

Functional structure and specialization in three tropical plant–hummingbird interaction networks across an elevational gradient in Costa Rica

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Understanding causes of variation in multispecies assemblages along spatial environmental gradients is a long-standing research topic in ecology and biogeography. Ecological networks comprising interacting species of plants and pollinators are particularly suitable for testing effects of environmental gradients on the functional structure and specialization in multispecies assemblages. In this study, we investigated patterns in functional assemblage structure and specialization of hummingbirds at the individual and species level along a tropical elevational gradient. We mist-netted hummingbirds at three elevations in Costa Rica in seven temporally distinct sampling periods and used the pollen carried by hummingbird individuals to construct plant–hummingbird networks at each elevation. We measured four functional traits of hummingbird species and quantified different metrics of functional community structure. We tested the effect of elevation on functional metrics of hummingbird assemblages and specialization within the networks, employing the variability across sampling periods and hummingbird species to compare the respective metrics among elevations. Hummingbird species and individuals were more specialized at low and mid elevations than at the highest elevation. This pattern corresponded to a more even and over-dispersed assemblage structure at the lower elevations throughout the year and suggests a high level of floral resource partitioning in functionally diversified communities. In contrast, an uneven and clustered functional structure of the highland assemblage across all sampling periods suggests that this assemblage was structured by environmental filtering and by niche expansion of hummingbird individuals and species at this elevation. We conclude that high degrees of specialization on specific floral resources might be crucial for the coexistence of hummingbird species in diversified lowland communities. Spatial variation in animal resource use may be an important crucial driver of spatial patterns in the functional structure of diversified species assemblages also in other types of ecological networks.

A primary aim of community ecology is to identify the processes that govern species assemblages across environmental gradients (McGill et al. 2006). Mountain ecosystems provide pronounced environmental gradients across relatively small spatial scales and have proved to be suitable systems to investigate patterns and determinants of species diversity and community structure (Körner 2000, Sanders and Rahbek 2012). In pollination systems, pollinator richness and abundance have been found to decrease with increasing elevation (Totland 2001). Although some studies have investigated the effects of elevational gradients on structural properties of plant–pollinator networks such as nestedness or specialization (Olesen and Jordano 2002, Ramos-Jiliberto et al. 2010, Benadi et al. 2013), such studies are still scarce, especially in the tropics. Here, we studied the effects of elevation on the functional structure of tropical hummingbird assemblages and specialization in plant–hummingbird interaction networks.

The structure of ecological communities can be described by species' functional traits, defined as measurable properties of individuals that influence their performance (McGill et al. 2006). Community trait composition can principally be examined by two distinct components: mean trait values of species, weighted by their relative abundances (i.e. community-weighted means of trait values), and multivariate measures of functional diversity (Dias et al. 2013). Functional diversity describes the range, distribution and abundance of trait values of species in a community (Tilman et al. 1997, Díaz and Cabido 2001) and has frequently been used to infer potential mechanisms of community assembly, such as environmental filtering and competition (Cornwell et al. 2006). However, different mechanisms can lead to similar patterns of functional diversity (Herben and Goldberg 2014) and especially the relationship between the prevalence of competition and functional community structure is controversial (HilleRisLambers et al. 2012, Dehling et al.

2014a, Fritschie et al. 2014). Environmental filtering tends to increase the functional similarity among species by reducing the range of trait values within a community (i.e. functional clustering) (Keddy 1992). It also appears to be an important mechanism that constrains particular functional roles within hummingbird assemblages at high elevations (Graham et al. 2009). In contrast, competition and resource partitioning tends to limit the functional similarity between co-existing species (i.e. functional over-dispersion) (MacArthur and Levins 1967, Mouchet et al. 2010), for example manifested by the partitioning of nectar plants among hummingbird species. In the presence of high degrees of interspecific competition, pollinators are expected to become more specialized by increasing resource partitioning (Schoener 1974, Inouye 1978). Thus, structural properties of mutualistic networks, such as specialization, may be related to patterns in the functional structure of species assemblages (Plein et al. 2013).

A comprehensive understanding of the processes leading to community assembly in plant–pollinator networks requires an understanding of the processes occurring at the level of both species and individuals. As stated in the niche variation hypothesis, individuals within populations may differ substantially in their resource use (Van Valen 1965). Large between-individual variation in resource use may contribute to niche expansion (Araújo et al. 2010), leading to reduced specialization of species assemblages (Bolnick et al. 2003). An important mechanism related to specialization is competition (Schoener 1974), both among individuals of the same species and among individuals of different species (MacArthur and Levins 1964, Araújo et al. 2008). Individual-based networks may be a powerful tool to assess competition and have been used to study intra-population patterns of resource partitioning in vertebrates (Pires et al. 2011) and changes in foraging preferences of consumer species (Araújo et al. 2008). However, to date only a few empirical studies have applied network analysis to explore patterns of ecological interactions between plants and their pollinators at the individual level (Tur et al. 2013). To our knowledge, differences in specialization of plant–pollinator networks among elevations have so far not been analysed at the individual level.

