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Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands

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Abstract As for many other taxa, hummingbird diversity declines away from the equator, but the causes for this decline are still disputed and might involve, among others, climatic factors or the availability of food resources. Because hummingbirds are one of the classical examples for plant–animal coevolution, it has been proposed that the diversity of hummingbird assemblages might depend on the diversity of food plants available. We tested this hypothesis by studying the hummingbird assemblages and their food plants for 1 year at six sites along a 660-km-long transect in Bolivian lowland forests extending from the southernmost Amazonian rain forests to dry Chaco forests. Hummingbird diversity was higher in the northern three sites as compared to the southern ones, with an abrupt decline in species numbers and a corresponding change in taxonomic composition at the boundary from evergreen to drought deciduous forests. Hummingbird diversity and abundance were only weakly correlated to climatic factors or to the diversity of humming-visited flowers, but strongly to the seasonal abundance of flowers. The overlap in nectar diet between hummingbird species depended on the number of plant species: when numerous species were available, the hummingbirds segregated by feeding preferences, but when few flowers were available, all hummingbirds fed on the same plants. We conclude that the local diversity of hummingbird species is not primarily determined by the diversity of food plants, but rather by the abundance of flowers available at any given point in time.

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Introduction

The causes determining geographical patterns of species richness remain debated (e.g., Rahbek and Graves 2001; Currie et al. 2004; Hawkins et al. 2007). One of the most commonly documented relationships is the decline of species richness of major taxonomic groups away from the Equator. This decline goes along with decreasing temperatures and precipitation (e.g., Flores-Rodriguez et al. 2007; Keil et al. 2008; Buisson et al. 2008). However, the mechanisms leading to this relationship are still poorly explored, and may involve both evolutionary and historical aspects, such as phylogenetic niche conservatism of taxa that originated in the tropics (Wiens and Donoghue 2004; Wiens et al. 2009; Kissling et al. 2009) or current ecological factors that limit the number of species that can co-occur in a given ecosystem (e.g., H-Acevedo and Currie 2003; Evans et al. 2009; Kissling et al. 2009). Much of the argument resolves around the idea that climatic conditions strongly influence plant development and hence ecosystem productivity, and that ecosystems with higher productivity have quantitatively and qualitatively more resources that can be partitioned onto species (Evans et al. 2005). Yet, few of the different potential mechanisms by which this partitioning may be achieved have been studied in detail (Evans et al. 2005).

Among the major taxonomic groups, birds may be the most intensively studied for both large-scale (e.g., Rahbek 1997; Jetz and Rahbek 2001; Hawkins et al. 2003; Rahbek et al. 2007) and small-scale patterns of species richness

(e.g., Hennessey et al. 2003; Macleod et al. 2005; Abrahamczyk et al. 2008), mainly because they are the taxonomically and biogeographically best-known major group of organisms (Bibby et al. 2000). Several studies have shown that the diversity of birds in general is weakly correlated to the diversity and abundance of plants at broad scales (Currie 1991; Kissling et al. 2007, 2008), while at the local scale correlations tend to be moderately high (e.g., Schulze et al. 2004; Sodhi et al. 2005). The causes for these relationships are uncertain, and may involve the use of plant resources (mainly fruits and nectar) by birds (Kissling et al. 2007), niche diversity as mediated by structural vegetation complexity (Verschuyl et al. 2008), or shared physiological traits or evolutionary histories that may cause a covariance of species numbers between the taxa without a direct causal link (Kissling et al. 2007, 2008). Untangling these relationships will depend on obtaining quantitative ecological data on birds and their food plants (Kissling et al. 2007). In particular, if bird richness is determined by the availability of food resources, it is unclear whether it is the abundance of food or the diversity of food types (or both) that influence the richness of birds.

Hummingbirds are the most species-rich family of nectarivorous birds (Fleming and Muchhala 2008). Because they are one of the bird families most tightly linked to a specific food resource, they represent one of the classical examples of plant–animal coevolution (Fleming and Muchhala 2008). They are therefore a highly suitable group to study the way in which plants may mediate the numbers of bird species. Because of the strong dependence of hummingbirds on their food plants, it has been proposed that the diversity of hummingbirds is at least partly determined by the diversity of food plants that determine the niche space of the species (Wolf et al. 1976; Stiles 1981; Heß 1990). However, other authors have found that diversity and abundance of hummingbirds are related more to flower abundance than diversity (Wolf 1970; Stiles 1980; Cotton 2007). As with other bird groups (Kissling et al. 2007, 2008), it is therefore unclear whether bird diversity is mediated by the diversity of food resources or the abundance of food.

A further complication arises from spatial scale. The above-mentioned studies of hummingbird assemblages were typically carried out at single localities. While they provide insights into the number of species that co-occur at a given site at any given time, they cannot be scaled up to deduce regional patterns of hummingbird diversity on the biome or even continental level. Such a large-scale view was taken by Rahbek and Graves (2000), who mapped hummingbird species numbers at a scale of 1°×1° lat–long cells. At this scale, climatic and topographic factors are usually the parameters that are most closely related to taxonomic diversity (e.g., Currie 1991; Rohde 1992; Kerr

and Packer 1997). In contrast, local studies, by being restricted to single sites, lack spatial variation in climate or topography. The challenge thus is to relate continental and local patterns to regional studies containing both biotic and abiotic factors.

