Esto permite la conclusión que la mayoría de las plantas visitadas por colibríes realmente son ornitófilas. La disponibilidad del nectar se caracteriza por cambios abruptos en la cantidad y la composición de néctar. Desde el punto de vista de las flores y energía, la disponibilidad máxima de recursos ocurre durante un mes de alta precipitación (abril), mientras que el mínimo se encuentra en un mes de baja precipitación (enero). Sin embargo, no se puede comprobar una correlación significativa entre la precipitación y el ofrecimiento de flores, individuos y energía. En total, solamente 27 de las 67 especies de plantas visitadas por colibríes fueron determinados en contribuir considerablemente en el recurso del nectar. Estás especies eran en floración por lo menos una tercera parte del año o contribuierón por lo menos una vez con más de 10% al valor total del recurso en una control. En total, la disponibilidad de plantas visitadas por colibríes en el bosque montano del Ecuador está sujeto a una alta dinámica temporal y espacial.

Zusammenfassung

PAULSCH C., STEVENS A.-D. & GOTTSBERGER G. 2012. Dynamics of nectar resources of hummingbird-visited plants in a montane forest of southern Ecuador. [Dynamik der Nektarressourcen kolibribesuchter Pflanzen in einem Bergregenwald Süd-Ecuadors] – Phyton (Horn, Austria) 52 (1): 121–138, with 2 figures.

In den Ost-Anden Süd-Ecuadors wurde die Dynamik der Nektarressourcen kolibribesuchter Pflanzen auf einem Hektar über den Zeitraum eines Jahres untersucht. Insgesamt wurden 3186 blühende Pflanzenindividuen aus 12 Familien, 29 Gattungen und 67 Arten von Kolibris besucht. Das durchschnittliche Nektarvolumen pro Blüte und Tag lag bei 38,6 µl (SD 153,5 µl) [ohne die Fledermausblumen von *Ceiba* berechnet: 20,2 µl (SD 30,2 µl)]. Die durchschnittliche Zuckerkonzentration betrug 18,8% (SD 4,4%). Mittels HPLC wurde bei einem Teil der Pflanzenarten die Zuckerzusammensetzung untersucht und belegte eine Saccharosedominanz. Dies stützte die These, dass die untersuchten Pflanzen größtenteils ornithophil und kolibribestäubt sind. Die beobachtete Dynamik war durch kurzfristige Wechsel in Menge und Zusammensetzung der Nektarressourcen gekennzeichnet. Das Maximum der verfügbaren Energie lag in einem regenreichen Monat (April) und das Minimum in einem trockenen Monat (Januar). Jedoch war eine signifikante Korrelation zwischen Niederschlagswerten und Blütenzahl/Energie nicht nachweisbar. Von den 67 kolibribesuchten Pflanzenarten trugen nur 27 substantiell zur Nektarverfügbarkeit bei: diese Arten blühten mindestens während eines Jahresdrittels (mit weniger als 10% des Gesamtenergieangebotes/Tag) oder sie trugen mindestens zu einem Beobachtungszeitpunkt mehr als 10% zum jeweiligen Gesamtenergieangebot bei. Die vorliegende Untersuchung belegt, dass die durch kolibribesuchte Pflanzen bereitgestellte Energieressource im Bergregenwald Ecuadors einer hohen zeitlichen und räumlichen Variablilität unterliegt.

1. Introduction

Knowledge concerning interactions between species in tropical rainforests is still comparatively limited (Stork 1993, Simon 1995, May 1996). Several authors have emphasized the need for studies on pollination and reproductive biology in the species-rich tropical ecosystems, because these phenomena can be seen as a basic part of the life history of all organisms (Heithaus 1974, Feinsinger 1987, Gentry 1990, Orians & al. 1996). Since pollination by animals is an important phenomenon particularly in the tropics (e.g. Bawa 1979, 1990), investigations of whole plant-pollinator communities are particularly relevant to better understand the functioning of these ecosystems.

Hummingbirds are important vertebrate pollinators in several Neotropical biomes. They cover most of their energy needs by floral nectar, normally presented for a short time and in small quantities by certain flowers (e.g., Baker 1975, Wolf & al. 1976, Kodric-Brown & Brown 1978, Sazima & Sazima 1990, Arizmendi & Ornelas 1990, McDade & Weeks 2004a, 2004b, Lasprilla & Sazima 2004, Machado & Semir 2006, Piacentini & Varassin 2007). Because hummingbirds are able to use almost 100% of the energy provided by the nectar they take up (Hainsworth 1974), a quantification of nectar production allows a close estimation of the food resources available for hummingbirds. Such an estimation of the amount of energy provided by different plant species can be achieved by comparing their nectar and sugar production. Though laborious, determination of the amount of nectar produced per flower and recording the flowering time is manageable.

Competition for limited resources has a key function for the structuring of communities and their diversity. We therefore investigated the dynamics of floral nectar resources of hummingbird-visited plants in a tropical montane rainforest in southern Ecuador. Any variation in temporal and/or spatial nectar production in the hummingbird-visited community should influence the behavior of the birds and their effects on pollination and reproduction of the plants they visit.

2. Material and Methods

The investigation was carried out near the Podocarpus National Park (province of Zamora Chinchipe), in the area of the 'Reserva Biológica San Francisco' (4° 00′ S, 79° 05′ W) in South Ecuador. The study site is located on a slope in NNW to NE exposition, ranging from 1920 to 2100 m a.s.l. altitude and is characterized by a strong inclination (up to 60°). The prevailing humid climate shows little seasonal variation (Bendix & Lauer 1992); the yearly precipitation is up to 2280 mm and average annual temperature is 17° C (Maldonado 1985). The inhomogeneous vegetation is composed of a small-scale mosaic of differently structured, primary montane rainforest.

The 67 hummingbird-visited plant species found in the investigation area belong to 29 genera and 12 families (Table 1). In the investigated area they received visits from 26 species of Trochilidae and additional visits by two species of Coerebidae (honeycreepers) (Dziedzioch & al. 2003).

Temporal changes in nectar resources offered by hummingbird-visited plant species were surveyed on a one hectare area over the course of a full year (October 1998 to October 1999). All plant species were considered on which feeding by hummingbirds was observed. Not all of these "hummingbird-visited" species, however, are necessarily pollinated by hummingbirds. Records were done in two transects of 500 m length and 10 m width at 14-day intervals and included: the verification of plant species in flower, the number of their flowering individuals, and the total number of their open flowers on that day. A three-dimensional description code enabled us to locate individual hummingbird-visited plants without altering the area by tagging or marking. Each plant species was once observed for a minimum of three hours through the study year with respect to records of hummingbird visits. For detailed information about the plant species and their visitors see Dziedzioch & al. 2003.

