

Feeding Specialization of Flies (Diptera: Richardiidae) in Aroid Infructescences (Araceae) of the Neotropics

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Abstract

Evolution and radiation between insects and flowering plants are both opportunistic and obligatory when the former feeds on the reproductive structures of the latter, whereas direct and indirect effects can influence the fitness of individuals, populations, and plant communities. The Araceae family constitutes an important element of the tropical rainforest of the Neotropics, and its morphology and floral biology provide a remarkable system for studying trophic interactions with insects, including the Richardiidae flies (Diptera). We studied the trophic interactions of the aroid-fly system, assessing infestation rates under natural conditions over an annual cycle. In the Neotropical region, we discovered for the first time that seven aroid species became infested by four richardiid species: *Beebeomyia tuxtlaensis* Hernández-Ortiz and Aguirre with *Dieffenbachia oerstedii* Schott and *D. wendlandii* Schott; *B. palposa* (Cresson) with *Xanthosoma robustum* Schott; *Beebeomyia* sp.3. in association with *Philodendron radiatum* Schott, *P. tripartitum* (Jacq.) Schott, and *P. sagittifolium* Liebm.; while *Sepsisoma* sp. only infested *Rhodospatha wendlandii* Schott. Infestation rates differed significantly among hosts, but comparisons with morphological traits did not provide evidence of a causal factor of the infestation. In contrast, larval density and time of development both exhibited significant differences between hosts. The findings suggest the high specialization of the flies, and that intrinsic factors of the plants, such as the presence of secondary metabolites and their maturation periods, may influence their infestation rates.

Key words: herbivory, antagonistic interaction, natural history, host plant

Half of all insect species feed on vascular plants, but these phytophagous organisms are basically restricted to 9 of the 30 extant orders (Kristensen 1981, Strong et al. 1984). It is estimated that over 70% of insects are highly host-specific either feeding on plants or as parasites (Jaenike 1990). Plant–herbivore interactions affect the ability of both interactants to survive because plants exert a selective pressure on the features of herbivores and herbivores exert a selection on the plant defense traits, while different host plants can promote insect speciation (Futuyma and Moreno 1988, Matsubayashi et al. 2010). Insects also spend a significant part of their life cycle (sometimes from birth to reproduction) within the host plant, which even provides shelter for diapause and against potential predators, along with a site to find partners for sexual reproduction and carry out oviposition (Kergoat et al. 2017).

Specialization occurs in the more advanced Neopteran insect orders, such as the Paraneoptera and Endopterygota (Bush and Butlin 2004, Schoonhoven et al. 2005). The importance of specialization in insect diversification is suggested because phytophagous insects are more diverse than their relatively generalized nonherbivorous sister

clades (Mitter et al. 1988, Futuyma and Agrawal 2009, Wiens et al. 2015). The host range of most herbivorous insects is restricted to a few plant genera or families because the attributes that restrict their exploitation by insects are usually similar among related plants (Mitter et al. 1988, Futuyma 1991, Futuyma and Mitter 1999). A preference for specific parts of plants is also a common feature, and insect species that feed inside plants are usually more specialized (Spencer 1990, Bernays and Chapman 1994, Novotny and Basset 2005, Kergoat et al. 2017). Florivory is associated with damage to structures related to potential reproductive output, whereas seed predation (both pre- and post-dispersal) is associated with the consumption of already-fertilized ovules at later life-history stages (McCall and Irwin 2006).

The family Araceae has a high diversity in the tropics, represented by 2,113 species in the Neotropical region (Boyce and Croat 2011). Nearly 109 species occur in Mexico, and 55 have been recorded in the state of Veracruz (Croat and Acebey 2015). Aroids possess a typical inflorescence consisting of a spadix and spathe, where female and male flowers are displayed, and all other morphologies

observed in these plants can be viewed as variations thereof (Bown 2000). Inflorescences in this group of plants are almost entirely entomophilous and, as such, they display strategies such as thermogenesis and the presentation of a number of other rewards to attract a great diversity of insects (Mayo et al. 1997, Gibernau 2003). Insect–aroid interactions have been recorded in nearly 200 species from 67 genera and mainly focus on pollination systems (Gibernau et al. 1999, 2000; Gibernau 2003, 2011, 2016; Gibernau and Barabé 2002). Neotropical studies related to the consumption of aroid flowers, fruits and seeds, most involving species of Coleoptera, Hymenoptera, and Diptera, are scarce. For instance, *Erioscelis emarginata* (Coleoptera) feeds on flowers of two *Philodendron* species (Maldonado et al. 2015), and the hymenopteran, *Exurus* aff. *gallicola* (Eulophidae) is associated with the formation of fruit galls and predation of seeds of *P. solimoense* (Gibernau et al. 2002).