In the Western Hemisphere, hummingbirds (Trochilidae) are considered to be effective pollinators (Castellanos et al. 2003). They have been classified into two distinct ecological groups: hermits and non-hermits, which differ mainly in their elevational distribution and their level of specialization on floral resources (Stiles 1978). Hermit hummingbirds mostly occur in wet lowland forests and are specialized on specific floral resources (Snow and Snow 1972). Non-hermit hummingbirds may be found along a wide range of elevations and are in general less specialized than hermits (Feinsinger and Colwell 1978). Hummingbird assemblages comprise species that differ in their morphology and functional roles (e.g. co-occurring hermit and non-hermit species) as well as in their degree of specialization. These assemblages are thus a suitable system to study functional community structure and floral resource partitioning in plant–pollinator networks. In seven sampling periods across one year, we mist-netted hummingbirds at three elevations in Costa Rica and used the pollen carried by hummingbird individuals to

construct plant–hummingbird interaction networks at the individual and species level.

By employing the observed variability across hummingbird species, individuals and sampling periods, we investigated whether patterns of specialization of hummingbirds varied across elevations at the individual and species level and explored whether these patterns corresponded to patterns in the functional structure of hummingbird assemblages. More specifically, we addressed the following questions and hypotheses: a) does the functional structure of hummingbird assemblages change with elevation? We expect that the hummingbird assemblage at the highest elevation has a clustered functional structure throughout the year because only a narrow spectrum of species and functional roles could occur and coexist in harsh environments. b) Do individual-level and species-level specialization change across elevations? We hypothesized that on average hummingbird species and individuals are more specialized at lower than at high elevations because high levels of competition might cause pronounced resource partitioning in highly diversified lowland assemblages.

Material and methods

Study area and data collection

The study was conducted at La Selva Biological Station located in the lowlands of northeastern Costa Rica (10°26'N, 84°01'W) and adjacent Braulio Carrillo National Park. This study region constitutes a corridor of continuous forest from sea level at La Selva Biological Station (LS) to elevations higher than 2900 m a.s.l. at the Braulio Carrillo National Park. Our study sites were located at three different elevations: low (50 m) in LS, mid (1000 m) and high elevation (2000 m) in the park. According to Holdridge's (1967) life-zone classification, forests represented at those three elevations are tropical wet, pre-montane and lower montane wet forest. All sites were located in old-growth forest. Canopy heights were approximately 35 m at LS, 30 m at 1000 m, and 20 m at 2000 m (Hartshorn and Peralta 1988). Mean annual temperature ranges from 25°C at LS to 14°C in the highlands, while mean annual precipitation ranges from 4300 mm in the lowlands to 2200 mm in the highlands (Blake and Loiselle 2000). The dry season lasts from January to April and the wettest months are July and October–November.

We conducted the study from May 2011 to April 2012, covering an entire study year and focused on the understory hummingbirds and their foraging plants. During the year of sampling, we repeatedly collected data on abundances and functional traits of hummingbirds. We also sampled pollen loads carried by hummingbirds to determine plant–hummingbird interactions. Hummingbird abundances and functional traits were collected during seven sampling periods of approximately 10 d each. Repeated sampling periods were separated by at least one month. Pollen loads were analysed for a subset of four periods covering both the wet and the dry season, that is, we identified pollen samples from plant species that bloomed at different times of the year.

Hummingbird abundances and traits

We placed at each elevation 12–14 standard mist nets (12 × 3 m) for approximately 6 h after dawn (Ralph et al. 1993). We used 30 mm mesh mist nets, which are efficient for capturing small birds (Karr 1979). To ensure a representative sampling of the hummingbird community in the understory, mist nets were located across different habitat types at each study site. All hummingbirds captured were identified to species level (according to Stiles and Skutch 1989) and banded with numbered aluminium bands allowing for individual identification. The total number of hummingbird individuals captured during each sampling period was used as an estimate of species' abundance for each elevation and sampling period; recaptured individuals within the same sampling period were discarded. Recaptures of hummingbirds in different sampling periods were rare (16% of all captures). We measured functional traits of hummingbird species that have been reported to affect their interactions with plant species, such as bill length and curvature (Hainsworth and Wolf 1972, Temeles et al. 2010), as well as body mass (Dalsgaard et al. 2008, 2009) and wing length (Stiles 2004). For each captured hummingbird individual, we measured bill length (exposed culmen) and length of the closed (folded) wing to the nearest 0.1 mm using dial calipers. To measure bill curvature, we placed the bill on graph paper so that the angle of deflection could be calculated using simple trigonometry (Kershaw 2006). We applied arcsinus-sqrt-transformation to bill curvature prior to analysis. Body mass was measured to the nearest 0.1 g with a digital scale. Body mass as well as the other morphological traits were measured within the same period in the morning (i.e. between 6:00 and 12:00). Morphological traits were measured from 773 individuals belonging to 28 hummingbird species. Wing length was excluded for further analysis due to its strong collinearity with body mass ($r = 0.88$, $p < 0.001$).

