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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Plant–hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size

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Abstract Floral phenotype and pollination system of a plant may be influenced by the abiotic environment and the local pollinator assemblage. This was investigated in seven plant–hummingbird assemblages on the West Indian islands of Grenada, Dominica and Puerto Rico. We report all hummingbird and insect pollinators of 49 hummingbird-pollinated plant species, as well as six quantitative and semi-quantitative floral characters that determine visitor restriction, attraction and reward. Using nonmetric multidimensional scaling analysis, we show that hummingbird-pollinated plants in the West Indies separate in floral phenotypic space into two gradients—one associated with the abiotic environment and another with hummingbird size. Plants pollinated by large, long-billed hummingbirds had flowers with long corolla tube, large amounts of nectar and showy orange-red colouration. These attracted few or no insect species, whereas plants pollinated by small, short-billed hummingbirds were frequently pollinated by insects, particularly lepidopterans. The separation of plants related to environmental factors showed that species in the wet and cold highlands produced large amounts of dilute nectar, possessed no or a weak odour, and were associated with few insects, particularly few hymenopterans, compared to plants in the dry and warm lowlands. The most specialised hummingbird-pollinated plants are found in the West Indian highlands where they are pollinated by mainly large, long-billed hummingbirds. At the other extreme, highly generalised plants growing in the dry and warm lowlands are pollinated by small, short-billed hummingbirds and numerous insect species. This illustrates that, even within the hummingbird-pollinated flora, pollination syndrome and the degree of specialisation may vary tremendously depending on pollinator morphology and environment.

Keywords Floral phenotype · Insect pollinator · Ornithophilous syndrome · Plant–pollinator interaction · Specialisation gradient

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Introduction

Plant–pollinator interactions have often been stated to be highly coevolved, resulting in certain floral phenotypes or "pollination syndromes", which are expected to be specialisations to particular types of pollinators (Faegri and van der Pijl 1979). However, during the last decade, the concept of pollination syndromes has been reassessed (e.g. Waser et al. 1996; Hingston and Mcqillan 2000; Ollerton and Watts 2000; Fenster et al. 2004; Wilson et al. 2004;

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Ollerton et al. 2009). Although in a number of cases pollinator type can be predicted from floral phenotype (Ollerton et al. 2009), pollinator preference often seems weak (Pleasants and Waser 1985), ecological generalisation on multiple pollinators may be the rule rather than the exception (Waser et al. 1996) and clear-cut predictions of pollinator type based on pollination syndromes seem therefore hazardous and cannot replace field observations (Johnson and Steiner 2000; Ollerton et al. 2009).

Moreover, plant–pollinator interactions change with environment, at both species and community level (e.g. Cruden 1972; Primack and Inouye 1993; Hingston and Mcqillan 2000; Olesen and Jordano 2002; Aizen 2003; Medel et al. 2007; Devoto et al. 2005). For instance, pollinator species richness and composition vary with elevation, rainfall and temperature (Arroyo et al. 1982; Olesen and Jordano 2002; Aizen 2003; Devoto et al. 2005), affecting specialisation level (Elberling and Olesen 1999) and pollinator mode (Cruden 1972; Stiles 1978; Aizen and Ezcurra 1998; Aizen 2003; Kessler and Krömer 2000; Kay and Schemske 2003; Krömer et al. 2006). Insects, especially hymenopterans, have low species richness in areas with cold and rainy weather (Cruden 1972; Aizen and Ezcurra 1998; Devoto et al. 2005), whereas vertebrates are expected to be less affected by these environmental factors (Stiles 1978; Bleiweiss 1998). In Central and South America, where hummingbirds are part of the pollinator fauna, many plant species are specialised on hummingbird–pollination in cold and rainy environments, often prevailing at high elevations (Cruden 1972; Stiles 1978; Aizen and Ezcurra 1998; Bleiweiss 1998; Kessler and Krömer 2000; Aizen 2003; Krömer et al. 2006). As an example, in the cold highlands and in wet areas of the eastern Andes, bromeliads are primarily hummingbird-pollinated, whereas in arid habitats they are mainly insect-pollinated (Kessler and Krömer 2000; Krömer et al. 2006). Similarly, in the tropical highlands, *Costus* species are pollinated by hummingbirds, whereas lowland species are pollinated by either euglossine bees or hummingbirds (Kay and Schemske 2003).

