

# Speciose opportunistic nectar-feeding avifauna in Cuba and its association to hummingbird island biogeography

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**Abstract** Island organisms often have wider feeding niches than mainland organisms, and migratory birds breeding on continents often widen their niches when overwintering on islands. Cuba's low hummingbird richness has puzzled ornithologists for decades. Here, we show that the Cuban hummingbird fauna is less rich than expected based on Cuba's elevation, when compared to the rest of the West Indian islands. Thereafter, we report nectar-feeding behaviour by 26 non-Trochilidae bird species in Cuba, encompassing pigeons/doves, woodpeckers and passerines, and endemic, resident and migratory species. We discuss if Cuba's speciose non-Trochilidae nectar-feeding avifauna may be associated with its depauperate hummingbird fauna.

**Keywords** Bird–plant mutualism · Caribbean · Columbidae · Passeriformes · Picidae · West Indies

## Zusammenfassung

**Zusammenhang zwischen einer artenreichen opportunistischen nektarfressenden Avifauna auf Kuba und der dortigen Biogeographie von Kolibris**

Das Ernährungsspektrum von Inselbewohnern ist oftmals größer als das von Landbewohnern. Zugvögel, die auf dem Kontinent brüten, können ihre Nahrungsnischen ausdehnen, wenn sie auf Inseln überwinteren. Die geringe Anzahl von Kolibris auf Kuba gilt unter Ornithologen schon lange als Rätsel. Wir zeigen, dass im Vergleich zu den anderen Westindischen Inseln Kuba weniger Kolibris als erwartet hat, wenn man die Höhe über dem Meeresspiegel berücksichtigt. Außerdem dokumentieren wir das Nektarfressen von 26 Arten, die nicht zu den Trochilidae gehören, beispielsweise Tauben, Spechte und Singvögel sowie resident endemische Arten und Zugvögel auf Kuba. Wir erörtern, ob die artenarme Kolibrifauna auf Kuba in Zusammenhang steht mit der artenreichen sonstigen Nektarivoren avifauna.

