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RESEARCH ARTICLE

Flesh flies (Diptera: Sarcophagidae: Sarcophaginae) from the Colombian Guajira biogeographic province, an approach to their ecology and distribution

César Valverde-Castro[1], Eliana Buenaventura[2,3], Juan David Sánchez-Rodríguez[1], Marta Wolff[1]

[1]*Entomology group, Instituto de Biología, Universidad de Antioquia. Calle 67 # 53-108, Laboratory 7-311, Medellín, Colombia.*
[2]*Natural History Museum of Denmark. Universitetsparken 15, DK-2100 Copenhagen, Denmark.*
[3]*National Museum of Natural History, Smithsonian Institution. Washington, DC, United States of America.*
Corresponding author: César Valverde-Castro (cesarvalverdec@gmail.com)

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ABSTRACT. Sarcophaginae is the most diverse subfamily of Sarcophagidae with 51 genera and more than 1,800 species and it is widely distributed in the Neotropical Region. Sarcophaginae flies of forest, rural, and urban habitats of the seven departments comprising the Colombian Guajira biogeographic province were surveyed. Van Someren Rydon traps baited with fermented fruit, decomposing fish, and human feces were active for 72 hours with samples collected every 12 hours (day/night) between 2010 and 2014. A total of 14,223 sarcophagines (78% females and 22% males) were collected, which belong to 28 species of nine genera. *Oxyvinia excisa* (Lopes, 1950) is a new record for Colombia. The richest genera were *Oxysarcodexia* Townsend, 1917 and *Peckia* Robineau-Desvoidy, 1830, with eleven and nine species, respectively. Some of the species with the highest affinity to urban habitats were *Oxysarcodexia bakeri* (Aldrich, 1916), *Oxysarcodexia aurata* (Macquart, 1851), and *Oxysarcodexia timida* (Aldrich, 1916); to rural habitats were *Oxysarcodexia diana* (Lopes, 1933), *Ravinia columbiana* (Lopes, 1962), and *Ravinia effrenata* (Walker, 1861); and to forest habitats were *Helicobia rapax* (Walker, 1849), *Oxysarcodexia avuncula* (Lopes, 1933), and *Oxysarcodexia major* Lopes, 1946. We also discuss diet, habitat, and activity periods of the species. Species composition of Sarcophaginae in the Guajira province was very homogenous across the habitats, with the forest as the richest habitat. Scavenger habits of Sarcophaginae are confirmed, as well as their strong association with anthropic environments.

KEY WORDS. Caribbean, Colombia, ecology, Guajira province, Sarcophaginae.

INTRODUCTION

The Neotropical Region comprises three sub-regions (Antillean, Brazilian, and Chacoan), two transition zones (Mexican and South American), seven dominions (Mesoamerican, Pacific, Boreal Brazilian, Southwestern Amazonian, Southeastern Amazonian, Chacoan, and Parana), and 53 provinces (Morrone 2014). The Brazilian sub-region is divided into the Mesoamerican and Pacific dominions. The latter is subdivided into twelve provinces, one of which is the Guajira biogeographic province, which encompasses northern Colombia and northwestern Venezuela (Morrone 2014). Dry forests and shrubs, short trees, scrubs, and cardones (Cactaceae) characterize the Guajira biogeographic province, but it also includes wet forests and swamps maintained by periodic floods (Morrone 2001). This province is also known as the pre-Caribbean arid belt, which is divided into the tropical desert, tropical sub-xerophytic, and hydric zono-biomes (Hernández and Sanchez 1992), and it is nearly 132.000 km^2. According to Holdridge (1967), dry and very dry tropical forests define the Guajira biogeographic province. This biogeographic province is characterized by a selection of endemic species of plants, birds, and beetles (Morrone 2014), although other endemic organisms are present as well, but not yet studied. Some of the few Diptera families reported for this province are Drosophilidae, Ephydridae, Simuliidae (Morrone 2001), and Calliphoridae (Santodomingo et al. 2014). However,

there is no information about Sarcophagidae, known as a widely-distributed family in the Neotropical Region, with species of forensic, medical, and ecological importance (Amorim et al. 2002, Courtney et al. 2009, Carvalho and Mello-Patiu 2008, Ramos and Wolff 2011, Pape and Thompson 2013).

Many flesh fly species seem to be closely associated with humans and domestic animals, and they are found in dung and organic decaying matter (Oliveira et al. 2002). Some species are pathogen vectors of protozoans, helminths, enteropathogenic bacteria, and enteroviruses (Greenberg 1971), and others cause myasis in vertebrates (Dodge 1955, Crump and Pounds 1985, Hagman et al. 2005, Stevens et al. 2006, Bermudez et al. 2010, Mello-Patiu and Luna-Dias 2010). Thus, these flies have medical and veterinary importance. They are also considered a public health problem, mainly because of their eusynanthropic behavior and pathogen vector capacity (Sukontason et al. 2006, Vasconcelos et al. 2015).