In the present study, we set out to bridge the gap between continent-wide macroecological studies and punctual local studies by inventorying the hummingbirds and food plant assemblages along a 660-km-long latitudinal transect in the Bolivian lowlands that reaches from Amazonian hummingbird assemblages of medium richness to species poor assemblages of the Chaco (Rahbek and Graves 2000). This transect thus corresponds to a gradient of precipitation and to shifts in forest seasonality, reaching from evergreen wet Amazonian forests in the north to the drought–deciduous spiny forests of the Chaco in the south. As such, it represents an area where both hummingbird diversity and precipitation decline in parallel, raising the possibility to unravel whether this relationship is mediated by the diversity and/or abundance of food plants. Our main question was to which degree the species richness of hummingbirds is related to different aspects of climatic conditions and to hummingbird food plants: namely (1) environmental factors that influence flower availability, (2) the number of food plants species, (3) the number of flowers, and (4) the seasonality of food plants and the number of flowers.

Methods

Our study was conducted at six sites (Villa Tunari: 16°57′59S, 65°24′44W; Sacta: 17°06′03S, 64°47′02W; Buena Vista: 17°30′49S, 63°38′16W; Santa Cruz: 17°46′48S, 63°04′02W; Río Seco: 18°42′44S, 63°11′35W; Corbalán: 21°36′15S, 62°27′45W; Fig. 1). Along this transect, mean annual precipitation decreases from 6,258 mm at Villa Tunari to 410 mm at Corbalán, while seasonality in temperature and precipitation increases (Kessler et al. 2007; Table 1).

The study sites consisted off primary, occasionally slightly disturbedf forest and lay between 200 and 440 m elevation. All forests are part of a larger forest system extending from Amazonia to the Gran Chaco. Each locality was visited twice for 16 days each between November 2007 and October 2008, once during the dry season (May–October) and once during the rainy season (November–April). At each site, we established a 1.5-km-long transect along a path through the forest whose minimum distance to the forest border was 150 m to avoid edge effects (Murcia 1995; Debinski and Holt 1999; Hausmann et al. 2005; Grimbacher et al. 2006). Each transect was visited for 13 days continuously between 7:30 am and 15:30 pm.
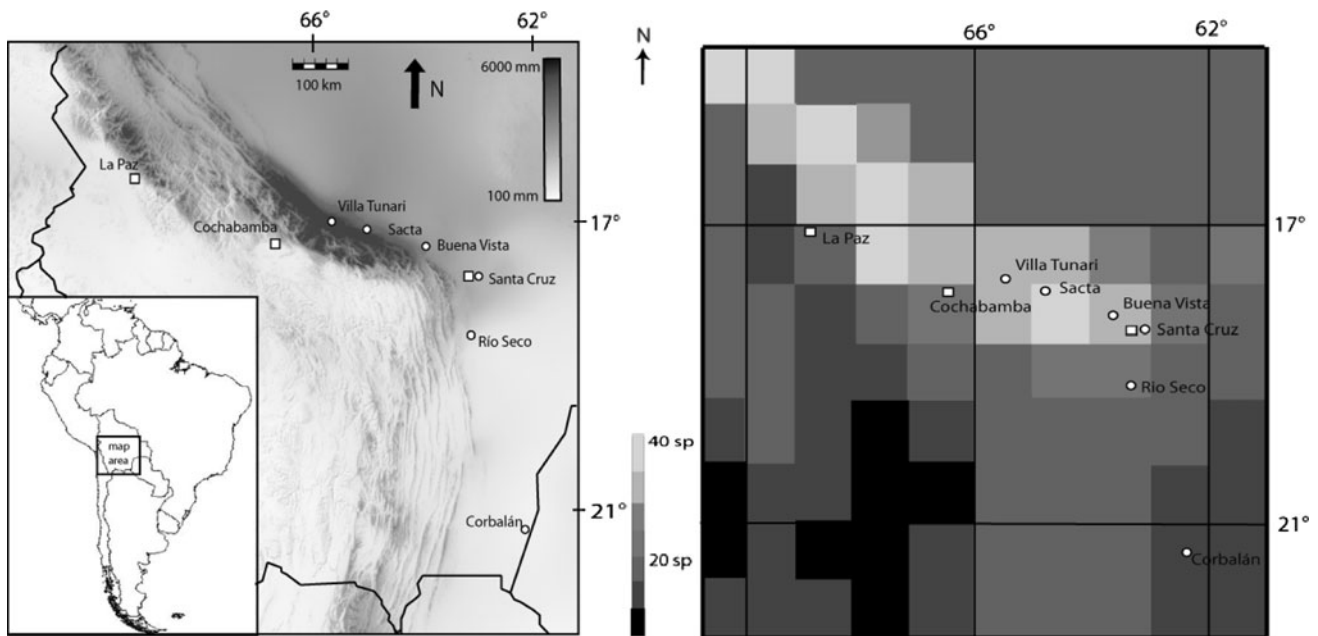
Fig. 1 Precipitation map (from Kessler et al. 2007) and map of hummingbird distribution of Bolivia (adapted from Rahbek and Graves 2000) with the six study sites (*circles*) and the main cities (*squares*)