Pollen analysis

Plant–pollinator interactions were quantified by examining pollen loads carried by mist-netted hummingbirds. We used fuchsin-stained gelatine (Beattie 1971) to gently remove pollen loads from the bill, head and throat plumage of each bird (Kearns and Inouye 1993). We used one small cube of gelatine to wipe dorsally from the bill tip to the nape of the neck and a second cube to sample the underside of the bill and the entire throat. Separation of samples in two parts allowed an easier identification of pollen grains within two small samples. Each collected pollen sample was placed in a separate vial for later analysis. We were careful to ensure that the same amount of time and effort was used for each bird, as well as similar amounts of gelatine. In addition, we sealed the Petri dishes containing the gelatine to avoid contamination and we manipulated hummingbirds carefully to prevent pollen transfer among individuals. Most pollen structures (e.g. exines) are colourless whereby small quantities of basic fuchsin used to stain the gelatine allowed for more accurate pollen identification.

The pollen identification process was done by two persons skilled in palynological techniques. We mounted

each cube of gelatine on a slide, melted the sample and covered it with glass coverslips to produce a single layer of stained pollen grains. These were observed under a light microscope at 400–1000 × magnification. We identified pollen grains by comparison with reference collections, taken from understory plants at the study sites during each seasonal sampling, as well as the literature (Roubik and Moreno 1991). Collecting pollen samples from all blooming plant species in the understory (i.e. up to 10 m above the ground) at each sampling period allowed us to reduce the number of potential plant species with similar pollen. Voucher specimens of plant species were deposited at the Inst. Nacional de Biodiversidad and the pollen reference collection at the Universidad Estatal a Distancia (Costa Rica).

Overall, we analysed pollen samples from 21 species of the total hummingbird species captured in mist nets. We did not include five species in our pollen analysis because the small sample sizes would not be representative of the interactions for these species (*Klais guimeti*, *Microchera albocoronata*, *Phaacroa cuvieri*, *Colibri thalassinus* and *Hylocharis eliciae*). *Selasphorus flammula* and *S. scintilla* are altitudinal migrants and they were not present in our study area for the time periods selected for pollen identification (Supplementary material Appendix 1, Table A2). Pollen grains were identified to plant species level whenever possible, and to morphospecies if pollen from closely related species or genera were indistinguishable (Feinsinger et al. 1987). In cases where species, or genus or family could not be determined, we classified pollen grains in morphotypes, based on their size, shape, type and number of apertures, and exine sculptures. The proportion of pollen in the three categories was 43, 10 and 47% for species, morphospecies and morphotypes, respectively. Hereafter, we will refer to morphotype of either pollen identified to species level, or pollen identified to morphospecies or morphotype level. The number of hummingbird individuals carrying pollen of a particular morphotype was used as a measure of the interaction frequency between that hummingbird species and a plant morphotype. Hummingbird individuals recaptured during the same sampling period and carrying the same pollen morphotype more than once were counted as a single individual.

Statistical analyses

Taxonomic and functional structure of hummingbird assemblages

To describe the taxonomic diversity of hummingbird assemblages, we estimated the abundance of hummingbird species and the species richness of the assemblage as the number of captured species for each sampling period and elevation. We also calculated the exponent of Shannon entropy (e^H), where H is the mean (one-dimensional) Shannon diversity of hummingbird assemblages for each sampling period and elevation (Jost 2006), to compute the effective number of species in a community (Jost 2006). To compare hummingbird abundance, species richness and the effective number of species e^H among the three elevations, we fitted linear mixed effect models with elevation as fixed effect and sampling period as random effect. Thus, we tested whether differences between elevational belts were consistent over time, accounting for random variation due to temporal

autocorrelation. Prior to analysis, estimates of hummingbird abundance were log-transformed. In addition, we estimated Bray–Curtis dissimilarity indices to quantify the beta-diversity across sampling periods for each elevation.

To determine the functional structure of hummingbird assemblages for each sampling period, we calculated two components of community trait composition based on the three selected hummingbird traits: a) the average trait values of the species, quantified by community-weighted mean trait values (CWM) and b) the degree to which trait values differ among hummingbird species, quantified by three measures of functional diversity (FD). Both components were calculated for each elevation and sampling period. CWM (Lavorel et al. 2008) was quantified as the mean trait value of all hummingbird species present in the community, weighted by their relative abundances from mist-netting during the respective sampling period. To calculate FD, species were projected into a trait-space based on pairwise Euclidean distances, as calculated from the functional traits using principal coordinate analysis (Villéger et al. 2008). Instead of choosing a single metric for measuring functional diversity (FD), we computed metrics of three complementary families of FD metrics, each accentuating different attributes of the concept (Mason et al. 2005, Villéger et al. 2008). We measured the following FD metrics: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis). FRic measures the entire functional space filled by the species in a community at a given time. FRic of each assemblage was standardized by the ‘global’ FRic that included all species across all elevations and sampling periods. Since FRic is mostly determined by the extreme values of trait combinations, we also calculated the FEve of each assemblage. FEve measures how regular the distances and abundances of individual species are distributed in the trait space along a minimum spanning tree (Villéger et al. 2008). In addition, FDis measures the spread of species in the functional space as the weighted distance to the assemblage centroid across all species (Laliberté and Legendre 2010) and is thus a measure of the functional specialization in a community (Plein et al. 2013). Unlike to FRic, FDis and FEve were weighted by the abundances of the species in a community at a given time. We compared the CWM and the different indices of FD among the three elevations with linear mixed effect models, including elevation as fixed effect and sampling period as random effect, assuming normally distributed error terms. Thus, we tested whether spatial variation in community structure was consistent over the seven sampling periods at each elevation, accounting for potential effects of temporal autocorrelation.