Sarcophagidae is the second largest family within Oestroidea, with approximately 171 genera and 3,094 species (Pape et al. 2011). It includes the subfamilies Miltogramminae, Paramacronychiinae, and Sarcophaginae, the latter being the most diverse in the Neotropical Region with around 780 species (Pape 1996). The Sarcophaginae have a large variety of feeding habits, especially in their larval stages. These habits include coprophagy (Pape et al. 2002), parasitism (Dodge 1955, Crump and Pounds 1985, Pape 1994, Stevens et al. 2006, Hagman et al. 2005, Bermúdez et al. 2010, Mello-Patiu and Luna-Días 2010), kleptoparasitism (Spofford and Kurczewski 1989), predation (Pickens 1981, Pape and Dahlem 2010), and necrophagy (Pape 1996, Pape et al. 2004, Barros et al. 2008, Buenaventura et al. 2009, Yepes-Gaurisas et al. 2013). Adult flies feed on nectar, fruit juice, and proteins taken from decomposing matter such as excrements and carrion (Mello-Patiu et al. 2014).

Sarcophagines are pioneers in the entomological succession in human corpses and considered relevant indicators of Post-Mortem Interval (PMI) and other forensic estimations (Pape 1996, Wells et al. 2001, Buenaventura et al. 2009, Buenaventura and Pape 2013). However, their use in criminal investigations is still limited due to: (1) most females and larvae are poorly known, and their taxonomic identification might not be reliable, (2) collection of sarcophagine larvae might not be representative as they spread out up to 10 meters from the cadaver, and (3) knowledge on the ecology, behavior, and distribution is scarce (Jordaens et al. 2013).

The geographic distribution and habitat preference of Neotropical Sarcophagines is still little known but synanthropy studies have provided valuable data in this regard (Ferreira 1979, Linhares 1981, Dias et al. 1984, D'Almeida 1984, Yepes-Gaurisas et al. 2013). In Colombia, records of this fly subfamily are scarce, with the little information being mostly the result of recent studies on forensic entomology (Wolff et al. 2001, Pérez et al. 2005, Martínez et al. 2007, Buenaventura et al. 2009, Barrios and Wolff 2011, Ramos and Wolff 2011, Ramírez-Mora et al. 2012, Amat et al. 2013, Yepes-Gaurisas et al. 2013, Ramos-Pastrana et al. 2014, Mello-Patiu 2016). The catalogue of Sarcophagidae from Colombia (Mello-Patiu 2016) listed 102 species in 26 genera and two subfamilies, of which 96 species belong to Sarcophaginae. In this study, we aimed to contribute to the knowledge on the diversity and ecology of Sarcophaginae, their diet and habitat preferences, as well as their activity periods (day/night) in the Guajira biogeographic province.

MATERIAL AND METHODS

Flies of Sarcofaginae were collected in the western part of the Guajira biogeographic province, which comprises the Colombian departments of La Guajira, Cesar, Magdalena, Atlantico, Bolivar, Sucre, and Cordoba (Fig. 1, Table 1).

Three habitats with differential anthropic intervention were selected in each department. The urban habitat consisted of residential areas in the capital of each department, and was characterized by having drinking water, sewage system, and periodical garbage collection. The rural habitat was an isolated dwelling with septic tanks, farm animals, fishponds, or vegetable crops. The forest habitat was a protected dry forest area.

Six Van Someren Rydon traps placed at 1.5 m height and spaced by 50 m were hung for 72 hours in each habitat on a linear transect of 250 m. Traps were alternately baited with fermented fruit mixture, decomposing fish, and human feces. Specimens were collected every 12 hours (06:00 am and 06:00 pm) and transferred to 96% ethanol. Samples were collected from June 2010 to April 2014 in the three different habitats studied (urban, rural, forest) in each of the seven departments, for a total of 21 localities sampled (Table 1).

Taxonomic identification included only males. Flies were identified using taxonomic keys and descriptions by Mello-Patiu and Pape (2000), Carvalho and Mello-Patiu (2008), Méndez et al. (2008), Buenaventura et al. (2009), Giroux and Wheeler (2009), Pape and Dahlem (2010), Silva and Mello-Patiu (2010), Pinto et al. (2011), Buenaventura and Pape (2013), and Carvalho-Filho et al. (2014). Taxonomic characters of each species were also compared to reference specimens of the Entomological Collection of Universidad de Antioquia, Medellin, Colombia (CEUA). All specimens were deposited in the CEUA (National Record of Biological Collections # 036).

Species preferences for habitat and type of bait were assessed using a Monte Carlo serial analysis (Brower and Kyle 1988), with an input of 30 random matrices. In order to identify the most diverse habitat, we calculated the Shannon-Wiener diversity index (H'). We also tested for statistically significant differences between the abundance and remaining variables using paired Student's t-Tests, considering the normality assumption (Shapiro Wilk). A Correspondence Analysis (CA) was used to estimate the correlation of species vs. habitats and species vs. baits. All analyses were carried out using the statistical program PAST version 3.06 (Hammer et al. 2001).