Table 1 Environmental data of the study sites

Precip. total annual precipitation, *temp. ampl.* mean annual temperature amplitude, *min. temp.* minimal annual temperature

	Altitude (m)	Precip. total (mm)	Temp. ampl. (°C)	Min. temp. (°C)	No. arid months
Villa Tunari	400	6,258	3	6	0
Sacta	204	3,457	4	5	0
Buena Vista	424	2,000	4	3	0
Santa Cruz	397	1,166	5	1	2
Río Seco	434	729	5	−1	6
Corbalán	268	410	7	−3	8

All hummingbirds and plants visited by hummingbirds or showing the anatomical adaptation to hummingbird pollination (Protor et al. 1996) found 3 m to both sides of the transect were recorded (Jones et al. 2006). Because some hummingbird species normally live in the tree crowns and only come down to lower vegetation levels along forest edges, on the remaining 3 days we visited a 350-m-long section of the forest border. However, according to Bawa (1990), only about 2% of the plant species flowering in rainforest canopy have hummingbird-pollination, whereas in the understory and subcanopy ca. 18% of the species are hummingbird-pollinated, suggesting that our focus on the understory plants captures the majority of hummingbird–plant interactions in these forests. During the monitoring, the hummingbird species, activity, and the visited plant species were noted. Additionally, hummingbird observations while walking on the transect were recorded. Hummingbird species abundance was grouped into three categories: 1–3 (rare species), 4–9 (occasional species), and 9+ individuals seen per visit (common species).

No direct individual counts were attempted due to their mobility. Flower abundance per plants species was grouped into five categories: 1–10, 11–50, 51–200, 201–1,000, and 1,000+ flowers along the transect.

In addition to raw species and individual numbers, hummingbird diversity was also calculated with several convenient indices (ACE Mean, ICE Mean, Chao 1 Mean, Chao 2 Mean, Jack 1 Mean, Jack 2 Mean, Bootstrap Mean, MMRuns Mean) by using Estimate*S* (Colwell et al. 2004) in order to assess the influence of species abundances on the observed species numbers. To detect similarities in the composition of the hummingbird communities between the study sites, we used a canonical correspondence analysis (CCA) provided by PCOrd 5.0. The CCA was based on the number of individuals of the recorded hummingbird species, using the quantitative Sorensen similarity (Bray–Curtis) index. To test whether the hummingbird species and individual number, the plant species and flower number, and the environmental conditions were significantly different between the two biomes comprised, respectively, of the

three northern and the three southern study sites recognized by the CCA analysis, we used *t* tests. To assess the overlap of bird and plant species between the study sites and the overlap in nectar diet per study site and season, we employed the qualitative Sorensen index. To quantify the overlap of hummingbird and plant species per study site between the seasons, we used the quantitative Sorensen similarity (Bray–Curtis) index due to differences in data structure (Magurran 2004). To test the correlation between traits of hummingbird assemblages (individual number, species number, overlap in nectar diet) against explanatory variables (plant species number, flower number, change in the relative plant species number, environmental characters), we conducted pair-wise linear regressions. Further, we used a linear model in R to search for the best combination of biotic and abiotic factors for explaining hummingbird species numbers. A linear mixed model in R was used to control for the effect of site on hummingbird diversity. We decided to define an additional level of marginal significance at $P = 0.1$ because of the small number of study sites. Hummingbird nomenclature followed Gill and Wright (2006), and for plant names we used http://www.tropicos.org.

Results

In total, we found 21 hummingbird species, 7 of which were observed only once (Abrahamczyk and Kessler 2010). The highest total number of species (11) was found in Buena Vista and Sacta and the lowest number (3) occurred in Santa Cruz and Corbalán. Both during the dry season and rainy season, there was a roughly continuous increase of hummingbird species richness and abundance from arid Corbalán to humid Sacta (Table 2). Only the wettest site at Villa Tunari had a conspicuously lowered species richness compared to the nearest locality (Sacta). The calculation of several abundance and diversity indices with EstimateS revealed that the low number of species at Villa Tunari was not an artifact of a low number of

individuals recorded (data not shown) and that it thus represents a real pattern.

Based on the CCA (Fig. 2) and on the Sorensen similarity index of the hummingbird species shared between the study sites (Table 3), we were able to recognize two clearly defined hummingbird assemblages corresponding to the two biomes represented by axis 1: a diverse northern one (18 species) living in the tropical rainforests (localities: Villa Tunari, Sacta, Buena Vista) and a species-poor southern one (6 species) inhabiting the deciduous forests (Santa Cruz, Río Seco, Corbalán). The similarity in species composition of the study sites was explained by axis 2. No hummingbird species was assigned to an ordination space intermediate between the assemblages. Using the Sorensen similarity (Bray-Curtis) index to compare the similarity in species composition, we found that only 38.5% of the species were shared between the northern and southern assemblages. If we exclude *Amazilia chionogaster*, *Hylocharis cyanus*, and *Campylopterus largipennis* from the southern sites, where they were only seen once and can be regarded as occasional visitors or vagrants, we even get a similarity in species composition of 17.4%, which reflects the shared occurrence of *Phaethornis subochraceus* and *Thalurania furcata* between some northern and southern sites (Table 2). The northern assemblage had a significantly higher number of species (*t* test, $P = 0.005$) and individuals (*t* test, $P = 0.045$). The two communities further differed significantly relative to mean annual precipitation (*t* test, $P = 0.023$), minimum annual temperature (*t* test, $P = 0.020$), and marginally significant to the number of arid months (*t* test, $P = 0.069$) and temperature amplitude (*t* test, $P = 0.076$).

