

# *Bourreria havanensis*: a nectar oasis in the serpentine shrub-wood of Lomas de Galindo?

## *Bourreria havanensis*: ¿un oasis de néctar en el cuabal de Lomas de Galindo?

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### ABSTRACT

The Cuban flora is the richest in the Caribbean and contains a high percent of endemic species. A significant amount of this richness is located in the ultramafic soils, which occupy only the 7 % of the island. The genus *Bourreria* is typical of the thickets of these areas. One of the species, *B. havanensis*, is distributed either in these ecosystems and other types of soils. The population of Lomas de Galindo occupies an ultramafic area in Western Cuba. *Bourreria havanensis* blooms throughout the year, although with high abundance between July and August. In this period, it attracts a high diversity of floral visitors. We studied this diversity in the flowering period of the years 2018 and 2019, and measure different variables that could modulate these interactions. The flowers of *B. havanensis* were visited by 47 species of floral visitors. Although the most frequent visitor was the bee *Centris poecila*, 80 % of the visitor species were butterflies and moths, similar to other *Bourreria* species. *Bourreria havanensis* has a generalist pollination system with white and short corollas, which allows the interactions with different groups. The attraction of floral visitors depended mainly on the floral display of the plants, specifically abundance of flowers and the dimensions of the individuals. The flowers produced low volumes of nectar, which force floral visitors to increase the number of visits to acquire enough nectar. In conclusion, *B. havanensis* attracts the floral visitors because of the floral display, and not because it offers high amounts of floral resources.

**Keywords:** *Boraginaceae*, Mayabeque, pollination, serpentine, ultramafic soils, water stress

### RESUMEN

La flora de Cuba es la más rica del Caribe y contiene un elevado endemismo. Una parte significativa de esta riqueza se concentra en los suelos ultramáficos, los cuales ocupan solamente el 7 % de la isla. El género *Bourreria* es típico de los matorrales de estas áreas. Una de sus especies, *B. havanensis*, está distribuida tanto en estos ecosistemas como en otros tipos de suelos. La población de Lomas de Galindo ocupa un área ultramáfica de Cuba occidental. *Bourreria havanensis* florece durante todo el año, aunque con más abundancia entre los meses de julio y agosto. En este período, atrae una alta diversidad de visitantes florales. Se estudió dicha diversidad en el período de floración de los años 2018 y 2019, y se midieron diferentes variables que podrían modular estas interacciones. Las flores de *B. havanensis* fueron visitadas por 47 especies de visitantes florales. Aunque el visitante más frecuente fue la abeja *Centris poecila*, el 80 % de las especies fueron mariposas y polillas, similar a otras especies del género. *Bourreria havanensis* tiene un sistema de polinización generalista con corolas blancas y cortas, lo que permite las interacciones con diferentes grupos. La atracción de los visitantes florales dependió solamente del despliegue floral de las plantas, específicamente la abundancia de flores y las dimensiones de los individuos. Las flores produjeron bajos volúmenes de néctar, lo cual ocasiona que los visitantes aumenten el número de visitas para adquirir suficiente néctar. En conclusión, *B. havanensis* atrae a los visitantes florales debido al despliegue floral, y no debido a la producción de grandes cantidades de néctar.

**Palabras clave:** *Boraginaceae*, Mayabeque, polinización, serpentina, suelos ultramáficos, estrés hídrico

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### INTRODUCTION

Cuba is the biggest island of the Caribbean hotspot and contains between 7 000 and 7 500 species of vascular plants, 53 % of them endemic (González-Torres & al. 2016). However, this diversity is not homogeneously distributed in the island. Some areas, such as ultramafic soils, contain a higher percent of the plant diversity of Cuba (Borhidi 1988). Controversially, these areas occupy only the 7 % of Cuban territory (Reeves & al. 1999). Several features of the soil influence the vegetation that develops over it, which is characterized by xeric thickets (Proctor 1999).

Ultramafic soils, commonly named serpentines by biologists, contain high concentrations of heavy metals such as iron, nickel,

magnesium, chromium and cobalt (Proctor 1999). Moreover, oligotrophy is a common feature due to the low concentrations of nutrients such as phosphorous, potassium and calcium (Proctor 1999). These soils are usually rocky with low water-retention capacity (Proctor & Woodell 1975). All these selective pressures caused the high diversity and endemism of the ultramafic flora in Cuba and other areas in the world (Borhidi 1996, Siebert & al. 2001, Safford & al. 2005). In Cuba, two vegetation types of thickets developed in ultramafic soils: the xeromorphic thorny thicket formation ("cuabal") and the xeromorphic sub-thorny thicket on serpentinite ("charrasca") (Capote & Berzaín 1984).