Nectar samples were taken from all 67 hummingbird-visited plant species. Nectar was collected from flowers which were bagged for 24 h. Nectar extraction was performed with Hamilton syringes (Type 802, 805, 810). For each plant species, the mean of the daily floral nectar secretion (in µl/day) was calculated from samples of at least 10 flowers per species. Species with less than 10 nectar samples are marked with * in Table 1.

The sugar concentration was immediately determined with a pocket refractometer (made and modified for volumes of less than 0.5 µl by Bellingham & Stanley, UK), as sucrose equivalents (sugar concentration in g per 100 g solution). For well accessible plant species with sufficiently abundant flowers, nectar was collected and sugar analyses were accomplished by high-performance liquid chromatography (HPLC), allowing the determination of nectar sugar composition. For each of these plant species, samples were collected as a mixture from ten flowers (2 µl per flower) in a clean plastic container with a known volume of alcohol (70%, for preservation) and kept in a refrigerator until analysis by HPLC. The analyses on a Waters HPLC were performed isocratic using an acetonitril-water mixture (72/28%) as eluent at a flux rate of 1.4 ml/min. A Waters High Performance Carbonhydrate Column was used at 35 °C. Sugars (standards: glucose, fructose, sucrose) were detected with a refraction index detector 410 and quantified with the Millennium 32 Software from Waters (Version 3.5.01).

The energy provided by the nectar was calculated from the mean sugar concentration, as indicated by the refraction index, and the mean nectar volume secreted per day and flower. Hainsworth & Wolf 1972 pointed out that the refraction index of an equimolar concentration of glucose and fructose is approximately half that of equimolar sucrose; glucose and fructose also provide only half the energy of sucrose. Hence the energy content of floral nectar is more or less independent of the nectar sugar composition (Hainsworth & Wolf 1972, Hainsworth 1973). As stated by several authors (e.g., Baker & Baker 1979, Krömer & al. 2008), sucrose is dominant over fructose and glucose in the floral nectar of hummingbird plants. Therefore, we used sucrose equivalents for the energy calculation; the energy content of sucrose (1 µg sucrose provides 0.01648 J) is given by Kearns & Inouye 1993. To change sucrose percentage (g sucrose/g solution) into g sucrose/l nectar, the conversion table of Kearns & Inouye 1993 was used. For calculation of the energy resource the mean was used under the assumption that the values for nectar volume per species would follow a normal distribution, if the number of samples is large enough. Furthermore, a comparison between calculations based on means versus median values did not show major differences for the energy resource.

3. Results

A total of 67 plant species were found to be visited by Trochilidae (hummingbirds), and along the year these species were present with 3186 flowering individuals in the one hectare investigated.

3.1. Nectar Production

1443 nectar samples were taken from the 67 hummingbird-visited plant species (Table 1). The sugar concentration was quite uniform across species with an average sugar content of 18.7% (SD 4.4%) (minimum 5.6%, maximum 29%). Interspecific variation of nectar volume was comparably high. The average nectar volume was 38.6 µl (SD 153.5 µl) per flower per day. The minimal average volume of 0.53 µl was produced by an orchid with small flowers (*Elleanthus bifarius*), whereas the large chiropterophilous flowers of *Ceiba* cf. *pentandra* (*Bombacaceae*) produced a maximum average nectar volume of 1252 µl. If the calculation is done without *Ceiba* cf. *pentandra*, the average nectar volume was 20.2 µl (SD 30.2 µl).

The energy provided as calculated from sugar concentration and nectar volume varied significantly between species, depending mainly on volume variation. The average energy production per day per flower was

Table 1. Hummingbird-visited plants from a tropical montane forest in southern Ecuador, the nectar volume produced by their flowers, the nectar sugar concentration and the energy provided by the sugars. – Abbr. = symbol used for species names, SD = standard deviation, n = number of samples, * = plant species represented by less than 10 nectar samples.