Over all sites, we obtained visitation observations of 19 hummingbird species on 39 plant species (Table 4). We also found an additional 6 species of putative hummingbird food plants for which we obtained no observations of hummingbird visits. These species were also included in the regression analyses. During the dry season, we found a higher number of hummingbird food plant species in the

Table 2 Hummingbird diversity (*No. hum. sp.*) and overlap in nectar diet (based on the Sorensen similarity index) of the study sites (%) during the rainy (*R*) and the dry season (*D*), and overlap of hummingbird species and hummingbird food plant species (based on the Bray–Curtis index) between rainy and dry season

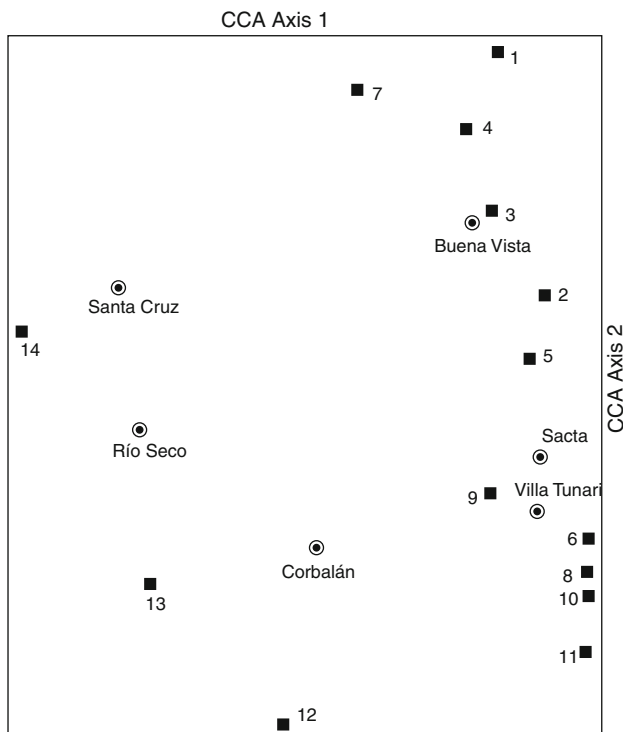|	No. hum. sp. R	No. hum. sp. D	Overlap in nectar diet R	Overlap in nectar diet D	Hum. sp. overlap	Plant sp. overlap
Villa Tunari	5	4	0	48	80	31
Sacta	8	6	18	13	42	24
Buena Vista	9	6	74	46	69	15
Santa Cruz	3	2	67	0	80	48
Río Seco	3	3	100	67	50	44
Corbalán	3	3	22	100	60	59

Fig. 2 Canonical correspondence analysis of the study sites based on the abundance composition of their hummingbird assemblages. Axis 1 explains 43% and axis 2 explains 29%. Squares illustrate the position of the hummingbird species relative to the sites: 1 *Anthracothorax nigricollis*, *Chaetocerus mulsantii*, cf. *Heliodoxa leadbearteri*, *Phaethornis stuarti*, *Phaethornis hispidus*; 2 *Florisuga mellivora*; 3 *Hylocharis cyanus*; 4 *Amazilia chinogaster*; 5 *Campylopterus largipennis*; 6 *Amazilia fimbriata*, *Lophornis delattrei*, *Coeligena torquata*; 7 *Phaethornis subochraceus*; 8 *Phaethornis ruber*; 9 *Thalurania furcata*; 10 *Glaucis hirsutus*, *Phaethornis malaris*; 11 *Threnetes leucurus*; 12 *Heliomaster furcifer*; 13 *Chlorostilbon aureoventris*; 14 *Hylocharis chrysura*

Table 3 Overlap (%) of hummingbird species (Hum. sp.) and hummingbird food plants (based on the Sorensen similarity index) between adjacent study sites

	Hum. sp. overlap	Food plants sp. overlap
Corbalán—Río Seco	25	27
Río Seco—Santa Cruz	50	0
Santa Cruz—Buena Vista	14	15
Buena Vista—Sacta	36	10
Sacta—Villa Tunari	59	17

northern than in the southern localities (*t* test, $P = 0.042$), while in the rainy season this pattern was not evident (*t* test, $P = 0.398$). We did not find a significantly higher number of flowers between the northern and the southern study sites during either the rainy (*t* test: $P = 0.210$) or dry (*t* test: $P = 0.671$) seasons. The overlap in food plant

species composition between the rainy and the dry season was significantly higher in the southern localities than in the northern ones (*t* test, $P = 0.014$).