In addition, flies of the family Richardiidae (Diptera) exploit aroid plant tissues for oviposition sites and larval development. The family is restricted to the Neotropics and represented by 178 known species (Hancock 2010, Pape et al. 2011). However, its biology is poorly understood because some species exhibit saprophagous habits, such as *Automola rufa* on decaying *Opuntia* sp., or *Epiplatea hondurana* reared from a diseased coconut palm (Steyskal 1958). Other studies show *Melanoloma viatrix* feeding on pineapple fruits (Henao and Ospina 2008); *Beebeomyia* spp. preying flowers of *Heliconia* (Seifert and Seifert 1976) and *Gearum brasiliense* (Bogner and Gonçalves 1999); *Beebeomyia taccarivora* (formerly misidentified as *Melanoloma* sp.) feeding in flowers and fruits of *Taccarum ulei* (Maia et al. 2013, Wendt et al. 2018); and *Beebeomyia tuxtlaensis* reared from inflorescences of *Dieffenbachia oerstedii* (Hernández-Ortiz and Aguirre 2015).

Despite the importance of internal feeders in understanding the causes that lead to specialization, and in contrast to studies dealing with external herbivores, such as leaf-chewers (Marquis 1991, Novotny et al. 2005), data are scarce pertaining to larvae feeding inside plants. Because aroids are an important component of hemiepiphytic vegetation and the tropical rainforest understory, the aim of this study was to characterize the trophic interactions of flies of the family Richardiidae as endophages of aroid infructescences in the Los Tuxtlas Biosphere Reserve (LTBR), Mexico. The specific objectives were to 1) identify interspecific aroid-Richardiid fly interactions in the LTBR and assess the infestation rates produced in each host plant; 2) determine whether the physical traits of the infructescences, such as, weight, width, and length, are related to the specific infestations; and 3) examine whether significant differences in larval density occur among different host plants.

Materials and Methods

Study Site

The LTBR is located in southeastern Veracruz, Mexico (18°05′–18°43′N; 94°35′–95°25′W). The region is considered the northern distributional limit of the evergreen tropical rainforest in the Americas (Dirzo and Miranda 1991). The climate of the region is tropical humid in the lowlands, and temperate very humid in the highlands. Average temperatures range between 18 and 22°C, with a maximum of 36°C (Soto 2004). Annual rainfall is 4,700 mm/yr, with a relatively dry season from March to May (Gutiérrez-García and Ricker 2011). The dominant vegetation is a lowland tropical rainforest, largely comprising Neotropical vascular plants, although Nearctic elements also occur at higher elevations (Ibarra-Manríquez et al. 1997). Floristic studies by Ibarra-Manríquez et al. (1997) and

Castillo-Campos and Laborde (2004) describe the natural vegetation of the LTBR as characterized by trees of over 30 m in canopy height, such as *Ficus* spp., *Ceiba pentandra*, *Poulsenia armata*, *Nectandra ambigens*, *Brosimum alicastrum*, among others, whereas the understory comprises palms, especially *Astrocaryum mexicanum* and *Chamaedorea* spp. The aroids are an important component of both the understory and epiphytic vegetation, comprising 34 species of nine genera, distributed from sea level up to 1,600 m asl at the summit of the San Martín volcano. The most represented genera are *Philodendron*, *Anthurium*, *Monstera*, and *Syngonium* (Acebey and Krömer 2008).