Abbr.	plant species	volume (µl/24h x flower)					sugar concentration % (g/100g)					Energy value (kJ/flower per 24h)
		mean	SD	median	range	n	mean	SD.	median	range	n	mean
A	***Alstroemeriaceae***											
A1	*Bomarea pardina* Herb.	14,1	7,5	14,75	2 - 31,0	26	12,1	1,8	12	9,0 - 18,0	27	29,4
A6	*Bomarea dissitifolia* Baker	2,0	1,7	1,5	0,5 - 6,0	23	23,7	7,4	21,25	13,0 - 38,6	22	8,5
A7	*Bomarea* sp.	13,8	7,6	7	4,0 - 28,0	10	15,2	1,0	15,5	14,0 - 16,0	10	36,5
B	***Bromeliaceae***											
B1	*Vriesea rubeobracteata* Rauh	2,7	2,1	10	1,5 - 10,0	10	14,2	4,3	22	6,0 - 23,8	10	6,6
B5*	*Tillandsia* sp.	5,6	1,6	8	3,0 - 8,0	8	22,1	3,1	21,3	19,0 - 29,1	8	22,1
B7	*Tillandsia complanata* Benth.	10,4	1,9	10	7,5 - 13,0	10	20,6	1,6	20,85	18,4 - 22,8	10	37,9
B9	*Guzmania besseae* H. Luther	77,5	27,6	82	8,0 - 120,0	15	17,7	2,2	18	9,8 - 19,0	15	242,3
B10	*Racinaea undulifolia* (Mez) H. Luther	0,9	0,5	1	0,5 - 2,0	10	24,6	7,5	29	14,0 - 32,0	10	4,0
B11*	*Pitcaimia riparia* Mez	23,5	21,9	23,5	8,0 - 29,0	2	19,5	2,1	19,5	18,0 - 21,0	2	81,5
B12	*Tillandsia confinis* L.B. Sm.	20,1	6,2	20	10,0 - 28,0	11	18,4	3,2	19	11,8 - 23,0	11	65,1
B13*	*Racinaea tetrantha* (Ruiz & Pavon) M. A. Spencer & L. B. Sm	12,6	7,6	13	3,0 - 21,5	6	18,5	2,8	17,2	14,8 - 22,4	9	41,2
B14	*Guzmania gloriosa* (André) André ex Mez	32,3	16,2	27	10,0 - 57,0	10	18,9	2,1	19,4	14,0 - 21,2	10	108,5
B16*	*Racinaea seemannii* (Baker) M.A. Spencer & L.B. Sm.	7,2	5,8	6	0,0 - 35,0	7	18,4	5,0	17,9	10,0 - 27,8	6	23,2
B17	*Pitcaimia* sp.	84,3	60,1	70	5,0 - 281	35	18,5	1,7	19	15,0 - 22,4	38	275,2
B18*	*Bromeliaceae,* gen. sp.	11,0	6,4	11	4,0 - 35,0	9	15,9	4,5	14,2	10,0 - 25,0	8	30,6
B22	*Tillandsia* sp.	21,9	17,0	15,5	2,0 - 56,0	50	17,4	0,8	17,4	13,0 - 19,0	50	66,9
B23	*Tillandsia barbeyana* Wittm.	8,8	2,6	8	4,0 - 16,5	55	23,3	1,9	23,8	17,0 - 26,0	57	37,1
B24	*Vriesea incurva* (Griseb.) Read	6,9	5,4	5,5	1,0 - 15,0	18	22,3	2,8	21,25	19,0 - 27,0	19	27,5
B25*	*Guzmania paniculata* Mez	5,0	0,4	5	4,5 - 5,0	5	21,9	6,4	25	14,0 - 27,5	5	19,7
B27*	*Vriesea appendiculata* (L. B. Sm.) L. B. Sm.	25,2	16,8	19	10,0 - 56,0	6	19,0	6,0	21,35	7,0 - 23,4	6	84,8
B31*	*Guzmania coriostachya* (Grisebach) Mez	14,0	-	-	-	1	20,0	-	-	-	1	49,9
B32*	*Tillandsia truncata* L. B. Sm.	10,8	-	-	-	1	17,0	-	-	-	1	32,3
B33*	*Guzmania* aff. *killipiana* L.	17,5	10,6	17,5	10,0 - 25,0	2	21,0	2,8	21	19,0 - 23,0	2	65,8
B35*	*Guzmania confusa* L. B. Smith var. *foetida* Rauh	18,6	-	-	-	1	21,0	-	-	-	1	69,9
BO	***Bombacaceae***											
BO1*	*Ceiba* cf. *pentandra* (L.) Gaertn.	1252,0	411,2	1440	620 - 1740	9	11,6	1,6	11,9	9,5 - 13,2	9	2502,2
CL	***Clusiaceae***											
CL1*	*Clusia alata* Triana & Planch.	10,8	5,7	9,5	5,0 - 20,0	6	13,3	2,6	13,5	11,0 - 17,0	6	24,4
E	***Ericaceae***											
E2	*Orthaea* cf. *abbreviata* Drake	19,9	14,2	21	0,0 - 64,0	169	16,3	2,2	17	10,0 - 24,0	278	57,1
E3	*Cavendishia nobilis* Lindl. var. *capitata* (Benth.) Luteyn	31,7	12,5	29	16,0 - 66,0	20	14,7	2,6	14,9	9,7 - 18,2	24	81,2
E8	*Macleania mollis* A. C. Smith	10,7	6,9	9	2,0 - 32,0	51	18,7	1,7	19	14,0 - 23,8	69	35,6
E10	*Ceratostema reginaldii* (Sleumer) A. C. Smith	35,9	25,6	45	3,0 - 75,0	11	18,7	2,0	19	16,0 - 21,0	11	118,8
E11*	*Semiramisia speciosa* (Benth.) Klotzsch	187,3	27,7	180	141 - 230	9	19,1	0,7	19	18,0 - 20,0	9	636,0