Resource use by hummingbirds at the species level

To investigate the structure of plant–hummingbird networks at the species-level, we built matrices with the interaction frequency between hummingbird species and plant morphotypes for each elevation. In order to quantify species’ level specialization across the entire year, we pooled the observations across sampling periods. Interaction frequency equalled the number of hummingbird individuals carrying pollen of a particular plant morphotype. Based on these matrices, we calculated the following indices for hummingbird species: complementary specialization d' ,

paired differences index (PDI) and standardized degree. The index d' is a sampling-robust measure of specialization derived from Kulback–Leibler distances and quantifies how strongly a species deviates from a random sample of interacting partners (Blüthgen et al. 2006). This index compares the observed frequency distribution of interactions with an expected probability distribution and thus estimates the degree of complementary specialization (i.e. niche partitioning) (Blüthgen et al. 2008, Blüthgen 2010). The index d' ranges from 1 for a completely specialized to 0 for a fully generalized species (Blüthgen et al. 2006).

We additionally used a normalised version of the PDI index proposed originally by Poisot et al. (2011), where values of 1 indicate perfect specialists and 0 indicate generalists. This index contrasts the species’ strongest interaction on a resource with those over all remaining resources. In addition, we calculated the standardized degree as the sum of interactions per species scaled by the number of possible partners (Dormann et al. 2013). We did not control these metrics for differences in the number of caught bird individuals among species because the number of captured individuals reflects the abundance of a species in the community. However, in statistical comparisons we weighted the species-specific indices by the number of individuals sampled per hummingbird species to account for potentially inaccurate estimates of specialization for rare species. To compare the different indices among the three elevations, we performed linear mixed effect models with elevation as fixed effect and species identity as random effect, accounting for the fact that we calculated the indices from three different networks. Thus, we tested whether species-level specialization varied consistently among elevations.

Resource use by hummingbirds at the individual level

To assess patterns of resource use of hummingbirds at the individual level, we used the number of pollen morphotypes carried by each hummingbird individual as a measure of individual specialization. We assumed that the number of pollen morphotypes carried by an individual was associated to the degree of ecological specialization, i.e. few morphotypes of carried pollen indicate high specialization. To assess the effect of elevation on the number of pollen morphotypes, we fitted a generalized linear mixed effect model with Poisson error distribution including elevation as fixed effect and species identity and sampling period as random effects. Thus, this model accounts for taxonomic and temporal autocorrelation and tests whether individual-level specialization consistently differs among the three elevations across different sampling periods and species.

In addition, we used pollen loads carried by hummingbirds to build binary interaction matrices of hummingbird individuals by plant morphotypes for each elevation. To partition the variation in resource use among hummingbird species and individuals, separately for each elevation, we performed a permutational multivariate analysis of variance, with the function *adonis* in the package *vegan* (Oksanen et al. 2014). In this analysis, Sørensen distances were calculated based on the binary interaction matrices. We separately included the two pollen samples (dorsal and ventral) per individual to measure also the variability within individuals (i.e. at different parts of the body). The analysis included

recaptures of the same individuals ($n = 47$ recaptures) and thus also captures the variability between recaptures of the same individuals. Thus, overall variation in hummingbirds' resource use was partitioned among species and individuals, whereas unexplained variance in the residuals accounted for the variation within individuals and between recaptures of the same individuals. The significance of the analysis of variance was assessed against 999 randomizations using a permutation test, based on pseudo F-ratios.

All statistical analyses were conducted with R statistical software ver. 3.0.0 (R Development Core Team) including the packages bipartite (Dormann et al. 2013), car (Fox et al. 2014), FD (Lalibert   et al. 2014), lme4 (Bates et al. 2014), rgl (Adler et al. 2014) and vegan (Oksanen et al. 2014).

Data associated with this paper are deposited at the Biodiversity and Climate Research Center Metacat Repository.

Results

Structure of hummingbird assemblages

We captured a total of 28 hummingbird species at the three elevations. Total abundance over all hummingbird species per sampling period (low vs high elevation, $t = -0.93$, $p = 0.36$; mid vs high elevation, $t = 0.85$, $p = 0.41$) and species richness (low vs high elevation, $t = 0.31$, $p = 0.76$; mid vs high elevation, $t = 0.50$, $p = 0.62$) did not differ significantly among elevations (Fig. 1A, B). In contrast, the effective number of hummingbird species (e^H) was higher at low ($t = 2.46$, $p = 0.02$) and mid elevations ($t = 2.35$, $p = 0.03$) compared to the highlands (Fig. 1C). Species turnover in the hummingbird communities among elevations was high between low and mid elevations (3 shared species, 14% overlap) and between low and high elevations (1 shared species, 3% overlap). In contrast, mid and high elevations had a lower turnover (7 shared species, 37 % overlap). Beta-diversity across sampling periods was high at all elevations (low elevation: range 0.32–0.79, mean 0.52; mid elevation: range 0.18–0.75, mean 0.45; high elevation: range 0.19–0.83, mean 0.47).