Collecting and Rearing of Biological Samples

Sampling was conducted along three transects of approximately 1,000 m in length at different elevations as follows: Station of Tropical Biology Los Tuxtlas (STBLT) 150 m (18°35′05″N, 95°04′27″W); Ejido La Perla de San Martín 600 m (18°34′15″N, 95°07′02″W); and Ejido Calería 1,100 m (18°32′36″N, 95°08′43″W). Mature infructescence of 17 aroid species were collected as available during five sampling events, from August 2015 to March 2017. Samples were labeled and stored individually in fine-mesh bags to allow ventilation but prevent the movement of larvae among hosts during transportation. In the laboratory, each sample was separated in plastic rearing chambers to continue the ripening process under laboratory conditions (24°C ± 4; RH = 70% ± 10) and diurnal cycles of approximately 12 h (Hernández-Ortiz and Aguirre 2015). The morphological measurements width and length of the infructescence were taken with a digital caliper (CD-s6, Mitutoyo Corp., Kawasaki, Japan) and the weight was obtained using a precision balance (Scout Pro, Ohaus SP402 AM, 400 g capacity, 0.01 g readability). Mature infructescences were dissected for inspection, and all richardiid specimens (larvae and pupae) were placed in a rearing chamber until emergence of adults, recording the abundance and date of emergence for each species. Adults were preserved in 75% ethanol, and some specimens were dry mounted for identification. Voucher specimens were deposited in the IEXA entomological collection (Instituto de Ecología AC, Xalapa, Mexico).

Statistical Analysis

Analyses of infestation rates and time of development among hosts were performed through generalized linear models (GLM) with negative-binomial and quasi-Poisson distributions, using the MASS package (Venables and Ripley 2002), followed by Tukey post hoc pairwise comparisons and Westfall-corrected P values with the Multcomp package (Bretz et al. 2002). The effects of morphological variables on larval numbers per infructescence were assessed by a generalized linear mixed model with binomial-negative distribution, using the package lme4 in R (Bates et al. 2015). Host species, length, width, and weight were the explanatory factors, whereas the collection event was the random variable.

Prior to the statistical analyses, all data were subjected to the Shapiro-Wilk test of normality, and the Fligner–Killeen test of homogeneity of variances. Comparisons of the morphological traits of the infructescence (weight, width, length), the time of larval–pupal development, and the density index among hosts were analyzed through an ANOVA with the White adjustment, which allowed for unequal variances, using the Car Package version 3.0-2 (Fox and Weisberg 2011), followed by Westfall-corrected Tukey’s post hoc tests. The time of larval–pupal development per host was calculated as the average number of days from sample collection to adult emergence.

The larval density per unit of biomass (DI) was calculated for each host using the following formula:

$$DI = \frac{100 \sum_{i=1}^n \frac{\text{individuals}_i}{\text{weight}_i}}{n}$$

where DI = density index; individuals = number of specimens (larvae, pupae, adults) per infructescence; weight = weight of the infructescence i ; n = number of infructescences sampled.

All statistical analyses were performed in R version 3.5.0 (R Core Team 2018).

Results

Trophic Interactions

In total, 454 infructescences from 17 aroid species belonging to the genera *Anthurium* (1), *Dieffenbachia* (2), *Monstera* (4), *Philodendron* (5), *Rhodospatha* (1), *Syngonium* (3), and *Xanthosoma* (1) were examined. Seven of these plant species (represented by 231 infructescences) were found to be infested by four richardiid fly species, as follows:

Beebeomyia tuxtlaensis feeding on *D. wendlandii* (Ejido Adolfo López Mateos, 26-III-2014) and *D. oerstedii* (La Perla, 24-VIII-2015, 09-VIII-2016, 14-VI-2016, 28-II-2017; STBLT, 03-V-2016, 10-VIII-2016, 02-III-2017). *Beebeomyia palposa* in *X. robustum* (Calería, 15-XI-2016; STBLT, 8-X-2015, 10-VIII-2016, 16-XI-2016, 02-III-2017). *Beebeomyia* sp.3 infesting three distinct hosts: *P. radiatum* (STBLT, 16-XI-2016, 02-III-2017); *P. sagittifolium* (La Perla, 02-V-16, 28-II-2017, 01-III-2017; STBLT, 03-V-2016, 02-III-2017); and *P. tripartitum* (La Perla, 09-VIII-2016; STBLT 10-VIII-2016, 16-XI-2016). *Sepsisoma* sp. infesting infructescences of *R. wendlandii* (STBLT 16-IX-2016, 02-III-2017; La Perla 14-XI-2016). With the exception of a previous report of *B. tuxtlaensis* infesting *D. oerstedii* (Hernández-Ortiz and Aguirre 2015), all other findings are the first host plant records for these flies in the Neotropical region. *Beebeomyia palposa* represents the first record for Mexico, whereas *Beebeomyia* sp.3 and *Sepsisoma* sp. are new species that will be described further.