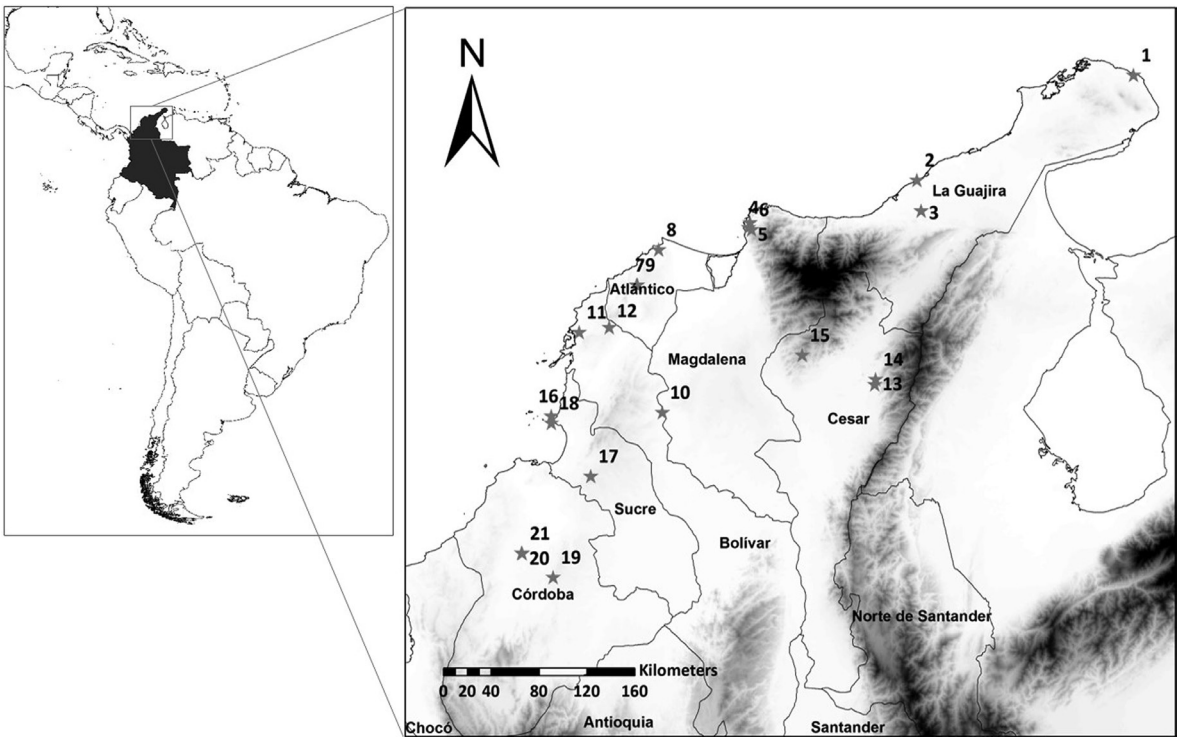


Figure 1. Map with collection localities in the Guajira province, Colombia.

Table 1. Collection localities in the Colombian Guajira province.

Location in the map	Departments	Municipalities	Location collects	Geographical coordinates	Altitude (msnm)	Habitat
1	La Guajira	Uribia	Vereda Santa Ana	12°19′52.3″N, 71°17′55.5″W	16	Rural
2		Riohacha	Barrio Jorge Pérez	11°32′25.02″N, 72°55′47.45″W	10	Urban
3		Riohacha	Caserío El Abra	11°18′36.69″N, 72°53′55.83″W	44	Forest
4	Magdalena	Santa Marta	SENA Agropecuario	11°11′01.2″N, 74°11′55.1″W	36	Rural
5		Santa Marta	Universidad del Magdalena	11°13′18.36″N, 74°11′10.89″W	20	Urban
6		Santa Marta	Reserva Lalguana Verde	11°10′07.2″N, 74°10′37.4″W	207	Forest
7	Atlántico	Usiacury	Reserva Luriza	10°45′04.99″N, 75°02′33.61″W	125	Rural
8		Barranquilla	Universidad del Atlántico	11°01′07.58″N, 74°52′28.19″W	48	Urban
9		Usiacury	Reserva Luriza	10°45′10.72″N, 75°02′08.59″W	187	Forest
10	Bolívar	Zambrano	Finca La Esmeralda	9°47′38.80″N, 74°50′52.22″W	16	Rural
11		Cartagena	Barrio Las Palmeras	10°23′51.04″N, 75°28′28.29″W	6	Urban
12		Villanueva	Finca El Peligro	10°25′57.59″N, 75°14′52.01″W	302	Forest
13	Cesar	Agustín Codazzi	CORPOICA	10°00′08.4″N, 73°14′54.7″W	113	Rural
14		Agustín Codazzi	Colegio Cooperativo	10°02′31.7″N, 73°14′28.9″W	129	Urban
15		Copey	Vereda Tierras Nuevas	10°13′34.0″N, 73°47′38.9″W	493	Forest
16	Sucre	Rincón del Mar	Cabecera Municipal	9°45′56.69″N, 75°41′00.15″W	2	Rural
17		Sincelejo	Institución Educativa Para Estudiantes Especiales	9°18′49.70″N, 75°23′11.69″W	193	Urban
18		San Onofre	Reserva Sanguaré	9°42′45.09″N, 75°41′00.15″W	16	Forest
19	Córdoba	San Carlos	Vereda Guacharacal	8°33′13.7″N, 75°40′13.6″W	141	Rural
20		Montería	Barrio Santa Fé	8°44′8.7″N, 75°54′26.1″W	47	Urban
21		Montería	Sierra Chiquita	8°43′57″N, 75°54′10.2″W	26	Forest