We found no significant correlation of hummingbird and plant richness and abundance relative to any environmental parameter (Table 1), except for marginal significance for a reduction of the number of hummingbird species during the rainy season with increasing number of arid months ($R = -0.73$, $P = 0.100$) and a decrease in hummingbird food plant species number with increasing altitude ($R = -0.71$, $P = 0.099$; Table 5). Additionally, we did not find any significance when we tested for the effects of site on hummingbird species number. Further, there was no significant correlation between either hummingbird richness or hummingbird abundance in any season to food plant richness (Fig. 3). Significant relationships were only recovered between hummingbird richness and abundance relative to the abundance of flowers in the rainy season and marginally over the year (Table 5). When we used a mixed model controlling which biotic or abiotic factors in combination best explain hummingbird species number, we found that the number of flowers ($P = 0.023$), the different biomes ($P = 0.002$), and the season ($P = 0.036$) had the highest explanatory impact (total: $R^2 = 0.87$; $P = 0.0007$). Finally, we found that a seasonal decrease in food plant species richness resulted in an increase in the overlap in nectar diet of the hummingbirds ($R = -0.85$, $P = 0.031$; Fig. 4).

Discussion

This is the first study to relate the species richness and abundance of hummingbirds to biotic and abiotic factors along a climatic gradient. Instead of a gradual change in hummingbird diversity and community composition corresponding to the gradual change of climatic conditions (precipitation, temperatures) from north to south we found two distinct hummingbird assemblages inhabiting two distinct biomes (Fig. 1; Table 3). The species-rich northern assemblage (Villa Tunari, Sacta, Buena Vista) had a significantly higher number of species compared to the southern one (3.7 vs. 9.3 species per site) and shared only two regularly occurring species with the southern sites. The northern assemblage occurred in Amazonian rainforests and shared many species with hummingbird assemblages reported from other lowland forests in Peru and Colombia (Terborgh et al. 1984; Cotton 1998b). The southern assemblage inhabited the deciduous dry forests from Santa Cruz southwards (Santa Cruz, Río Seco, Corbalán) and showed some similarities to an assemblage in similar habitats in the southern Pantanal in Brazil (Araujo and Sazima 2003).

Table 4 Food plant abundance in the examined study sites during rainy season (*R*) and dry season (*D*)

	Corbalán R	Corbalán D	Río Seco R	Río Seco D	Santa Cruz R	Santa Cruz D	Buene Vista R	Buena Vista D	Sacta R	Sacta D	Villa Tunari R	Villa Tunari D
Anisacanthus boliviensis (Nees) Wassh.				4								
Aphelandra aurantiaca (Scheidw.) Lindl.											1	
Justicia appendiculata (Ruiz & Pav.) Vahl								2				
Justicia dumentorum Morong.												
Justicia tenuistachys (Rusby) Wassh. & J. R. I. Wood	1	2										4
Pachystachys spicata (Ruiz & Pav.) Wassh.										3		
Ruellia inflata Rich.											1	2
Suessenguthia multisetosa (Rusby) Wassh. & J. R. I. Wood[b]								5				
Mandevilla angustifolia (Malme) Woods.	3											
Marsdenia spec.					3	1						
Arrabidea triplinervia (Mart. ex DC.) Baill ex Bureau				3								
Dolichandra unguis-cati (L.) L. G. Lohmann[b]						3						
Pithecoctenium crucigerum (L.) A. H. Gentry					2							
Chorisia insignis Kunth		2										
Bromelia hieroyimi Mez	1											
Pseudananas sagenarius (Arruda) Camargo						3						
Tillandsia lorentziana Griseb.	2											
Cleistocactus samaipatensis (Cardenas) D. R. Hunt	1	1		1								
Stetsonia coryne (Salm-Dyck) Britton & Rose[b]	4											
Bauhinia pentandra (Bong.) A. Dietr.			4	2								
Capparis retusa Griseb.[b]	3											
Capparis salicifolia Griseb.		1		3								
Capparis speciosa Griseb.[b]	3	3										
Erythrina dominguezii Hass.								4				
Fabaceae												
Besleria rotundifolia Rusby											2	2
Besleria spec.									1	1		
Drymonia semicordata (Poepp.) Wiehler									1	1	2	2
Juanulloa parasitica Ruiz & Pav.									2	1	2	2
Heliconia acuminata Rich.									1			
Heliconia episcopalis Vell.									3	1		
Heliconia subulata Ruiz & Pav.							3	3			2	
Leonotis leonurus (L.) R. Br.[a]										3		1
Tripodanthus acutifolius (Ruiz & Pav.) Van Tiegh[b]		5										
Calathea spec. I									2	2		

Table 4 continued

	Corbalán R	Corbalán D	Río Seco R	Río Seco D	Santa Cruz R	Santa Cruz D	Buene Vista R	Buena Vista D	Sacta R	Sacta D	Villa Tunari R	Villa Tunari D
Calathea spec. II									2			
Calliandra haematocephala Hassk.								1				
Zygia coccinea (G. Don) L. Rico											3	
Passiflora coccinea Aubl.						1		1				2
Hamelia patens Jacq.									3	3		
Palicourea guianensis Aubl.											3	2
Palicourea lasiantha K. Krause							1		5			
Erythrochiton fallax Kallunki							5	4				
Lantana spec.										4		