Of the seven species that became fly infested, only six were included in our analysis because individualized data of the infructescence infestations were not available for *D. wendlandii*.

Nearly half of all infructescences examined (57.3%, $n = 129$) were infested by a total of 2,634 fly larvae. In addition, nearly 30 morphospecies from other insect groups were found associated with the infructescences; these are being identified and under review. The highest percentages of richardiid-infested infructescences were found in *D. oerstedii* (88.3%, $n = 77$) and *X. robustum* (70%, $n = 20$), whereas moderate infestations were found in *P. radiatum* (61.1%, $n = 18$), *P. sagittifolium* (50%, $n = 38$) and *R. wendlandii* (42.1%, $n = 19$), and the lowest proportion of occupied infructescences occurred in *P. tripartitum* (16.9%, $n = 53$). Hosts showed significant differences in the mean values of larval infestation (GLM $\chi^2 = 70.392$, $df = 5$, $P < 0.0001$). Highest averages occurred in *R. wendlandii* (28.6 ± 11.1 , larvae/infructescence; mean \pm SE), *X. robustum* (18.7 ± 6.8), and *D. oerstedii* (15.6 ± 2.1), whereas significant variations were observed among the three *Philodendron* species (all infested by *Beebeomyia* sp.3); *P. radiatum* showed the highest average (15.1 ± 3.7), whereas *P. sagittifolium* (5.0 ± 1.2) and *P. tripartitum* (1.0 ± 0.4) exhibited the lowest infestation rates (Table 1, Fig. 1).

Morphological Traits of Hosts

Comparisons between the morphological features of the infructescence among hosts yielded prominent differences in the weight ($F = 196.56$, $df = 5, 219$; $P < 0.0001$; Fig. 2A), width ($F = 142.33$; $df = 5, 221$; $P < 0.0001$; Fig. 2B), and length ($F = 34.277$; $df = 5, 221$; $P < 0.0001$; Fig. 2C). *Xanthosoma robustum* and *P. radiatum* presented the widest (54.3 ± 2.4 ; 51.5 ± 1.3 mm) and heaviest (152.2 ± 18.5 ; 211.7 ± 6.9 g) infructescences, respectively, contrasting with the lowest values observed in *D. oerstedii* and *R. wendlandii* for width (23.2 ± 0.3 mm; 23.3 ± 1.0 mm) and weight (21.1 ± 0.6 ; 42.5 ± 4.7 g). In the same way, the infructescences displayed a length gradation, the longest corresponded to *D. oerstedii* (223.0 ± 4.0) and *P. radiatum* (221.9 ± 6.34), whereas the shortest were found in *X. robustum* (135.2 ± 5.9 ; Fig. 2). The regression analysis used to compare the three morphological variables of infructescences with larval abundance revealed a significant effect only of the weight of

Table 1. Aroid infructescences sampled at Los Tuxtlas Biosphere Reserve, Mexico, and their infestation rates produced by flies of the family Richardiidae (Diptera)

Aroid species	Host code	Infructescences sampled	Infructescences Infested (%)	Fly species encountered	Number of Larvae per infructescence (mean \pm SE)
<i>Anthurium schlechtendalii</i>	ANSC	9	—	—	—
<i>Dieffenbachia oerstedii</i>	DIOE	77	88.3	<i>Beebeomyia tuxtlaensis</i>	15.64 ± 2.10
<i>Dieffenbachia wendlandii</i>	DIWE	6	—	—	4.5^a
<i>Monstera acuminata</i>	MOAC	5	—	—	—
<i>Monstera deliciosa</i>	MODE	1	—	—	—
<i>Monstera egregia</i>	MOEG	78	—	—	—
<i>Monstera tuberculata</i>	MOTU	1	—	—	—
<i>Philodendron inaequilaterum</i>	PHIN	9	—	—	—
<i>Philodendron radiatum</i>	PHRA	18	61.1	<i>Beebeomyia</i> sp.3	15.11 ± 3.69
<i>Philodendron sagittifolium</i>	PHSA	38	50	<i>Beebeomyia</i> sp.3	5.0 ± 1.24
<i>Philodendron seguine</i>	PHSE	11	—	—	—
<i>Philodendron tripartitum</i>	PHTR	53	17	<i>Beebeomyia</i> sp.3	1.0 ± 0.38
<i>Rhodospatha wendlandii</i>	RHWE	19	42.1	<i>Sepsisoma</i> sp.	28.58 ± 11.09
<i>Syngonium angustatum</i>	SYAN	5	—	—	—
<i>Syngonium chiapense</i>	SYCH	25	—	—	—
<i>Syngonium podophyllum</i>	SYPO	79	—	—	—
<i>Xanthosoma robustum</i>	XARO	20	70	<i>Beebeomyia palposa</i>	18.65 ± 6.82

^aIndividualized data not available.