Names of the genera *Oxysarcodexia* and *Oxyvinia* are abbreviated as "*Oxys*." and "*Oxyv*.", respectively. Similarly, *Sarcofarhtiopsis* is abbreviated as "*Sarcof*.", *Sarcophaga* as "*Sarcop*.", *Tricharaea* as "*Tr*.", and *Titanogrypa* as "*Ti*.". Genera *Helicobia*, *Peckia*, and *Ravinia* are abbreviated with their inicials.

RESULTS

A total of 14,223 sarcophagines (11,094 females and 3,129 males) were collected, which belong to 28 species of nine genera. *Oxyvinia excisa* (Lopes, 1950) is a new record for Colombia (Table 2). The new records increased to 97 the number of Sarcophaginae species and to 103 the number of flesh flies known to the country.

According to the diversity analysis, the forest was the most homogenous habitat (H' = 2.580), followed by the rural (H' = 2.071) and urban (H' = 2.058) habitats. However, all habitats had regular values as indicated by the Shannon-Wiener diversity index.

Oxysarcodexia bakeri (Aldrich, 1916), *Oxysarcodexia timida* (Aldrich, 1916), *Tricharaea occidua* (Fabricius, 1794), and *Oxysarcodexia conclausa* (Walker, 1861) were the most abundant species in urban environments. The species *Tr. occidua*, *Ravinia columbiana* (Lopes, 1962), *Oxys. conclausa*, *Oxys. bakeri*, *Ravinia effrenata* (Walker, 1861), and *Oxysarcodexia diana* (Lopes, 1933) were the most abundant in rural areas, while *Oxys. conclausa*, *Oxys. timida*, *Tr. occidua*, and *Oxysarcodexia amorosa* (Schiner, 1868) were the most abundant taxa in forest habitats (Table 2).

Table 2. Abundance of Sarcophaginae species (males) collected in the Colombian Guajira province (suc = Sucre, at = Atlántico, mag = Magdalena, lg = La Guajira, ce = Cesar, bl = Bolivar, cor = Cordoba). Species codes in first column are used in the Correspondence Analysis. Taxa are presented by genus, according to their abundance. New record for Colombia are indicated with *.

Genus	Code	Species	Departments	Habitats			Baits			Period of activity		Total
				Urban	Rural	Forest	Fruit	Faeces	Fish	Day	Night	
	1	*Oxys. bakeri* (Aldrich, 1916)	suc, at, mag, lg, ce, bl, cor	263	146	36	81	146	218	344	101	445
	2	*Oxys. conclausa* (Walker, 1861)	suc, at, mag, lg, ce, bl, cor	85	169	136	22	154	214	303	87	390
	3	*Oxys. amorosa* (Schiner, 1868)	suc, at, mag, lg, ce, cor	20	35	70	7	28	90	109	16	125
	4	*Oxys. diana* (Lopes, 1933)	suc, at, mag, ce, bl, cor	29	118	17	5	121	38	152	12	164
	5	*Oxys. sarcinata* Lopes, 1953	suc, at, ce, cor	0	1	15	1	4	11	16	0	16
Oxysarcodexia	6	*Oxys. aurata* (Macquart, 1851)	suc, at, mag, ce, bl, cor	54	29	35	39	12	67	89	29	118
	7	*Oxys. timida* (Aldrich, 1916)	suc, at, mag, ce, bl, cor	228	95	130	50	159	244	322	131	453
	8	*Oxys. angrensis* (Lopes, 1933)	ce, bl, cor	2	0	4	1	0	5	4	2	6
	9	*Oxys. avuncula* (Lopes, 1933)	ce	0	0	9	0	0	9	9	0	9
	10	*Oxys. major* Lopes, 1946	ce	0	0	4	0	0	4	4	0	4
	11	*Oxys. occulta* Lopes, 1946	ce	0	0	2	0	0	2	2	0	2
	12	*P. chrysostoma* (Wiedemann, 1830)	suc, at, mag, lg, ce, bl, cor	41	22	19	12	19	51	69	13	82
	13	*P. pexata* (Wulp, 1895)	mag, lg, ce, bl, cor	1	8	8	2	0	15	15	2	17
	14	*P. lambens* (Wiedemann, 1830)	suc, at, mag, lg, ce, bl, cor	15	10	41	9	0	57	41	25	66
	15	*P. ingens* (Walker, 1849)	at, mag, lg, ce, bl, cor	1	10	17	0	16	12	17	11	29
Peckia	16	*P. gulo* (Fabricius, 1805)	suc	0	0	8	1	0	7	5	3	8
	17	*P. collusor* (Curran & Walley, 1934)	ce	0	0	2	0	2	0	2	0	2
	18	*P. hirsuta* (Hall, 1933)	suc	0	0	1	0	0	1	1	0	1
	19	*P. intermutans* (Walker, 1861)	ce	0	0	1	0	0	1	1	0	1
	20	*P. anguilla* (Curran & Walley, 1934)	ce	0	0	1	0	0	1	0	1	1
Ravinia	21	*R. columbiana* (Lopes, 1962)	suc, at, mag, lg, ce, bl, cor	46	194	57	54	163	80	231	66	297
	22	*R. effrenata* (Walker, 1861)	suc, at, mag, lg, ce, bl, cor	34	144	42	56	109	55	172	48	220
Tricharaea	23	*Tr. occidua* (Fabricius, 1794)	suc, at, mag, lg, ce, bl, cor	120	461	75	44	339	273	505	151	656
Sarcophaga	24	*Sarcop. ruficornis* (Fabricius, 1794)	suc, lg	2	0	0	0	1	1	2	0	2
Titanogrypa	25	*Ti. placida* (Aldrich, 1925)	at, lg, bl	3	0	2	1	0	4	5	0	5
Oxyvinia	26	*Oxyv. excisa* (Lopes, 1950)*	at	0	1	1	0	2	0	2	0	2
Helicobia	27	*H. rapax* (Walker, 1849)	mag	0	0	4	0	0	4	4	0	4
Sarcofahrtiopsis	28	*Sarcof. cuneata* (Townsend, 1935)	lg, cor	0	0	5	5	0	0	5	0	5
Total abundance				944	1443	742	390	1275	1464	2431	698	3129
Number of species				16	15	27	17	15	25	27	16	28