Across the seven sampling periods, the distribution of morphological traits within the hummingbird assemblages differed among elevations (Fig. 2). At low and mid eleva-

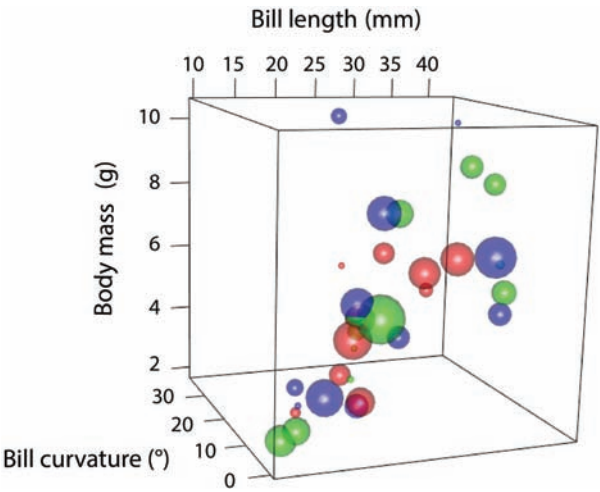


Figure 2. Distribution of functional traits of hummingbird species in a tri-dimensional space at three elevations in Costa Rica (50, 1000 and 2000 m a.s.l.). Each data point represents one hummingbird species at a given elevation ($n = 28$); 8 species occurred at two study sites and 1 species occurred at the three study sites. Traits were bill length, bill curvature and body mass. Symbol size corresponds to weights by the number of individuals mist-netted for each hummingbird species (log-transformed) at the respective elevation. Symbol colours indicate the communities at each elevation: red, blue and green for low, mid and high elevation, respectively.

tions, traits were more evenly distributed among species and species were on average more distant to the community centroid than in the highlands (Fig. 3B, C; Table 1). Throughout the year, functional richness was similar at all elevations (Fig. 3A; Table 1). At low and mid elevations, we found higher CWMs for bill length and, especially, bill curvature than in the highlands, while the CWM for body mass tended to increase with elevation, but this trend was not significant (Fig. 3D, E, F; Table 1).

Resource use by hummingbird species

We identified 208 unique pollen morphotypes collected on 357 individuals of 21 hummingbird species, corresponding to 1273 plant–hummingbird interactions (see Supplementary material Appendix 1, Table A1 and A2 for species lists). We

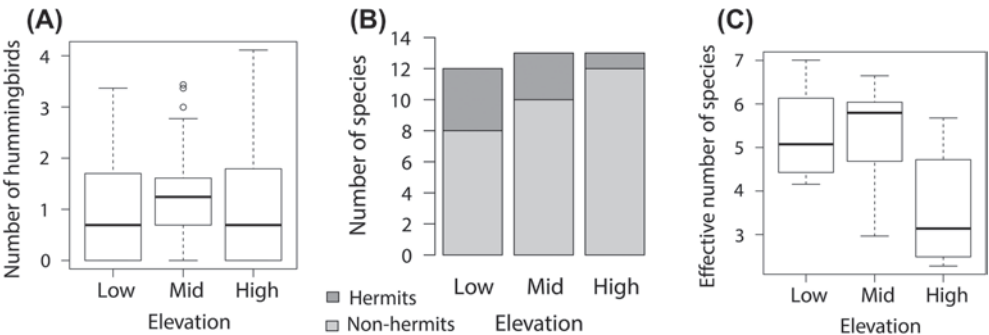


Figure 1. Number of hummingbird individuals captured in mist nets (A), number of hummingbird species (B) and the effective number of hummingbird species (C) at three elevations in Costa Rica (50, 1000 and 2000 m a.s.l.). In the stacked bar graph (B), each bar is divided into the two groups of hummingbird species (hermits vs non-hermits) and each of the three bars represents the total number of hummingbird species at each elevation. In the boxplots (A, C), thick horizontal lines are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range and circles are outliers.

