



Rove beetle species diversity and the patterns of interactions with their host plants in primary and secondary tropical forests

Diana M. Méndez Rojas¹ · Juan Márquez² · José L. Navarrete-Heredia³ · Ana Paola Martínez Falcón² · J. Manuel Lobato-García¹ · Julieta Benítez Malvido¹

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Abstract

In tropical disturbed forests, it is relatively unknown the extent insect communities are experiencing shifts in species diversity and the consequences for ecosystem functions and services. In southern Mexico, we used the rove beetle community associated to *Heliconia wagneriana* bracts, as a model system, to investigate differences in community attributes and feeding habits between old-growth and human induced secondary forests. We tested if the beta diversity components of rove beetle communities were influenced by forest type and bract traits. Furthermore, we described the topology of individual-based heliconia-rove beetle ecological networks. Overall, we recorded 26 rove beetle species with significantly greater abundance in secondary forests. High compositional dissimilarity between forest types was observed with saprophagous species being more likely detected in old-growth forests; whereas predatory species in secondary forests. Heliconia-rove beetle networks showed a significant nested pattern with incidence data for old-growth forests and incidence and abundance data for secondary forests. Compared to old-growth forests, the rove beetle community in secondary forests showed strong shifts in species composition, diversity and differences in the detection probability of feeding habits, with consequences for ecosystem functioning. We further discuss these findings according to the forest disturbance and phytotelm systems. Implications for insect conservation: Individuals of *H. wagneriana* represent biodiversity reservoirs for invertebrates, especially in human-modified landscapes.

Keywords Disturbance · Heliconia · Staphylinids · Phytotelmata · Compositional dissimilarity · Ecological networks

Introduction

Tropical rainforest deforestation and consequent habitat loss, usually distress plant and animal populations and the different types of biotic interactions among them. Generally, specialist species preferentially inhabit old-growth preserved forests, while generalist species are present in both preserved and disturbed forests (Melo et al. 2013; Kormann et al. 2018). In the Neotropics, herbaceous species in the

Heliconiaceae (Zingiberales) are able to establish in a wide range of environmental conditions, including human-modified landscapes, but with modifications in their vegetative and chemical traits and in their biotic interactions with different organisms (Berry and Kress 1991; Benítez-Malvido et al. 2014, 2016). In tropical southern Mexico, effects of human disturbances on the physical and chemical characteristics of *Heliconia* species (i.e., leaf size, number of shoots, toughness and condensed tannins, etc.) have been observed (Santos and Benítez-Malvido 2012). Furthermore, heliconias in old-growth continuous forests harbor greater arthropod diversity and ecological networks with higher diversity of interactions, as compared with individual plants inhabiting secondary forests and forest fragments (Benítez-Malvido et al. 2014, 2016).

The erect inflorescences of some *Heliconia* species, represent ephemeral small ecosystems known as phytotelmata where water is retained in the floral bracts. Phytotelmata maintain diverse animal communities and are considered

✉ Diana M. Méndez Rojas
dianamendez04@gmail.com

¹ Laboratorio de Ecología del Hábitat Alterado, Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES)-UNAM, Morelia, Mexico

² Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo (UAEH), Pachuca de Soto, Mexico

³ Centro de Estudios en Zoología, CUCBA, Universidad de Guadalajara, Guadalajara, Mexico

as biodiversity reservoirs for invertebrates (Seifert 1982; Kitching 2000). These ephemeral microhabitats are used by terrestrial and aquatic invertebrate species for feeding, refuge and reproduction (Seifert 1982; Aristizábal et al. 2013; de Oliveira et al. 2018; Sayers et al. 2019). In some cases, the physical and chemical conditions in phytotelmata influence the abundance and the species richness of invertebrates inhabiting them, promoting high invertebrate species turnover (Jalinsky et al. 2014; de Oliveira et al. 2018). Invertebrate communities in the phytotelmata of bromeliads and heliconias exhibit different trophic guilds and a positive size-diversity relationship (Seifert and Seifert 1976; Antiqueira et al. 2018). Therefore, *Heliconia* species represent an ideal study system for evaluating the impact of forest disturbance on animal diversity, trophic guilds, and their patterns of interactions with their host plants.

Beetle species within the Staphylinidae (commonly known as rove beetles) are abundant and frequent opportunistic floral visitors (Thayer 2016; Sayers et al. 2019), and commonly found in *Heliconia* inflorescences (Seifert and Seifert 1976; Frank and Barrera 2010; Frank and Morón 2012; Bersosa et al. 2014; Jalinsky et al. 2014; de Oliveira et al. 2018). Rove beetle species present numerous feeding habits (e.g., predators, phytophagous, parasitoids and saprophagous), and are often observed preying actively on fly larvae and pupae (Frank and Barrera 2010; Frank and Morón 2012; López-García and Marín-Gómez 2018) and feeding on decomposing organic matter in the bracts of heliconias (Frank and Barrera 2010; López-García et al. 2011). Rove beetles are not directly involved in pollination however, as floral visitors they could affect plant fitness by consuming floral parts and pollen or by preying on insect folivores (McCall and Irwin 2006; Klimaszewski et al. 2010; Thayer 2016; Sayers et al. 2019). Therefore, the interaction between plants and rove beetles could range from commensalistic to mutualistic or antagonistic, but further research about the natural history of rove beetles inhabiting heliconias is required (Sayer et al. 2019).

Despite of the high species diversity of rove beetles worldwide (e.g., approximately 63,000 known species, Irmeler et al. 2018) and of their functional importance in ecosystems, little is known about their interactions with their host plants and the role of phytotelmata as habitat refuges for the preservation of rove beetle species in human-modified landscapes (Sayers et al. 2019). In this study, we compared the rove beetle community inhabiting *Heliconia wagneriana* Petersen inflorescences present in old-growth and human induced secondary tropical forests. Firstly, we tested if rove beetle species diversity and their feeding habits differed between old-growth and secondary forests. Secondly, we evaluated if phytotelmata traits and forest type influence rove beetle species composition. Finally, we described the topological structure of individual-based heliconia-beetle

ecological networks in each forest type. We expected that rove beetle community attributes and interactions were affected by forest type while phytotelmata traits influence species composition (Benítez-Malvido et al. 2014, 2016). We also discussed and highlighted the ecological role of *Heliconia* herbs as microhabitats for different native rove beetle species in human-modified landscapes.

Material and methods

Study area

The study was conducted in the Lacandona rainforest region, in the state of Chiapas, southeastern Mexico (16° 03'N; 90° 64'W, 170 m, Fig. 1). This region contains the Montes Azules Biosphere Reserve (MABR, 331,200 ha) and some protected areas in the Marqués de Comillas municipality. The MABR has around 4000 species of vascular plants (Medellín 1994), is one of the most biodiverse regions in Mexico and is considered the largest remnant of tropical rainforest of Mesoamerica (Mendoza and Dirzo 1999). Temperature ranges between 18° and 32 °C, and annual precipitation averages 3000 mm (Meave del Castillo 1990). Human activities, such as cattle ranching, forestry and agriculture, are the main causes of deforestation (Durand 2019). Two contrasting common forest types in the region were considered for this study including: old-growth continuous forests and secondary forests. Forest types are divided by the Lacantún River, which forms the southern boundary of the MABR. The old-growth forest corresponds to well-preserved lowland tropical rainforest within the MABR, while the secondary forests areas have regrown after forest clearance and are close to human settlements with paved and unpaved roads (see details in Benítez-Malvido et al. 2016).

Study species

In the Lacandona rainforest, eight natives *Heliconia* species are found, including the following: *Heliconia aurantiaca* Ghiesbreghtii ex Lemaire, *H. bourgaeana* Petersen, *H. collinsiana* Griggs var. *collinsiana*, *H. latispatha* Benthann cv. Orange Gyro, *H. librata* Griggs, *H. spissa* Griggs, *H. vaginalis* Benthann and *H. wagneriana* (Santos et al. 2009; Benítez-Malvido et al. 2014, 2016). Some of these *Heliconia* species are found in old-growth continuous forests and secondary forests concurrently, e.g., *H. latispatha*, *H. collinsiana*, and *H. wagneriana*. For the purposes of this study, we selected *H. wagneriana* because the species presents erect inflorescences arranged in concave bracts forming phytotelm systems and is commonly found in preserved and disturbed forests.