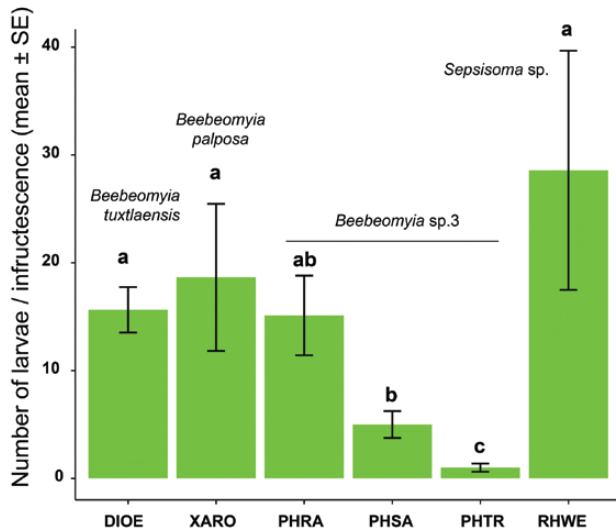


Fig. 1. Infestation of the infructescences of six aroid species by flies of the family Richardiidae (mean \pm SE) in Los Tuxtlas Biosphere Reserve, Mexico. Letters above bars indicate significant differences (Westfall-corrected Tukey post hoc analysis, $P < 0.05$). For species codes, see Table 1.

D. oerstedii ($\chi^2 = 4.80$, $df = 1$, $P < 0.0001$); a positive effect of infructescence length in *X. robustum* and *P. radiatum*, but a negative effect in *R. wendlandii* ($\chi^2 = 34.10$, $df = 5$, $P < 0.0001$); and also a negative effect of infructescence width in *P. radiatum* ($\chi^2 = 11.66$, $df = 5$, $P = 0.0397$; see Table 2). Nevertheless, the length of the infructescence of *Xanthosoma* is not comparable amongst hosts because the male section is lost following anthesis.

Infestation Density and Time of Development

Larval density per sample was estimated as the number of larvae per unit of host biomass, standardized to constant weight (density index). The results revealed significant differences in the concentration of larvae per unit of weight among hosts ($F = 15.099$; $df = 5, 215$; $P < 0.0001$). Two blocks of infructescences were found, the first characterized by high density indices recorded for *D. oerstedii* (72.2 ± 9.1 , density index \pm SE) and *R. wendlandii* (70.1 ± 25.9), the values of which were at least six times higher than in the hosts of the second block, represented by *X. robustum* (11.7 ± 5.1), *P. sagittifolium* (7.8 ± 3.2), *P. radiatum* (7.2 ± 1.8), and *P. tripartitum* (1.9 ± 0.7 ; Fig. 3).

Furthermore, assessment of the larval-pupal development inside the infructescence revealed differences among hosts ($F = 17.988$; $df = 5, 47$; $P < 0.0001$), in which *Beebeomyia sp.3* presented the longest development times in *P. radiatum* (60.9 ± 4 , days \pm SE) and *P. tripartitum* (60.2 ± 5.1), compared with its development in *P. sagittifolium* (43.1 ± 1.9), which was similar to *Sepsisoma sp.* in *R. wendlandii* (39.2 ± 2.6). Conversely, the development times recorded for *B. tuxtlaensis* and *B. palposa* were significantly shorter when infesting *D. oerstedii* (30.2 ± 2.2) and *X. robustum* (24.6 ± 1.7 ; Fig. 4).

Discussion

The relationship between female preference for oviposition sites and the performance of the offspring is a critical point in the theme of the evolutionary ecology of host association in plant-insect interactions (Thompson 1988). The offspring survive better on the plant types preferred by females, which lay more eggs on plant types that favor offspring performance (Gripenberg et al. 2010).