Plants of these vegetation types are morphologically and physiologically different from the rest of the species of Cuba.

Morphological changes include reduced growth forms, microphyllly, stenophyllly, sclerophyllly and the presence of thorns, all xeromorphic anatomical and morphological features (Berazaín 2001). Moreover, the metabolism of serpentine plants is slower than that of plants growing in other kind of soils; it is adapted to conserve mineral nutrients and several species hyperaccumulate nickel and other heavy metals in their tissues (Reeves & al. 1999, Belloeil & al. 2021). This hyperaccumulation can be toxic for the species that feed on these plants and also modulates the ecological interactions in these ecosystems (Martens & Boyd 1994). One of these interactions is pollination, because ultramafic plant species have small flowers, with low water availability for nectar production and toxicity in their tissues, including nectar and pollen (Meindl & al. 2013).

Insect pollination is the main pollination syndrome on plants from xeromorphic thorny thicket formations (Faife-Cabrera & al. 2012). However, pollination studies in plants of this vegetation type in Cuba are scarce, although several plant genera are characteristic of these areas, such as, *Bourreria*, *Buxus*, *Coccoloba*, *Coccothrinax*, *Copernicia*, *Leucocroton*, *Rondeletia* and *Tabebuia* (Capote & Berazaín 1984). Particularly, the genus *Bourreria* is composed by nine species in Cuba (Gottschling & Miller 2018). One of these species, *Bourreria havanensis* (Roem. & Schult.) Miers, occurs in scattered populations over southern Florida, Cuba and Hispaniola (Gottschling & Miller 2018). We observed that this species flowers massively and attracts many species of pollinators in Lomas de Galindo, a xeromorphic thorny thicket in Western Cuba. Because of this, the objectives of this study are the characterization of the diversity of floral visitors of *Bourreria havanensis* and relate it to the abiotic and biotic variables that could modulate the diversity of these interactions in the thicket of Lomas de Galindo.

## MATERIALS AND METHODS

### The species

*Bourreria havanensis* is a 3-8 meters tall shrub, typical from dry open thickets over serpentines but also in limestones. The species is distributed in six to seven populations scattered in Cuba, Haiti, Dominican Republic and the state of Florida of the United States of America (Gottschling & Miller 2018). Similar to other species of the genus, *B. havanensis* has hermaphroditic flowers, with white corollas, five stamens inserted on the corolla tube and a nectariferous disc located in the base of the carpels (Gottschling 2004). It has glabrous leaves, which distinguishes it from other small-leaved species of the genus. The flowering period of *B. havanensis* comprises almost every month of the year (Gottschling & Miller 2018).

### Study design

After two years of monthly observations, we noted a peak in the flowering period of *Bourreria havanensis* in Lomas de Galindo (Mayabeque province, Cuba), which occurs in July and August. For that reason, this study was performed during this moment, in the years of 2018 and 2019. In 2018, the species composition and abundance of floral visitors of *B. havanensis*

were registered in 23-time spans of 15 minutes. Sampling occurred between 09:00 and 16:00 hours around individuals of *B. havanensis*. In 2019, a pilot study in the same individuals of *B. havanensis* was performed to determine the moment of maximum activity of floral visitors, which occurred between 09:00 and 13:00 hours. Within this period in two consecutive days, two-time spans of 15 minutes were assigned randomly to ten individuals of *B. havanensis*, one-time span per day. In those time spans the composition and abundance of floral visitors were recorded, accompanied with predictor variables such as relative humidity, temperature, wind speed, height and maximum diameter of individuals of *B. havanensis* and number of flowers per plant. Predictor variables could potentially influence the composition and abundance of floral visitors; therefore, they were measured in every time span of every *B. havanensis* individual.

Relative humidity, temperature and wind speed were measured with a Kestrel device (*Kestrel 4 000 Pocket Weather Station*), with an accuracy of 0.1 %, 1 °C and 1 m/s, respectively. The height from base to top and the maximum diameter of the crowns of individuals were measured with a meter tape using an error of 1 cm. The abundance of flowers was measured by counting all the flowers of every individual. Additionally, the nectar volume was measured in 20-40 flowers of every individual distributed in the two consecutive days. Also, the nectar volume of 262 flowers was measured. For this, we used a capillary of 0.4 mm of internal diameter and 148 mm long.