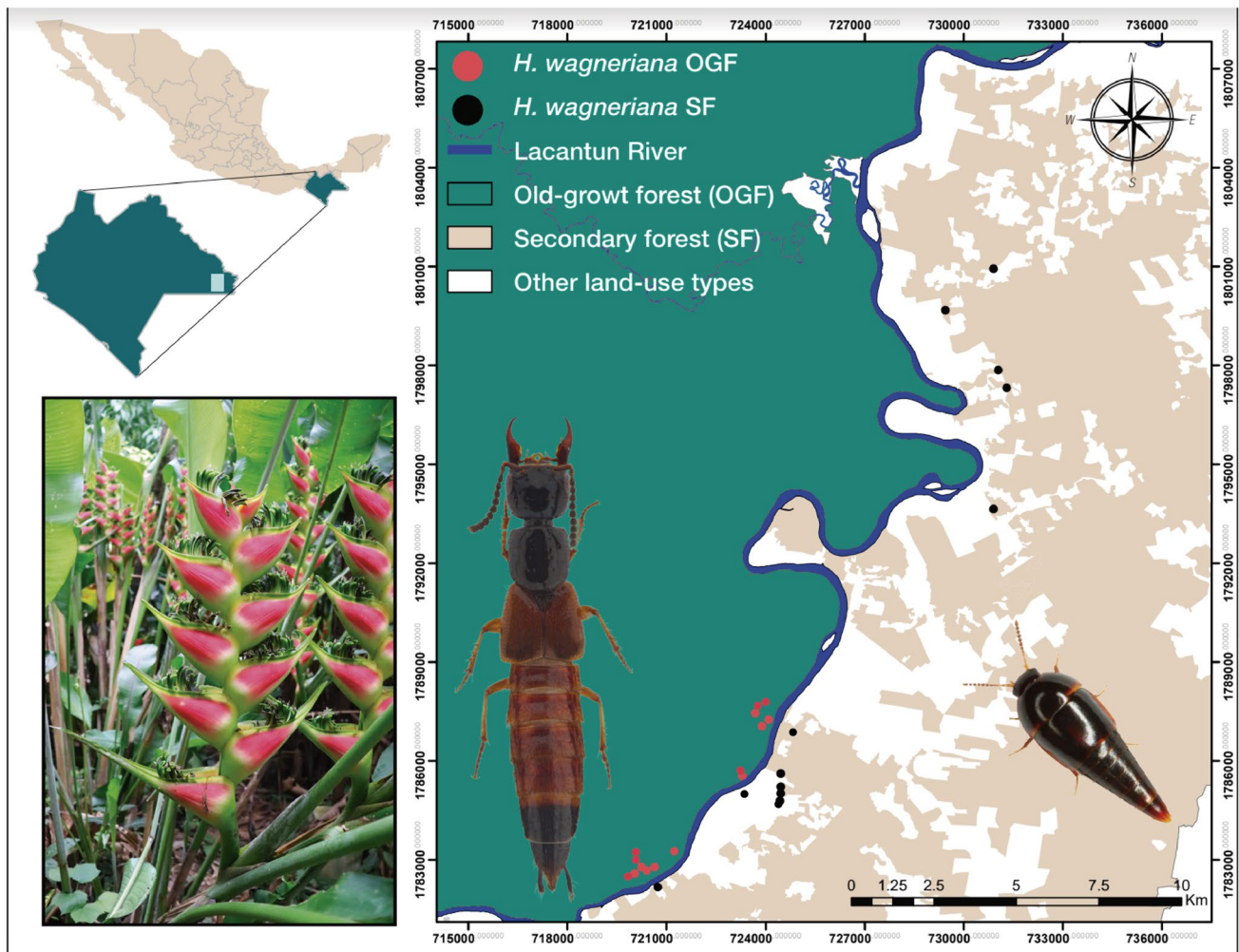


Fig. 1 The map shows the study area with the location of *Heliconia wagneriana* individuals (red and black dots) growing in old-growth continuous forests (OGF, green color) and secondary forests (SF, grey color) within the Lacandona rainforest region, Chiapas, Mexico. The

image shows two common beetle species visiting the heliconia bracts: *Belonuchus rufipennis* (predator, left-bottom side) and *Coproporus* sp. (saprophagous, right-bottom side). (Color figure online)

The species *H. wagneriana* is mainly distributed in Central America and the Caribbean; with a narrow blooming season during the dry season from March to April, in Mexico (Criley and Sakai 1997). The species attracts pollinators with long curved bills, such as the hummingbird species *Phaethornis longirostris* and *Campylopterus hemileucurus* (Stiles 1975; Berry and Kress 1991; Gannon et al. 2018). Furthermore, *H. wagneriana* can establish in open areas and tolerate up to 40% shade, its height ranges from 1 to 8 m, and the erect inflorescences are composed by 6–20 large bright pink and green bracts (approximately 200 flowers) forming phytotelms (Stiles 1975; Berry and Kress 1991). In the study area, *H. wagneriana* was relatively common in old-growth continuous forest gaps and in secondary forest regrowth, however individuals were not evenly distributed through the study area. In old-growth continuous forest, *H. wagneriana*

individuals were more aggregated and located along forest trails, paths and canopy gaps, while in secondary forest, the species was common along forest edges and clear-cut forest along paved and unpaved roads (Fig. 1).

Rove beetle sampling

In the southern boundary of MABR, we searched for individuals of *H. wagneriana* with their inflorescences at similar developmental stages (i.e., holding up to 12 bracts, with an average length of 45 ± 6.97 cm). In an area of 334 km² during the blooming season of 2022 and 2023, 20 different individuals of *H. wagneriana* in each forest type were located. The sample of individuals was constrained by the presence of fresh inflorescences and a minimum distance of 60 m between them. Given accessibility limitations within

the MABR, *H. wagneriana* individuals in old-growth continuous forest were located at an average distance of 554.7 ± 167.8 m from the river. Conversely, individuals in the secondary forests were more scattered and located at an average distance of 1218 ± 896 m from the river border close to human settlements (e.g., the ejido Boca de Chajul, Playón de la Gloria, Galicia and Zamora Pico de Oro). Though *H. wagneriana* is relatively common in the study region, the requirement for fresh inflorescences and accessibility limitations, influenced the differences in average distance among *H. wagneriana* individuals in old-growth continuous forests (60–750 m) and in the secondary forests (153–3729 m).

Sampled *H. wagneriana* individuals were used as independent sampling units. Two inflorescences per individual were removed from the most basal part of the plant and covered with plastic bags (i.e., 80 inflorescences from 40 plants in total). Each inflorescence was sectioned, the bracts split, and the floral contain was pulled apart in search of rove beetle adults. A total of 743 bracts, 371 bracts in secondary forests and 372 in old-growth forests, were examined. Beetles were captured manually and collected in vials filled with 90% alcohol. Rove beetle abundance, richness and feeding habits (assigned following Navarrete-Heredia et al. 2002) were recorded for each plant. Adult specimens were determined to the lowest possible taxonomic level using dichotomous keys for the Staphylinidae (Sharp 1884; Smetana 1995; Navarrete Heredia et al. 2002; Chani-Posse 2014; Márquez and Asiain 2022). All species were confirmed as independent taxonomic entities based on differentiating external characters and the extraction of male genitalia. Specimens were deposited in the Coleoptera Collection, at the Universidad Autónoma del Estado de Hidalgo (CC-UAEH).

Rove beetle species composition is strongly influenced by environmental and microhabitat variables (Irmeler and Gürlüch 2007; Gutiérrez et al. 2009). Therefore to assess if phytotelmata traits influenced rove beetle species composition between forest types, the following bract traits were recorded by using a measuring tape and a digital caliper: length, width and thickness. Using a digital water quality tester WALFRONT, three physicochemical variables of the liquid contained within the bracts were recorded for each bract, including the following: liquid pH, temperature and volume (Table S1).

Data analysis

Species diversity

Species diversity of the rove beetle community was estimated using Hill numbers (Hill 1973) or ${}^qD$ diversity (Jost 2006), which indicates the effective number of species in a sample. The exponent q determines the influence of species abundance on diversity values, whereas ${}^0D$ is equal to

species richness and ${}^1D$ gives a proportional weight to species based on their abundances and is known as the effective number of equally common species. Finally, the effective number of dominant species ${}^2D$ gives greater weight to those species that are the most abundant in the community. Diversity values were compared between forest types, using the sample-completeness profile through all ${}^qD$ values (${}^q\hat{C}_{max}$, Chao et al. 2020), which allows for fair comparisons under the replication principle (Jost 2006; Chao and Jost 2012). A cutoff for comparison was defined as the reference sample extrapolated up to double the reference sample size ($\hat{C}_{max} = 96\%$, Supplementary Information Table 1, Chao et al. 2020). Significant differences between ${}^qD$ were identified when there was no overlap with a confidence interval of 95% (Cumming et al. 2007).

Evenness is a measure of variation in species relative abundance. When species abundances are perfectly even, diversity of all orders ${}^qD \geq 0$ are identical and equal to species richness. When species abundances are not even, species diversity declines as the diversity order q increases. Therefore, the steepness of the slope reflects the unevenness of species abundances, but as ${}^0D$ only considers species richness, abundance is disregarded, and it is not meaningful to evaluate evenness (Chao and Ricotta 2019; Chao et al. 2020). Here, we focus on evenness measures of orders ${}^1D$ and ${}^2D$ at the coverage level of $\hat{C}_{max} = 96\%$; and the comparison between forest types was realized using 95% of confident intervals (Chao et al. 2020). The iNEXT-4-steps package for R.v.4.3.2 was used for calculating the values of ${}^qD$ ($\pm 95\%$ CI), the evenness and sample completeness profiles (Chao et al. 2020). To visualize rove beetle community structure between forest types, we constructed rank-abundance curves with the *BiodiversityR* package for R.v.4.3.2 (Kindt and Kindt 2019).