E13	*Thibaudia floribunda* H.B.K.	8,0	5,6	7	0,0 - 26,0	137	16,3	2,0	16,5	9,0 - 25,0	165	22,9
E15	*Psammisia guianensis* KLOTZSCH	15,4	11,1	16	0,0 - 60,0	44	21,4	2,4	22	14,0 - 25,0	48	59,1
E16	*Cavendishia* cf. *bracteata* (RUIZ & PAV. ex J. ST.-HIL.) HOEROLD	21,0	11,1	19,5	4,5 - 46,0	36	18,4	2,0	18,8	8,8 - 22,0	66	68,0
E17	*Oreanthes hypogaeus* A. C. SMITH	7,4	2,6	7	4,0 - 12,0	10	17,8	1,2	18	15,0 - 18,0	10	23,3
E21*	*Ericaceae*, gen.,sp.	18,7	-	-	-	1	18,6	-	-	-	1	61,7
G	***Gesneriaceae***											
G2	*Drymonia urceolata* WIEHLER	12,9	7,6	9	5,0 - 31,0	12	21,4	3,2	21	17,0 - 28,8	12	49,6
G5*	*Columnea inaequilatera* POEPP.	15,3	9,6	14	7,0 - 35,0	7	16,8	5,4	17	7,0 - 24,2	7	45,1
G6	*Columnea strigosa* BENTH.	9,2	10,7	5	0,5 - 38,0	29	19,0	6,0	21	7,0 - 29,5	27	31,1
G7*	*Dalbergaria* aff. *villosissima* (MAUSF.) WIEHLER	62,0	26,9	62	43,0 - 81,0	2	25,7	2,7	17	23,8 - 27,6	2	291,0
G8*	*Dalbergaria* aff. *archidonae* (CUATR.) WIEHLER	57,0	-	-	-	1	23,8	-	-	-	1	245,7
G11*	*Besleria* sp.	11,2	-	-	-	1	19,5		-	-	1	38,8
Ge	***Gentianaceae***											
Ge1*	*Symbolanthus calygonus* (RUIZ & PAV.) GRISEB. ex GILG	70,0	18,3	70	50,0 - 90,0	4	20,0	2,1	19	18,6 - 19,5	3	249,4
Ge3	*Macrocarpaea harlingii* J. S. PRINGLE	117,8	33,0	110	50,0 - 180	18	15,6	1,4	15,7	13,2 - 17,4	18	321,5
Ge5*	*Marcrocapaea* sp.	25,3	-	-	-	1	21,2	-	-	-	1	95,1
L	***Lobeliaceae***											
L3*	*Siphocampylus scandens* (KNUTH) G. DON	5,3	4,0	6	0,5 - 11,0	6	10,8	5,2	9	5,0 - 19,0	6	9,8
L10*	*Siphocampylus* sp.	24,4	-	-	-	1	12,9	-	-	-	1	54,4
M	***Moraceae***											
M1*	*Moraceae*, gen., sp.	1,0	-	-	-	1	18,0		-	-	1	3,2
OR	***Orchidaceae***											
OR4	*Elleanthus maculatus* (LINDL.) RCHB. f.	11,7	6,4	11	4,0 - 24,0	11	21,2	4,7	20	14,5 - 29,0	21	44,5
OR6	*Maxillaria aurea* (POEPP. & ENDL.) L. O. WILLIAMS	2,1	2,3	1	0,5 - 7,0	11	8,6	2,6	9,25	5,0 - 12,8	8	3,1
OR7	*Maxillaria jamesonii* (RCHB.f.) GARAY & C. SCHWEINF.	1,6	1,6	1	0,5 - 7,5	27	13,3	5,5	16	3,4 - 20,0	18	3,7
OR8	*Elleanthus* sp.	7,5	8,2	4	1,0 - 35,0	25	21,0	4,8	19,5	15,0 - 29,0	12	28,0
OR11	*Masdevallia deformis* KRAENZL.	1,9	1,0	5	0,5 - 5,0	62	23,1	5,9	23	7,0 - 35,0	47	7,9
OR13	*Elleanthus bifarius* GARAY	0,5	0,1	0,5	0,5 - 1,0	16	25,4	8,5	24,5	11,0 - 40,0	14	2,5
OR14*	*Maxillaria* sp.	4,4	2,3	3,23	2,0 - 8,0	8	5,6	2,3	5,2	3,1 - 8,0	8	4,1
OR15*	*Maxillaria* sp.	8,0	1,4	4	2,0 - 6,0	2	20,5	5,0		17,0 - 24,0	2	29,2
OR21*	*Elleanthus amethystinoides* GARAY	6,4	-	-	-	1	21,0	-	-	-	1	24,0
OR28*	*Elleanthus* sp.	3,2	-	-	-	1	23,0	-	-	-	1	13,3
OR29*	*Elleanthus* sp.	1,5	-	-	-	1	29,0	-	-	-	1	8,0
OR30*	*Maxillaria* sp.	1,0	0,8	1	0,5 - 1,5	2	23,0	-	-	-	1	4,1
OR31	*Maxillaria* sp.	2,7	3,1	2,5	1,0 - 21,5	15	20,5	3,6	20	13,0 - 27,5	10	9,8
P	***Polemoniaceae***											
P1*	*Cantua* sp.	8,2	-	-	-	1	18,0	-	-	-	1	26,1
R	***Rubiaceae***											
R3	*Palicourea luteonivea* C. M. TAYLOR	12,1	4,0	11	5,0 - 12,0	49	18,3	2,4	19	13,0 - 25,0	75	38,9
R5	*Palicourea canarina* C. M. TAYLOR	14,7	10,1	12	1,0 - 38,0	97	8,9	2,6	9	4,0 - 14,0	90	22,2
R6*	*Palicourea angustifolia* H.B.K	6,8	3,8	6	3,0 - 13,0	9	15,1	3,5	16,4	7,0 - 19,0	9	18,0
R8	*Rubiaceae* , gen., sp.	9,1	5,6	7	1,0 - 22,0	10	18,3	2,4	18	13,0 - 25,0	10	29,5
R10*	*Palicourea subtomentosa* (RUIZ & PAV.) C.M. TAYLOR subsp. *lojana* C. M. TAYLOR	1,7	0,8	1,5	1,0 - 3,0	7	28,8	4,3	27,5	25,0 - 34,0	6	9,0

103.2 J (minimum 2.5 J, maximum 2502 J). Comparing the three most abundant families, *Ericaceae* showed the highest average energy production with 116.4 J (SD 184.8 J) per flower per day, whereas bromeliads offered 66.3 J (SD 69.6 J), and orchids only 14.0J (SD 13.2 J).

For 29 plant species, an HPLC-analysis of the sugar composition was performed (Table 2).Two plant species showed only sucrose, in all other 27 species sucrose was predominant, followed by glucose and fructose.

3.2. Resource Dynamics

The temporal resource dynamics of the hummingbird-visited plants were remarkably high (Tables 1 and 3, Fig. 1) and accompanied short-time changes in amount and composition of the nectar. Variation depended on the level of organisation: the number of flowering species varied 1.7-fold between 17 and 29, the number of flowering individuals varied 6-fold, and the number of flowers varied 22-fold. This resulted in a 20-fold variation in energy production. On average over the year, 23.0 (SD 3.5) flowering species had 378.0 (SD 191.4) flowering individuals, presenting 2219.0 (SD 2134.7) flowers that offered 81.7 (SD 89.3) kJ/ha per day. Based on flower numbers and energy content, the maximum of resources was offered during the rainy period in April, whereas the minimum was observed in the drier January. Maximum and minimum were calculated using the numbers of flowers and energy production, because these factors are more strongly determining the hummingbird community than just the numbers of flowering species or individuals.

Although there was a significant correlation between precipitation and number of flowering species, no significant correlation was detected between precipitation and number of flowering individuals, number of flowers or energy production (Table 3).

As it is to be expected, the number of flowering individuals, the number of flowers, and nectar volume were unevenly distributed among plant species (data for April given as an example; see Fig. 2). For example, considering flowering individuals, two species were dominant in April: *Elleanthus maculatus* and *Tillandsia confinis*. Both species had their main flowering period during the rainy period in April when 80% of their individuals were in flower. Within that period, these two species represented 62% of all flowering individuals of all species (38% *E. maculatus*; 24% *T. confinis*). However, considering the number of flowers, a third species codominated in April: *Orthaea* cf. *abbreviata* (*Ericaceae*) provided many flowers albeit presenting only a few flowering individuals. The three species together were responsible for 85% of all open flowers (*E. maculatus* 56%, *O.* cf. *abbreviata* 17%, *T. confinis* 12%). And finally, at the level of nectar production per species per ha and day, a member of the family of *Gentianaceae* (*Macrocarpaea harlingii*) was conspicuous, offering a high