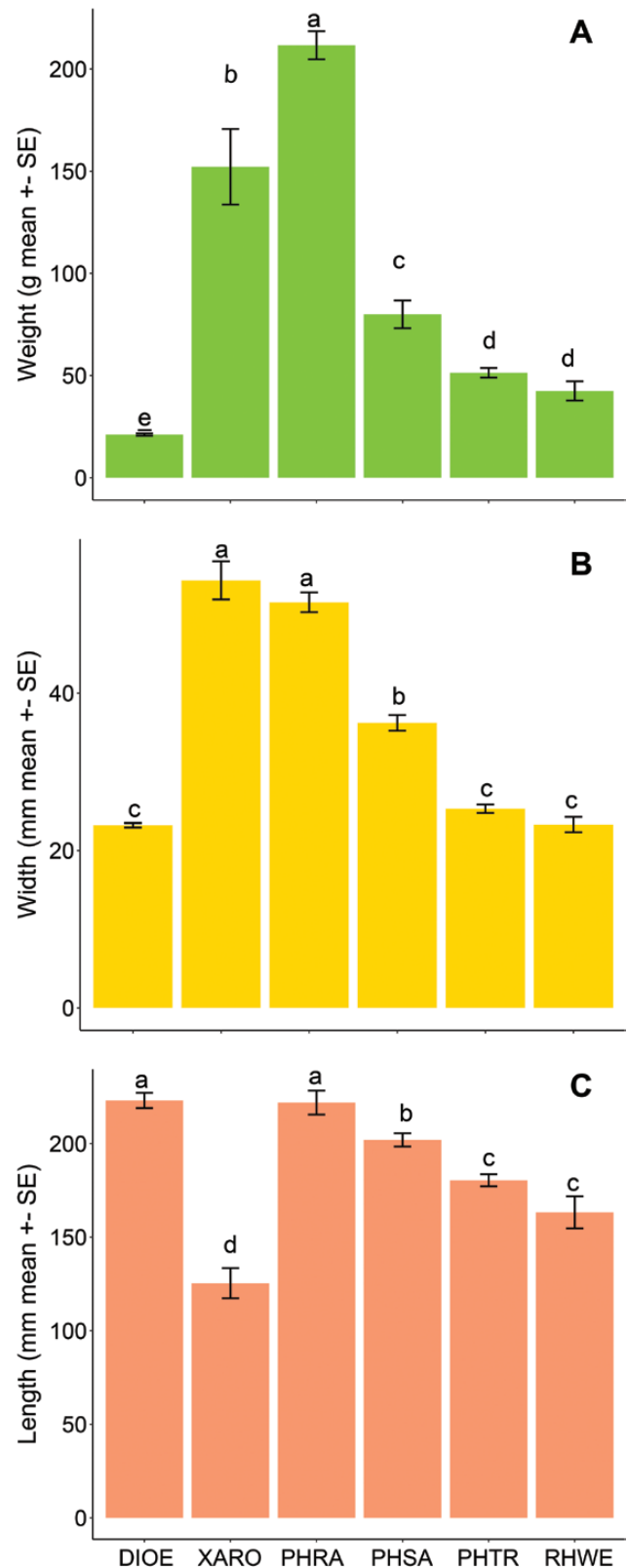


Fig. 2. Differences in weight (A), width (B), and length (C) of the infructescences in six aroid species in Los Tuxtlas Biosphere Reserve, Mexico. Different lowercase letters indicate significant differences (Westfall-corrected Tukey post hoc analysis, $P < 0.05$). For species codes, see Table 1.

Previous studies stated that Richardiid larvae are saprophagous (Steyskal 1958, Hancock 2010), whereas some others reported phytophagous habits in larvae infesting plant tissues of Bromeliaceae,

Table 2. Regression analysis results comparing the effects of morphological characteristics of infructescence weight, width, and length on the number of individuals per infructescence

Aroid species	Weight (g)		Width (mm)		Length (mm)	
	z^a	P^a	z^a	P^a	z^a	P^a
<i>Dieffenbachia oerstedii</i>	3.711	0.0002***	-0.677	0.4985	0.151	0.8799
<i>Xanthosoma robustum</i>	-1.375	0.1693	-1.482	0.1383	3.444	0.0006***
<i>Philodendron radiatum</i>	0.182	0.8553	-2.604	0.0092**	5.087	<0.0001***
<i>Philodendron sagittifolium</i>	-0.684	0.4937	0.05	0.9602	1.908	0.0564
<i>Philodendron tripartitum</i>	-0.182	0.8557	-0.849	0.3958	1.272	0.2034
<i>Rhodospatha wendlandii</i>	-0.363	0.7165	-0.049	0.96123	-2.007	0.0448*

^a P and z values calculated using a generalized linear mixed model.
Statistical significance: * $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$.