To assess changes in rove beetle species abundance between forest types, a generalized linear model with negative binomial error was fitted with *glm.nb* function in MASS package (R Core Team 2020). The GLM was compared with a null model using ANOVA (Chi-squared LR test) in Stats package (R Core Team 2020). The probability of finding one feeding habit in each forest type was estimated using generalized linear models with a binomial distribution. A two-column matrix—used as a response variable—was constructed using the *cbind* function in R (i.e., “cbind (Predators, Saprophagous)”, which represents the abundance of predator or saprophagous species found in each inflorescence by forest type; these were the only two feeding habits found in our samples (Rodríguez-Peña et al. 2023). The models were fitted and compared with null model using the *glm* and *anova* function (Chi-squared test) for Stats package R.v.4.3.2 (R Core Team 2020), and the heteroscedasticity and normality assumptions of all generalized linear models were evaluated with residual plots (Burham and Anderson 2002).

Table 1 Rove beetle species collected in the inflorescences of *Heliconia wagneriana* in old-growth and secondary forests in the Lacandona rain-forest region, Mexico

Subfamily	Species	Feeding habits	Code	Old-growth forest	Secondary forest
Aleocharinae	Aleocharinae sp. 1	Predator	A1	3	101
	Aleocharinae sp. 2	Predator	A2	0	3
	Aleocharinae sp. 3	Predator	A3	2	4
	Aleocharinae sp. 4	Predator	A4	1	103
	Aleocharinae sp. 5	Predator	A5	0	59
Osoriinae	<i>Naceus</i> sp.	Saprophagous	O1	0	1
	<i>Thoracophorus</i> sp.	Saprophagous	O2	1	11
Paederinae	<i>Lithocharis</i> sp. 1	Predator	Pa1	0	12
	<i>Lithocharis</i> sp. 2	Predator	Pa2	1	1
	<i>Scopaeus</i> sp.	Predator	Pa3	0	2
	<i>Deroderus</i> sp.	Predator	Pa4	0	1
Piestinae	<i>Piestus</i> sp. aff. <i>mexicanus</i> Laporte, 1835	Saprophagous	Pi1	0	47
	<i>Piestus</i> sp.	Saprophagous	Pi2	3	16
	<i>Hypotelus</i> sp.	Saprophagous	Pi4	0	1
Staphylininae	<i>Belonuchus rufipennis</i> (Fabricius, 1801)	Predator	S1	1	17
	<i>Belonuchus bidens</i> Sharp, 1885	Predator	S2	1	0
	<i>Belonuchus iridescence</i> Solsky, 1868	Predator	S6	1	0
	<i>Belonuchus</i> sp. 1	Predator	S3	17	2
	<i>Belonuchus</i> sp. 2	Predator	S5	1	0
	<i>Quedius</i> sp.	Predator	S7	0	1
	<i>Paederomimus</i> sp.	Predator	S11	1	0
Tachyporninae	<i>Coproporus</i> sp. 1	Saprophagous	T1	35	24
	<i>Coproporus</i> sp. 2	Saprophagous	T2	13	12
	<i>Coproporus</i> sp. 3	Saprophagous	T5	1	1
	<i>Coproporus</i> sp. 4	Saprophagous	T6	39	2
	<i>Coproporus</i> sp. 5	Saprophagous	T7	0	2
Sample coverage ($\hat{C}_{max}$)				0.62	0.962
No individuals				191	473
Observed species richness				16	22
Species richness (^0D)				24	22
Number of equal effective species (^1D)				4.86	9.64
Number of dominant species (^2D)				3.14	7.31

Rove beetle species composition and phytotelmata traits

Compositional dissimilarity based on the Jaccard index (β_{cc}) was used to determine the variation of rove beetle species composition in *H. wagneriana* bracts between forest types. Compositional dissimilarity (β_{cc}) is separated into two additive components: replacement (β_{repl} , species replacement) and richness difference (β_{rich} , loss or gain of species, Podani and Schmera 2011; Carvalho et al. 2013). These measures are insensitive to undersampling (Cardoso et al. 2009) and do not overestimate the species turnover component (Carvalho et al. 2012). The compositional dissimilarity matrices were calculated with the *betamulti* and

beta function in the BAT package for R.v.4.3.2 (Cardoso et al. 2015). By using a Mantel test with Spearman's correlation and 9,999 permutations (Legendre and Legendre 2012) there was no significant relationship between compositional dissimilarity of rove beetles and geographic distance among plants for either forest type: old-growth forest (Mantel test, $r=0.138$ and $p=0.142$) and secondary forest (Mantel test, $r=-0.09$ and $p=0.73$). In order to evaluate if forest type and physical and chemical variables of *H. wagneriana* inflorescences determine the rove beetle species composition, we use the non-metric multidimensional scaling (NMDS, Legendre and Legendre 2012). Goodness-of-fit measure for NMDS configuration was inspected by stress values, i.e., the sum of the squared differences between fitted and original

distances (Legendre and Legendre 2012) and by Shepard diagrams, which compare the distances among objects in the ordination plot with the original distances. Replacement (β_{repl}) and richness difference (β_{rich}) dissimilarity matrix were used for NMDS with *metaMDS* function for Vegan package (Oksanen et al. 2015), the non-metric fit (based on stress) and linear fit (the correlation between fitted values and ordination distances) were provided. The *envfit* function was used to calculate multiple regression of bract trait variables and forest type with ordination axes of each NMDS (i.e., for the replacement and richness difference component), with the length of the arrow proportional to the correlation with the ordination. Biplots of species and *envfit* vectors were generated to visualize.

Ecological networks

We assessed the topological structure of individual-based *H. wagneriana*-rove beetle networks in old-growth and secondary forests. Each individual-based heliconia-beetle network was built with an adjacency matrix *A*, where a_{ij} is the number of interactions from an individual plant *j* by rove beetle species *i* (Bascompte et al. 2003). To describe the topological structure of the heliconia-beetle network in old-growth and secondary forests, and to assess how connected are the networks the following metrics were calculated (Tylianakis et al. 2007; Benítez-Malvido et al. 2014, 2016). Connectance is the sum of links divided by the total number of cells within the interaction matrix. Links per species indicate the sum of connections divided by the number of species. The network metrics were calculated using the *networklevel* and *plotweb* functions in the bipartite package for R (Dormann et al. 2009).

To assess the degree of nestedness of each network per forest type, the NODF metric was used for incidence data in ANINHADO (Almeida-Neto et al. 2008) and the wNODF metric was used for abundance data with NODF software (Almeida-Neto and Ulrich 2011). To assess if nestedness values are higher than those expected by chance, 1000 random networks were generated using Null Model II-CE for incidence networks (Bascompte et al. 2003), and Null Model RC for abundance networks (Almeida-Neto and Ulrich 2011). In these null models, the probability of an interaction occurring is proportional to the number of interactions between beetles and plant inflorescences (Bascompte et al. 2003). Nestedness values range from 0 (non-nested) to 100 (perfectly nested). Using a simulated annealing algorithm, we calculated modularity (index *M*, from 0 to 1 for non-subgroups and completely separated subgroups) with the MODULAR software (Marquitti et al. 2014). In a nested network, peripheral species (i.e., beetles with few visits) interact with a subgroup of inflorescences that are also visited by a generalist core species (i.e., beetles with a higher

number of visits). The core-periphery measure was evaluated to determine the core groups (i.e., highly connected nodes) and peripheral groups (i.e., poorly connected nodes) using the formula proposed by Dáttilo et al. (2013).

Results

Rove beetle species diversity

In the 80 *H. wagneriana* inflorescences sampled from 40 different individuals, a total of 26 species within six Staphylinidae subfamilies and 11 genera were recorded (*N* = 664 individuals, Supplementary Information, Table 1). All individuals of *H. wagneriana* were inhabited by at least one rove beetle species (range from 1 to 13 species in one plant). Rove beetle abundance was significantly higher in secondary forests than in old-growth forests ($Z = -2.753$, *df* = 76, and $p = 0.005$; Shapiro test *W* = 0.95; $p = 0.008$; Chi-squared *LR* = 7.03, $p = 0.008$). Both forest types showed a sample completeness profile of 100% for ${}^0D$ values > 0, but 78% for species richness in secondary forest and 28% in old-growth forests (Fig. 2a). Total rove beetle species richness (${}^0D$) did not differ between forest types (Fig. 2b, ${}^0D \pm 95\%$), while the effective number of equally common species (${}^1D$) and dominant species (${}^2D$) was twice as diverse in secondary forests than in old-growth continuous forests (Fig. 2b). The evenness profile showed a more uneven distribution for old-growth forests than for secondary forests (Fig. 2c), coinciding with the rank-abundance curves where the secondary forest reveals a more equitable abundance distribution among species (Fig. 2d). Two species in the genus *Coproporus* were dominant in the old-growth forest (Fig. 2b): *Coproporus* sp. 1 (T1, Fig. 2b) and *Coproporus* sp. 4 (T6, Fig. 2b), and represented about 75% of the total abundance, while two Aleocharinae species were dominant in the secondary forests with 43% of the total abundance.