Plant species adapted to hummingbird–pollination often have flowers that are showy orange-red, scentless, have a long, narrow, tubular corolla and produce a large amount of dilute nectar, which broadly correspond to hummingbird sensory capabilities, morphology and high energetic demands. However, floral phenotype may vary among populations within the same species (Stiles 1978; Devoto et al. 2006; Nattero and Cocucci 2007; Medel et al. 2007), species groups (Krömer et al. 2006) and among communities (Aizen 2003) in association with differences in both the abiotic environment (Aizen 2003; Devoto et al. 2006) and the local pollinator assemblage (Nattero and Cocucci 2007; Medel et al. 2007). For instance, natural selection may modify corolla morphology, nectar reward and colouration, causing changes in hummingbird and insect accessibility and attractiveness (Bradshaw et al. 1995; Bradshaw and Schemske 2003; Wilson et al. 2006). Hence, floral phenotype of hummingbird-pollinated plants may be adaptations to a mixture of hummingbird and insect foraging (Stiles 1981; Hurlbert et al. 1996; Mayfield et al. 2001; Castellanos et al. 2004). Indeed, as most researchers studying plant–hummingbird interactions have observed, hummingbirds and insects, in particular lepidopterans and bees, often pollinate the same plants (e.g. Snow and Snow 1972; Feinsinger and Colwell 1978; Carpenter 1979; Stiles 1981; Feinsinger et al. 1982; Arizmendi and Ornelas 1990; Mayfield et al. 2001; Medel et al. 2007; Dalsgaard et al. 2008). This may especially be the case for plants pollinated by small hummingbirds (e.g. Stiles 1981; Feinsinger et al. 1982; Arizmendi and Ornelas 1990; Dalsgaard et al. 2008), plants in dry lowland habitats where insects are reliable and effective pollinators (Cruden 1972; Bleiweiss 1998), and on islands, where pollination systems are expected to be more generalised than on comparable mainland (e.g. Linhart and Feinsinger 1980; Feinsinger et al. 1982; Olesen et al. 2002; Rivera-Marchand and Ackerman 2006; Timmermann et al. 2008).

Floral phenotype may consequently vary with environment, local pollinator assemblage and size of hummingbird pollinator. Thus, hummingbird-pollinated flowers might not fit into a single category, such as the traditional ornithophilous pollination syndrome (Ollerton et al. 2009). In this study, we examine the relationships between floral phenotype, hummingbird type, insect generalisation level and environment in seven plant–hummingbird assemblages varying in altitude, rainfall and temperature on the West Indian islands of Grenada, Dominica and Puerto Rico. We ask: (1) can we separate the plant species in floral phenotypic space in relation to the type of hummingbird visitor and environment, i.e. can we identify gradients associated with hummingbird size and environment? (2) How is floral phenotypic separation related to insect visitor fauna, and how is insect species richness related to hummingbird size and environment? (3) Finally, we identify representatives of the most specialised and generalised plant species, and discuss the pros and cons of having a generalised pollination system in the West Indies.

Methods

Study sites and species

The study was carried out in the West Indian islands of Grenada (12°07′N, 61°40′W), Dominica (15°25′N, 61°20′W) and Puerto Rico (18°15′N, 66°30′W). The seven

plots were distributed at lowland and highland sites, enabling us to observe all hummingbird species on each island and to examine the patterns of plant–pollinator interactions along an environmental gradient of altitude, rainfall and temperature (Tables 1, 2). Fieldwork was conducted from 10 April to 17 July 2005 (Dominica), 10 March to 25 June 2006 (Grenada) and 3 March to 15 June 2006 (Puerto Rico).

Flower visitors

All flowering plant species, regardless of pollination syndrome, were identified and surveyed for hummingbird and insect flower visitation, but only hummingbird-pollinated plant species (i.e. plants where hummingbirds made legitimate visits, defined as drinking nectar and touching reproductive floral parts) are reported in this study. Thus, illegitimate interactions in which plants were nectar robbed without being pollinated are not included in these analyses. Visitation by hummingbirds was systematically monitored for all flowering plant species in 30-min observation periods (a total of 1,420 h) from a distance of approximately 10 m. Observations were conducted during dry and calm weather between 0600 and 1800 hours (Dominica) and 0600 and 1400 hours (Grenada and Puerto Rico). We divided our plots into 10 × 5 m segments and, on the day prior to each survey, we randomly chose the order and segment of each plant species to be observed (Dominica) or

Table 1 Description of study sites

Study site	Plot size	Habitat type	Altitude (m a.s.l.)	Annual rainfall (mm)	Annual temperature (°C)[a]	No. hummingbird-pollinated plant species
Dominica lowland	400 × 5 m[b]	Dry scrub woodland	9	1,905	27.1	11
Dominica highland	400 × 5 m[b]	Cloud forest	813	7,506	21.9	12
Grenada lowland	200 × 5 m	Dry scrub woodland	38	1,287	27.2	3
Grenada highland 1	200 × 5 m[c]	Rainforest, hurricane disturbed	500	3,868	24.2	7
Grenada highland 2	200 × 5 m	Cloud forest	705	3,868	22.9	7
Puerto Rico lowland	200 × 5 m	Dry scrub woodland	10	799	25.4	5
Puerto Rico highland	200 × 5 m	Cloud forest	1,154	1,914	17.7	10