### Data analysis

Floral visitor diversity was estimated using Hill numbers of order 0, 1 and 2 (Hill 1973, Ellison 2010). For this analysis, the data of the flowering periods of 2018 and 2019 were gathered and sampling units were represented by 15 minutes time spans. In total, the data includes 43-time spans of 15 minutes, 23 of the sampling period of 2018 and 20 time spans of 2019. Moreover, only binary data (presence/absence) were used. This analysis was performed using the *iNEXT* package (Hsieh & al. 2016) of *R v.4.0.3* (R Core Team 2020).

Relationships between the predictor variables measured in 2019 and the abundance of every floral visitor species were assessed using a set of competitive linear models. For this, the dependent variable abundance of interactions was log-transformed to homogenize the variances. Nine models were built based on the biological relationships between the dependent variables and predictor variables relative humidity, temperature, wind speed, height and maximum diameter of *Bourreria havanensis* individuals and number of flowers. Nectar volume was not included in these models because it was measured in flowers where the interactions did not occur. Model selection using corrected Akaike Information Criterion (*AICc*) was used to select the models that better fit to the data. The models with  $\Delta AICc < 2$  were selected as the best models. This analysis was performed using the package *AICcmodavg* (Mazerolle 2020) of *R v.4.0.3* (R Core Team 2020).

## RESULTS

The flowers of *Bouyeria havanensis* interacted with 54 species of floral visitors (Table I). All floral visitors, except the bird *Chlorostilbon ricordii*, were insects. Amongst them, butterflies and moths (Lepidoptera) represented 80 % of the species present in both years. The observed richness of floral visitors did not reach the asymptote of the estimation curve using Hill number of order 0. However, the observed diversity of floral visitors was closed to the estimated one using Hill numbers of order 1 and 2 (Figure 1).

We recorded 285 and 1 843 interactions of floral visitors with *Bouyeria havanensis* flowers in 2018 and 2019, respectively. In 2018, the butterfly *Urbanus proteus domingo* was the most common floral visitor, while in 2019 three species maintain the highest number of interactions: the bees *Centris poecila* and *Apis mellifera*, and the hawkmoth *Aellopos blaini* (Figure 2). The interactions of these three species represented 80 % of all interactions of 2019. Particularly, *C. poecila* was highly frequent in the flowers of *B. havanensis*.

Two models were equally supported based on *AICc* values because both of them had  $\Delta AICc < 2$  (Table II). The first one includes the flower abundance as the only predictor variable, and had  $\Delta AICc = 0$ . The second one, which includes the

plant height and maximum plant diameter, was close to the former ( $\Delta AICc = 1.02$ ). Both models were related to the floral display of the plant. The rest of the models had values of  $\Delta AICc > 2$ .

No nectar was found in 189 of the 262 flowers measured (Figure 3). However, in the other 73 flowers with nectar, the average production was  $0.21 + 0.23 \mu\text{L}$  (mean + SD).

## DISCUSSION

The flowers of *Bouyeria havanensis*, attract floral visitors from different groups, mainly bees, moths and butterflies. This diversity of functional groups indicates that *B. havanensis* has a generalist pollination system (Fenster & al. 2004). The bee *Centris poecila* was the most frequent floral visitor, in part because this species is widespread in the island and it is abundant in various ecosystems (Alayo 1976). *Centris poecila* has been recorded as the main pollinator of different plant species in Cuba from several families (*Orchidaceae*, *Malpighiaceae* and *Ochnaceae*) (Vale & al. 2011), indicating thereby a generalized diet. The bees of the genus *Centris* are polylectic, which means that can consume nectar and pollen of different plant families, usually the most abundant floral resources in the community (Quiroz-García & Arreguin-Sánchez 2006, Moure & al. 2007).