Only two feeding habits were recorded in the bracts of *H. wagneriana*, saprophagous and predator species. A total of 315 individuals in 10 species and 349 individuals in 16 species for saprophagous and predatory species, respectively, were found in both forest types (Fig. 3, Table 1). The detection probability of saprophagous and predator rove beetles was significantly influenced by forest type, where saprophagous species were predominantly found in old-growth forests ($Z = 10.95$ and $p < 0.001$ in Fig. 3), and predator rove beetles in secondary forests ($Z = -10.95$ and $p < 0.001$ in Fig. 3).

Rove beetle species composition and phytotelmata traits

A high compositional dissimilarity of rove beetle species was found between forest types ($\beta_{cc} = 87.07\%$). The

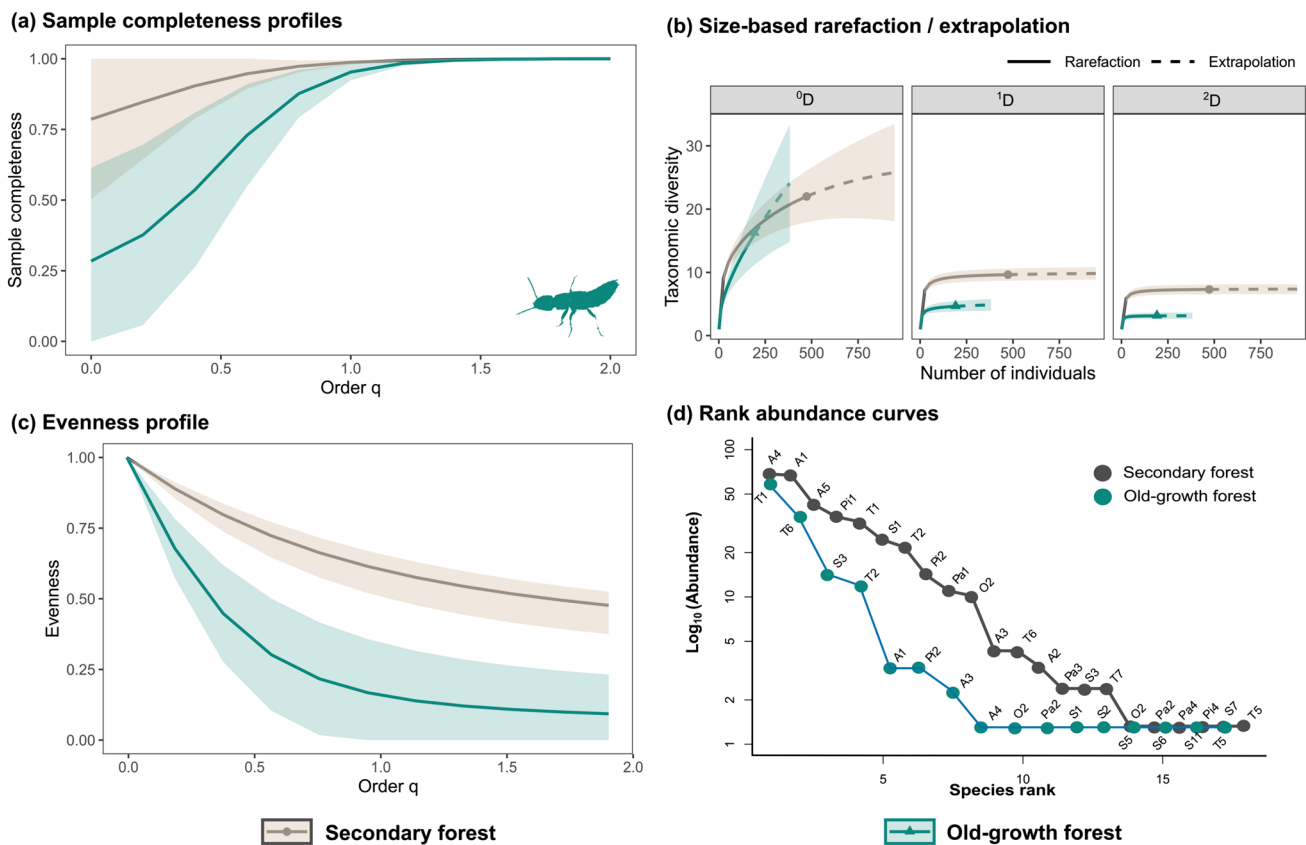


Fig. 2 Patterns of rove beetle species diversity (${}^0D$) in *Heliconia wagneriana* inflorescences in two forest types of the Lacandona rain-forest region; where **a** sample completeness profile; **b** sized-based rarefaction and extrapolation curves for species richness (${}^0D \pm 95\%$

CI), the effective number of equally common species (${}^1D \pm 95\%$ CI), the effective number of dominant species (${}^2D \pm 95\%$ CI); **c** evenness profile; and **d** rank abundance curves. Species abbreviations are described in Table 1

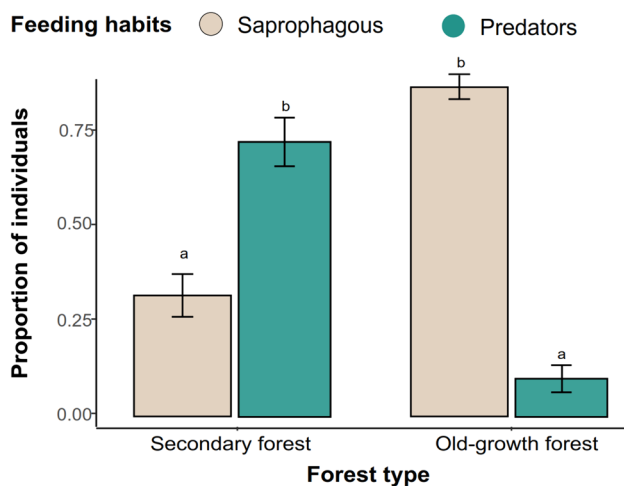


Fig. 3 Proportion of individuals by rove beetle feeding habits in old-growth and secondary forest. Data are presented by means and standard errors. Different letters show significant differences between feeding habits ($p < 0.05$)

richness difference component ($\beta_{rich} = 47.95\%$) had a slightly higher contribution than the replacement component ($\beta_{repl} = 39.11\%$). Twelve species were shared between forest types, four species were recorded exclusively in old-growth forests, and ten species were unique to secondary forests. The NMDS ordination showed that the rove beetle dissimilarity composition by forest type was better explained in the replacement component β_{repl} ($R^2 = 0.22$, $p = 0.001$) than in the richness difference component β_{rich} ($R^2 = 0.032$, $p = 0.311$, Fig. 4b). Nevertheless, the relationship between compositional dissimilarity and bract traits showed significant values only with the β_{rich} matrix, where liquid temperature ($R^2 = 0.29$, $p = 0.003$), volume ($R^2 = 0.26$, $p = 0.006$) and bract width ($R^2 = 0.16$, $p = 0.037$, Fig. 4a) were the bract traits that best explained the variation in beetle species composition between forest types (Supplementary material, Table S2). The inflorescences in secondary forest with relatively smaller bracts and higher liquid temperature showed higher number of rove beetle species (see grey arrow in Fig. 4b). The bract traits were not significant for the replacement component (Supplementary material, Table S2).

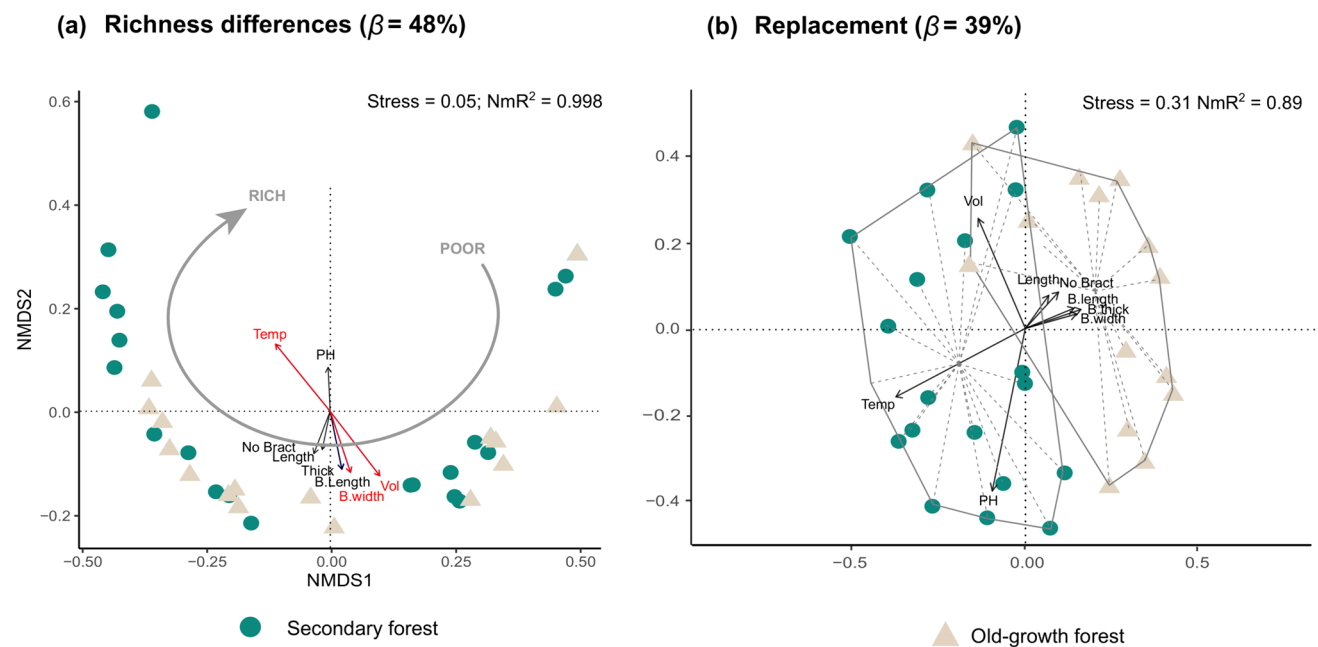


Fig. 4 Non-metric multidimensional scaling (NMDS) for richness difference component (a, β_{rich}) and replacement component (b, β_{repl}). Stress value and non-metric fit R^2 (NmR^2) are provided. Bract

traits are presented in black arrows for those no significant and red arrows for those significant $P < 0.001$ (see abbreviation in Supplementary material, Table S2)