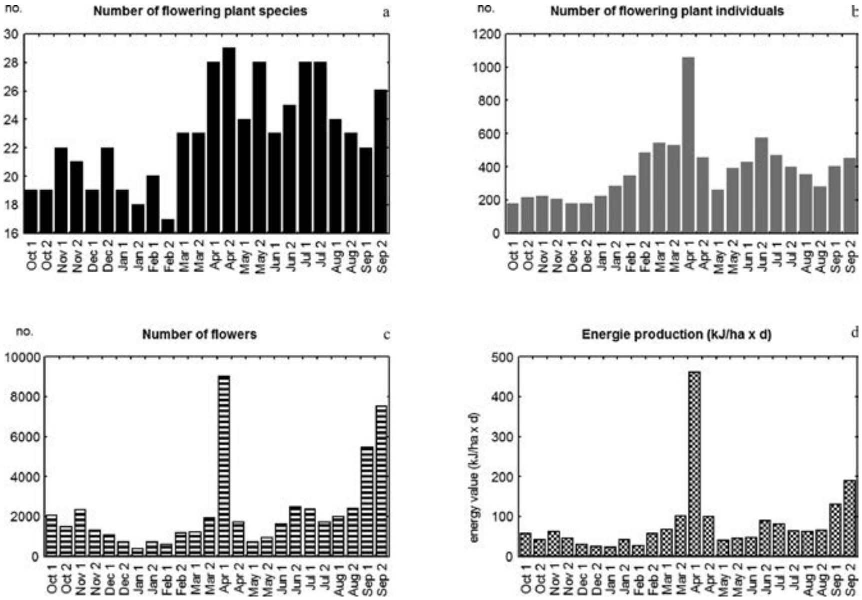

Fig. 1. Dynamics of floral nectar resources based on two-weekly records for each month (e.g. Oct 1 and Oct 2). – a. Number of species in flower. – b. Number of individuals in flower. – c. Total number of open flowers of all individuals. – d. Energy produced by all open flowers at the respective record date (kJ/ha x d).

nectar volume with only few flowers on few flowering individuals. In the first half of April, these four species together were responsible for 92% of total nectar production.

In contrast to the flowering maximum in April the minimum is not as easily to be determined: regarding the number of flowers (396) and the energy value (22.71kJ/ha per d) the minimum falls into January, whereas on the level of flowering individuals the minimum would be the first half of October (174) and, regarding flowering species, the second half of February (17). As for the hummingbirds the offered energy value is the most important variable the minimum resource availability is in the first half of January, being nearly 20 times lower than in April (461.53 kJ/ha per d). During this minimum period only one plant species (*Tillandsia confinis*) dominates the resource offer on the levels of flowering individuals, number of flowers and energy value, although *T. confinis* has not its flowering maximum in January.

At any given data record, only a few species dominated energy production (Fig. 2). In most data records, 1–4 species were the dominant energy producers. The contribution of a plant species to the total energy production on different levels of investigation can be analysed by temporal

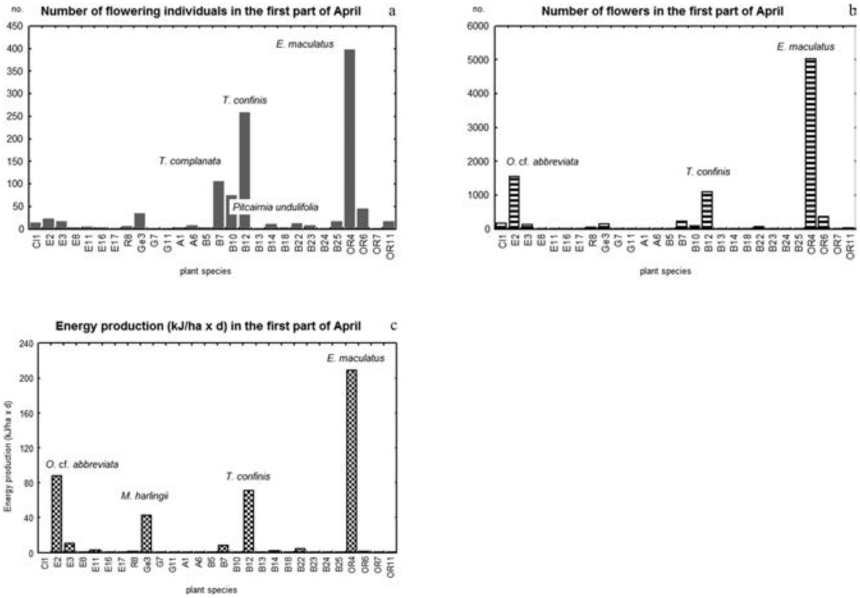

Fig. 2. Example of dynamics of floral nectar resources for the first half of April. – a. Number of flowering individuals. – b. Total number of open flowers of all individuals. – c. Energy produced by all open flowers. – Note that several values are so low that they do not show up in the graph. – E = *Elleanthus*, M = *Macrocarpaea*, O = *Orthaea*, T = *Tillandsia*.

or quantitative approaches. To qualify a plant species as a **C**onsiderable **N**ectar **S**ource (CNS-species), we defined the following criteria: it either contributed at least during one third of the year (i.e. eight out of 24 data records) to the produced energy or it contributed in at least one record more than 10% to the total energy produced at that record. The majority (63%) of the species failed to fulfill any of these CNS criteria. The 27 species of six families (dominated by *Ericaceae* and *Bromeliaceae*) which were CNS are listed in Table 4. According to the criteria explained above, the CNS-species fall into two groups: 13 species contributed continuously for at least eight records, but never reached more than 10% (pattern 1), while the other 14 species peaked with over 10% energy contribution in at least one record. Within the second group, some species like *Elleanthus maculatus* (OR4) or *Orthaea* cf. *abbreviata* (E2) contributed for a short time only but with many individuals or flowers. Others, especially four members of the *Bromeliaceae* and *Rubiaceae*, flowered for longer periods with a high contribution (highlighted in grey in Table 4). Outstanding was *Tillandsia confinis*, a species which contributed more than 30% energy during a quarter of its flowering time and twice even reached more than 80% of the total energy production.

Table 2. Percentage of sugar content (S= sucrose, F= fructose, G= glucose) in the nectar of 29 hummingbird-visited plants.