TABLE I

Floral visitors recorded in the flowers of *Bouyeria havanensis* in Lomas de Galindo, Mayabeque, Cuba, during the peak of the flowering seasons of 2018 and 2019

TABLA I

Visitantes florales registrados en las flores de *Bouyeria havanensis* en Lomas de Galindo, Mayabeque, Cuba, durante las temporadas de máxima floración de 2018 y 2019

Order	Family	Species	2018	2019	
Aves	Trochilidae	<i>Chlorostilbon ricordii</i> (Gervais, 1835)		X	
Diptera	Asilidae	<i>Efferia</i> sp.		X	
	Syrphidae	Syrphidae sp.		X	
Hymenoptera	Apidae	<i>Apis mellifera</i> Linnaeus, 1758	X	X	
		<i>Centris poecila</i> Lepeletier, 1841	X	X	
		<i>Centris</i> sp.		X	
		<i>Centris fulviventris</i> Cresson, 1865	X		
		<i>Melipona beecheii</i> Bennett, 1831		X	
		<i>Xylocopa cubaecola</i> Lucas, 1857	X	X	
		Scoliidae	<i>Campsomeris atrata</i> (Fabricius, 1775)	X	
		Vespidae	<i>Polistes</i> sp.		X
Lepidoptera	Erebidae	<i>Pseudocharis minima</i> (Grote, 1867)	X		
		<i>Syntomeida wrighti</i> (Gundlach, 1881)	X		
		<i>Zelatilla columbia</i> Dyar, 1914	X		
	Hesperiidae	<i>Asbolis capucinus</i> (Lucas, 1857)	X		
		<i>Atalopedes m. mesogramma</i> (Latreille, [1824])	X	X	
		<i>Burca c. concolor</i> (Herrich-Schäffer, 1865)		X	

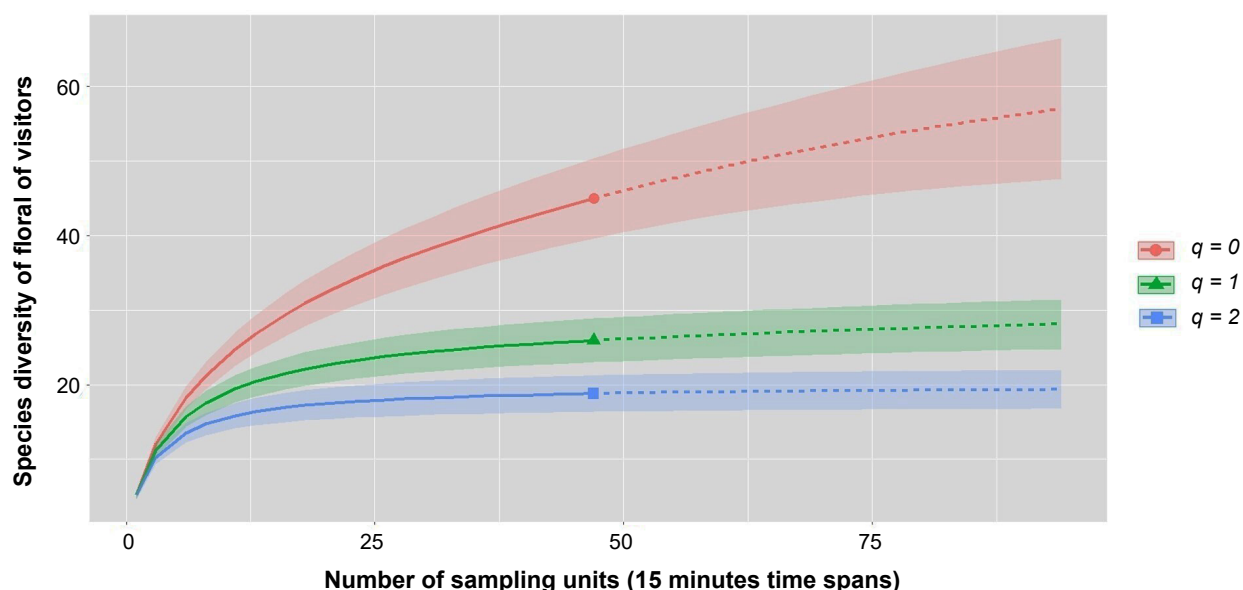
TABLE I

Floral visitors recorded in the flowers of *Bourreria havanensis* in Lomas de Galindo, Mayabeque, Cuba, during the peak of the flowering seasons of 2018 and 2019 (Continue)