1 1–10 flowers, *2* 11–50 flowers, *3* 51–200 flowers, *4* 201–1,000 flowers, *5* >1,000 flowers

[a] Introduced

[b] Mainly insect pollinated

The transition between the two hummingbird assemblages was not gradual but rather abrupt, with less than 70 km in a direct line between Buena Vista (north) and Santa Cruz (south). In their continent-wide analysis, Rahbek and Graves (2000) provided the first hints of a dramatic decline in hummingbird diversity in the transition zone between evergreen and deciduous lowland forests in central Bolivia. This abrupt transition between the two assemblages corresponds to the shift in biomes from tropical to subtropical conditions (Linares-Palomino et al. 2008a, b). The northern area has no climatically arid months, the yearly amplitude of temperature is lower, and frost is completely absent, whereas the south has marked seasonality in precipitation and temperatures as well as nocturnal winter temperatures close to or even below the freezing point. Due to these environmental conditions, the plant communities differ enormously between the two regions. From Buena Vista northwards, we find evergreen rain forests with *Heliconia* species, Melastomataceae, and a large number of fern, herb, and tree species which are characteristic for the Amazon region (Navarro and Maldonado 2002). The south has seasonally drought deciduous forests in which terrestrial cacti and other succulent plants are common.

In contrast to the climatic factors, hummingbird diversity showed a close relationship to the availability of food plants. Most importantly, we found that the number of flowers available, rather than the diversity of food plants, was important. This corresponds to previous conjectures on hummingbird–food relationships based on local-scale studies (Stiles 1980; Araujo and Sazima 2003; Cotton 2007). Further, we found that the relationships of hummingbird diversity to flower number were only evident when the seasons were analyzed separately. In addition, the higher number of hummingbird species in the less seasonal northern part of the transect suggests that the most important factor determining hummingbird diversity is the continuous availability of food which is not given at the southern study sites. The influence of climate on the hummingbird assemblages thus appears to depend primarily on the threshold between evergreen and drought-deciduous forests (ca. 1,600 mm mean annual precipitation; Gentry 1995). This threshold leads to a reduction of flowers during the peak of the dry season in the southern part of the transect. Above and below this limit, there appears to be little direct influence of climate on the hummingbirds.

The impact of food availability even in the less seasonal northern part of the gradient becomes particularly evident when focusing on the Villa Tunari site which did not fit into the general pattern of a decrease of hummingbird diversity and abundance from north to south. This site had few hummingbird-pollinated flowers, especially in the wet season, presumably because of nutrient poor soils

Table 5 R values of the different parameters for regression analysis: number of arid months, number of flower individuals and number of plant species versus the number of hummingbird species and individuals, the number of flower individuals and the number of plant species

	Hum. sp. total	Hum. sp. R	Hum. sp. D	Hum. ind. total	Hum. ind. R	Hum. ind. D	Flower ind. total	Flower ind. R	Flower ind. D	Plant sp. total	Plant sp. R	Plant sp. D
Altitude	−0.20	−0.19	−0.30	−0.24	−0.04	−0.48	−0.29	−0.48	−0.05	−0.71*	−0.68	−0.66
Precip. total	0.37	0.38	0.40	0.14	0.10	0.16	0.13	0.08	−0.28	0.54	0.59	0.68
Temp. ampl.	−0.60	−0.58	−0.53	−0.45	−0.40	−0.44	−0.03	−0.23	0.26	−0.12	−0.08	−0.47
Min. temp.	0.65	0.66	0.62	0.40	0.44	0.29	0.06	0.37	−0.22	0.40	0.34	0.67
No. arid month	−0.68	−0.73*	−0.61	−0.54	−0.62	−0.37	−0.17	−0.43	0.10	−0.19	−0.09	−0.47
Flower ind. total	0.71	0.77*	0.78*	0.79*	0.83**	0.64				0.39		
Flower ind. R	0.91**	0.90**	0.92***	0.71	0.87**	0.45					0.13	
Flower ind. D	0.38	0.48	0.48	0.69	0.62	0.66						−0.02
Plant sp. total	0.36	0.41	0.53	0.06	0.16	0.04	0.39					
Plant sp. R	0.06	0.10	0.23	0.26	0.18	0.31		0.13				
Plant sp. D	0.64	0.60	0.72	0.18	0.30	0.03			−0.02			

Hum. sp. Hummingbird species, *Hum. ind.* number of individual hummingbirds, *Flower ind.* number of individual flowers, *Plant sp.* plant species, *Precip. total* annual precipitation (mm), *Temp. amplitude* ampl. of annual mean temperatures (C°), *Min. temp.* minimum annual temperature (C°), *R* rainy season, *D* dry season