hummingbird-visited plant species	**fructose (%)**	**glucose (%)**	**sucrose (%)**	**S/(F+G)**
Bomarea pardina	40,2	4,3	55,5	1,2
Bomarea setacea	19,4	1,8	78,8	3,7
Guzmania besseae	19,0	17,8	63,3	1,7
Guzmania gloriosa	12,6	13,4	74,0	2,8
Pitcairnia sp.	14,4	15,2	70,3	2,4
Racinaea tetrantha	37,9	38,6	23,5	0,3
Tillandsia barbeyana	16,4	14,8	68,9	2,2
Tillandsia complanata	15,2	14,1	70,7	2,4
Tillandsia confinis	12,4	10,8	76,8	3,3
Cavendishia cf. *bracteata*	7,6	7,0	85,4	5,8
Cavendishia nobilis var. capitata	3,9	3,3	92,8	12,8
Ceratostema reginaldii	5,9	3,3	90,8	9,9
Macleania mollis	4,0	3,6	92,4	12,1
Oreanthes hypogaeus	1,4	1,8	96,8	30,6
Orthaea cf. *abbreviata*	7,4	4,4	88,2	7,5
Psammisia guianensis	14,5	11,5	74,0	2,9
Semiramisia speciosa	0,0	0,0	100,0	–
Thibaudia floribunda	3,5	3,5	93,0	13,3
Columnea inaequilatera	18,4	6,7	74,9	3,0
Columnea strigosa	14,5	2,2	83,2	5,0
Dalbergaria aff. *villosissima*	17,4	1,2	81,5	4,4
Drymonia urceolata	19,1	8,5	72,4	2,6
Macrocarpaea harlingii	38,2	33,0	28,8	0,4
Siphocampylus sp.	34,4	3,6	62,0	1,6
Elleanthus maculatus	2,9	2,6	94,5	17,2
Maxillaria aurea	0,0	0,0	100,0	–
Palicourea angustifolia	16,4	14,7	69,0	2,2
Palicourea luteonivea	20,6	14,0	65,4	1,9
Palicourea sulphurea	30,5	19,8	49,7	1,0

4. Discussion

The typical nectar sugar concentration of plants specialised for hummingbird pollination is considered to be approximately 20% (Baker 1975). The average of 18.8% (SD 4.4%) found in the present study corresponds to this expectation and gave among other floral features reason to the presumption that most of the hummingbird-visited plants were really ornithophilous (exceptions are the chiropterophilous *Ceiba* cf. *pentandra* and the supposedly melittophilous *Clusia alata*). As nectar viscosity not only depends on sugar concentration but also on temperature, Hainsworth & Wolf 1972, Cruden & al. 1983, and Freeman & Head 1990 assumed a decreasing sugar concentration with increasing altitude in order to keep viscosity constant despite declining temperatures. The average of nearly 19% nectar sugar concentration at the study site at 2000 m a.s.l. was not so different from the results of other studies, with 23.5% (Kraemer 1998) and 19.8% (Cotton 1998) for lowland forests, 16.3% for a forest at 2200-2400 m a.s.l. (Schmitt 2000), and only 14.5% for páramo vegetation (Kraemer & Schmitt 1991; see also McDade & Weeks 2004a, Lasprilla & Sazima 2004). Nectar collected from ornithophilous *Bromeliaceae* mainly from

Table 3. Numbers of species, individuals and open flowers, and the total of energy provided at the respective record date.

record	no. of species	no. of individuals	no. of open flowers	energy value (kJ/ha per d)	precipitation (mm)
Oct 1	19	174	2069	57,73	47
Oct 2	19	212	1507	42,44	85
Nov 1	22	222	2343	61,73	45
Nov 2	21	206	1321	45,45	76
Dec 1	19	175	1075	29,38	0
Dec 2	22	178	719	25,08	163
Jan 1	19	220	396	22,71	28
Jan 2	18	285	764	42,13	197
Feb 1	20	344	633	26,41	54
Feb 2	17	484	1175	57,65	85
Mar 1	23	540	1220	67,59	71
Mar 2	23	530	1937	101,78	126
Apr 1	28	1055	9028	461,53	183
Apr 2	29	456	1719	101,38	233
May 1	24	258	767	40,20	160
May 2	28	389	940	45,70	159
Jun 1	23	425	1609	46,96	187
Jun 2	25	572	2472	89,71	85
Jul 1	28	467	2409	80,57	92
Jul 2	28	397	1733	64,35	146
Aug 1	24	353	1985	61,85	96
Aug 2	23	277	2434	65,43	77
Sep 1	22	399	5463	131,04	45
Sep 2	26	449	7519	191,23	79

correlations	Spearman R	p-Level
no. of species / no. of individuals	0,555	< 0,01
no. of species / no. of flowers	0,469	< 0,05
no. of species / energy value	0,585	< 0,01
no. of species / precipitation	0,483	< 0,05
no. of. flowers / no. of individuals	0,935	< 0,001
no. of. flowers / energy value	0,439	< 0,05
no. of. flowers / precipitation	–0,047	n,s,
no. of individuals / energy value	0,67	< 0,001
no. of individuals / precipitation	0,352	n,s,
energy value / precipitation	0,126	n,s,

plants grown in tropical glasshouses had a comparable sugar concentration of 20.1% (SD 3.9%) (Krömer & al. 2008). The general tendency seems indeed a decrease in sugar concentration with increasing altitude in floral nectar of bird-pollinated plants.

Although nectar has very different components (Baker 1975), the sugars sucrose, fructose, and glucose are quite regularly present (Baker & Baker 1979, Stiles & Freeman 1993). The sugar composition found in the nectar of a plant species is more or less species-specific and varies only slightly due to environmental conditions (Freeman & Head 1990, Villarreal & Freeman 1990). Within the 29 plant species whose sugars were determined, in 27 sucrose dominated over glucose and fructose, while in 2 species sucrose was found exclusively. This parallels the results of Baker & Baker 1990, Stiles & Freeman 1993, Krömer & al. 2008 and Schmid & al.

Table 4. List of the 27 species that were considerable nectar sources, either contributing nectar continuously for at least eight data records but not reaching 10% of the total nectar production (pattern 1), or reaching at least 10% of the total nectar production for at least one recording date during the year (pattern 2). – Plant species abbreviations as in Table 1.

	plant species	**no. of records**	**Contribution to the nectar supply**								
			0–10%	**10–20%**	**20–30%**	**30–40%**	**40–50%**	**50–60%**	**60–70%**	**70–80%**	**>80%**
pattern 1	**B14**	8	8								
	OR11	8	8								
	E10	9	9								
	OR7	9	9								
	B23	11	11								
	B25	12	12								
	B1	13	13								
	B22	13	13								
	E8	14	14								
	A6	17	17								
	E16	19	19								
	B5	19	19								
	B1	20	20								
pattern 2	**R8**	6	4		1			1			
	B13	8	7	1							
	B27	8	2	3		1	1	1			
	OR4	9	6	2			1				
	Ge3	9	5	3	1						
	R3	10	5	1	2	2					
	E13	11	8		1				2		
	R6	12	5	3	1	2	1				
	B12	13	3	4	1		1	1	1		2
	E15	16	13	1	2						
	E3	16	12	3	1						
	E11	16	9	3	3	1					
	E2	20	16	2	2						
	B7	23	22	1							

2011 who documented sucrose dominance in nectar preferred by hummingbirds. For discussion of effects when nectar is removed during anthesis, see, e.g., McDade & Weeks 2004a and Ordano & Ornelas 2004.