TABLA I

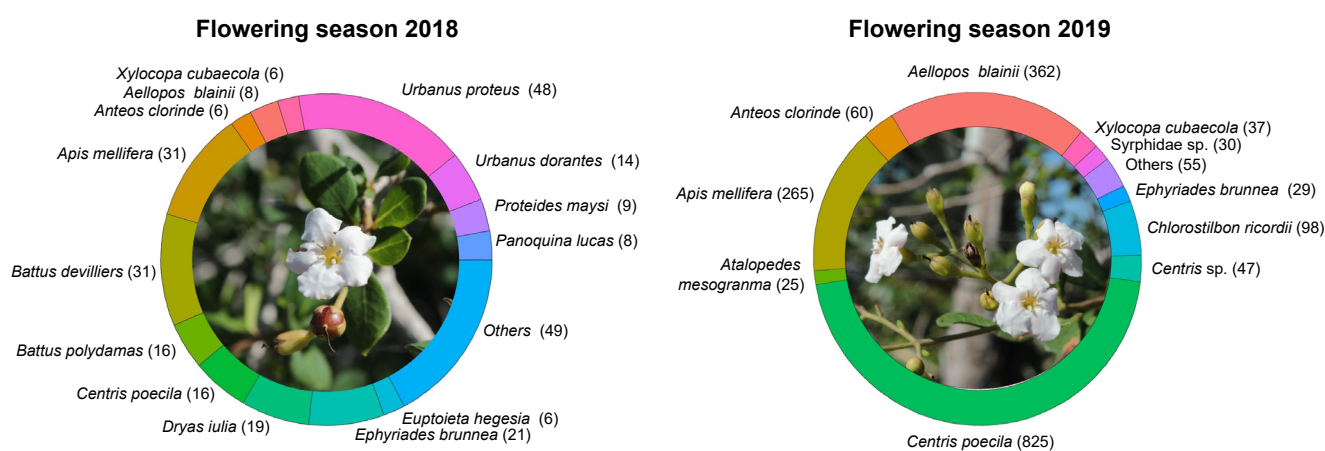
Visitantes florales registrados en las flores de *Bourreria havanensis* en Lomas de Galindo, Mayabeque, Cuba, durante las temporadas de máxima floración de 2018 y 2019 (Continuación)

Order	Family	Species	2018	2019		
Lepidoptera	Hesperiidae	<i>Choranthus radians</i> (Lucas, 1857)		X		
		<i>Eantis papinianus</i> (Poey, 1832)	X			
		<i>Ephyriades b. brunnea</i> (Herrich-Schäffer, 1865)	X	X		
		<i>Erynnis zarucco</i> (Lucas, 1857)		X		
		<i>Hylephila p. phylaeus</i> (Drury, 1773)	X			
		<i>Panoquina corrupta</i> (Herrich-Schäffer, 1865)	X	X		
		<i>Panoquina l. lucas</i> (Fabricius, 1793)	X			
		<i>Perichares p. philetus</i> (Gmelin, 1790)	X			
		<i>Phocides pigmalion batabano</i> (Lucas, 1857)	X			
		<i>Proteides maysi</i> (Lucas, 1857)	X			
		<i>Proteides mercurius sanantonio</i> (Lucas, 1857)	X			
		<i>Pyrrhocalles antiqua orientis</i> Skinner, 1920	X			
		<i>Synapte m. malitiosa</i> (Herrich-Schäffer, 1865)	X			
		<i>Urbanus dorantes santiago</i> (Lucas, 1857)	X			
		<i>Urbanus proteus domingo</i> (Scudder, 1872)	X	X		
		Lycaenidae	<i>Electrostrymon angelia</i> (Hewitson, 1874)			X
			Nymphalidae	<i>Agraulis vanillae insularis</i> Maynard, 1869	X	
				<i>Anartia jatrophae guantanamo</i> Munroe, 1942	X	
		<i>Dryas iulia nudeola</i> (Bates, 1934)		X	X	
	<i>Euptoieta h. hegesia</i> (Cramer, 1779)	X		X		
	<i>Heliconius charithonia ramsdeni</i> Comstock & Brown, 1950	X		X		
	<i>Junonia c. coenia</i> Hübner, 1822	X				
	Papilionidae	<i>Junonia evarete zonalis</i> Felder & Felder, 1867	X			
		<i>Phyciodes phaon phaon</i> (Edwards, 1864)	X			
		<i>Siproeta stelenes biplagiata</i> (Fruhstorfer, 1907)	X			
		<i>Battus devilliers</i> (Godart, 1823)	X			
		<i>Battus polydamas cubensis</i> (Dufrane, 1946)	X			
		<i>Heraclides a. andraemon</i> Hübner, [1823]	X			
		<i>Heraclides androgeus epidaurus</i> (Godman & Salvin, 1890)	X			
<i>Heraclides aristodemus temenes</i> (Godart, 1819)		X				
Pieridae		<i>Anteos clorinde</i> (Godart, [1824])	X	X		
		<i>Aphrissa neleis</i> (Boisduval, 1836)	X			
	<i>Aphrissa statira cubana</i> D'Almeida, 1939		X			
	<i>Glutophrissa drusilla poeyi</i> (Butler, 1872)	X				
	<i>Phoebis argante fornax</i> (Butler, 1869)	X				
	<i>Phoebis sennae sennae</i> (Linnaeus, 1758)	X				
		<i>Aellopos blaini</i> Herrich-Schäffer, [1869]	X			