Table 2 Ecological networks descriptors of rove beetle species associated to *Heliconia wagneriana* inflorescences in old-growth and secondary forests. (*) indicates $P < 0.001$ i.e., significantly nested

Network descriptor	Old-growth forest	Secondary forest
No. of rove beetle species	16	22
No. of inflorescence	20	20
Link per species	1.4	2.66
Connectance	0.16	0.25
NODF	47.82*	50.93*
wNODF	33.86	31.95*
Modularity	0.42	0.25

Ecological networks

The individual-based heliconia-beetle networks descriptors differed between forest types, the connectance values and the link per species were higher in secondary forests (Table 2). No modular pattern was found, but nested significant patterns with incidence data in old-growth forest and with incidence and abundance data in secondary forest, were found (Table 2, Fig. 5). The *Coproporus* genus showed the greater number of links in both forest types and was the most important species in determining the nested pattern; *Coproporus* sp. 1., and *Coproporus* sp. 4 constituted the old-growth forest core species and concentrated 75% of the total abundance; whereas *Coproporus* sp. 1, *Coproporus* sp. 2,

Aleocharinae sp. 4, Aleocharinae sp. 1 and Aleocharinae sp. 5 formed the secondary forest core species and concentrated 70% of the total abundance.

Discussion

This study is the first attempt to estimate the diversity of rove beetle communities associated with a tropical host plant, *H. wagneriana*, throughout feeding habits and ecological networks in old-growth and secondary forests. According to our predictions, forest type originated from tropical rainforest disturbance affected rove beetle diversity, the incidence of feeding habits and the network structure. The study highlights the important role of *H. wagneriana* inflorescences in the community structure of associated rove beetles. Furthermore, our results indicate that *H. wagneriana* act as an important microhabitat for rove beetle species in conserved and disturbed tropical forests.

Rove beetle feeding habits and species diversity

In our study, although total species richness was similar in old-growth and secondary forests, we found differences between forest types when comparing equally common (^1D) and dominant (^2D) species diversity. Inflorescences of *H. wagneriana* in secondary forests hold twice as diverse (^1D , ^2D) rove beetle species than those in old-growth forests.

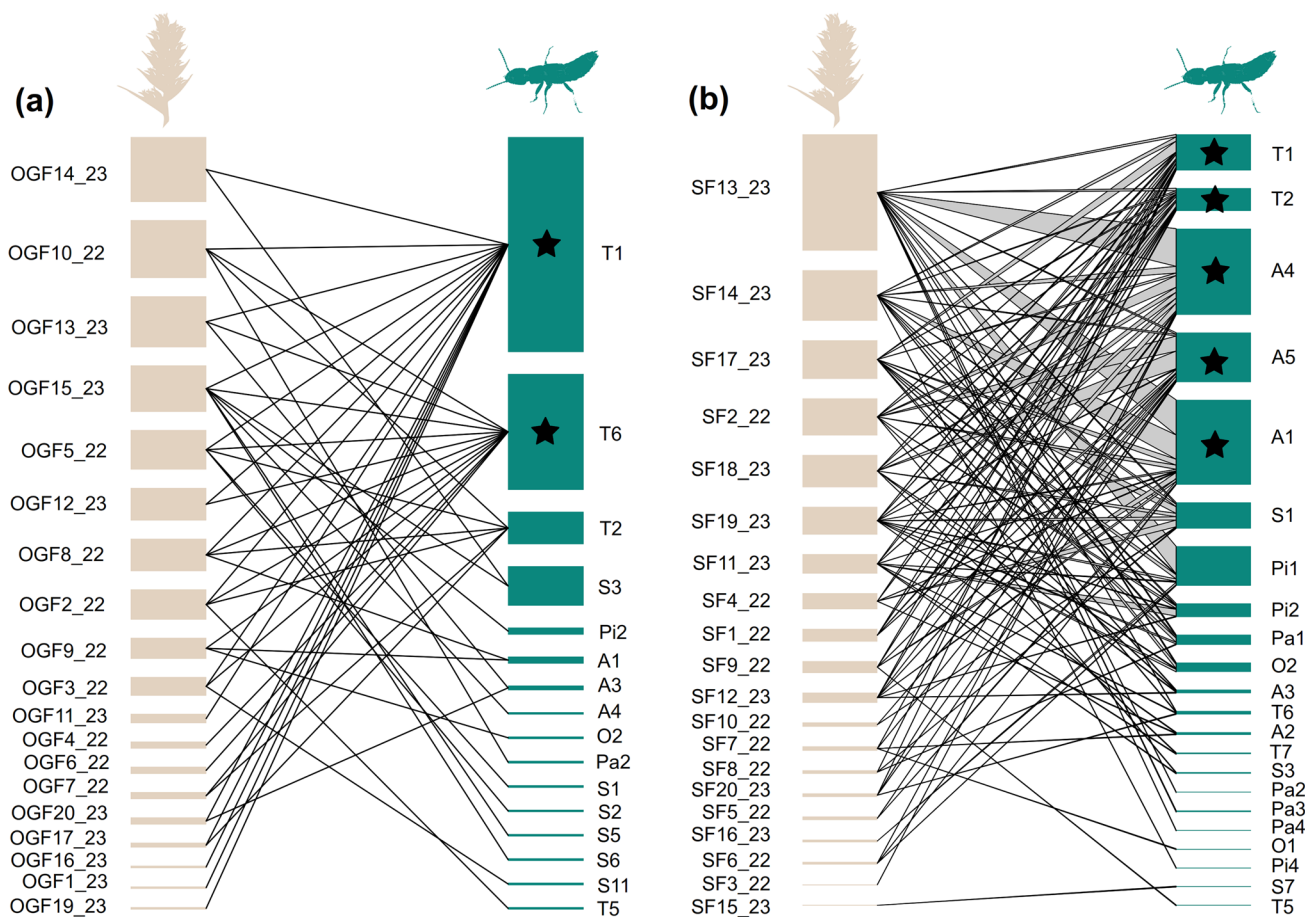


Fig. 5 Ecological networks between *Heliconia wagneriana* and their associated rove beetles showing a significant nested pattern for incidence data in old-growth forests (**a**), and both incidence and abundance data in secondary forests (**b**). Core species are indicated by a

star. The lines represent the number of interactions between each rove beetle species (dark green squares) with individuals of *H. wagneriana* (gray squares). The left codes represent different individuals of *H. wagneriana* and rove beetle species code are presented in Table 1

Species richness (^0D) is the most difficult diversity expression to estimate because of the high influence of rare species (Chao et al. 2020). The sample completeness analyses showed higher rare undetected species in old-growth forests than in secondary forests. Old-growth forests present a greater number of ephemeral microhabitats for opportunistic rove beetle species such as decomposing tree trunks and litter, fallen rotten fruits, mushrooms, bromeliads, and other *Heliconia* species (Arnan et al. 2011). Thus, the large extension of the old-growth continuous forest and its high offer of ephemeral resources contributes to the high proportion of rare undetected species. Furthermore, the dominance of species in the saprophagous genus *Coproporus* in old-growth forests generated an uneven distribution of species abundance compared with secondary forests. Seasonality is also another important factor in the structure of rove beetle communities, some species are dominant during the dry season while others during the rainy season (Reyes-Hernández and Navarrete-Heredia 2021). The herbaceous species *H.*

wagneriana, may represent a shelter and feeding source for rove beetle species during the dry season. The rove beetles associated to inflorescences are restricted to the blooming season, however.