Although seasonality in the tropics is not as pronounced as at higher latitudes, many studies showed relatively strong temporal rhythms for plants and animals even in aseasonal tropical lowland forests (e.g., Wolf 1970, Stiles 1985, van Schaik & al. 1993, Szarzynski & al. 2000). Differences in precipitation or sun intensity are thought to be responsible for these rhythms. Thus, strong dynamics of nectar resources of the hummingbird-visited plants in the montane rainforest of Ecuador were to be expected as well. Trochilid activity is closely related to the flowering rhythms of plants because nectar covers most of their energy needs (Wolf 1970). Although nectar is available as a resource throughout the entire year, there is however a strong variability with a maximum of energy production at our study site occurring in rainy April and a minimum in dry January. These results support that of Schmitt 2000. However, no significant correlation between amount of precipitation and the total energy resources could be shown in our study.

Energy resources from nectar showed high short-time variability. One extreme case was the more than fourfold increase within only two weeks in April caused by the abundant flowering of *Elleanthus maculatus*. Other abrupt increases or decreases were caused by the unsteady flowering of several species of *Ericaceae*. STILES 1980 and SNOW 1981 stated with respect to hummingbirds that life phases with high energy costs like reproduction, moulting, or migration should be synchronized with food resources. However, it seems improbable that hummingbirds living in such species-rich communities can react or adapt to such short-time variations as were observed in the present study. Also MONTGOMERIE & GASS 1981 doubted that hummingbirds are able to closely adapt their high energy consuming life phases to strongly varying local food resources.

In addition to variation of the total amount of nectar resources at the study site, there is also strong variation of the contribution of each plant species to these nectar resources along the year. However, the main part of the total resource was provided by only 1-4 plant species. In total, only 27 of 67 hummingbird-visited plant species were classified as considerable nectar resources. Of these species, 13 flowered at least for one third of the year but never reached more than 10% of the total energy resource, while another 14 contributed at least at one record date more than 10% to the total energy production. Within the latter 14 species (which consisted mainly of members of *Bromeliaceae, Ericaceae,* and *Rubiaceae*), two patterns or strategies were detected: The first group was characterised by few individuals providing many flowers for a short time. Most members of the *Ericaceae* belonged to that group. The second group comprised species that contributed at least 10% of total resources for more than half of their flowering time. Consequently, these plants provided a reliable nectar resource over longer periods. *Bromeliaceae* and *Rubiaceae* species with many individuals and extended flowering phases followed this pattern. In particular, resident hummingbird species were observed visiting plants of the latter pattern, underlining the importance of a constant nectar resource for at least the more resident bird species. Notwithstanding, the high seasonal variability and the constantly changing composition of food resources force hummingbirds to be flexible in their foraging behavior and management of their energy budget (see also TIEBOUT 1991 and MCDADE & WEEKS 2004b).

Although epiphytes were the dominant nectar-providing life form throughout most of the year, this dominance changed in the drier months between September and December. During this period, phanerophytes dominated, represented by four understory tree species, three of them belonging to the *Rubiaceae* family, and one to the *Ericaceae* (*Thibaudia floribunda*).

In conclusion, the energy resources provided by hummingbird-visited plants in the investigated Ecuadorian montane forest showed a high temporal and spatial variability characterised by short-time changes in the total amount of resources and the contribution of different plant species, mainly in the subcanopy and understory. Responsible for these rapid changes were plant species, mostly *Ericaceae*, with few individuals providing many flowers for a short period. These plants have irregular flowering periods so that nectar resources provided by them are hard to predict. Most members of the *Bromeliaceae* on the other hand, also an important plant family with regard to nectar resources, are known to flower just once at the end of their life and thus do not follow a yearly reproductive cycle. This supports the results of STILES 1977 who investigated the yearly changing flowering periods of species visited by shade hummingbirds (hermits) in lowland rainforests in Costa Rica. Altogether, the dynamics of nectar resources in an Andean montane forest probably do not follow a yearly pattern. Thus, although our study demonstrated a high temporal and spatial variability of nectar resources, there was no clear seasonal or other pattern detectable. Quite contrarily, the results of our study are indicative that there is no clear yearly rhythm but a rhythm that changes from year to year.

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6. References

ARIZMENDI M. DEL CORO & ORNELAS J. F. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. – Biotropica 22 (2): 172–180.

BAKER H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. – Biotropica 7(1): 37–41.

BAKER H. G. & BAKER I. 1979. Sugar ratios in nectar. – Phytochem. Bull. 12: 43–45.

BAKER H. G. & BAKER I. 1990. The predictive value of nectar chemistry to the recognition of pollinator types. – Israel J. Bot. 39: 157–166.

BAWA K. S. 1979. Breeding systems of trees in a tropical wet forest. – New Zeal. J. Bot. 17: 521–524.

BAWA K. S. 1990. Plant-pollinators interaction in tropical rain forests. – Annual Rev. Ecol. Syst. 21: 399–422.

BENDIX J. & LAUER W. 1992. Die Niederschlagsjahreszeiten in Ecuador und ihre klimadynamische Interpretation. – Erdkunde 46: 118–134.

COTTON P. A. 1998. The hummingbird community of lowland Amazonian rainforest. – Ibis 140: 512–521.

Cruden R. W., Hermann S. M. & Peterson S. 1983. Pattern of nectar production and plant-pollinator coevolution. – In: Bentley B. & Elias T. (eds.), The biology of nectaries, pp. 80–125. – Columbia University Press, New York.

Dziedzioch C., Stevens A.-D. & Gottsberger G. 2003. The hummingbird plant community of a tropical montane rain forest in southern Ecuador. – Plant Biol. 5: 331–337.

Feinsinger P. 1987. Approaches to nectarivore-plant interactions in the New World. – Revista chilena Hist. natur. 60: 285–319.

Freeman C. & Head K. 1990. Temperature and sucrose composition of floral nectars in *Ipomopsis longiflora* under field conditions. – Southwestern Naturalist 35: 423–426.

Gentry A. H. 1990. Evolutionary patterns in Neotropical *Bignoniaceae*. – Mem. New York bot. Gard. 55: 118–129.

Hainsworth F. R. 1973. On the tongue of a hummingbird: its role in the rate and energetics of feeding. – Comp. Biochem. Physiol. 46: 65–78.

Hainsworth F. R. 1974. Food quality and foraging efficiency: the efficiency of sugar assimilation by hummingbirds. – J. comp. Physiol. 88: 425–431.