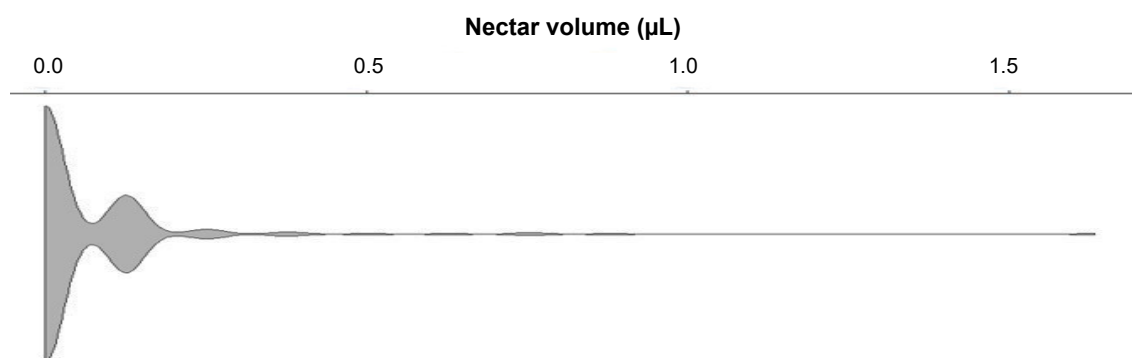
**Fig. 1.** Diversity estimations of floral visitors in the flowers of *Bourreria havanensis* during the peak of the flowering periods of 2018 and 2019 in Lomas de Galindo, Mayabeque, Cuba. The curves depict the estimation using three orders of Hill numbers ( $q = 0, 1, 2$ ). Rarefaction is represented with continuous lines while extrapolation with dotted ones. The data was extrapolated to 86 sampling units, which is the double of the reference sample.

**Fig. 1.** Estimación de la diversidad de visitantes florales en las flores de *Bourreria havanensis* durante las temporadas de máxima floración de 2018 y 2019 en Lomas de Galindo, Mayabeque, Cuba. Las curvas representan la estimación mediante el uso de los tres órdenes de los números de Hill ( $q = 0, 1, 2$ ). La rarefacción se representa con líneas continuas mientras que la extrapolación con líneas punteadas. Los datos fueron extrapolados hasta 86 unidades de muestreo, lo cual es el doble de la muestra de referencia.



**Fig. 2.** Abundance of floral visitors in the flowers of *Bourreria havanensis* during the sampling period of 2018 and 2019 in Lomas de Galindo, Mayabeque, Cuba. The number of interactions of every species is represented between parentheses. The label “Others” of the peak of the flowering season of 2018 includes the species with less than 5 interaction each (*Atalopedes mesogramma*, *Heraclides androgeus*, *Anartia jatrophae*, *Heraclides aristodemus*, *Agraulis vanillae*, *Aphrissa neleis*, *Panoquina corrupta*, *Panoquina lucas*, *Phoebis argente*, *Phoebis sennae*, *Asbolis capucinus*, *Campsomeris atrata*, *Helichonius charithonia*, *Junonia evarete*, *Junonia coenia*, *Phocides pigmalion*, *Pseudocharis minima*, *Centris fulviventris*, *Eantis papinianus*, *Glutophrissa drusilla*, *Heraclides andraemon*, *Hylephila phylaeus*, *Perichares philete*, *Proteides maysi*, *Proteides mercurius*, *Pyrrhocalles antiqua*, *Siproeta stelenes*, *Synapte malitiosa*, *Syntomeida wrighti*, *Zelatilla columbia*). The label “Others” of the flowering season of 2019 includes the species with less than 15 interactions each (*Helichonius charithonia*, *Aphrissa statira*, *Chorantus radians*, *Dryas iulia nudeola*, *Urbanus proteus domingo*, *Erynnis zarucco*, *Polistes sp.*, *Burca concolor*, *Electrostrymon angelia*, *Euptoieta hegesia*, *Melipona beecheii*, *Panoquina corrupta* and *Efferia sp.*).