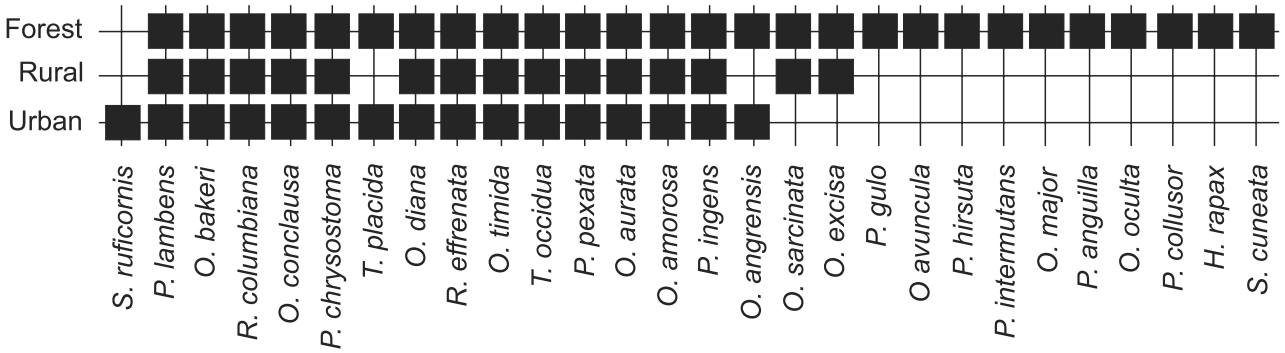
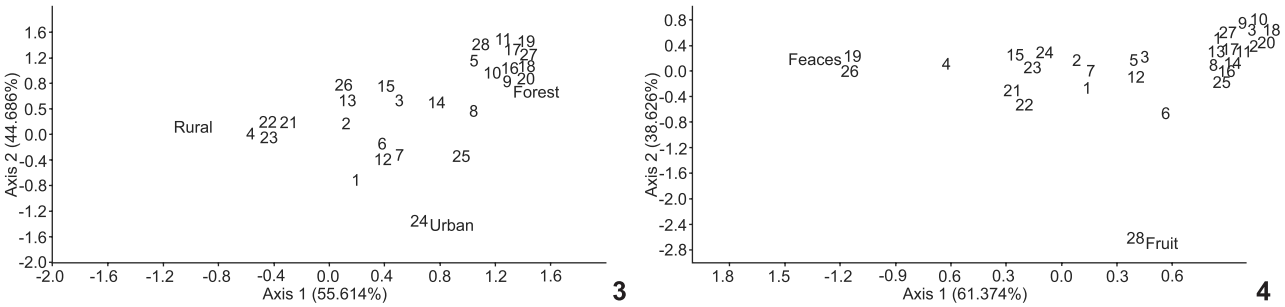


Figure 2. Serial analysis of distribution of species of Sarcophaginae in the Guajira province between habitats (Monte Carlo method with 30 random matrices = 0.878).



Figures 3–4. Correspondence analysis: (3) between the 28 Sarcophaginae species collected in the Guajira province and the three types of habitat (urban, rural, and forest); (4) between species and baits. Species were coded with the numbers from 1 to 28 (see Table 1) to simplify the graphic.