The proportion of rove beetles within different feeding habits shifted between forest types. Saprophagous species are generally more sensitive to microclimatic changes than generalist predator species (Nagy et al. 2015), which could explain the higher detection probability of saprophagous species in old-growth forests. The prevalence of different microhabitats in old-growth forests could explain greater resource availability for saprophagous and other undetected species. For instance, *Piestus* beetles were observed consuming fallen decomposing fruits of *Pouteria* sp. in old-growth forest (D.M. Méndez, personal observation). Four *Coproporus* species were the most abundant (60% of collected individuals) and occupied more than 50% of *H. wagneriana* inflorescences in both forest types. Little it is known about *Coproporus* life history, but larvae and adults

have mainly saprophagous habits and can be found in leaf litter, dung, carcasses, fungi, decomposing fruits and cacti (Navarrete-Heredia et al. 2002; Thayer 2016). Since *H. wagneriana* inflorescences accumulate their own organic matter in the bracts, they represent a favorable environment for saprophagous species such as *Coproporus*. Species in the genus *Coproporus*, have also been found in inflorescences with high humidity and organic matter content, such as *Heliconia stricta*, *Calathea lutea* and *Etlingera elatior* (López-García et al. 2011; Jalinski et al. 2014).

Conversely predator species were less likely detected in old-growth forests than in secondary forests probably because generalist predator species present high dispersal capability, are less sensitive to environmental conditions and have opportunistic habits (Rusch et al. 2015; Hanson et al. 2016). Nevertheless, habitat specificity could change among Staphylinidae's subfamilies. Six predator species of the Staphylininae subfamily were found in old-growth forests, and only three species in secondary forests, while predator species of Aleocharinae and Paederinae prevail in secondary forest. It is likely that predator species used *Heliconia* inflorescence for feeding on dipteran larvae that are more abundant in secondary forests, as has been shown for other invertebrates associated to heliconias (Benítez-Malvido et al. 2014). Greater abundance of invertebrates could result in greater prey availability for rove beetles. It has been reported that *Belonuchus*, *Platydracus*, *Chroaptomus* and *Paederomimus* species visit heliconia inflorescences for hunting (Seifert and Seifert 1976; Frank and Barrera 2010; Frank and Morón 2012; de Oliveira et al. 2018). Congeneric species of heliconia like *H. bihai* in Venezuela (i.e., four *Belonuchus* species, Frank and Barrera 2010) and Brazil (i.e., one *Paederomimus*, de Oliveira et al. 2018), *H. stricta* in Peru (i.e., one *Philonthus* species Jalinski et al. 2014) and *H. bourgaeana* in Veracruz, Mexico (i.e., four *Platydracus* and one *Chroaptomus* species, Frank and Morón 2012) also supported rove beetle predator species.

Rove beetle species composition in *H. wagneriana* inflorescences

At a local scale, the species composition of rove beetle communities tend to be explained by environmental conditions (Irmeler and Gürlüch 2007; Caballero et al. 2009) and, at the landscape scale, by the degree of habitat loss and forest fragmentation (Golden and Crist 2000). Our study showed that forest type and the physical and chemical traits of the bracts influenced the beta diversity components in rove beetle communities. The ephemeral nature of heliconia inflorescences ensures high turnover of insect communities offering food and shelter for many rove beetle species (Jalinsky et al. 2014). Our results reveal the importance of two different components of beta diversity, although 12 common species

were shared between forest types, species replacement β_{repl} (39% of beta diversity) was mainly explained by the loss of old-growth forests species (Carvalho et al. 2012). Assuming that old-growth forests were our experimental control, we found that different rove beetle species were replaced by others in secondary forests. Predator species such as *Paederomimus* and those within the genus *Belonuchus* (i.e., *B. bidens*, *B. iridescens*, *Belonuchus* sp. 1 and *Belonuchus* sp. 2) were unique to old-growth forests; and were replaced by predator species unique to secondary forest such as *Lithocharis* sp. 1, *Scopaeus* sp., *Deroderus* sp., *Quedius* sp., and two Aleocharinae species.

Physical and chemical conditions of heliconia bracts could have contributed to rove beetle species turnover due to space availability and to the amount of prey that bracts can sustain. It has been reported that arthropod abundance and species richness are influenced by bract size and resource heterogeneity in *H. imbricata* (Naeem 1990). In our study, bract size (i.e., width bract and volume) and temperature contributed to explain only the richness difference component β_{rich} (i.e., 48% of total composition dissimilarity). The beta diversity component known as richness difference is referred to the number of different species that each inflorescence contained (Carvalho et al. 2012). The NMDS from the richness difference component revealed an indirect gradient, ordering individual inflorescences from those with higher number of rove beetle species and individuals, to those with lower number of species and individuals. Particularly some inflorescences in secondary forest with smaller bracts and greater liquid temperature, hosted up to 13 rove beetle species. In contrast, inflorescences that showed lower liquid temperature and larger bracts housed only one beetle species in both forest types. Our results highlighted the importance of intraspecific trait differences among *H. wagneriana* individuals in rove beetle species composition. Ten species including *Coproporus* sp. 5, *Naceus* sp., *Hypotelus* sp., and *Piestus* aff. *mexicanus* were unique in secondary forests. These species are generally found inhabiting the leaf-litter and are usually locally restricted, but in secondary forest they were also found in *H. wagneriana* inflorescences above the soil level (Anderson and Ashe 2000; Navarrete-Heredia et al. 2002).

Heliconia-rove beetle interaction networks

Our study contributes to untangling the structure of rove beetle communities that exploit ephemeral, rare and unpredictable resources in preserved and disturbed tropical rainforests. Overall, the individual-based heliconia-rove beetle networks were significantly nested. As it has been documented, some networks descriptors usually employed in ecological interactions are quite sensitive to data category (Miranda et al. 2019). In mutualistic plant-ant interactions, nested patterns

are more commonly found with binary networks (93%) than quantitative networks (21%), while binary and quantitative data are less commonly found (14%, as seen in Dáttilo et al. 2014). In our study, nestedness differed with incidence and abundance data between forest types. Moreover, nestedness was detected only with incidence data in old-growth forests. Although *Coproporus* sp. 4 and *Coproporus* sp. 1 were core species inhabiting 15 of 20 individual plants, all interactions in networks with binary data are ecological equivalent because the strength of the interaction is not represented (Almeida-Neto and Ulrich 2011).

In secondary forests, nestedness was detected in abundance and incidence data, where only one *H. wagneriana* individual showed up to 13 species with 30% of the total beetle abundance recorded. This could be related to intrinsic plant traits, resource availability and competition with other arthropod species. The blooming season of *H. wagneriana* is between January and April (Stiles 1975; Berry and Kress 1991), with greater resources offered to invertebrate species in the dry season. The inflorescence life span is up to five months. Some rove beetle species and other invertebrate species could take advantage of this time window with higher resource availability for visiting the inflorescences more frequently. It is likely that greater resource availability may contribute to beetle abundance within a bract. An abundant and rich community of ants, earwigs, bugs and other beetle families (e.g., Carabidae, Chrysomelidae, Curculionidae, and Hydrophilidae) has been reported in *H. latispatha*, *H. collinsiana*, *H. stricta* and *H. bihai* (Benítez-Malvido et al. 2014; Jalisnki et al. 2014; de Oliveira et al. 2018), which is an indicator that phytotelmata environments form more complex interaction networks than shown at present.

A nested pattern for individual-based heliconia-invertebrate (Benítez-Malvido et al. 2014, 2016) and cactus-Syrphidae ecological networks have been reported (Martínez-Falcón et al. 2010). Connectance values of the heliconia-rove beetle networks were also similar to those found for invertebrate networks in *H. collinsiana* and *H. latispatha* at the same study region ($C=0.3$ – 0.4 ; Benítez-Malvido et al. 2014) and for one cactus species in a semiarid region ($C=0.35$; Rosano-Hinojosa et al. 2019) but higher for palm-rove beetle networks (Niño-Pérez and Nuñez-Avellaneda 2018; $C=0.078$). Low connectance is generally an indicator of low specialization, which could be expected for rove beetle floral visitors. The rove beetle species associated with heliconia inflorescences are mostly generalists. The most abundant species (*Coproporus* spp.) were core species in the networks and suggesting that these species could be permanent residents in *H. wagneriana* inflorescences and developing part of their life cycle therein. Predators could be considered as peripheral species because they are more itinerant moving to other substrates or visiting *H. wagneriana* clumps with greater number of inflorescences. Until now, there have been

no reports of direct mutualistic interaction between rove beetles and heliconias (Seifert 1982; Frank and Barrera 2010; Frank and Morón 2012; Aristizábal et al. 2013; de Oliveira et al. 2018). Nevertheless, the high abundance and species richness of rove beetles in heliconia inflorescences could indicate indirect mutualistic interactions. While heliconias offer shelter and resources, some rove beetles may consume herbivores that cause floral damage.

Conclusions

Our study revealed the impact of forest disturbance on the rove beetle community associated to *H. wagneriana* inflorescences. Species diversity, compositional dissimilarity, proportion of feeding habitats and nestedness varied between forest types. The structural and environmental complexity that characterize preserved forests offer greater resource availability and microhabitats for rove beetle species, where many rare rove beetle species were undetected. By contrast, *H. wagneriana* inflorescences inhabiting secondary forests are suitable microhabitats for many rove beetle species not recorded in old-growth forests.