**Fig. 2.** Abundancia de los visitantes florales en las flores de *Bourreria havanensis* durante los períodos de muestreo de 2018 y 2019 en Lomas de Galindo, Mayabeque, Cuba. El número de interacciones de cada especie se representa entre paréntesis. La etiqueta “Others” de la temporada de máxima floración de 2018 incluye a las especies con menos de 5 interacciones cada una (*Atalopedes mesogramma*, *Heraclides androgeus*, *Anartia jatrophae*, *Heraclides aristodemus*, *Agraulis vanillae*, *Aphrissa neleis*, *Panoquina corrupta*, *Panoquina lucas*, *Phoebis argente*, *Phoebis sennae*, *Asbolis capucinus*, *Campsomeris atrata*, *Helichonius charithonia*, *Junonia evarete*, *Junonia coenia*, *Phocides pigmalion*, *Pseudocharis minima*, *Centris fulviventris*, *Eantis papinianus*, *Glutophrissa drusilla*, *Heraclides andraemon*, *Hylephila phylaeus*, *Perichares philete*, *Proteides maysi*, *Proteides mercurius*, *Pyrrhocalles antiqua*, *Siproeta stelenes*, *Synapte malitiosa*, *Syntomeida wrighti*, *Zelatilla columbia*). La etiqueta “Others” de la temporada de máxima floración de 2019 incluye a las especies con menos de 15 interacciones cada una (*Helichonius charithonia*, *Aphrissa statira*, *Chorantus radians*, *Dryas iulia nudeola*, *Urbanus proteus domingo*, *Erynnis zarucco*, *Polistes sp.*, *Burca concolor*, *Electrostrymon angelia*, *Euptoieta hegesia*, *Melipona beecheii*, *Panoquina corrupta* y *Efferia sp.*).



**Fig. 3.** Violin plot of the nectar volume produced in the flowers of *Bourreria havanensis* in Lomas de Galindo, Mayabeque, Cuba, during the peak of the flowering season of 2019. The width of every part of the violin indicates the number of flowers with the specified nectar volume. Of the 262 flowers measured, 189 were empty.

**Fig. 3.** Gráfico de violín del volumen de néctar producido en las flores de *Bourreria havanensis* en Lomas de Galindo, Mayabeque, Cuba, durante la temporada de máxima floración de 2019. El ancho de cada porción del violín indica el número de flores con el volumen de néctar respectivo. De las 262 flores medidas, 189 estaban vacías.

**TABLE II**

**Models and model selection parameters based on Akaike Information Criterion (AICc) of the relationship between predictor variables and the abundance of interactions of floral visitors in the flowers of *Bourreria havanensis* in Lomas de Galindo, Mayabeque, Cuba, during the peak of the flowering season of 2019**

The global model includes all predictor variables: temperature, relative humidity, flower abundance, plant height, plant diameter, wind speed and floral visitor identity (species). LogL: likelihood function; K: number of parameters of every model;  $\Delta AICc$ : difference of the Akaike Information Criterion relative to the smallest AIC value in the set of models;  $w_i$ : Akaike weights.

**TABLA II**

**Modelos y parámetros de selección de los modelos basados en el Criterio de Información de Akaike (AICc) de las relaciones entre las variables predictoras y la abundancia de interacciones de visitantes florales en las flores de *Bourreria havanensis* en Lomas de Galindo, Mayabeque, Cuba, durante la temporada de máxima floración de 2019**

El modelo global incluye a todas las variables predictoras: temperatura, humedad relativa, abundancia de flores, altura de la planta, diámetro de la planta, velocidad del viento e identidad del visitante floral (especie). LogL: función de verosimilitud; K: número de parámetros de cada modelo;  $\Delta AICc$ : diferencia del Criterio de Información de Akaike relativo al menor valor AIC del conjunto de modelos;  $w_i$ : pesos de Akaike.