*$P < 0.1$, **$P \leq 0.05$, ***$P \leq 0.01$

Fig. 3 Regression of the number of flowers versus the number of hummingbird individuals/species number at all study sites during the rainy and dry seasons
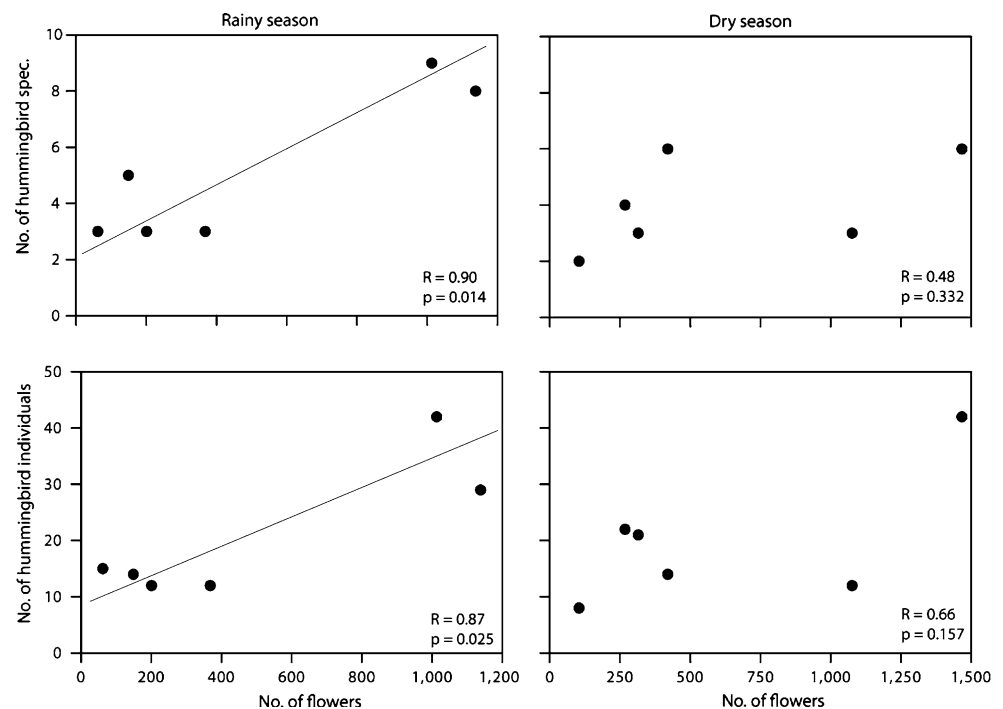
(Abrahamczyk and Kessler, unpublished data). It thus fit perfectly well into the pattern relating hummingbird diversity to flower abundance, as opposed to a direct influence of climate. The paucity of food resources during the peak of the rainy season has also been hypothesized to be the limiting factor for hummingbird diversity and abundance in tropical wet forests of Costa Rica (Stiles 1978) and Colombia (Cotton 2007).

The only site that did not match the pattern of reduced hummingbird diversity and abundance with limited flower abundance was Corbalán during the dry season, where the number of flowers was very high. This was due to the large number of flowers of *Tripodanthus acutifolius,* a hemiparasitic Lorantaceae (Table 4). However, this is a primarily bee-pollinated species that produces a limited amount of nectar per flower and which is only used as a
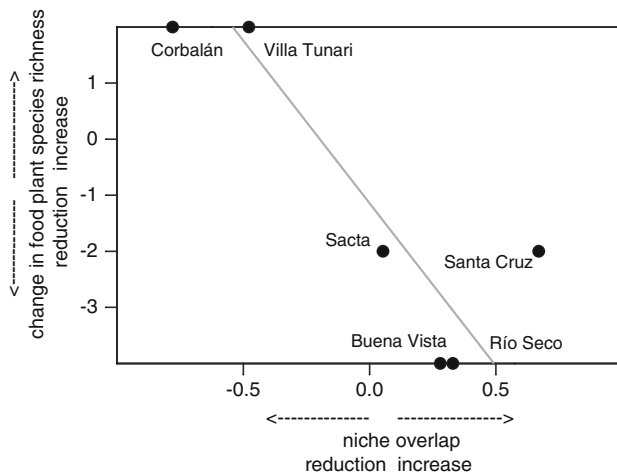
Fig. 4 Regression of the relative seasonal change in hummingbird overlap in nectar diet (based on the Sorensen similarity index) versus the relative seasonal change in food plant species richness at all study sites (rainy season–dry season); $R = -0.85$, $P = 0.031$

subsidiary resource by generalistic hummingbird species. Such a use of mainly insect-pollinated plants by hummingbirds was an exception in our study. In contrast to the studies by Snow and Snow (1980) or Dalsgaard et al. (2009), only 6 of the 45 hummingbird food plant species found by us were mainly insect-pollinated (Table 4). Five of them were found at Corbalán, the southernmost and most seasonal study site. Such high levels of hummingbird food plants that are primarily entomophilous have previously only been reported from naturally fragmented forest patches of the Brazilian ''capões'' (Araujo and Sazima 2003) and on Caribbean Islands (Dalsgaard et al. 2009).