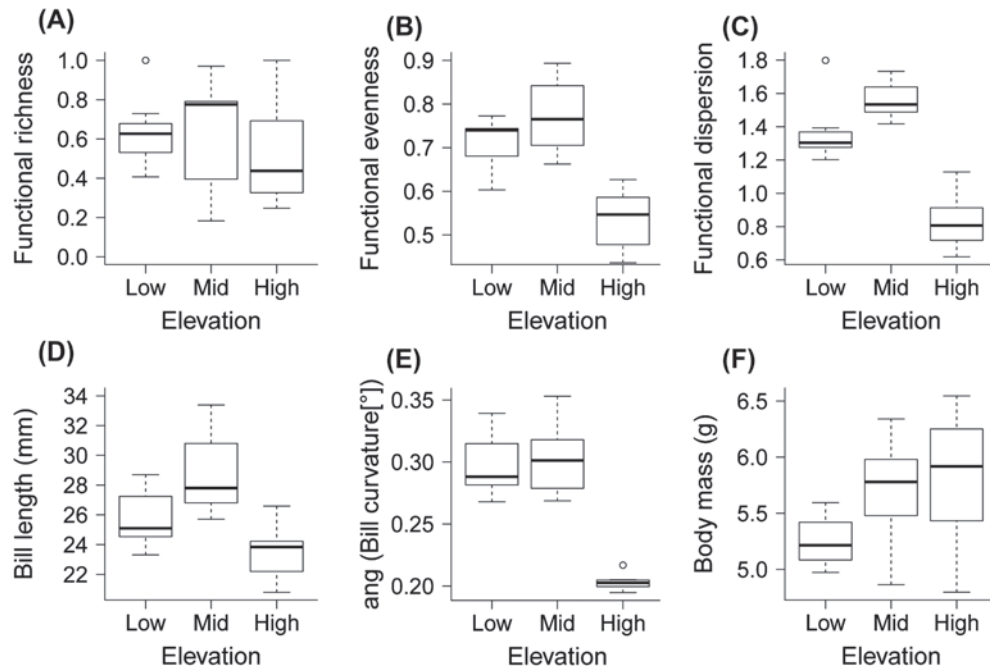


Figure 3. The functional structure of hummingbird assemblages at three elevations in Costa Rica (50, 1000 and 2000 m a.s.l.). Metrics were based on three functional traits (bill length, bill curvature and body mass) measured in 28 hummingbird species. (A, B, C) Indices of functional diversity: functional richness, functional evenness and functional dispersion. (D, E, F) Community weighted means of functional traits. Statistics are provided in Table 1. Variability per elevation corresponds to the temporal variability among sampling periods; horizontal lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range and circles are outliers.

did not detect pollen grains on 29 individuals (8% of all sampled birds) of ten hummingbird species.

All indices at the species level showed significant variation among elevations across species. Specialization index d' was higher at the low and mid elevations compared to the highlands (Fig. 4A, Table 2). The PDI index also

indicated higher specialization of hummingbird species at low ($PDI = 0.92 \pm 0.01$) and mid elevation ($PDI = 0.95 \pm 0.01$) than at the highest elevation ($PDI = 0.90 \pm 0.02$) (Table 2). Moreover, standardized degree was higher in the highlands compared to the other elevations, which indicates that hummingbird species visited on average more of the available plant species in the highlands than species at the other elevations (Fig. 4B, Table 2).

Table 1. Linear mixed effect models of the relationships between different metrics of the functional structure of hummingbird assemblages and elevation in Costa Rica. Three indices of functional diversity and community weighted means of functional traits were calculated based on three functional traits (bill length, corolla length and body mass) and 28 hummingbird species. Differences in functional metrics among the three elevations were tested against the temporal variability in functional metrics, as derived from seven sampling periods of hummingbird abundance at each elevation. Sampling period was included as a random effect in each model. The reference level (intercept) was the high-elevation assemblage in all models.

Response variable	Elevation	β	t value	p
Indices of functional diversity				
Functional richness	Low	0.40	0.73	0.477
	Mid	0.32	0.57	0.572
Functional evenness	Low	1.37	3.94	0.001
	Mid	1.81	5.22	<0.001
Functional dispersion	Low	1.52	6.11	<0.001
	Mid	2.07	8.29	<0.001
Community weighted means				
Bill length	Low	0.74	1.86	0.079
	Mid	1.69	4.26	<0.001
Bil curvature	Low	1.83	7.64	<0.001
	Mid	1.91	7.97	<0.001
Body mass	Low	-1.03	-2.05	0.055
	Mid	-0.19	-0.39	0.703

Resource use by hummingbird individuals

The number of pollen morphotypes carried by hummingbird individuals differed across elevations, with individuals at low ($z = -4.58$, $p < 0.001$) and mid elevations ($z = -4.71$, $p < 0.001$) carrying fewer pollen morphotypes than individuals in the highlands (Fig. 4C).

Most of the variation in resource use by hummingbirds at all elevations was explained by species and individual identity, with a rather low variance residing among samples (i.e. among recaptures and different body parts; residuals < 25% at all elevations) (Table 3). Individual hummingbirds differed strongly in their use of nectar plants at the three elevations, with over 60% of the variation in resource use explained by individual identity in all cases. In contrast, variation at the species level was smaller than at the individual level ($\leq 20\%$ in all cases, Table 3).

Discussion

Our findings show consistent patterns in the functional structure of hummingbird assemblages and specialization of

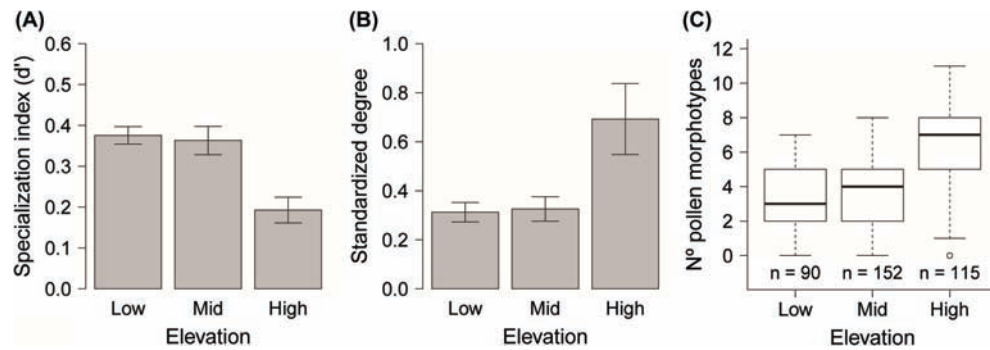


Figure 4. (A and B) Relationship between specialization indices at the species-level (specialization d' and standardized degree) and elevation. Means and standard errors shown in the bar plots were weighted by the number of individuals sampled per hummingbird species at the respective elevation and were computed from the variability among species at the respective elevation. (C) Number of pollen morphotypes carried by individual hummingbirds at three different elevations in Costa Rica ($n = 357$ individuals). Thick horizontal lines are medians, boxes indicate 25th and 75th percentiles, and whiskers indicate the data range across hummingbird individuals captured at the respective elevation.