Serial analysis (Fig. 2) showed that *Helicobia rapax* (Walker, 1849), *Oxys. avuncula* (Lopes, 1933), *Oxys. major* (Lopes, 1946), *Oxys. occulta* (Lopes, 1946), *P. anguilla* (Curran & Walley, 1934), *P. collusor* (Curran & Walley, 1934), *P. gulo* (Fabricius, 1805), *P. hirsuta* (Hall, 1933), *P. intermutans* (Walker, 1861), and *Sarcofahrtiopsis cuneata* (Townsend, 1935) are exclusively found in forested areas, while *Sarcophaga ruficornis* (Fabricius, 1794) is found only in urban habitats. In general, we observed that *Oxys. amorosa*, *Oxys. bakeri*, *Oxys. conclausa*, *Oxys. diana*, *Oxys. timida*, *Oxys. aurata* (Macquart, 1851), *P. ingens*, *P. lambens*, *P. chrysostoma* (Wiedemann, 1830), *P. pexata* (Wulp, 1895), *R. columbiana*, *R. effrenata*, and *Tr. occidua* were found in all habitats, making up for 97.8% of the individuals collected (Fig. 2).

Our CA showed association between *H. rapax*, *Oxys. avuncula*, *Oxys. major*, *Oxys. occulta*, *Oxys. sarcinata*, *P. anguilla*, *P. collusor*, *P. gulo*, *P. hirsuta*, *P. intermutans*, and *Sarcof. cuneata* and the forest, and between *Oxys. diana*, *R. columbiana*, *R. effrenata*, and *Tr. occidua* and the rural habitat. *S. ruficornis* was the only taxon associated with the urban habitat, although *Oxys. bakeri*, *Oxys. aurata*, *Oxys. timida*, *P. chrysostoma*, and *Titanogrypa placida* (Aldrich, 1925) showed also slight preference for this habitat. The remaining species did not show a preference for any of the three habitats (Fig. 3).

Paired Student's *t*-Tests showed no significant difference between the habitats, but it revealed differences between the type of baits and the activity periods. This indicates that most of the species were collected during the day with fish and feces bait (Tables 2 and 3).

The most effective bait as measured by species richness was fish with 25 species, followed by fruit with 17, and feces with 15. Fish was also the most effective bait as measured by abundance, attracting 47% of the specimens, followed by feces with 41% and fruit with 12% (Table 1).

Results of the CA between species and baits showed that *Oxyv. excisa* and *P. intermutans* were associated with feces, while *Sarcof. cuneata* showed preference for fruit. Fish was the preferred substrate for most of the species, with the following species showing strong affinity *Oxysarcodexia angrensis* (Lopes, 1933), *Oxys. avuncula*, *Oxys. bakeri*, *Oxys. conclausa*, *Oxys. major*, *Oxys. occulta*, *P. anguilla*, *P. collusor*, *P. gulo*, *P. hirsuta*, *P. lambens*, *P. pexata*, and *Ti. placida*. Other species were collected from three baits without specific affinity to any particular bait (Fig. 4).

According to the CA, all species were active during day except *P. anguilla*, which was collected at night with a single individual (Table 2).

Table 3. Comparison of the abundances of species through paired Student's *t*-Tests between the habitats, baits and period of activity of Sarcophaginae flies in the Colombian Guajira province.

Comparisons		t	(p-value)
Habitats			
Forest	Rural	-1.51385	0.141272
Forest	Urban	-0.393244	0.697117
Urban	Rural	1.15808	0.256615
Baits			
Faeces	Fish	0.139035	0.890418
Faeces	Fruit	2.46099	0.0202824*
Fruit	Fish	-3.14418	0.0039202*
Period of activity			
Day	Night	3.44142	0.0018352*

* Significant difference to 95% confidence intervals.

DISCUSSION

The habitats showed no statistically significant difference in species composition, which indicates that flesh flies are, generally speaking, uniformly distributed throughout the Colombian Guajira province (Suppl. material 1). This region originally comprised mostly dry and very dry tropical forest, located in lowlands below 1,000 m altitude. Due to agricultural expansion (Espinal and Montenegro 1977, Etter et al. 2008) in the lowlands of the region, these forests have been drastically reduced and fragmented, which apparently allows the most adapted species to expand their distribution range.

In terms of dietary habits, Sarcophaginae adult flies showed higher preference for decomposing fish than for feces and fermented fruit. The high frequency of adults visiting the decomposing fish seems to be related to the high fat and protein content in animal tissues, which are needed by females for developing eggs (Pape 1996), as well as for first instar larvae to grow and develop on these substrates (Stevens 2003). Human feces and fruits probably do not provide the necessary amount of nutrients for larval development of Sarcophaginae flies. However, other fly families like Muscidae, Calliphoridae, Drosophilidae, and Stratiomyidae, among others, can develop on these media.