[a] The temperature at each study site was calculated using the wet adiabatic lapse rate (0.65°C/100 m), annual long-term sea-level temperature close to each of our lowland study sites (NOAA National Weather Service) and the elevation of each study site

[b] In Dominica, we had 400 × 5 m plots. In 200 × 5 m we observed all plant-pollinator interactions (as in Grenada and Puerto Rico), whereas we in the remaining 200 × 5 m only observed plant-insect interactions when a plant species was recorded to be hummingbird-pollinated. However, since we only added one hummingbird-pollinated plant species both in the Dominican highland and lowland plots by having the additional 200 × 5 m, we in the subsequent field seasons in Grenada and Puerto Rico only had 200 × 5 m plots

[c] Grenada highland 1 was the only plot where we were unable to observe the canopy flowers accounting for ca. 30% of the entire flower community. However, according to Bawa (1990) the rainforest canopy has only ca. 2% hummingbird-pollination, whereas the understory and subcanopy have ca. 18%, i.e. hummingbird-pollination is nine times as frequent in the understory/subcanopy as the canopy. Assuming the same in the rainforest of Grenada, we would be missing very few hummingbird-pollinated plant species

Table 2 Hummingbird characteristics and study sites where present

Hummingbird species		Body mass (g)[a]	Bill length (mm)[a]	Study sites present[b]
Common name	Scientific name			
Antillean crested hummingbird	*Orthorhyncus cristatus*	2.71	10.72	All sites in the Lesser Antilles
Puerto rican emerald	*Chlorostilbon maugaeus*	2.93	13.62	PtR-low, PtR-high
Blue-headed hummingbird	*Cyanophaia bicolor*	4.55	16.41	Dom-high
Green-throated carib	*Eulampis holosericeus*	5.60	22.74	Dom-low, Gre-high 1, Gre-high 2
Antillean mango	*Anthracothorax dominicus*	5.66	24.13	PtR-low
Green mango	*Anthracothorax viridis*	6.60	24.40	PtR-high
Rufous-breasted hermit	*Glaucis hirsuta*	6.82	32.25	Gre-high 1
Purple-throated carib	*Eulampis jugularis*	8.67	23.59	Dom-high

[a] Hummingbird body mass and bill length (exposed culmen) are according to Brown and Bowers (1985), except for the green mango (Kodric-Brown et al. 1984). The hummingbirds are arranged by increasing size. Notice the division of the hummingbirds into two size classes of three small, short-billed species and five large, long-billed species

[b] *Dom-high* Dominica highland, *Dom-low* Dominica lowland, *Gre-low* Grenada lowland, *Gre-high 1* Grenada highland 1, *Gre-high 2* Grenada highland 2, *PtR-low* Puerto Rico lowland, *PtR-high* Puerto Rico highland. See Table 1 for description of study sites

randomly chose a starting segment and observed all plant species not previously observed within this segment, before moving on to the next segment (Grenada and Puerto Rico). In both cases, we made the restrictions that plants should preferably be sampled at different individuals and times of the day, i.e. a semi-random method. Whenever possible, several plant species were observed simultaneously. Additional plant–hummingbird interactions opportunistically observed between the 30-min observation periods were also included in the dataset. All hummingbird-pollinated plant species were observed for insect visitation in 10-min observation periods (a total of 110 h) in dry and calm weather between 1000 and 1600 hours (Dominica) and 0600 and 1400 hours (Grenada and Puerto Rico). As for hummingbirds, plant species were selected semi-randomly and only visits where insects touched anthers and/or stigmas were included in these analyses. When observing plants for insect visitation, we observed only one plant species at a time. Insects that could not be identified in the field were caught for later identification and assignment to distinct morphospecies at family level using Triplehorn and Johnson (2005) and Michener (2000). Vouchers are kept at the University of Aarhus, Denmark. For each plant species in each plot, we calculated the average morphology (body mass and bill length) of visiting hummingbird species, and the hummingbird and insect pollinator species richness (see ESM S1 for details).

Floral variables

For each hummingbird-pollinated plant species, we measured six quantitative and semi-quantitative floral variables grouped pair-wise: "restriction" (internal corolla depth and corolla width), "reward" (nectar volume and nectar concentration) and "attraction" (colour and odour). These six variables enabled us to quantitatively describe different floral types, ranging from flowers fitting the traditional ornithophilous syndrome (i.e. long and narrow corolla, large amount of dilute nectar, orange-red and scentless flowers) to flowers that would be traditionally considered to be entomophilous. For each plant species in each plot, we used the average value for each of the six floral traits (see ESM S2 for details).