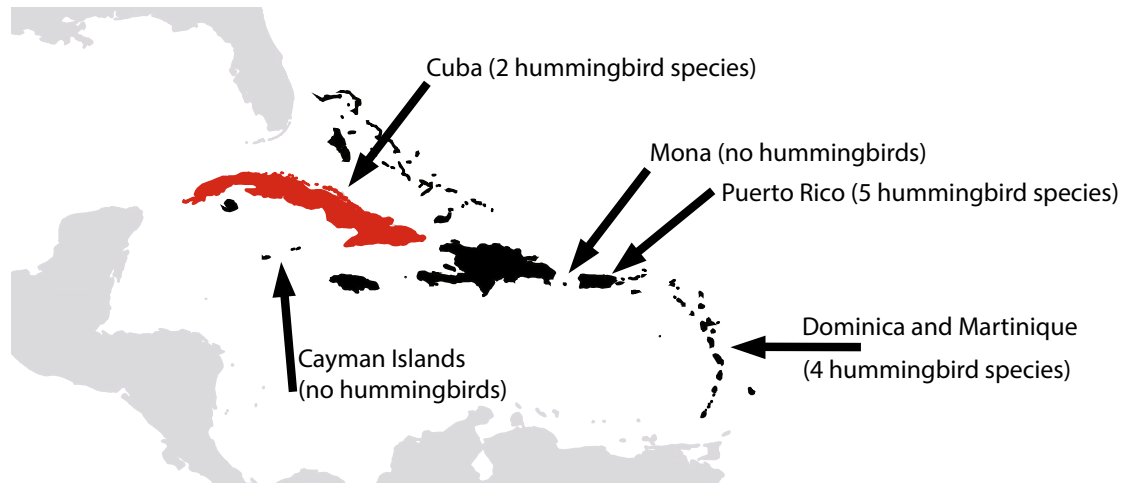
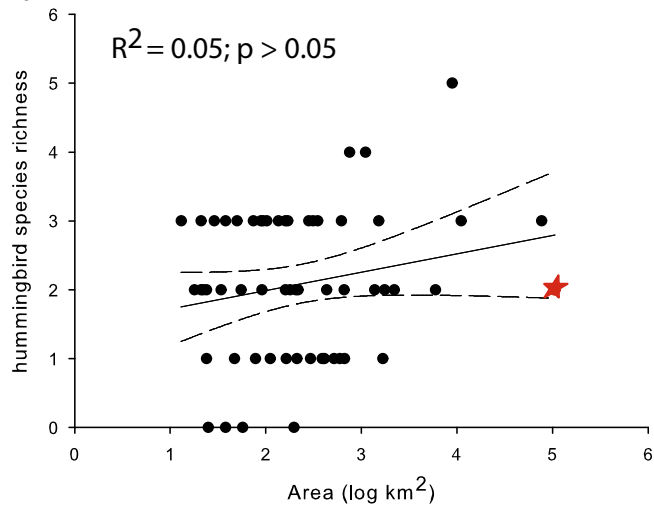
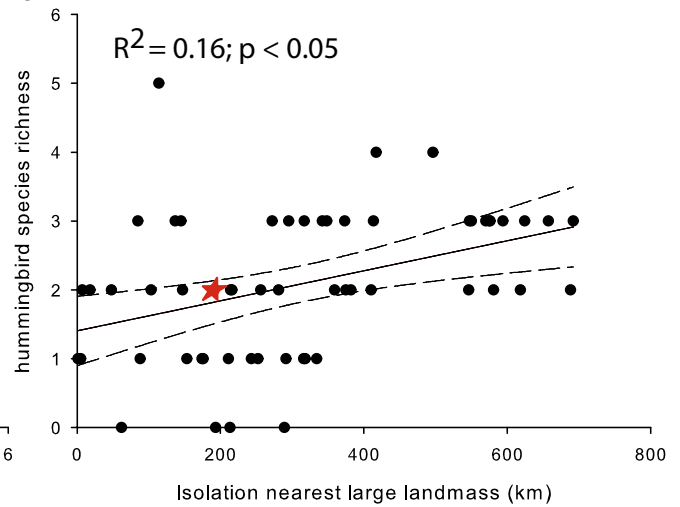
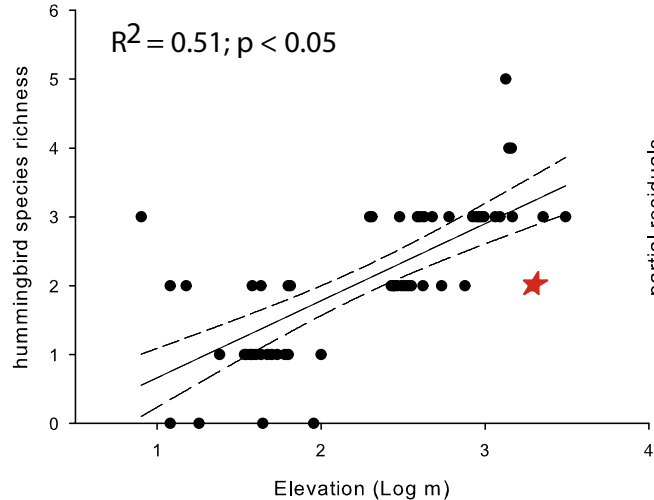
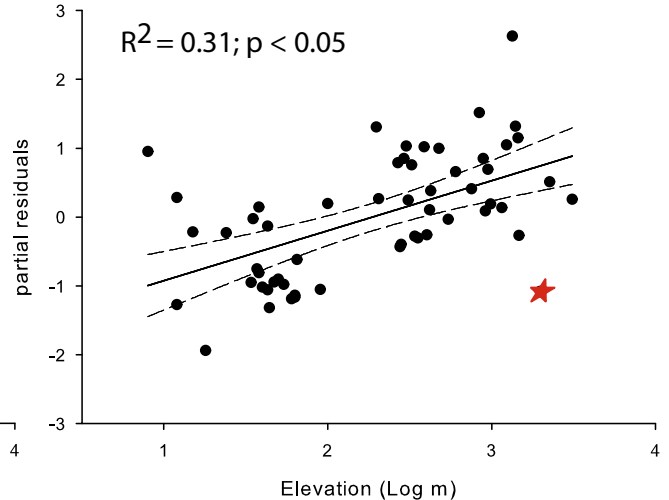
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## Introduction