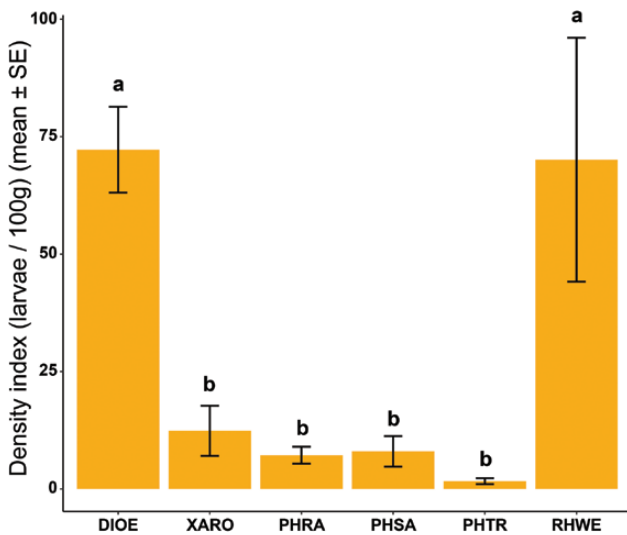


Fig. 3. Density index (mean ± SE) showing differences among six aroid species. Different letters above bars indicate significant differences (Westfall-corrected Tukey post hoc analysis, $P < 0.05$). For species codes, see Table 1.

Heliconiaceae, and Araceae (Seifert and Seifert 1976, Bogner and Gonçalves 1999, Kitching 2000, Henao and Ospina 2008, Maia et al. 2013, Hernández-Ortiz and Aguirre 2015, Wendt et al. 2018). Our results confirmed that four fly species of Richardiidae are exclusively phytophagous because their larvae consume the fresh floral tissues and developing fruits of different species of *Philodendron* and *Rhodospatha*, even consuming the spadix of *Dieffenbachia* and *Xanthosoma*. These flies proved to be highly specialized in terms of their use of hosts because they presented monophagous habits in *B. palposa* and *Sepsisoma* sp., each feeding on a single host, whereas two stenophagous species were raised from closely related plants, *B. tuxtlaensis* from two *Dieffenbachia* species, and *Beebeomyia* sp.3 infesting three *Philodendron* hosts.

In a broad sense, our results demonstrate that there was no correlation between increased infestation and increased resource size because some examples even showed negative effects such as those of the width of *P. radiatum* and the length of *R. wendlandii*. Thus, no conclusive evidence was found that such morphological traits of the infructescence have a significant influence on infestation levels. This suggests that other intrinsic features of the flies or certain plant attributes, such as chemical traits, could be limiting factors in the use of such resources, affecting their infestation levels and leading to greater specialization.

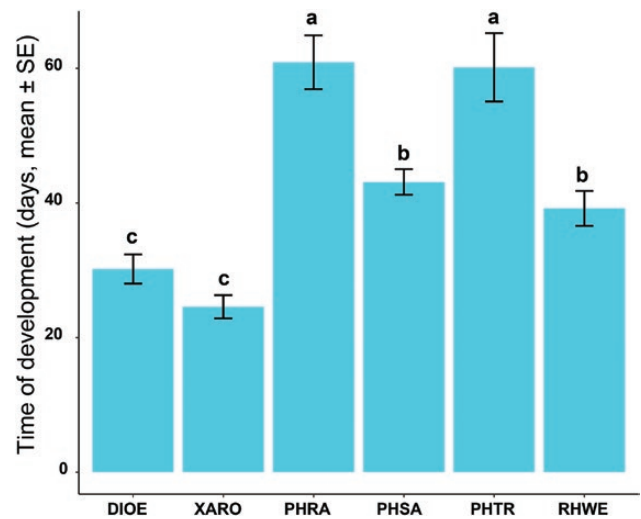


Fig. 4. Time of larval-pupal development recorded for six aroid species in Los Tuxtlas Biosphere Reserve, Mexico. Different letters above bars indicate significant differences (Westfall-corrected Tukey post hoc analysis, $P < 0.05$). For species codes, see Table 1.