Model	K	LogL	AICc	$\Delta AICc$	$w_i$	Biological hypothesis of the model
Flower abundance	3	-130.69	267.68	0.00	0.48	The number of flowers is a visual element that attracts pollinators.
Plant height + Plant diameter	4	-130.10	268.70	1.02	0.29	The size of the plant influences its visibility by pollinators
Flower abundance + Plant height + Plant diameter	5	-129.66	270.09	2.41	0.14	A combined measure of the attraction features of the plant for pollinators.
Null model	2	-133.88	271.92	4.24	0.06	Abundance of interactions is random
Wind speed	3	-133.79	273.88	6.20	0.02	The majority of pollinators are flying insects, which cannot fly at a certain wind speed.
Species identity	24	-105.38	279.11	11.42	0.00	The abundance of interactions depends only in the species of pollinator involved.
Wind speed + Species identity	25	-105.27	282.96	15.28	0.00	The speed of wind at which pollinators cannot fly is specific of every species.
Temperature + Relative humidity	11	-129.31	284.29	16.61	0.00	The majority of floral visitors were insects, which are ectothermic and their activity depends on these variables.
Global model	36	-86.78	302.25	34.57	0.00	The abundance of interactions depends on all predictor variables considered.

Although the most frequent visitor was the bee *Centris poecila*, the majority of the species were butterflies and moths (order Lepidoptera), which comprises a significant proportion of all visitors. This high abundance of butterflies in the flowers of *Bourreria havanensis* is also typical in other species of the genus, for example, *Bourreria succulenta* Jacq. in the island of San Salvador, Bahamas (Rathcke 2001). However, the effect of ultramafic soils could be the principal reason for the diversity of lepidopterans, which included nine endemic species in Lomas de Galindo. Ultramafic areas contain a large number of Lepidoptera species and high levels of endemism, particularly if it is considered the small areas that occupy ultramafic soils in Cuba (Barro & al. 2003). One of the species with high abundance in the flowers of *B. havanensis* was the hawkmoth *Aellopos blaini*, an endemic species of Cuba (Barro & Núñez 2011).

*Aellopos blaini*, such as other species of the genus *Aellopos* (Young 1985), has diurnal activity and it is scarce in Cuban ecosystems (Barro & Núñez 2011). Therefore, *B. havanensis* could be a key resource in the lifecycle of this moth and the rest of the lepidopterans.

There is a high confidence that the most frequent visitors observed are the only principal visitors in the flowers of *Bourreria havanensis*, because of the high sampling completeness showed in the curves of Hill numbers of order 1 and 2. However, it is expected that other species of floral visitors could be recorded with more sampling effort, due to the low sampling completeness showed in the curve of order 0.

The attraction of visitors to the flowers of *Bourreria havanensis* depends only on floral display, particularly in the abundance of flowers and the size of the plants. Diurnal pollinators use visual cues for foraging (Faegri & van der Pijl 1979), and this species blooms massively during the summer months. The combination of a generalist pollination system and the floral display are the principal characteristics for the attraction of the high diversity of floral visitors. Usually the abundance of flowers and the phenology of the species in the community modulate the pattern of pollination interactions (Encinas-Viso & al. 2012, Olito & Fox 2015).

Although *Bourreria havanensis* attracts a diverse assemblage of floral visitors and flowers massively, the nectar in the flowers is scarce. However, *B. succulenta*, a related species with a population in Bahamas, produces eight times more nectar, although it is scarcely visited by pollinators (Rathcke 2001). The most plausible explanation for this result is the effect of ultramafic soils in nectar production. High temperature and water stress diminish several features of flowers, including nectar volume (Descamps & al. 2018, 2020). Both features are the cornerstone of ultramafic soils, with a strong influence in the plants of these habitats (Berazain 2001). *Bourreria havanensis* could produce low quantities of nectar on its flowers because of the low water availability in the soil. This leads insects to visit more flowers, similar to the observations of Descamps & al. (2018) in *Borago officinalis* L., a species of the same

family. Floral visitors must increase the number of visits to the flowers to obtain a significant amount of nectar, with an increase in the pollination success of *Bourreria havanensis*.

## CONCLUSIONS

*Bourreria havanensis* attracts a wide variety of floral visitors, making it an "oasis" in the harsh environment of the thicket of Lomas de Galindo. However, the main cause of this phenomenon is not the availability of nectar, but the floral display of this plant and its generalist pollination system.

## AUTHOR'S CONTRIBUTION

A. Barro conceived the original idea, participated in the investigation design and took part of the data. D. Alameda participated in the investigation design, took and processed the data and, wrote the first version of the manuscript. A.J. Corso, A.P. González and A. Tejada took and processed the data and participated in the results discussion. All authors participated actively in the discussion of the results and the critical review of the manuscript.

## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interest:* The authors declare that they have no conflict of interest.

*Ethics approval:* All authors have carried out fieldwork and data generation ethically, including obtaining appropriate permitting.

*Consent for publication:* All authors have consented to publishing this work.

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