This is the first attempt to quantify the topology of ecological networks in *H. wagneriana* inflorescences and their associated rove beetles growing in different forest type. Despite the increasing knowledge regarding rove beetles in heliconia inflorescences, their functional roles and their direct or indirect mutualistic interactions are still poorly understood. It is unclear which rove beetle species are permanent residents or itinerant visitors in heliconia inflorescences, and we still ignore if they cause some indirect advantages to heliconias by hunting herbivores.

The ephemeral and scattered nature of heliconia inflorescences in human-modified landscapes may serve as biodiversity reservoirs hosting rich invertebrate communities. Bracts offer food, shelter and sites for mating, oviposition and development for a diverse invertebrate community; and the aggregated distribution of heliconias (i.e., clumps) form complex ecological micro-systems hosting different trophic guilds. Different heliconia species can commonly growth in disturbed forest, along roadside, on riverbanks and patches of secondary forest, became an important shelter for insect conservation in tropical human-modified landscapes. In addition, heliconias represent important landscape elements in the control of soil erosion (Alvarado and Zúñiga 2018), therefore we propose the use of heliconia species as landscape elements for maintaining distinct insect communities.

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Author contributions DMMR and JBM designed the study. DMMR and JMLG performed the rove beetle sampling. JM and JLNH helped in the taxonomic identification of beetles and their knowledge about natural history of species. APMF helped in data analysis. DMMR analyzed data and wrote the first draft of the manuscript. All authors contributed significantly in discussing the data and revising the manuscript.

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Data availability Data is provided within supplementary information file and are also available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

Ethical approval Not applicable.

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References

- Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. *Environ Model Softw* 26:173–178. <https://doi.org/10.1016/j.envsoft.2010.08.003>
- Almeida-Neto M, Guimarães P, Guimarães PR Jr et al (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239. <https://doi.org/10.1111/j.2008.0030-1299.16644.x>
- Alvarado V, Zúñiga MA (2018) Plantas nativas para el control de erosión. *Tecnológica De Costa Rica*. <https://doi.org/10.3232/SJSS.2014.V4.N1.07>
- Anderson RS, Ashe JS (2000) Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae). *Biodivers Conserv* 9:617–653. <https://doi.org/10.1023/A:1008937017058>
- Antiqueira PAP, Petchey OL, Romero GQ (2018) Warming and top predator loss drive ecosystem multifunctionality. *Ecol Lett* 21(1):72–82. <https://doi.org/10.1111/gcb.14314>
- Aristizábal LF, Ospina KA, Vallejo UA et al (2013) Entomofauna associated with *Heliconia* spp. (Zingiberales: Heliconiaceae) grown in the central area of Colombia. *Fla Entomol* 96:112–119. <https://doi.org/10.1653/024.096.0114>
- Arnan X, Bosch J, Comas L, Gracia M, Retana J (2011) Habitat determinants of abundance, structure and composition of flying Hymenoptera communities in mountain old-growth forests. *Insect Conserv Divers* 4(3):200–211
- Bascompte J, Jordano P, Melián CJ, Olesen JM (2003) The nested assembly of plant-animal mutualistic networks. *Proc Natl Acad Sci USA*. <https://doi.org/10.1073/pnas.1633576100>
- Benítez-Malvido J, Martínez-Falcón AP, Dáttilo W, Del Val E (2014) Diversity and network structure of invertebrate communities associated to *Heliconia* species in natural and human disturbed tropical rain forests. *Glob Ecol Conserv* 2:107–117. <https://doi.org/10.1016/j.gecco.2014.08.007>
- Benítez-Malvido J, Dáttilo W, Martínez-Falcón AP et al (2016) The multiple impacts of tropical forest fragmentation on arthropod biodiversity and on their patterns of interactions with host plants. *PLoS ONE* 11:1–15. <https://doi.org/10.1371/journal.pone.0146461>
- Berry F, Kress WJ (1991) *Heliconia*: an identification guide. Smithsonian Institution Press, Washington
- Bersosa F, Simbaña W, Moreno S (2014) Invertebrados asociados a brácteas de *Heliconia rostrata* y *Heliconia spathocircinata* (Heliconiaceae) en la estación biológica Jatun Sacha, Provincia de Napo: un análisis preliminar. *La Granja: Revista de Ciencias de la Vida* 2:20–28
- Burham KP, Anderson DR (2002) *Model Selection and Multimodel Inference*. Springer, New York, p 488
- Caballero U, León-Cortés JL, Morón-Ríos A (2009) Response of rove beetles (*Staphylinidae*) to various habitat types and change in Southern Mexico. *J Insect Conserv* 13:67–75. <https://doi.org/10.1007/s10841-007-9121-6>
- Cardoso P, Borges PAV, Veech JA (2009) Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. *Divers Distrib* 15:1081–1090. <https://doi.org/10.1111/j.1472-4642.2009.00607.x>
- Cardoso P, Rigal F, Carvalho JC (2015) BAT—Biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *MEE* 6:232–236. <https://doi.org/10.1111/2041-210X.12310>
- Carvalho JC, Cardoso P, Gomes P (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Glob Ecol Biogeogr* 21:760–771. <https://doi.org/10.1111/j.1466-8238.2011.00694.x>
- Carvalho JC, Cardoso P, Borges PAV et al (2013) Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. *Oikos* 122:825–834. <https://doi.org/10.1111/j.1600-0706.2012.20980.x>
- Chani-Posse M (2014) An illustrated key to the New World genera of Philonthina Kirby (*Coleoptera: Staphylinidae*), with morphological, taxonomical and distributional notes. *Zootaxa* 3755:62–86. <https://doi.org/10.11646/zootaxa.3755.1.3>
- Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93:2533–2547. <https://doi.org/10.1890/11-1952.1>
- Chao A, Ricotta C (2019) Quantifying evenness and linking it to diversity, beta diversity, and similarity. *Ecology* 100:e02852. <https://doi.org/10.1002/ecy.2852>
- Chao A, Kubota Y, Zelený D, Chiu CH, Li CF, Kusumoto B, Yasuhara M, Thorn S, Wei Ch, Costello MJ, Colwell RK (2020) Quantifying sample completeness and comparing diversities among assemblages. *Ecol Res* 35:292–314. <https://doi.org/10.1111/1440-1703.12102>