In this regard, aroid inflorescences are known to contain substances dissuasive to herbivory, such as calcium oxalate, proteolytic enzymes, and toxins, that act to protect the ovules, embryos, and pollen (Mayo et al. 1997, Barabé et al. 2004, Coté 2009, Coté and Gibernau 2012, Maldonado et al. 2015). Such defensive strategies could limit the consumption of certain reproductive structures by richardiids because drosophilid larvae prefer staminodes or decaying flowers of *Dieffenbachia* (Valerio 1984, Cuartas-Hernández 2006). Similar feeding behavior was observed for *Erioscelis emarginata* on *Philodendron*, which presents a preference for consuming sterile male flowers, as these contain less calcium oxalates than fertile flowers (Maldonado et al. 2015).

However, high larval infestations by richardiid flies have also been reported, harming both fertile flowers and developing fruits (Maia et al. 2013, Hernández-Ortiz and Aguirre 2015) and the variability in use of these resources could therefore also be related to the maturation process of reproductive structures of different hosts, when proteolytic enzymes and toxins decline, or also to the senescence of the male section or the presence of a spathe that provides protection to the fruits following anthesis (Madison 1979, Mayo et al. 1997).

The density-index results revealed the presence of two host groups; the first characterized by larval densities that were seven to

nine times higher in *D. oerstedii* and *R. wendlandii*, compared with the second group integrated by *X. robustum* and three *Philodendron* species, all with significantly lower larval densities.

In accordance with these results, the first group of hosts showed the lowest values of mean infructescence weight and, following our laboratory observations, their maturation and decay occurred within a shorter period (2–3 wk) compared with the second group, which presented longer ripening times (4–6 wk). It is therefore likely that the rapid degradation of secondary metabolites allows faster larval development with high rates of occupancy of the resource. For instance, the larval development of *Colocasiomyia alocasiae* and *C. xenalocasiae* (Drosophilidae: Diptera) is conditioned by the reproductive biology of their host plant, *Alocasia odora* (Araceae). The former species has shorter larval cycles because it feeds only on the male section that decays earlier than female section, whereas the latter species feeds exclusively on female section and presents longer larval cycles (Yafuso 1994).

It should be noted that hosts with higher larval density indices also exhibited very dissimilar variances because *D. oerstedii* infested 88.3% of the total sample (72.3 ± 9.1 larvae/100g), whereas *R. wendlandii* showed a high variance (70.1 ± 25.9 larvae/100g), being concentrated in only 42.1% of the sampled infructescences. This fact may be supported by the lifestyle of each host: while *Dieffenbachia* is a patch-growing terrestrial plant in the forest understory, *Rhodospatha* is an epiphytic plant distributed across the habitat, making it harder to detect by the insects. Some factors such as the abundance, distribution and dispersal of individual plants are particularly important for their location by the insects, since they primarily respond to visual and olfactory stimuli, and these signals may change with distance, affecting the detectability of the plants (Bernays and Chapman 1994, Bruce et al. 2005, Schoonhoven et al. 2005, Nobre et al. 2015).

Average larval–pupal development intervals of between 24 and 60 d showed that *Beebeomyia* sp.3 experienced cycles that were nearly three times longer when infesting two *Philodendron* species. Such variation in the duration of the developmental cycle divergence in the cycle of development may be linked to the timing of oviposition during growth of the infructescence but is more likely to be related to the time of maturation phase following anthesis. Oviposition in *Taccarum ulei* takes place in several ripening stages, from newly emerging inflorescences to late male inflorescences (Maia et al. 2013). Conversely, oviposition in *D. oerstedii* occurs in developing inflorescences before anthesis, after which the female marks the structure with a deterrent pheromone (Hernández-Ortiz and Aguirre 2015).

The highly specialized habits involved in feeding on reproductive structures mean that flies are strongly linked to the biology of their hosts and are entirely dependent on the plants for their larval stage development. Similarly, the reproductive condition of the plant is adversely affected by the presence of the fly larvae as a result of the consumption of flowers, developing fruits or seeds. These adult flies have not been shown to be involved in pollination (Bogner and Gonçalves 1999, Maia et al. 2013) and, because oviposition takes place before or during anthesis, such interactions are harmful to the plants.

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