Extant hummingbirds colonised the West Indies allegedly ~5 million years ago (McGuire et al. 2014), which roughly coincides with the colonization of most of their nectar-food plants (Abrahamczyk et al. 2015). However, some of the present-day hummingbird-dependent plants colonised the West Indies a few million years before extant hummingbirds arrived (Abrahamczyk et al. 2015). Thus, it has been suggested that hummingbirds may have colonised the West Indies earlier than currently estimated, but that those hummingbird species have since gone extinct,

**a****b****c****c****d**

**Fig. 1** Hummingbird island biogeography, illustrating **a** map of the West Indies with all islands in *black*, except Cuba highlighted in *red*. In addition to highlighting Cuba, the *arrows* highlight islands with an abnormally high number of hummingbird species (Puerto Rico, Dominica and Martinique) and no hummingbird species (Mona and Caymans constituting of three islands). *Grey* is the North, Central and South American mainland. We also illustrate the association between number of hummingbird species and: **b** island area, **c** island isolation to nearest landmass >10,000 km<sup>2</sup>, **d** island elevation, and **e** partial residual plot illustrating the association between hummingbird richness and elevation when accounting for area and isolation. For all associations, we show the regression (*bold lines*) and 95 % confidence interval (*dashed lines*). Cuba is highlighted with a *red star*. Note that for isolation, we present only the association to distance to nearest large landmass, because distance to nearest mainland was unimportant. See the text and Table 1 for details on the statistics

explaining how hummingbird-dependent plants could establish and reproduce prior to ~5 million years ago (Abrahamczyk et al. 2015). An alternative explanation, though, could be that those plants were pollinated by animals other than hummingbirds in their early history in the West Indies. Island organisms are known to be generalists, incorporating an array of food items into their diet; for instance, lizards are known to act as pollinators on islands, but rarely on the mainland (Olesen and Valido 2003) and some North American insectivorous passerine birds feed on nectar while wintering in the West Indies (e.g. Wunderle 1995; Raffaele et al. 1998; Garrido and Kirkconnell 2000; Latta and Faaborg 2002; Graves 2014). Thus, at least two

hypotheses could explain the disparity between colonisation time of extant West Indian hummingbirds and some of their nectar plants.

In the West Indies, Cuba is the largest island with one of the highest topographic reliefs and species-rich avifauna (e.g. Lack 1973; Dalsgaard et al. 2014). However, in Cuba only two hummingbird species breed, which is typical of most sizeable islands with little topographic relief, whereas other mountainous West Indian islands have an extra hummingbird community in the highland and, thus, are inhabited by three to five species (Lack 1973). For instance, four hummingbird species breed in Dominica and Martinique, which are relatively small mountainous islands in the Lesser Antilles (Lack 1973), and Puerto Rico with its mountains and five species is the most species-rich island (Lack 1973; Fig. 1a). Thus, Cuba is an anomaly in respect to hummingbird island biogeography, which for decades has puzzled ornithologists (Lack 1973). However, because Cuba is situated close to the North American mainland, many migrant passerine species winter in Cuba, some of which are known to drink nectar while in the West Indies (e.g. Wunderle 1995; Raffaele et al. 1998; Garrido and Kirkconnell 2000; Latta and Faaborg 2002; Graves 2014). Additionally, some endemic Cuban birds are known to opportunistically feed on nectar (e.g. Raffaele et al. 1998; Garrido and Kirkconnell 2000; Dalsgaard 2011). Thus, one possibility for the depauperated hummingbird fauna in Cuba could be that these other species of opportunistic

**Table 1** Models using island area, elevation, distance to nearest mainland, and distance to nearest large landmass (i.e. >10,000 km<sup>2</sup>) as predictors of number of hummingbird species

	OLS			SEVM		
	$\Sigma w_i$	Averaged	MAM <sup>a</sup>	$\Sigma w_i$	Averaged	MAM
Area	0.49	+0.16	+0.17	0.95	+0.28	+0.28
Elevation	1.00	+0.63	+0.59	1.00	+0.48	+0.48
Isolation mainland	0.24	−0.02		0.23	−0.00	
Isolation large landmass	0.88	+0.26	+0.29	0.24	+0.04	
AIC <sub>c</sub>			131.19			117.91
Moran's index			≤0.21*			≤0.07 <sup>NS</sup>
$R^2$			0.58			0.66
$R^2_{\text{area}}$			0.02			0.05
$R^2_{\text{elevation}}$			0.28			0.16
$R^2_{\text{isolation}}$			0.06			0.00