- Criley RA, Sakai WS (1997) *Heliconia wagneriana* Petersen is a short-day plant. HortScience 32(6):1044–1045. <https://doi.org/10.21273/HORTSCI.32.6.1044>
- Cumming G, Fidler F, Vaux DL (2007) Error bars in experimental biology. J Cell Biol 177:7–11. <https://doi.org/10.1083/jcb.200611141>
- Dáttilo W, Guimarães PR, Izzo TJ (2013) Spatial structure of ant-plant mutualistic networks. Oikos 122:1643–1648. <https://doi.org/10.1111/j.1600-0706.2013.00562.x>
- Dáttilo W, Sánchez-Galván I, Lange D et al (2014) Importance of interaction frequency in analysis of ant-plant networks in tropical environments. J Trop Ecol 30:165–168. <https://doi.org/10.1017/S0266467413000813>
- De Oliveira TRS, De MSR, Da CDD et al (2018) Interaction and Distribution of Beetles (Insecta: Coleoptera) Associated with *Heliconia bihai* (Heliconiaceae) Inflorescences. Fla Entomol 101:160–165. <https://doi.org/10.1653/024.101.0202>
- Dormann CF, Fründ J, Blüthgen N, Gruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. Open Ecol J 2:7–24. <https://doi.org/10.2174/1874213000902010007>
- Durand L (2019) Power, identity and biodiversity conservation in the Montes Azules biosphere reserve, Chiapas, Mexico. J Political Ecol 26:19–37. <https://doi.org/10.2458/v26i1.23160>
- Frank JH, Barrera R (2010) Natural history of *Belonuchus Nordmann* spp. and allies (Coleoptera: Staphylinidae) in *Heliconia* L. (Zingiberales: Heliconiaceae) flower bracts. Insecta Mundi 0110:1–12
- Frank JH, Morón MA (2012) Natural history of four species of *Platydracus* Thomson (Coleoptera: Staphylinidae) in *Heliconia bourgaeana* Petersen (Zingiberales: Heliconiaceae) flower bracts. Insecta Mundi 0258:1–12
- Gannon DG, Kormann UG, Hadley AS, Betts MG, Jones FA (2018) The “jack-in-the-box” stamens of *Heliconia wagneriana* (Heliconiaceae). Ecology 99(2):488–490
- Golden DM, Crist TO (2000) Experimental effects of habitat fragmentation on rove beetles and ants: patch area or edge? Oikos 90:525–538. <https://doi.org/10.1034/j.1600-0706.2000.900311.x>
- Gutiérrez-Chacon C, Zuñiga MDC, Van Bodegom P, Chara J, Giraldo LP (2009) Rove beetles (Coleoptera: Staphylinidae) in Neotropical riverine landscapes: characterizing their distribution. Insect Conserv Divers 2(2):106–115
- Hanson HI, Palmu E, Birkhofer K, Smith HG, Hedlund K (2016) Agricultural land use determines the trait composition of ground beetle communities. PLoS ONE 11:e0146329. <https://doi.org/10.1371/journal.pone.0146329>
- Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432. <https://doi.org/10.2307/1934352>
- Irmeler U, Gürlich S (2007) What do rove beetles (Coleoptera: Staphylinidae) indicate for site conditions? Faunistisch-Ökologische Mitteilungen 8:439–455
- Irmeler U, Klimaszewski J, Betz O (2018) Introduction to the biology of rove beetles. In: Betz O, Irmeler U, Klimaszewski J (eds) Biology of rove beetles (Staphylinidae). Springer, Cham, pp 1–4
- Jalinsky JR, Wertenberger RA, Radocy TA, Chaboo CS (2014) Insects Inhabiting Two Host Plants, *Heliconia stricta* Huber (Heliconiaceae) and *Calathea lutea* Schult (Marantaceae), in Southeastern Peru. J Kans Entomol 87:299–311. <https://doi.org/10.2317/JKES130816.1>
- Jost L (2006) Entropy and diversity. Opinion 2:363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kindt R, Kindt MR (2019) Package ‘BiodiversityR.’ Package Commun Ecol Suitabil Anal 2:1–181
- Kitching RL (2000) Food webs and container habitats: the natural history and ecology of phytotelmata, 1st edn. Cambridge University Press, Edimburg
- Klimaszewski J, Pace R, Center TD, Couture J (2010) A remarkable new species of *Himalusa* Pace from Thailand (Coleoptera, Staphylinidae, Aleocharinae): phytophagous aleocharine beetle with potential for bio-control of skunkvine-related weeds in the United States. ZooKeys 35:1–12. <https://doi.org/10.3897/zookeys.35.329>
- Kormann UG, Hadley AS, Tscharnkte T et al (2018) Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. J Appl Ecol 55:1288–1298. <https://doi.org/10.1111/1365-2664.13084>
- Legendre P, Legendre L (2012) Numerical ecology. Elsevier, Amsterdam
- López-García M, Méndez-Rojas D, García-Cárdenas R (2011) Staphylinidae y Nitidulidae (Coleoptera) asociados a inflorescencias de *Etilingera elatior* (Zingiberaceae). Rev Colomb Entomol 37:357–359. http://www.scielo.org.co/scielo.php?script=sci_arttext&pid=S0120-04882011000200033&lng=en&nrm=iso. ISSN 0120–0488.
- López-García M, Marín-Gómez OH (2018) Description and notes on natural history of a new species of *Parosus* Sharp 1887 (Coleoptera, Staphylinidae, Oxytelinae) living in floral bracts of *Columnea medicinalis* L. (Gesneriaceae). Zootaxa 4394:559–566. <https://doi.org/10.11646/zootaxa.4394.4.6>
- Márquez J, Asiain J (2022) Taxonomy of the Mexican species of *Belonuchus Nordmann* (Coleoptera: Staphylinidae). Zootaxa 5152:1–129. <https://doi.org/10.11646/zootaxa.5152.1.1>
- Marquitti FMD, Guimarães PR, Pires MM, Bittencourt LF (2014) MODULAR: software for the autonomous computation of modularity in large network sets. Ecography 37:221–224. <https://doi.org/10.1111/j.1600-0587.2013.00506.x>
- Martínez-Falcón AP, Ángeles Marcos-García M, Díaz-Castelazo C, Rico-Gray V (2010) Seasonal changes in a cactus-hoverfly (Diptera: Syrphidae) network. Ecol Entomol 35:754–759. <https://doi.org/10.1111/j.1365-2311.2010.01236.x>
- McCall AC, Irwin RE (2006) Florivory: the intersection of pollination and herbivory. Ecol Lett 9:1351–1365. <https://doi.org/10.1111/j.1461-0248.2006.00975.x>
- Meave del Castillo J (1990) Estructura y composición de la selva alta perennifolia de los alrededores de Bonampak. Colección Científica Serie Arqueológica Instituto Nacional de Antropología e Historia. México, DF
- Medellín R (1994) Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conserv Biol 8:780–799. <https://doi.org/10.1046/j.1523-1739.1994.08030780.x>
- Melo FPL, Arroyo-Rodríguez V, Fahrig L et al (2013) On the hope for biodiversity-friendly tropical landscapes. Trends Ecol Evol 28:462–468. <https://doi.org/10.1016/j.tree.2013.01.001>
- Mendoza E, Dirzo R (1999) Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. Biodivers Conserv 8:1621–1641. <https://doi.org/10.1023/A:1008916304504>
- Miranda PN, da Silva Ribeiro JE, Luna P, Brasil I, Delabie JH, Dáttilo W (2019) The dilemma of binary or weighted data in interaction networks. Ecol Complex 38:1–10. <https://doi.org/10.1016/j.ecocom.2018.12.006>
- Naeem S (1990) Resource heterogeneity and community structure: a case study in *Heliconia imbricata* phytotelmata. Oecologia 84:29–38. <https://doi.org/10.1007/BF00665591>
- Nagy DD, Magura T, Debnár Z, Horváth R, Tóthmérész B (2015) Shift of rove beetle assemblages in reforestation: does nativity matter? J Insect Conserv 19:1075–1087. <https://doi.org/10.1007/s10841-015-9823-0>
- Navarrete Heredia JL, Newton AF, Thayer MK et al (2002) Guía ilustrada para los géneros de Staphylinidae (Coleoptera) de México. Universidad de Guadalajara, CONABIO
- Niño-Pérez AE, Nuñez-Avellaneda LA (2018) Diversidad y especificidad de estafilínidos (Coleoptera, Staphylinidae) asociados con

- inflorescencias de palmas silvestres en el Pacífico colombiano. *Rev Biodivers Neotrop* 8:94–107
- Oksanen J, Blanchet FG, Kindt R et al (2015) Package ‘vegan.’ *Commun Ecol Package Vers* 2:1–295
- Podani J, Schmera D (2011) A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. *Oikos* 120:1625–1638. <https://doi.org/10.1111/j.1600-0706.2011.19451.x>
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Reyes-Hernández JL, Navarrete-Heredia JL (2021) Composition and seasonality of *Staphylinidae* (Coleoptera) collected with carrion traps in a cloud forest in Jalisco. *Mexico Proc Entomol* 123(3):596–614. <https://doi.org/10.4289/0013-8797.123.3.595>
- Rodríguez-Peña ON, Oropeza Sánchez MT, González-Di Pierro AM (2023) Variable effects of tourist presence on the activity budget of *Alouatta pigra*. *Trop Conserv Sci* 16:1–7. <https://doi.org/10.1177/19400829231188622>
- Rosano-Hinojosa AM, Martínez-Falcón AP, Martínez-Hernández S, Ramírez-Hernández A (2019) Temporal shifts and cactus-beetle networks in an intertropical semiarid zone in Mexico. *Environ Entomol* 48:88–96. <https://doi.org/10.1093/ee/nvy175>
- Rusch A, Birkhofer K, Bommarco R, Smith HG, Ekbom B (2015) Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *BAAE* 16:250–259. <https://doi.org/10.1016/j.baae.2015.02.003>
- Santos BA, Benítez-Malvido J (2012) Insect herbivory and leaf disease in natural and human disturbed habitats: lessons from early-successional *Heliconia* herbs. *Biotropica* 44:53–62. <https://doi.org/10.1111/j.1744-7429.2011.00765.x>
- Santos BA, Lomera R, Benítez-Malvido J (2009) New records of *Heliconia* (Heliconiaceae) for the region of Chajul, Southern Mexico, and their potential use in biodiversity-friendly cropping systems. *Rev Mex Biodivers* 80:857–860. http://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S1870-34532009000300027&lng=es&nrm=iso. ISSN 2007–8706
- Sayers TDJ, Steinbauer MJ, Miller RE (2019) Visitor or vector? The extent of rove beetle (*Coleoptera: Staphylinidae*) pollination and floral interactions. *Arthropod Plant Interact* 13:685–701. <https://doi.org/10.1007/s11829-019-09698-9>
- Seifert RP, Seifert FH (1976) Natural History of insects living in inflorescences of two species of *Heliconia*. *JNY Entomol Soc* 84:233–242. <https://www.jstor.org/stable/25009025>
- Seifert RP (1982) Neotropical *Heliconia* insect communities. *Q Rev Biol* 57:1–28. <https://www.jstor.org/stable/2825133>
- Sharp D (1884) Fam. Staphylinidae. In: Godman and Salvin (eds) *Biologia Centrali-Americana. Insecta, Coleoptera*, Vol. 1. Taylor and Francis, London
- Smetana A (1995) Rove beetles of the subtribe Philonthina of America North of Mexico (Coleoptera: Staphylinidae) classification, phylogeny and taxonomic revision. Associated Publishers
- Stiles GF (1975) Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285–301. <https://doi.org/10.2307/1934961>
- Thayer MK (2016) Staphylinidae Latreille 1802. In: Beutel RG, Leschen RAB (eds) *Handbook of Zoology: Arthropoda: Insecta, Coleoptera, Beetles Morphology and Systematics* (Archostemata, Adephaga, Myxophaga, Polyphaga Partim). De Gruyter, Berlin, pp 394–442
- Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* 445:202–205. <https://doi.org/10.1038/nature05429>

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