hummingbird species and individuals at the three elevations. Across sampling periods, hummingbird assemblages varied from being functionally even and over-dispersed in the two lower elevations to uneven and clustered in the high-elevation assemblage. Accordingly, hummingbird species and individuals were more specialized at low and mid elevations than at the highest elevation. These corresponding trends suggest that changes in the specialization of hummingbird species and individuals extend to the functional structure of the hummingbird assemblages.

Structure of hummingbird assemblages

Total abundance, species and functional richness of hummingbird assemblages remained similar across the three elevations. At all study sites and across sampling periods, hummingbird assemblages were characterized by a diverse pool of species with different functional roles, comprising territorial and trap-lining species, as well as species with distinct morphologies (Fig. 2, see also Feinsinger and Colwell 1978). Hermit hummingbirds, i.e. trap-lining species with long and curved bills, were captured across all elevations although there was a decreasing richness of this group with

increasing elevation. Despite the similarity in abundance and species richness among assemblages, the effective number of hummingbird species was significantly reduced at the highest elevation. While species abundances were rather evenly distributed across species at low and mid elevations, the highland assemblage was dominated by *Lampornis calolaema* that contributed on average 56% of the captured individuals at this elevation (range of dominance values across sampling periods: 41–77%). This trend of reduced effective species richness of hummingbirds is consistent with the general pattern of decreasing diversity with increasing elevation (Koch and Sahli 2012).

The functional structure of the highland assemblage was more uneven and clustered compared to the lower elevations, and this effect was consistent throughout the year. This may indicate that the assembly of the highland assemblage is subject to environmental filtering. This is in line with the interpretation of patterns in the phylogenetic structure of hummingbird assemblages in the tropical Andes (Graham et al. 2009, 2012, Weinstein et al. 2014). The hypothesis of environmental filtering assumes that environmental conditions act as a filter allowing only a narrow range of species and functional roles to coexist in harsh, high-elevation environments (Keddy

Table 2. Linear mixed effect models of the relationships between specialization indices at the species-level and elevation in Costa Rica. Indices were calculated from 1273 interactions between 21 hummingbird species and 208 plant species (identified from pollen morphotypes), separately for each elevation. Differences in specialization among the three elevations was tested against the variability in specialization among species. In all models, species identity was included as a random factor and indices were weighted by the number of individuals sampled per hummingbird species. The reference level (intercept) was the high-elevation network in all models.

Response variable	Elevation	β	t value	p
Specialization	Low	1.24	17.39	<0.001
	Mid	1.19	19.07	<0.001
PDI index	Low	0.20	2.40	0.027
	Mid	1.06	14.40	<0.001
Standardized degree	Low	-0.58	-5.47	<0.001
	Mid	-0.87	-10.10	<0.001

Table 3. Permutational multivariate analysis of variance on resource partitioning among hummingbird species and individuals at three different elevations in Costa Rica. Observations included 1273 interactions between 357 hummingbird individuals belonging to 21 hummingbird species and 208 plant species (identified from pollen morphotypes). Based on these observations, binary distance matrices based on Sørensen dissimilarities were constructed. Coefficients of determination (R^2) indicate the amount of variation in hummingbirds' resource use that is explained by: species and individual identity. Unexplained variance in the residuals includes the variation between dorsal and ventral samples within individuals and between recaptures of the same individuals.

Source of variation	Elevation					
	Low		Mid		High	
	R^2	p	R^2	p	R^2	p
Species	0.158	0.001	0.181	0.001	0.097	0.001
Individual	0.698	0.001	0.619	0.001	0.677	0.001
Residuals	0.144	–	0.200	–	0.226	–

1992, Mouchet et al. 2010, but see HilleRisLambers et al. 2012 and Fritschie et al. 2014). Consequently, trait values of species tended to be clustered in functional space. Hummingbird assemblages are likely to be strongly influenced by environmental filtering because of metabolic and aerodynamic challenges faced by hummingbirds at high elevations (Altshuler et al. 2004a, b). Moreover, a reduced functional diversity of plant resources could constrain the functional diversity of the dependent consumer guild (Dehling et al. 2014b).

In addition to environmental factors, competition is another factor influencing community structure and tends to limit the functional similarity of co-occurring species (MacArthur and Levins 1967). A high intensity of interspecific competition is expected to increase the spread of species traits within a community (Laliberté and Legendre 2010, but see Mayfield and Levine 2010, and Fritschie et al. 2014). Accordingly, we found a pattern of functional evenness and over-dispersion at low and mid elevations. This suggests that interspecific competition is particularly strong in these hummingbird assemblages with high effective species numbers (see also Graham et al. 2009, 2012). However, differential effects of competition on species assemblages along elevational gradients have been recently challenged and differences in functional structure could also derive from abrupt changes in environmental conditions or phylogenetic effects on species assemblages (Dehling et al. 2014a). Consistent with this proposition, the rarity of hermits at the high elevation may be one crucial driver for the observed pattern in our study, in addition to environmental filtering and competition for resources.