Statistical analysis

In order to examine whether we can separate the hummingbird-pollinated plants into phenotypic gradients or subgroups, we analysed the floral variables using nonmetric multidimensional scaling (NMS), an analysis previously used for this type of data (Ollerton and Watts 2000; Wilson et al. 2004; Ollerton et al. 2009). A few plant species (six out of 49 species) occurred in more than one study site. Since the purpose of this study was to examine the effect of both floral phenotype and environment, we used data from each site separately rather than the average of several sites (see ESM S1–S2 for details). Prior to analysis, each floral variable was standardised by subtracting the minimum score and dividing by the range of scores, giving each of the six variables the same weight (Wilson et al. 2004). We used the Euclidean distance measure and the recommended "autopilot" function "slow and thorough" in PC-ORD 5.0 (McCune and Mefford 2006). In our case, the recommended dimensionality was a three-dimensional (3D) solution. We showed the two axes related to hummingbird size and environment, and for illustration we rotated the axes in order to separate flowers according to hummingbird body mass. Hereafter, we correlated the axes with a second matrix containing the floral variables, the environmental descriptors, hummingbird size, hummingbird and insect species richness, sampling effort and plant origin (native/introduced).

Results

In our study sites, a total of 49 plant species from 25 families were hummingbird-pollinated (ESM S1). The most species-rich family was the Rubiaceae with nine species (18%), whereas the rest of the families, e.g. Acanthaceae, Bromeliaceae, Campanulaceae, Ericaceae, Gesneriaceae and Heliconiaceae, were each represented by one to four species. The small, short-billed hummingbirds were the exclusive hummingbird visitors of 28 (57%) and the main visitors of another 9 (18%) plant species. The large, long-billed hummingbirds were the exclusive hummingbird visitors of seven (14%) and the main visitors of five (10%) plant species. Hummingbirds as a group were the exclusive pollinators of 12 plant species (24%) whereas the remaining 37 (76%) were pollinated by both hummingbirds and insects. The most frequent insect pollinators were Hymenoptera (range 0–6 species per plant species, mean ± SD = 1.3 ± 1.6 species), Lepidoptera (0–14 species, 1.1 ± 2.4 species) and Diptera (0–3 species, 0.4 ± 0.8 mm), with only a few visitors from other insect orders (ESM S1). The plants varied greatly in their floral characters of corolla depth (range 0.0–48.8 mm, mean ± SD = 15.9 ± 12.8 mm), corolla width (0.8–21.5 mm, 4.1 ± 4.1 mm), nectar volume code (1–3, 2.0 ± 0.8), nectar concentration (9.8–50.2%, 27.6 ± 10.0%), colour code (1–4, 2.3 ± 0.9) and odour code (1–4, 2.4 ± 0.8) (ESM S2).

The NMS ordination resulted in a 3D solution (stress = 6.6, $R^2 = 0.97$, $P < 0.01$) with the variation related to hummingbird size being on axis 1 ($R^2 = 0.45$) and variation related to environmental descriptors on axis 2 ($R^2 = 0.20$; Fig. 1). Along axis 1, the main hummingbird pollinators of plants toward the left were small, short-billed

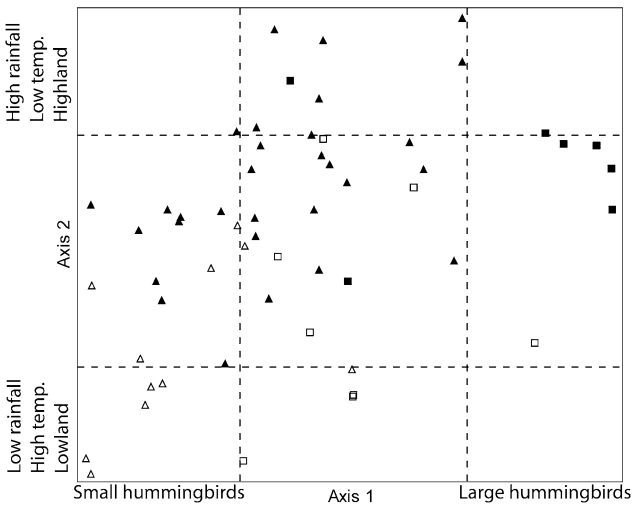

Fig. 1 Nonmetric multidimensional scaling (NMS) ordination based on six quantitative and semi-quantitative floral variables using a Euclidean distance measure. *Triangles* Plant species pollinated entirely or mainly by small hummingbirds, *squares* plant species pollinated entirely or mainly by large hummingbirds, *filled symbols* highland plants, *open symbols* lowland plants. The ordination space is rotated to optimise the separation of hummingbird body size along Axis 1. For correlation coefficients, see Table 3