Oxyvinia excisa is here reported for the first time from Colombia. This species has also been found in Brazil and Peru (Pape 1996). In Brazil, specimens of *Oxyv. excisa* were collected in forests using human feces (D'Almeida 1984, Lopes 1973), banana with brown sugar and decomposing "*Coccus comosa*" as baits (possibly *Cocos comosa* [Mart.]) (Lopes 1973). The habits of *Oxyv. excisa* from Peru are unknown. Additionally, the description of *Oxyv. excisa* by Lopes (1950) mentions the saprophagous habit of the larvae. Thus, both the habitat preference and the scavenger habit kown for *O. excisa* are consistent with our results.

The most abundant and generalist species were *Oxys. timida*, *Oxys. bakeri*, *Oxys. conclausa*, *Oxys. diana*, *Oxys. amorosa*, *Oxys. aurata*, *P. chrysostoma*, *R. columbiana*, *R. effrenata*, and *Tr. occidua*, found in all habitats along the Guajira province, and from all baits (Table 2). These species showed necrophagous and coprophagous behaviors. Visits to feces and carrion enable these species to transport pathogenic microorganisms on the adhesive ultrastructures of their legs, which might imply potential risks for public health (Sukontason et al. 2006). Besides this, some species such as *P. lambens* are knowning for cause myasis (Pape 1994, Hall and Wall 1995, Fernandes et al. 2009, Bermudez et al. 2010). As other studies indicated, the saprophagous behavior and preference for decaying substrates of the above metioned species (Oliveira-Costa et al. 2001, Barros et al. 2008), might point to their relevance for forensic estimations in the Guajira province.

Tricharaea occidua was the most abundant and widely distributed species in the Guajira province, with 656 specimens (21% of total specimens collected) (Table 2, Suppl. material 1). This species was also dominant in similar studies in a natural reserve in Buenos Aires, Argentina, where it was found associated with feces (Mariluis et al. 2007, Mulieri et al. 2008). In Brazil, it was the most abundant species in cow's lung tissue (Pereira de Sousa et al. 2015) and the second most abundant in pig carcasses (Barbosa et al. 2009), in buffalo excrements (Marchiori 2014), and the third most abundant in feces in the Archipelago Fernando de Noronha (Couri et al. 2008). In Colombia, Yepes-Gaurisas et al. (2013) recorded *Tr. occidua* feeding on chicken viscera, fish, and human feces. These authors also proposed this species as a potential vector in human disease transmission due to its high abundance, closeness to feces, and strong association with human settlements. However, *Tr. occidua* seems to be able to adapt to different environments and has been recorded in both open habitats and forests (Pereira de Sousa et al. 2015). All above is consistent with the abundance of this species in feces and fish. Our CA showed strong association of *Tr. occidua* with rural habitats, probably because of the abundance of barnyard animal excrements in this environment, as reported by Toyama and Ikeda (1976) in milk farms from Oahu-Hawaii. Our results suggest the importance of this species as a decomposer of carrion and feces and its high dispersion ability in the Neotropical Region.

Oxysarcodexia, with 11 species, was the most diverse and abundant genus in the present study, which confirmed its dominance in the Neotropical Region (Lopes 1973). This genus is considered of importance in forensic entomology studies in Brazil due to its abundance, diversity, and scavenger habits (Dias et al. 1984, Carvalho and Linhares 2001, Oliveira et al. 2002, Barros et al. 2008, Rosa et al. 2009, Barbosa et al. 2009). A study by Oliveira et al. (2002) reported 11 species in Rio de Janeiro, of which *Oxys. thornax* (Walker, 1849) was the most abundant species, while in the present study *Oxys. timida* was the most abundant species of *Oxysarcodexia* with 453 specimens (14.5%). The flesh fly *Oxysarcodexia timida* has been reported as

a PMI indicator (Barbosa et al. 2009, Bitar et al. 2013) and it is strongly associated with urban settlements (Yepes-Gaurisas et al. 2013). Our CA suggests this species as widely distributed in the Colombian Guajira province.

Oxysarcodexia bakeri was the third most abundant species (14.2%). It seems to be a generalist species, since our CA showed no correlation between this species and any particular habitat or bait. Other studies reported coprophagous (Flores and Dale 1995) or necrophagous (Yepes-Gaurisas et al. 2013) habits for this species.

Oxysarcodexia conclausa seems to be common in urban and peri-urban settlements where it showed strong preferences for necrophagous feeding mode (Ramirez-Mora et al. 2012, Yepes-Gaurisas et al. 2013). This is consistent with our results, since the greatest abundance of this species was on fish bait. However, our CA showed no preference of this species for any habitat.

Oxysarcodexia angrensis, *Oxys. amorosa*, *Oxys. occulta*, *Oxys. avuncula*, *Oxys. major*, and *Oxys. sarcinata* were associated with the forest, as confirmed our CA. Similarly, the three latter species were associated with non-disturbed environments and showed necrophagous habits in previous reports (i.e., Yepes-Gaurisas et al. 2013). In addition, *Oxys. avuncula* was found in human corpses (Barros et al. 2008) and pig carrion (Barbosa et al. 2009) in urban and forest areas in Brazil (Dias et al. 1984, Carvalho and Linhares 2001), which suggests its potential as a PMI indicator.