Hainsworth F. R. & Wolf L. L. 1972. Energetics of nectar extraction in a small, high altitude, tropical hummingbird, Selaphorus flammula. – J. comp. Physiol. 80: 377–387.

Heithaus E. R. 1974. The role of plant pollinator interactions in determining community structure. – Ann. Missouri bot. Gard. 61: 675–691.

Kearns C. A. & Inouye D. W. 1993. Techniques for pollination biologists. – Univ. Press, Colorado.

Kodric-Brown A. & Brown J. H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. – Ecology 59: 285–296.

Kraemer M. 1998. Struktur und Dynamik der Pflanzen-Kolibrigemeinschaft von Bajo Calima, Kolumbien. – Cuvillier-Verlag, Göttingen.

Kraemer M. & Schmitt U. 1991. Interaktionen zwischen andinen Kolibris (Trochilidae) und ihren Nahrungspflanzen im Páramo de Los Dominguez, Cordillera Central, Columbien. – Unpubl. Diploma thesis, University of Bonn.

Krömer T., Kessler M., Lohaus G., & Schmidt-Lebuhn A. N. 2008. Nectar sugar composition and concentration in relation to pollination syndromes in *Bromeliaceae*. – Plant Biol. 10: 502–511.

Lasprilla L. R. & Sazima M. 2004. Intracciones planta-colibrí en tres comunidades vegetales en la parte suroriental del Parque Nacional Natural Chiribiquete, Colombia. – Ornitol. Neotrop. 15 (Suppl.): 183–190.

Machado C. G., & Semir J. 2006. Flowering phenology and floral biology of some ornithophilous *Bromeliaceae* of an Atlantic Forest area in southeastern Brazil. – Revista bras. Bot. 29: 163–174.

Maldonado A. N. 1985. Contribución al estudio del clima en la provincia de Loja. – Rev. Estudios Univ., Universidad nacional de Loja, 1: 11–140.

May R. M. 1996. Introduction – In: Hochberg M. E., Clobert J. & Barbault R. (eds.), Aspects of the genesis and maintenance of biological diversity, pp. 1–15. – Oxford Univ. Press, Oxford.

McDade L. A. & Weeks J. A. 2004a. Nectar in hummingbird-pollinated Neotropical plants I: Patterns of production and variability in 12 species. – Biotropica 36: 196–215.

McDade L. A. & Weeks J. A. 2004b. Nectar in hummingbird-pollinated Neotropical plants II: Interactions with flower visitors. – Biotropica 36: 216–230.

Montgomerie R. D. & Gass C. L. 1981. Energy limitation of hummingbird populations in tropical and temperate communities. – Oecologia 50: 162–165.

Ordano M. & Ornelas J. F. 2004. Generous-like flowers: nectar production in two epiphytic bromeliads and a meta-analysis of removal effects. – Oecologia 140: 495–505.

Orians G. H., Dirzo R. & Cushman J. H. 1996. Introduction. – In: Orians G. H. & Dirzo R. (eds.), Biodiversity and ecosystem processes in tropical forests, pp. 1–9. – Springer, Berlin, Heidelberg.

Piacentini V.D. Q. & Varassin I.G. 2007. Interaction network and the relationships between bromeliads and hummingbirds in an area of secondary Atlantic rain forest in southern Brazil. – J. trop. Ecol. 23: 663–671.

Sazima M. & Sazima I. 1990. Hummingbird pollination in two species of *Vellozia* (*Liliiflorae: Velloziaceae*) in southeastern Brazil. – Bot. Acta 103: 83–86.

Schaik C. P. van, Terborgh J. W. & Wright S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. – Annual Rev. Ecol. Syst. 24: 353–377.

Schmid S., Schmid V., S., Zillikens A., Harter-Marques B. & Steiner J. 2011. Bimodal pollination system of the bromeliad *Aechmea nudicaulis* involving hummingbirds and bees. – Plant Biol. 13 (Suppl. 1): 41–50.

Schmitt U. 2000. Die Pflanzen-Kolibri-Gemeinschaft im Bergregenwald der Farallones de Cali, Reserva Natural Hato Viejo, Kolumbien. – Cuvillier-Verlag, Göttingen.

Simon H.-R. 1995. Arteninventar des Tierreiches. Wieviele Tierarten kennen wir? – Naturwissenschaftlicher Verein Darmstadt – Berichte 17: 103–121.

Snow D. W. 1981. Coevolution of bird and plants. – In: Forey P. L. (ed.), The evolving biosphere, pp 169–178. – Brit. Mus. Natur. Hist., Cambridge.

Stiles F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. – Science 198: 1177–1178.

Stiles F. G. 1980. Ecological and evolutionary aspects of bird-flower coadaptation. – In: Snow D. W. & Bock W. J. (eds.), Symposium on Co-Evolutionary Systems in Birds, ACTA XVII Congressus Internationalis Ornithologici, Bd. II. – Verlag der Deutschen Ornithologischen Ges., Berlin.

Stiles F. G. 1985. Seasonal patterns and coevolution in the hummingbird-flower community of a Costa Rican subtropical forest. – Ornithol. Monogr. 36: 757–785.

Stiles F. G. & Freeman C. E. 1993. Patterns in floral nectar characteristics of some bird-visited plant species from Costa Rica. – Biotropica 25: 191–205.

Stork N. E. 1993. How many species are there? – Biodiversity and Conservation 2: 215–232.

Szarzynski J., Engwald S., Schmit-Neuerburg V., Barthlott W. & Anhulf D. 2000. El Niño 1997/98: ein diversitätssteuernder Faktor bei Epiphyten im Kronenraum eines amazonischen Regenwaldes in Venezuela? – Jahrestagung Ges. Tropenökologie (gtö), Würzburg. Abstracts: p. 48.

Tiebout H. M. 1991. Daytime energy management by tropical hummingbirds: responses to foraging constraint. – Ecology 8: 199–210.

Villareal A. G. & Freeman C. E. 1990. Effects of temperature and water stress on some floral nectar characteristics in *Ipomopsis longiflora* (*Polemoniaceae*) under controlled conditions. – Bot. Gaz. 151: 5–9.

Wolf L. L. 1970. The impact of seasonal flowering of the biology of some tropical hummingbirds. – Condor 72: 1–14.

Wolf L. L., Stiles G.F. & Hainsworth F.R. 1976. Ecological organisation of tropical highland hummingbird community. – J. Animal Ecol. 45: 349–380.

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Artikel/Article: Dynamics of Nectar Recources of Hummingbird-visited Plants in a Montane Forest of Southern Ecuador 121-138