The number of food plant species found at each site was low (8.7) compared to other studies that found up to 72 species per site (Cotton 1998a; Dziedzioch et al. 2003) even if one notes that these localities were observed for a longer period of time. Indeed, one of the diverse, northern hummingbird assemblages was seasonally effectively supported by only two food plant species. Accordingly, the overlap in nectar diet between hummingbird species at a given locality changed markedly between the seasons. Importantly, the direction of this change, i.e., higher or lower degree of overlap in a given season, differed between localities. Further, the overlap in nectar diet space between co-occurring hummingbird species was significantly negatively correlated with the number of flowering plant species (Fig. 3). This suggests that like other groups of birds (e.g., Fjeldså 1983; Krebs and Cowie 1976) the hummingbird species studied by us had feeding preferences but reacted opportunistically to the absence or availability of food plants. Thus, when several different food plant species were flowering in sufficient numbers, the hummingbirds tended to segregate their feeding activity. In

contrast, when few species were flowering, all hummingbirds were forced to feed on the same species.

This partly resulted in high values of overlap in nectar diet between hummingbirds at a given locality, reaching values of up to 100% at Río Seco and Santa Cruz (Table 2). This contrasts with a study by Cotton (1998a), who only reported overlaps in nectar diet below 50% among co-occurring hummingbirds in Colombia. Further, this result does not match with the suggestions of several authors that flower morphology (size, length) closely determines which hummingbird species visit them and who interpreted this as an example of specialization and co-evolution (e.g., Wolf et al. 1976; Stiles 1981; Heß 1990). However, other authors (e.g., Snow and Snow 1980; Dziedzioch et al. 2003; Lara et al. 2009) have reported that hummingbirds regularly visit flowers that morphologically would not appear to be suitable food plants. In combination with these studies, our study indicates that many hummingbird species are opportunistic feeders that are not closely linked to specific food plants. Yet, even if all hummingbirds at a site feed on the same plant species, there might be some niche segregation. For example, in a hummingbird community in Central Mexico that was mainly supported by *Penstemon roseus* (Plantaginaceae), the hummingbirds used flowers differently depending on species and sex (Lara et al. 2009): smaller species mostly used the flowers in the center of the plant patches whereas larger ones used all flowers, and females often perched lower than males.

In conclusion, our study supports the notion that the diversity of hummingbird assemblages is predominantly determined by a constant, high availability of flowers on the regional as well as on the local scale. Climatic factors, determining the threshold between evergreen and seasonally green vegetation types and resulting in different rates of flower seasonality are more important on the larger scale. At the local scale, it is more the abundance of flowers that matters rather than their diversity. If only a limited number of food plant species are available that provide a sufficiently high amount of flowers, hummingbirds are surprisingly opportunistic in their feeding behavior resulting in an increase in nectar diet overlap between species. This suggests that the diversity of hummingbird assemblages, and perhaps also of other bird assemblages, depends more on the quantity of food available than on the number of different food resources. This may be one of the reasons why macroecological studies have so far only found rather weak links between bird and plant diversity (Kissling et al. 2007, 2008). On the other hand, our study supports the hypothesis that the diversity of a given assemblage depends on the energy available to it, and thus provides direct ecological support for the diversity–productivity relationship (H-Acevedo and Currie 2003; Evans

et al. 2005, 2009; Kissling et al. 2009). All these results indicate that a combination of several local studies can help to understand plant–animal interactions on a larger scale.

Zusammenfassung

Kolibridiversität, Nahrungswahl und die Zusammensetzung von Kolibrigemeinschaften entlang eines latitudinalen Niederschlagsgradienten im bolivianischen Tiefland

Ausgehend vom Äquator nimmt die Kolibridiversität wie auch die vieler anderer Taxa ab. Die Gründe für diese Abnahme sind umstritten, beinhalten aber wahrscheinlich klimatische Faktoren und die Verfügbarkeit von Nahrung. Da Kolibris eines der klassischen Beispiele für Pflanze-Tierkoevolution darstellen, wurde angenommen, dass die Diversität von Kolibrigemeinschaften von der Diversität ihrer Futterpflanzen abhängen. Wir haben diese Hypothese in einer einjährigen Feldstudie im bolivianischen Tiefland geprüft. Dabei wurden Kolibirgemeinschaften und ihre Futterpflanzen entlang eines 660 km langen Transekts vom amazonischen Regenwald bis in den saisonalen Trockenwald untersucht. Die höchste Kolibridiversität wurde in den nördlichen drei Gebieten beobachtet. Zu den südlichen Gebieten hin ergab sich an der Grenze vom immergrünen Regenwald zum saisonalen Trockenwald ein abrupter Abfall in der Artenzahl der Gemeinschaften verbunden mit einem Wechsel in der Artenzusammensetzung. Kolibridiversität und Abundanz waren nur schwach mit klimatischen Faktoren oder der Diversität der Futterpflanzen korreliert. Vielmehr hatte die saisonale Verfügbarkeit von geeigneten Blüten einen sehr starken Einfluss. Bei der Wahl der Futterpflanzen zeigten die verschiedenen Kolibriarten sehr unterschiedliche Überlappungsmuster: Waren geeignete Blüten vieler Arten verfügbar, spezialisierten sich die Arten sehr stark auf wenige Futterpflanzenarten. Waren nur wenige Futterpflanzenarten verfügbar, nutzen alle Kolibri-arten dieselben Pflanzenarten. Wir schlossen aus unseren Beobachtungen, dass die lokale Kolibridiversität nicht in erster Linie von der Diversität der Futterpflanzen, sondern von der dauerhaften Verfügbarkeit von Blüten abhängt.

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