hummingbirds and at the right were large, long-billed hummingbirds; in the middle there was a mixture containing flowers pollinated mainly by both small and large hummingbirds. This separation was related to an increase in corolla depth, nectar volume and orange-red colours as the average hummingbird's body mass and bill length increased. In other words, flowers pollinated by large, long-billed hummingbirds were longer, had more nectar and more frequently an orange-red colour, compared to flowers pollinated by small, short-billed hummingbirds (Table 3; Figs. 1, 2). Moreover, along axis 1, there was a positive correlation with hummingbird species richness (Table 3; Figs. 1, 2). This was caused by the large number of plant species to the left in the ordination space not attracting large hummingbirds, whereas most plants toward the centre in the ordination space were pollinated by both small and large hummingbirds, and some of the plants at the very right attracted three hummingbird species. However, all of the plant species at the very right were pollinated mainly by large hummingbirds, and some of them were also pollinated entirely by large hummingbirds (ESM S1). Along axis 2, plants separated according to the environment: only lowland plants were at the bottom of the phenotypic space, whereas only highland species were at the upper part; again with a mixture in the middle containing both lowland and highland plants. This partition was related to an increase in nectar volume, and a decrease in nectar concentration and odour as rainfall increased and temperature decreased with altitude (Table 3; Figs. 1, 2). In other words,

Table 3 Correlations between nonmetric multidimensional scaling (NMS) ordination axes and plant origin (native/introduced), floral traits, environment, hummingbird and insect visitors and sampling effort

Variable type	Variable	Axis 1, *r*	Axis 2, *r*	Axis 3, *r*
Plant origin and floral traits	Plant origin	−0.163	−0.019	0.133
	Corolla depth	0.773*	−0.076	−0.070
	Corolla width	0.285	−0.193	−0.698*
	Nectar volume	0.745*	0.626*	−0.640*
	Nectar concentration	−0.309	−0.741*	0.219
	Colour	0.785*	0.359	0.221
	Odour	−0.306	−0.711*	−0.572*
Environment	Altitude	0.208	0.578*	−0.030
	Rainfall	0.078	0.435*	−0.260
	Temperature	−0.227	−0.497*	−0.006
Hummingbird visitors and sampling effort	Body mass	0.678*	0.118	−0.234
	Bill length	0.694*	0.076	−0.125
	No. of hummingbird species	0.414*	0.327	−0.223
	Sampling effort	0.263	0.074	0.184
Insect visitors and sampling effort	No. of insect orders	−0.445*	−0.527*	−0.019
	No. of insect species	−0.424*	−0.476*	0.026
	No. of Hymenoptera species	−0.296	−0.479*	−0.096
	No. of Lepidoptera species	−0.441*	−0.306	0.168
	No. of Diptera species	−0.284	−0.283	−0.173
	Hymenoptera (%)	0.016	0.020	−0.296
	Lepidoptera (%)	−0.466*	−0.271	0.289
	Diptera (%)	−0.107	−0.102	−0.476*
	Sampling effort	0.184	0.146	0.151

In all quantitative or semi-quantitative variables, a positive correlation coefficient represents an increase, e.g. an increase in corolla depth. The only exceptions to this are colour (a positive correlation coefficient represents ornithophilous syndrome colours) and plant origin (a positive correlation coefficient represents introduced species)