We were able to identify functional traits, specifically bill traits, driving the changes in functional community structure. Analyses suggest that species with long and, in particular, curved bills were filtered out at the highest elevation, where mostly species with short and straight or slightly-curved bills occurred. This pattern may primarily arise from a reduced abundance of curved-billed hermit species at high elevations as only one hermit species was present at the highest elevation (*Phaethornis guy*). Throughout the tropics, hermits are mostly limited to lowlands and only a few species occur at high elevations (Snow and Snow 1972). Phylogenetic constraints in evolving traits to adapt to high elevations have been proposed to explain their limited ability to occupy highland habitats (Stiles 2004), e.g. the evolution of larger feet that permit hummingbirds to perch while extracting nectar, reducing hovering costs at high elevations.

Hummingbirds' resource use

Hummingbird species were on average less specialized at the highest elevation compared to the lower elevations. High specialization at low elevations may contribute to releasing species from competitors in highly diverse communities, due to increased resource partitioning (MacArthur and Levins 1967, Mouchet et al. 2010). This explanation is consistent with the findings of a study of plant–hummingbird networks along a latitudinal gradient that found increasing specialization towards species-rich lower latitudes

(Dalsgaard et al. 2011). In line with that, competition for resources has been found to be intense in hummingbird assemblages (Brown and Bowers 1985), favouring the evolution of specialized hummingbird morphologies. For example, hermit hummingbirds have evolved specific bill traits that match closely to the morphology of *Heliconia* flowers (Heliconiaceae) in tropical lowland forests. The *Heliconia*–hermit system represents a traditional example of coevolution and is one of the most specialized pollination systems in the Neotropics (Stiles 1975). Although we could not directly test the link between specialization and the intensity of interspecific competition in our study, our findings suggest that specialization in resource use might be crucial for allowing the coexistence of hummingbird species within highly diversified assemblages.

We found that hummingbird individuals were less specialized at the highest elevation, since they visited a larger number of plant species. Specialization, thus, followed the same pattern at the individual and species level. A possible driver for patterns in individual-level specialization could be changes in the intensity of intraspecific competition among the three elevations. Different degrees of specialization of hummingbird individuals along the elevational gradient could be associated with changes in floral resource availability. Previous studies have reported declines in flowering plant species richness as well as decreases in nectar production of hummingbird-visited plants with increasing elevation (Smith et al. 1995, Biesmeijer et al. 2006, Ornelas et al. 2007). Fewer floral resources at the highest elevation, where total hummingbird abundance was similar to the lowlands, suggests fewer floral resources per capita at this elevation. It is likely that reduced resource availability and increased intraspecific competition constrain the possibility of hummingbird individuals to specialize on specific floral resources and may favour their niche expansion at the highest elevation. Changes in competition, associated with varying degrees of resource diversity, are therefore likely to influence spatial patterns of ecological specialization in mutualistic networks (Schleuning et al. 2012).

Our results show strong variation in resource use among individuals and a rather low variation among hummingbird species across all elevations. These findings are in line with Tur et al. (2013) who found a high degree of heterogeneity in resource use among individuals in plant–insect mutualistic networks. The low specialization found in hummingbird individuals, especially at the highest elevation, may also be associated with high variation in resource use among individuals. Optimal foraging theory predicts that individuals tend to specialize on a few most-preferred resources (Stephens and Krebs 1986). However, under low resource availability, individuals may need to use also less preferred resources, leading to niche expansion and a decrease in specialization (Araújo et al. 2008). Niche expansion of individuals may be reflected by an increase in between-individual and a decrease in between-species variation in resource use, consistent with the niche variation hypothesis (Van Valen 1965). It is likely that the niche expansion of hummingbird individuals at the highest elevation may be a major driver of generalization in hummingbirds at this elevation and may be an important mechanism for driving spatial patterns in functional assemblage structure also in other taxa.

Conclusions

Our results show that the functional structure of hummingbird assemblages and specialization of plant–hummingbird networks are consistently affected by elevation throughout the year of study. Although we were unable to collect abundance, trait and interaction data from multiple sites per elevation, the consistent trends over time suggest an even and over-dispersed assemblages structure of hummingbirds at the lower elevations, consistent with high levels of floral resource partitioning and interspecific competition in specialized plant–hummingbird networks. Specialization on specific floral resources, also corroborated by the specialized bill morphologies at lower elevations, may facilitate the co-existence of hummingbird species within diversified assemblages at low- and mid elevations. In contrast, an uneven and clustered functional structure of the hummingbird assemblage at the highest elevation corresponds to more generalized individuals and species in this assemblage throughout the year. This may be the result of individual niche expansion as a consequence of a low availability of nectar plants and high intraspecific competition for floral resources in the highlands. We conclude that spatial variation in competition and animal resource use at the species and individual level may be a crucial mechanism for shaping the functional structure of highly diversified species assemblages and may also be important for structuring spatial patterns in other types of ecological networks and multispecies assemblages.

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