We report the standardized regression coefficients for ordinary least squares (OLS) and spatial eigenvector mapping (SEVM) regression, which is reported for both an averaged model based on weighted  $w_i$  and minimum adequate models, as in Dalsgaard et al. (2014). We also report the corrected Akaike information criterion (AIC<sub>c</sub>) and coefficients of determination ( $R^2$ ) from partial regression models separating the effect of island area, elevation, and isolation:  $R^2_{\text{area}}$ ,  $R^2_{\text{elevation}}$  and  $R^2_{\text{isolation}}$  reflect the unique variation explained by island area, elevation and isolation, respectively. Multicollinearity was not a problem in any of the MAMs, as indicated by the variance inflation factor  $VIF < 1.6$  and the condition number  $CN < 2.0$  (In SAM 4.0,  $VIF > 10$  and  $CN > 5$  indicate problems with multicollinearity).

<sup>a</sup> One model was equally fit (i.e.  $\Delta AIC_c < 2$ ) containing the following variables: (1) elevation, isolation large landmass

nectar-feeding birds—at least partly—compete with hummingbirds as pollinators; however, to date this idea has not been thoroughly reviewed.

To investigate this idea, we first identify how island area, elevation and isolation associate with island richness of hummingbirds in the West Indies, and identify how Cuba is an anomaly in this respect, i.e. whether Cuba has lower hummingbird richness than expected by its area, elevation or isolation, when compared to the rest of the West Indies. Based on this, we then use new information on opportunistic nectar-feeding by numerous non-Trochilidae bird species in Cuba to discuss if Cuba's speciose opportunistic nectar-feeding avifauna explain its depauperate hummingbird fauna.

## Methods

### Hummingbird island biogeography

We obtained the distribution of all 16 West Indian hummingbird species from an established database on the breeding distribution of all bird species across 57 islands in the West Indies (Dalsgaard et al. 2014). We followed the taxonomy of the American Ornithologists' Union checklist (<http://checklist.aou.org/>), which groups the red- and black-billed Jamaican Streamertails into one species (*Trochilus polytmus*), and included the extinct Brace's Hummingbird (*Chlorostilbon bracei*) from New Providence, Bahamas (Graves & Olson 1987). We also used the database of Dalsgaard et al. (2014) on (1) island area (km<sup>2</sup>), (2) island elevation (m), (3) distance (km) to nearest mainland, and (4) distance (km) to nearest large landmass irrespectively of mainland or island, using the island size threshold of 10,000 km<sup>2</sup> to be considered a large landmass, because these have previously been shown to be important predictors of bird distributions in the West Indies (Dalsgaard et al. 2014).

To identify the main predictors of hummingbird species richness across the West Indies, and to identify how Cuba is an anomaly compared to the rest of the West Indies, we used regression modelling. First, we regressed hummingbird species richness and each of the predictors (1–4, see above), and calculated 95 % confidence intervals to identify if Cuba had lower hummingbird richness than expected when compared to the rest of the West Indies. Second, we fitted regression models with all combinations of the predictor variables (1–4, see above) and used a model selection analysis based on information theory, as previously done on all breeding bird species in the West Indies (Dalsgaard et al. 2014). We used the corrected Akaike information criterion (AIC<sub>c</sub>) to identify minimum adequate models (MAMs). We report standardized regression

coefficients using ordinary least squares (OLS) regression for both an averaged model based on weighted  $w_i$  and for the MAM, as in Dalsgaard et al. (2014). As we observed spatial autocorrelation in the OLS models (see Table 1), we repeated the regression model procedure using spatial eigenvector mapping (SEVM) modelling. The analyses were conducted using the software Spatial Analysis in Macroecology (SAM) 4.0 (Rangel et al. 2010).

### Nectar-feeding by opportunistic birds in Cuba

During several years of fieldwork by JWW and shorter intensive fieldwork periods by BD, ACB, and JMO, we have observed opportunistic nectar-drinking by numerous bird species not normally considered nectarivorous. Only one of these observations has previously been published (Dalsgaard 2011). Whenever possible, we document these observations with photographs. In addition, we review the literature for all Cuban bird species, consulting both bird field guides (e.g. Raffaele et al. 1998; Garrido and Kirkconnell 2000) and Handbook of Birds of the World (del Hoyo et al. 2011), and searched at Google for combinations of “bird species name” and either “nectar” or “flower”.