* Correlation of $r^2 \geq 0.15$

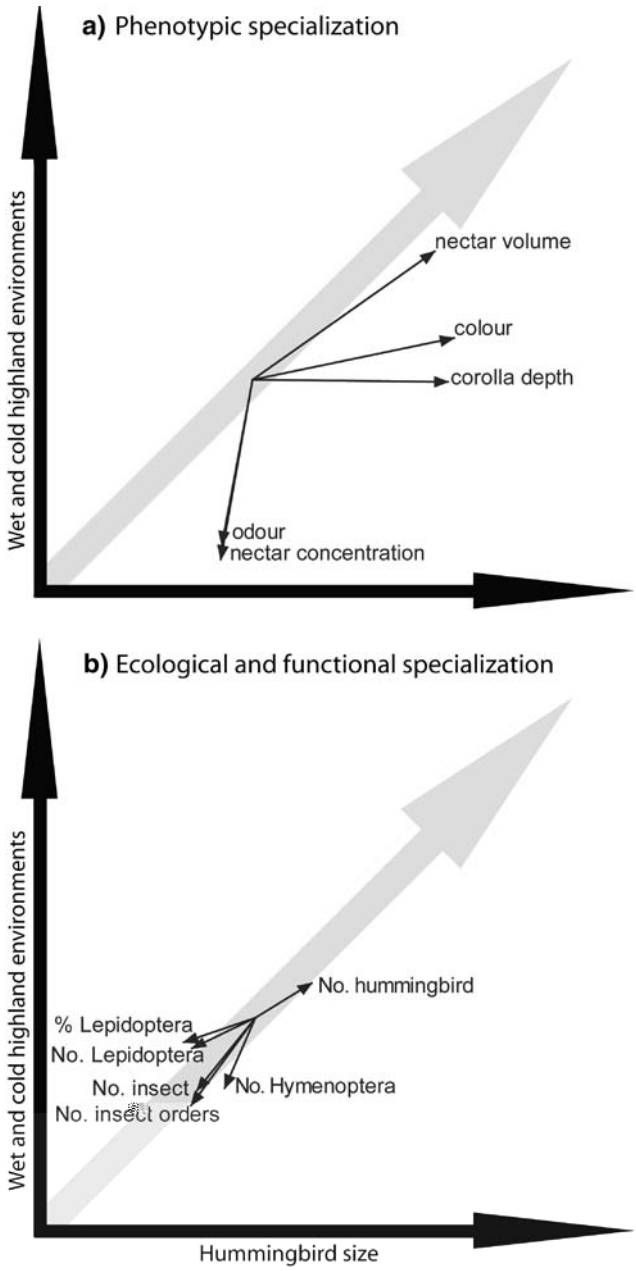

Fig. 2 Schematic version of the NMS ordination illustrating the relation between environmental setting, hummingbird pollinator size and (**a**) phenotypic specialisation and (**b**) ecological and functional specialisation. Shown are vectors from the NMS ordination with $r^2 \geq 0.15$. *Grey arrow* Overall direction of specialisation (phenotypic, ecological and functional) on hummingbird-pollination

hummingbird-pollinated flowers in the wet and cold highlands had large amounts of dilute nectar and no or weak odour, compared to hummingbird-pollinated flowers in the dry and warm lowland.

The separation of flowers according to hummingbird size and environment was also related to variation in insect pollinator species richness. Plants pollinated by small-sized hummingbirds were pollinated by more insect orders and species, in particular lepidopterans, than flowers pollinated by large-sized hummingbirds (Table 3; Figs. 1, 2). Likewise, plant species in lowland environments were also pollinated by more insect orders and species, in particular hymenopterans (Table 3). However, although the species richness of hymenopterans was higher on lowland plants, there was also a higher overall insect species richness, and therefore proportionally, there were no more hymenopterans at the lowland plants than at the highland ones. Along axis 3, unrelated to both hummingbird size and environment, there were proportionally more dipterans pollinating wide flowers with odour and a large amount of nectar. None of the above mentioned patterns were caused by variation in sampling effort or plant origin (Table 3).

Discussion

In this study, we have reported an analysis of West Indian plant–hummingbird interaction data covering 49 plant species and all eight hummingbird species of the islands of the Lesser Antilles and the Greater Antillean island of Puerto Rico. Most plant species (ca. 75%) were pollinated by both hummingbirds and insect species (ESM S1) and had a floral phenotype associated with insect pollination, e.g. short, blue- or white-coloured corolla and small amounts of often concentrated nectar (ESM S2), as has also been observed in the nearby continental islands of Trinidad and Tobago (Feinsinger et al. 1982). Although this indicates a general lack of specialisation on hummingbirds as pollinators in the West Indies, some plant species appear to be extremely specialised on hummingbird–pollination. Despite this apparent dichotomy, the floral phenotypes did not separate into distinct clusters of "sub-communities" or "sub-syndromes" (Fig. 1), but instead into two specialisation gradients—one associated with environment and another with hummingbird size (Fig. 2).

Specialisation level and hummingbird size

Although Kodric-Brown et al. (1984) separated the hummingbird-pollinated flowers in Puerto Rico into two largely non-overlapping sub-communities corresponding to and coevolving with the two hummingbird size classes found in the West Indies (Lack 1973), our larger dataset shows a considerable flower feeding niche overlap between hummingbird sizes, with ca. 30% of the plants shared by both hummingbird size classes. Thus, the fit between floral phenotype and hummingbird size is much less distinct than previously concluded by Kodric-Brown et al. (1984) resulting in a continuum of floral phenotypes along the hummingbird size axis (Fig. 1) rather than in distinct "sub-syndromes". Increased floral phenotypic specialisation on

hummingbird–pollination as hummingbird size increased was associated with flowers having a long corolla tube, producing a large amount of nectar and possessing orange-red colouration (Table 3; Figs. 1, 2), i.e. classical ornithophilous syndrome flowers (Proctor et al. 1996). Hence, plants pollinated by large, long-billed hummingbirds were phenotypically specialised (sensu Ollerton et al. 2007) on hummingbird pollination, whereas the smaller-sized hummingbirds often explored flowers traditionally considered entomophilous. Similar trends have been observed in Trinidad and Tobago, and in mainland Central and South America (e.g. Feinsinger et al. 1982; Snow and Snow 1980; Arizmendi and Ornelas 1990). Furthermore, in our study, we supported this interpretation by documenting high insect pollinator species richness, in particular lepidopterans, at those plant species pollinated by small hummingbirds and characterised by flowers possessing short corolla tube, blue-violet or white colouration and small nectar reward (Table 3; Figs. 1, 2).