Oxysarcodexia diana, *R. columbiana*, and *R. effrenata* were correlated with rural habitat, which is in agreement with reports by Yepes-Gaurisas et al. (2013), Faria (2013), and Pinilla et al. (2012). Particularly, *Oxys. diana* showed coprophagous and necrophagous habits (D'Almeida 1984, Dias et al. 1984, D'Almeida and Lima 1994, Barbosa et al. 2009). Our CA showed no correlation of *R. columbiana* and *R. effrenata* with any bait, although previous studies reported these species as necrophagous (Yepes-Gaurisas et al. 2013, Faria 2013, Pinilla et al. 2012).

Peckia, with nine species, was the second most abundant genus. Species of this genus have been widely studied due to their forensic importance and diversity (Carvalho and Linhares 2001, Barros et al. 2008, Buenaventura et al. 2009, Barbosa et al. 2009, Rosa et al. 2009, Buenaventura 2013, Buenaventura and Pape 2013, 2015, Yepes-Gaurisas et al. 2013). In Brazil and Colombia, *Peckia* was reported as the second most abundant genus in forensic studies, after *Oxysarcodexia* (Carvalho and Linhares 2001, Barros et al. 2008, Barbosa et al. 2009, Rosa et al. 2009, Yepes-Gaurisas et al. 2013).

We found *P. chrysostoma* as the most abundant species of *Peckia*. This species is widely distributed in the Neotropical Region (D'Almeida 1993, Pape 1996, Buenaventura 2013, Buenaventura and Pape 2013, 2015), and seems to adapt to open habitats and forests (Pereira de Sousa et al. 2015). In Colombia and Brazil, Linhares (1981), D'Almeida (1984), Oliveira et al. (2002), and Yepes-Gaurisas et al. (2013) reported it as eusynanthropic (strong affinity for human-modified habitats) species associated with carrion. In contrast, we found no affinity to any habitat.

Peckia lambens was the second most abundant species of *Peckia* with a wide distribution in all habitats studied in the Guajira province. This species showed necrophagous habit as observed in previous studies (Carvalho and Linhares 2001, Barros et al. 2008, Barbosa et al. 2009, Bitar et al. 2013, Yepes-Gaurisas et al. 2013, Vasconcelos et al. 2015, Pereira de Sousa et al. 2015), one of them including a report in human corpses (Oliveira-Costa et al. 2001). The broad biological spectrum of this species also includes parasitism, as it causes myiasis in birds (Bermúdez et al. 2010), anurans (Hagman et al. 2005), and humans (Queiroz de Leão et al. 1996, Fernandes et al. 2009).

Peckia ingens occurred in all three studied habitats, which is consistent with the study by Yepes-Gaurisas et al. (2013). Our CA showed a correlation of this species with feces and carrion baits. This species might have potential as a PMI indicator in forensic entomology, since previous studies found it as necrophagous on decomposing pig corpses in the Colombian amazon foothills (Ramos and Wolff 2011), and in a forest in Brazil (Carvalho and Linhares 2001).

Peckia pexata was found in all habitats, but it was highly associated with rural and forest habitats. Our CA showed correlation between this species and fish, which indicates necrophagous habits, also confirmed in other studies (Carvalho and Linhares 2001, Barros et al. 2008, Bitar et al. 2013). In Colombia, this species showed low abundance (Yepes-Gaurisas et al. 2013), which is further supported in this study with only 17 specimens collected.

Peckia collusor, *P. anguilla*, *P. hirsuta*, and *P. intermutans* were collected in low numbers in forest habitat. *Peckia collusor* has been collected in decomposing fish (Yepes-Gaurisas et al. 2013) and pig corpses (Carvalho and Linhares 2001, Barbosa et al. 2009, Bitar et al. 2013), which suggests necrophagous habits and some potential as a PMI indicator. In Brazil, *P. intermutans* is a relevant species in forensic entomology due to its scavenger habits (Carvalho and Linhares 2001, Barbosa et al. 2009, Rosa et al. 2009, Oliveira and Vasconcelos 2010, Amorim et al. 2014). According to D'Almeida (1984), *P. intermutans* rejects densely populated areas, which is in agreement with our study as this species was only found in forest habitats.

This is the first ecological approach to the subfamily Sarcophaginae in a specific biogeographic area within Colombia. Our study corroborates the necrophagous habits of some species of this subfamily. Species composition of Sarcophaginae in the Guajira province was very homogenous across the habitats, although the forest showed higher richness.

Historically, Sarcophaginae flies have been associated with anthropic environments, which is consistent with the results presented here. The performance of Sarcophaginae as bacteria carriers and its consequences for public health in this province has not been studied, however the present study highlighted their high dispersion ability and ubiquity in urban habitats. In addition, flesh flies of Sarcophaginae seem to be relevant decomposers of organic matter, thus playing a role as recyclers in terrestrial ecosystems.

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Supplementary material 1

Composition by departments of Sarcophaginae species collected in the Colombian Guajira province

Authors: César Valverde-Castro, Eliana Buenaventura, Juan David Sánchez-Rodríguez, Marta Wolff

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