## Results

Island elevation associated strongly and positively to hummingbird species richness, whereas we found weaker positive associations between area and isolation with hummingbird richness (Fig. 1). Cuba was an anomaly with respect to elevation, having less hummingbird richness than expected by its elevation (Fig. 1d–e), but was within the 95 % confidence intervals for area and isolation. The OLS regression models explained a total of 58 % of hummingbird species richness in the West Indies, with elevation (28 %) explaining much more unique variation than did isolation (6 %) and area (2 %). In SEVM models, elevation (16 %) was also the most important predictor of hummingbird richness, with area (6 %) and isolation (0 %) explaining less unique variation.

We report a total of 26 species of non-Trochilidae birds feeding on nectar in Cuba, including species of pigeons, doves, woodpeckers and passerines. They represent endemic, resident and migratory species (Table 2; Fig. 2).

## Discussion

Based on our field experience and knowledge of the literature, we are confident that our list of 26 non-Trochilidae birds feeding on nectar in Cuba represents more opportunistic nectar-feeding bird species than on any islands in

**Table 2** A total of 26 non-Trochilidae bird species observed to opportunistically drink floral nectar in Cuba

Bird species	Bird residence status	Plant species (family)	Plant status	Pollinating or robbing nectar	References
Plain Pigeon* <i>Patagioenas inornata</i>	Greater Antillean endemic	<i>Spathodea campanulata</i> (Bignoniaceae)	Introduced	Pollinating/robbing	JWW
White-winged Dove* <i>Zenaida asiatica</i>	Resident	<i>Stenocereus fimbriatus</i> (Cactaceae)	Native	Pollinating	JWW
		<i>Agave sisalana</i> (Agavaceae)	Introduced	Pollinating	JWW
Cuban Trogon <i>Priotelus temnurus</i>	Cuban endemic	–	–	–	<a href="http://www.staugustine-baracoa.org/">www.staugustine-baracoa.org/</a>
West Indian Woodpecker* <i>Melanerpes superciliosus</i>	Greater Antillean endemic	<i>Tabebuia heterophylla</i> (Bignoniaceae)	Native	Pollinating	JWW
		<i>Selenicereus grandiflorus</i> (Cactaceae)	Native	Pollinating	JWW
Cuban Green Woodpecker <i>Xiphidopicus percussus</i>	Cuban endemic	<i>Lysiloma latisiliquum</i> (Leguminosae)	Native	Pollinating	JWW
		<i>Tabebuia heterophylla</i> (Bignoniaceae)	Native	Pollinating/robbing	JWW
Cuban Vireo* <i>Vireo gundlachii</i>	Cuban endemic	<i>Cordia sebestena</i> (Boraginaceae)	Native	Pollinating	Dalsgaard (2011)
		<i>Callistemon [viminalis?] sp.</i> (Myrtaceae)	Introduced	Pollinating	JWW
Black-whiskered Vireo* <i>Vireo altiloquus</i>	Wintering	<i>Pavonia paludicola</i> (Malvaceae)	Native	Pollinating	BD
		<i>Vachellia farnesiana</i> (Leguminosae)	Native	Pollinating	JWW
Tennessee Warbler <sup>a</sup> <i>Vermivora peregrina</i>	Wintering	–	–	–	e.g. Raffaele et al. (1998)
Worm-eating Warbler* <i>Helmitheros vermivorum</i>	Wintering/transient	<i>Cordia sebestena</i> (Boraginaceae)	Native	Pollinating	JMO
		<i>Callistemon [viminalis?] sp.</i> (Myrtaceae)	Introduced	Pollinating	JWW
Cape May Warbler <sup>a</sup> <i>Setophaga tigrina</i>	Wintering/transient	<i>Callistemon [viminalis?] sp.</i> (Myrtaceae)	Introduced	Pollinating	JWW
Yellow Warbler* <i>Setophaga petechia</i>	Resident/transient	<i>Avicennia germinans</i> (Avicenniaceae)	Native	Pollinating	JWW
Blackpoll Warbler* <i>Setophaga striata</i>	Transient	<i>Vachellia farnesiana</i> (Leguminosae)	Native	Pollinating	JWW
Black-throated Blue Warbler <sup>a</sup> <i>Setophaga caerulescens</i>	Wintering/transient	<i>Lysiloma latisiliquum</i> (Leguminosae)	Native	Pollinating	JWW
		<i>Callistemon [viminalis?] sp.</i> (Myrtaceae)	Introduced	Pollinating	JWW
Prairie Warbler* <i>Setophaga discolor</i>	Wintering/transient	<i>Cordia sebestena</i> (Boraginaceae)	Native	Pollinating	JMO
Bananaquit <i>Coereba flaveola</i>	Rare visitor, possible resident	<i>Lysiloma latisiliquum</i> (Leguminosae)	Native	Pollinating	JWW
Red-legged Honeycreeper <i>Cyanerpes cyaneus</i>	Rare resident	–	–	Pollinating/robbing	Garrido and Kirkconnell (2000)
Western Spindalis <i>Spindalis zena</i>	Resident	<i>Byrsonima coriacea</i> (Malpighiaceae)	Native	Pollinating	JWW
		–	–	–	<a href="http://beautyofbirds.com">http://beautyofbirds.com</a>