Specialisation level and environmental gradient

A gradient of increasing phenotypic, functional and ecological specialisation (sensu Ollerton et al. 2007) on hummingbird pollination was also observed as the abiotic environment (temperature and rainfall) changed with altitude. The phenotypic specialisation gradient was caused by plant species in the wet and cold highlands having large amounts of dilute nectar and absent or weak odour, compared to species in the dry and warm lowland. This specialisation functionally and ecologically correlated with decreased insect pollinator species richness, in particularly hymenopterans, as altitude and rainfall increased and temperature decreased. In the Patagonian region in South America, an increased importance of hummingbird pollination along an east–west rainfall gradient (Aizen and Ezcurra 1998) was also associated with a decreased nectar concentration (Devoto et al. 2006) and decreased species richness of hymenopterans as rainfall increased (Devoto et al. 2005). The same may be the case in the wet and cold highlands of Central America (Cruden 1972; Stiles 1978; Wolda 1987). The dilute nectar of most hummingbird-pollinated flowers is not a preference of the hummingbirds (Montgomerie 1984) and it has been debated whether it could be a mechanism to prevent nectar foraging by bees or a way to overcome increased nectar viscosity at lower temperatures (Baker 1975; Bolton and Feinsinger 1978; Pyke and Waser 1981). Moreover, nectar reward is a plastic trait that depends on the environmental conditions, e.g. water availability and temperature (Stiles 1978; Arizmendi and Ornelas 1990; Aizen and Ezcurra 1998; Devoto et al. 2006). In the West Indies, the large amounts of dilute nectar and absence of odour in highland plants may therefore both be caused by the environmental conditions and be floral adaptations toward bird-pollination, resulting in an increased specialization on hummingbirds as pollinators with increasing altitude. The ultimate reason for this trend is most likely that insects are affected negatively by high rainfall and to a lesser extent low temperatures (Janzen 1973; Wolda 1987; Aizen and Ezcurra 1998; Devoto et al. 2005), whereas hummingbirds are endothermic and therefore physiologically less sensitive to these environmental conditions. In addition, the constant high energetic demands of hummingbirds make them dependent and reliable pollinators in rainy and cold environments often observed in the highlands (Cruden 1972; Stiles 1978; Bleiweiss 1998).

Super specialised and generalised pollination systems

The plant species most specialised on hummingbird pollination are therefore the ones growing in the wet and cold highlands, characterised by having a long corolla tube, large amounts of dilute nectar, orange-red colouration and no or weak odour; they are pollinated entirely or mainly by large, long-billed hummingbirds. However, with the present data it is difficult to determine whether these plants are more specialised than their mainland relatives, or simply "trapped" in this pollination mode and therefore pollinated by fewer species in depauperate island systems such as the West Indies (Bleiweiss 1998). Alternatively, it could be a combination of these scenarios. Depauperate insular pollinator faunas (Olesen and Jordano 2002) may, for the few highly specialised plants colonising or speciating in island systems, facilitate extreme fine-tuned specialisation, rarely seen in mainland settings. Using Trinidad and Tobago as a model system, Feinsinger et al. (1982) found that plant species adapted to hummingbird pollination had an inconsistent pollination service on the small, distant and depauperate island of Tobago compared to "mainland" Trinidad. However, the plants on Tobago partly compensated for this, showing an increased specialisation on hummingbirds by offering a greater amount of nectar reward. In our study, an example of such a locally extremely specialised pollination system is *Heliconia bihai* in the Dominican highland (Temeles and Kress 2003). In this species, floral morphology and energetic reward are co-adapted with bill length and energetic demand of the large purple-throated carib *Eulampis jugularis* (Temeles and Kress 2003). In Grenada, which is outside the range of the purple-throated carib, *H. bihai* is instead pollinated by several other hummingbirds (ESM S1). The same is also the case in Trinidad (Snow and Snow 1972). Here, even small, short-billed hummingbirds pollinate *H. bihai* (Snow and Snow 1972; ESM S1). Hence, *H. bihai* illustrates both a locally extremely specialised plant species, but also how

the local pollinator assemblage determines specialisation level.

At the other extreme, in our study the most generalised plants were growing in the dry and warm lowland and were pollinated by small hummingbirds and numerous insect species. They had a short corolla tube, small amounts of concentrated nectar, most often white or blue-violet colour and obvious odours. In fact, with the exception of a few plant species pollinated mainly by large hummingbirds (e.g. *Opuntia rubescens* in the Puerto Rican lowland), the entomophilous syndrome was the dominating floral phenotype utilised by lowland hummingbirds (ESM S1–S2). Similarly, in Trinidad and, especially, in Tobago in two lowland locations as dry as our Dominican lowland site, most of the hummingbird pollinated plants were also entomophilous (Feinsinger et al. 1982). This is in contrast to mainland setting, with the exception of Brazilian "capões"—natural fragmented forest patches resembling physical islands (Araujo and Sazima 2003), suggesting a widening of the niche of plants and hummingbirds on small, isolated and depauperate islands (Feinsinger and Swarm 1982; Feinsinger et al. 1982). In the Dominican lowland, an example of such a generalised plant is *Cordia globosa* (Boraginaceae), which was pollinated by the small antillean crested hummingbird *Orthorhyncus cristatus*, numerous lepidopterans, hymenopterans and dipterans as well as the passerine bananaquit *Coereba flaveola*.

Pros and cons of generalised pollination systems

Plants with such super-generalised pollination systems that use most of the available pollinator fauna are common on oceanic islands (Olesen et al. 2002). Yet, in absolute numbers, island plants are pollinated by fewer species since island systems have lower animal to plant ratios, than comparable mainlands (Olesen and Jordano 2002). Many island plants may therefore be left unvisited and their fruit set is pollinator limited (Linhart and Feinsinger 1980; Feinsinger et al. 1982; Spears 1987). Consequently, island plants are especially susceptible to pollinator fluctuations (Rathcke 2000, 2001). Insect populations fluctuate even in relatively stable tropical mainland environments (Wolda 1983, 1987) and may do so more on islands (Spears 1987). In the West Indies, hurricanes have devastating effects on nectarivorous bird populations (Wiley and Wunderle 1993), causing pollinator limitation in strictly bird-pollinated plant species (Rathcke 2000). On the other hand, plants with a mixed hummingbird and insect pollination may be ensured some pollination in the aftermath of hurricanes (Rathcke 2001). A generalised pollination system, with a pollinator fauna of both hummingbird and insect species, might therefore ensure pollination in periods of either hummingbird or insect scarcity (Fumero-Cabán and Meléndez-Ackerman 2007). This "back-up" pollination system (Mayfield et al. 2001; Timmermann et al. 2008) may, in the West Indies, also occur in plant species adapted for bat-pollination, another high energy demanding vertebrate negatively affected by hurricanes (Rivera-Marchand and Ackerman 2006). Hence, although hummingbirds are most efficient as pollinators when flower and hummingbird have complementary phenotypes (Fumero-Cabán and Meléndez-Ackerman 2007), a generalised pollination system may be favoured in highly variable and disturbed environments (Waser et al. 1996). Thus, in the West Indies, there is a trade-off between high pollination efficiency and susceptibility to breakdowns of mutualistic plant–pollinator interactions caused by, for example, hurricanes occurring cyclically in the West Indies (Rathcke 2000; Rathcke 2001; Rivera-Marchand and Ackerman 2006; Fumero-Cabán and Meléndez-Ackerman 2007). For these reasons, generalised lowland plants pollinated by both small hummingbirds and insects may be pollinated less efficiently but also be less susceptible to pollinator limitation in the aftermath of hurricanes, than highland plants specialised on large hummingbirds. Furthermore, because the vegetation recovers slowly in mountain forests, hurricanes may indirectly also have a large impact on nectarivorous and frugivorous birds, especially in the highlands (Wunderle et al. 1992).

Conclusions

The West Indies is a biological hotspot (Myers et al. 2000) characterised by high levels of environmental variation and disturbance (e.g. Wunderle et al. 1992; Wiley and Wunderle 1993; Rathcke 2000; Rathcke 2001; Rivera-Marchand and Ackerman 2006; Dalsgaard et al. 2007; Fumero-Cabán and Meléndez-Ackerman 2007), a depauperate and generalistic fauna (Tanaka and Tanaka 1982; Bleiweiss 1998; Dalsgaard et al. 2007), and a diverse environment ranging from dry scrub woodland in the lowlands to wet cloud forest in the highlands. Altogether, this may explain why the hummingbird pollinated flora of the West Indies has representatives of the most extreme ends of the specialisation gradient ranging from super-generalised flowers traditionally considered as entomophilous to classical ornithophilous flowers, with floral specialisation gradually increasing with size of visiting hummingbird and environmental settings which disfavour insect pollinators, i.e. the wet and cold habitats observed in the highland.

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