Table 2 continued

Bird species	Bird residence status	Plant species (family)	Plant status	Pollinating or robbing nectar	References
Cuban Grassquit <i>Tiaris canorus</i>	Cuban endemic	<i>Vachellia farnesiana</i> (Leguminosae)	Native	Pollinating	JWW
Yellow-faced Grassquit* <i>Tiaris olivaceus</i>	Resident	<i>Colpothrinax wrightii</i> (Arecaceae)	Native	Pollinating	JWW
		<i>Stenocereus fimbriatus</i> (Cactaceae)	Native	Pollinating	JWW
		<i>Antigonon leptopus</i> (Polygonaceae)	Introduced	Pollinating	ACB
		<i>Cordia sebestena</i> (Boraginaceae)	Native	Robbing	JMO
Red-shouldered Blackbird <i>Agelaius assimilis</i>	Cuban endemic	–	–	–	Garrido and Kirkconnell (2000)
Tawny-shouldered Blackbird <i>Agelaius humeralis</i>	Greater Antillean endemic	<i>Callistemon [viminalis?] sp.</i> (Myrtaceae)	Introduced	Pollinating	JWW
		<i>Tabebuia heterophylla</i> (Bignoniaceae)	Native	Robbing	JWW
		<i>Buchenavia capitata</i> (Combretaceae)	Native	Pollinating	JWW
		<i>Buchenavia capitata</i> (Combretaceae)	Native	Pollinating	JWW
		<i>Tabebuia heterophylla</i> (Bignoniaceae)	Native	Pollinating	JWW
		<i>Cordia sebestena</i> (Boraginaceae)	Native	Pollinating	JMO
		<i>Agave sisalana</i> (Agavaceae)	Introduced	Pollinating/robbing	JWW
Cuban Oriole <i>Icterus melanopsis</i>	Cuban endemic	<i>Callistemon [viminalis?] sp.</i> (Myrtaceae)	Introduced	Pollinating	JWW
		<i>Ochroma pyramidale</i> (Bombacaceae)	Native	Robbing	JWW
		<i>Tabebuia heterophylla</i> (Bignoniaceae)	Native	Robbing	JWW
		<i>Lysiloma latissilicium</i> (Leguminosae)	Native	Pollinating	JWW
Orchard Oriole <i>Icterus spurius</i>	Vagrant	–	–	–	del Hoyo et al. (2011)
Hooded Oriole <i>Icterus cucullatus</i>	Vagrant	–	–	–	Garrido and Kirkconnell (2000)
Baltimore Oriole <i>Icterus galbula</i>	Wintering/transient	<i>Lysiloma latissilicium</i> (Leguminosae)	Native	Pollinating	JWW

For each species, we report the residence status of the bird (following Raffaele et al. 1998), the name and family of the plant species visited, whether the plant is considered native or introduced (following “Flora of the West Indies” of the Smithsonian National Museum of Natural History: [www.botany.si.edu/antilles/WestIndies](http://www.botany.si.edu/antilles/WestIndies)), and whether the birds were robbing or potentially pollinating the plant (*dash*, if unknown). We do not present evidence that the birds in fact pollinated the plants, however, if noted as pollinating then the species approached the flowers in a way that they touched the stigma and stamens of the flowers and, thus, potentially act as pollinators. We only include species drinking nectar, excluding those eating the flowers, e.g. Cuban Bullfinch (*Melopyrrha nigra*), Cuban Parakeet (*Psittacara euops*) and Cuban Parrot (*Amazona leucocephala*). We note whether the information is based on the literature or our own records; in most cases it is based on our own field observations, since in the literature the plant species were normally not reported. However, this does not necessarily mean that the bird species had not previously been reported feeding on nectar. Species ( $n = 10$ ) that to our knowledge have not previously been reported to feed on nectar are marked with *asterisk* (\*). The species are arranged according to bird taxonomy. See Fig. 2 for illustrations of some of the reported bird-plant interactions

<sup>a</sup> In the North American breeding area, mainly insectivorous, but in the West Indies, mainly feeds on nectar (Raffaele et al. 1998)



**Fig. 2** Photographs documenting interactions between eight opportunistic nectar-feeding birds and nectar plants in Cuba: **a** West Indian Woodpecker feeding on *Selenicereus grandiflorus* (Cactaceae); **b** Cuban Green Woodpecker feeding on and likely pollinating *Lysiloma latisiliquum* (Leguminosae); **c** Cape May Warbler visiting flowers of the exotic bottlebrush *Callistemon [viminalis?] sp.* (Myrtaceae); **d** Black-throated Blue Warbler feeding and pollinating *Cordia sebestena* (Boraginaceae); **e** Yellow-faced Grassquit male robbing nectar from *Cordia sebestena* (Boraginaceae); **f** Tawny-shouldered Blackbird robbing nectar from *Tabebuia heterophylla* (Bignoniaceae); **g** Cuban Blackbird visiting and pollinating *Cordia sebestena* (Boraginaceae); **h** Cuban Oriole robbing nectar from *Tabebuia heterophylla* (Bignoniaceae). Note that the flowers represent both traditional bird syndrome flowers (**c–e, g**) and non-ornithophilous syndrome floral types (**a–b, f, h**), and that also hummingbirds visit some of these plant species (e.g. *T. heterophylla* and *C. Sebestena*; Dalsgaard et al. 2009; Dalsgaard 2011), thus, hummingbirds and the opportunistic nectar-feeding birds may compete for nectar. See Table 1 for more records of opportunistic nectar-feeding birds in Cuba



the West Indies (Table 2; Fig. 2). For instance, Dalsgaard et al. (2009) only observed hummingbirds and the Bananaquit *Coereba flaveola* as floral visitors during 1420 h of plant–bird observations on Puerto Rico, Dominica and

Grenada. Also, Cuba has more nectar-feeding blackbirds/orioles than any other West Indian island (Raffaele et al. 1998), and the Cuban woodpeckers are the only confirmed West Indian woodpeckers feeding on nectar (Dalsgaard

2011; Table 2). Additionally, the North American migratory species of wood warblers, which drink nectar while in the West Indies (e.g. Raffaele et al. 1998; Graves 2014; Table 2), overwinter in huge numbers on Cuba (JWW, pers. obs.). They are most common on Cuba, Caymans and Bahamas (Tennessee Warbler *Vermivora peregrina*) or entire Greater Antilles, Caymans and Bahamas (Cape May Warbler *Setophaga tigrina* and Black-throated Blue Warbler *Setophaga caerulescens*; Raffaele et al. 1998). Interestingly, the high number of opportunistic nectar-feeding birds coincides with Cuba being an anomaly in hummingbird richness from a biogeographical perspective, having less species than expected based on its elevation, when compared to the rest of the West Indies. It is also notable that island geography explains much less variation in hummingbird species richness (58 %; Table 1) than for total breeding bird richness (82 %) and overall endemic bird richness in the West Indies (69 %; Dalsgaard et al. 2014). Thus, island geography does—for unknown reasons—explain relatively little variation in hummingbird richness, with Cuba being an extreme case (Lack 1973; Fig. 1e). This raises the possibility that Cuba may have few hummingbird species because of its high number of opportunistic nectar-feeding birds (or other nectarivorous animals, such as bats and insects). Perhaps the migrant nectar feeders and the many endemic opportunistic nectar-feeding species have deterred hummingbird diversification in Cuba. Or, alternatively, do the opportunistic nectarivorous birds in Cuba explore a niche not yet fully filled by hummingbirds? Regardless of which explanation is correct, it is striking that Cuba has numerous opportunistic nectar-feeding birds and low hummingbird richness.

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