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Anthropic effects on sand fly (Diptera: Psychodidae) abundance and diversity in an Amazonian rural settlement, Brazil

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ABSTRACT

Sand flies (Diptera: Psychodidae) are responsible for the transmission of protozoan parasites that cause leishmaniases. They are found predominantly in forests, but some species exploit environments that have been subject to deforestation and subsequent human colonization. Studies conducted in Brazil over the past 30 years show that some species are adapting to peri-urban and urban settings. We evaluated sand fly diversity and abundance in the rural settlement of Rio Pardo, Presidente Figueiredo Municipality, Amazonas State, Brazil. Settlement households were divided into four categories. These categories were determined by the human population density and the degree of deforestation in the immediate area. We used CDC light traps to sample the area surrounding 24 households (6 households in each category). Samples were taken on six occasions during September–November 2009 and June–August 2010. A total of 3074 sand fly specimens were collected, including 1163 females and 1911 males. These were classified into 13 genera and 52 species. The greatest abundance of sand flies and the greatest richness of species were observed in areas where human population density was highest. Our results show that changes in the human occupancy and vegetation management in rural settlements may affect the population dynamics and distribution of sand fly species, thereby affecting the local transmission of cutaneous leishmaniases.

1. Introduction

Phlebotomine sand flies (Diptera: Psychodidae) are small insects of medical and veterinary relevance. The females of most species are hematophagous and are responsible for transmitting several etiological agents to vertebrate hosts. In the Amazon region, sand flies are vectors for *Leishmania* (Ross)—protozoan which cause leishmaniases—and for virus such as *Phlebovirus* (Acevedo and Arrivillaga, 2008; Casseb et al., 2013; Travassos et al., 1983). Cesário et al. (2011) have warned of the risks that sand flies pose as agents for the spread of bartonellosis, which is caused by *Bartonella bacilliformis* (Barton). In the Amazon forest, these flies can be found on tree trunks, in the canopy, in caves, and in animal burrows (Killick-Kendrick, 1999; Ready, 2013). These flies have also been found in rural environments, and, more recently, in urban environments. This indicates that sand flies are adapting to anthropic environments, particularly in peridomestic areas associated with animal shelters (Feitosa and Castellón, 2004; Nunes et al., 2008; Paes, 1991; Rangel and Lainson, 2009). In addition, some studies have shown that sand flies in peri-urban areas do bite humans, thereby increasing the risk of leishmaniasis infection in areas near dwellings (Carvalho et al., 2010; Nery et al., 2004; Salomón et al., 2006). It has been shown that deforestation is related to rises in the incidence of infectious diseases such as malaria, schistosomiasis, arboviroses, yellow fever, and leishmaniasis (Maroli et al., 2013; Walsh et al., 1993).

The main causes of deforestation include: the construction of hydropower plants, roads, and railways, selective logging, agriculture, livestock needs, and, in particular, the establishment of new settlements. In settlements the deforestation rate can be as much as 1.8% annually—four times higher than the average rate (Brandão

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and Souza, 2006). Historically in the Brazilian Amazon, the government offered financial incentives to encourage the ownership of land and the development of new agricultural settlements; this accelerated deforestation rates until the 1980s (Fearnside, 2005). In many cases, building a rural settlement provides new breeding sites for insect vectors. Insects can feed on people living near deforested areas, and this expands the focus of disease transmission. With a focus set, contact between vectors and humans can cause a local outbreak of disease if human population density is sufficiently high. Migration and emigration can then spread the disease to other areas (Jardine et al., 2008; Rezende et al., 2009; Walsh et al., 1993).

In Brazil, leishmaniases are currently thought to be rural (cutaneous and visceral) and forest (cutaneous) diseases. However, this profile has been modified in the North, Northeast, and Southeastern regions of Brazil, where urban epidemics of canine visceral leishmaniasis (VL) and cutaneous leishmaniasis (CL) have been documented over the past several decades. Human infection and sand fly vectors have also been identified in these regions (Amóra et al., 2010; Carvalho et al., 2010; Kawa et al., 2010). Thus, some species of sylvatic sand fly have adapted to urban environments and have established a peridomestic cycle (Desjeux, 2001; Feitosa and Bermúdez, 2009; Guerra et al., 2007; Lainson et al., 1994; Marzochi, 1992). Santarém Municipality, Pará State, is an area of endemic VL and CL, and, even though the abundance of the vectors is higher in rural zones, the process of synantropization among sand flies in urban areas is a fact (Feitosa et al., 2012).

Cases of cutaneous leishmaniasis have been recorded in metropolitan areas since 1987, including cases in Minas Gerais State, where sand flies have been collected (Araújo et al., 2013; Barata et al., 2011; Carvalho et al., 2010; Genaro et al., 1996; Mayrink et al., 1979; Saraiva et al., 2008). Similar observations have been reported in urban and peri-urban areas of Rio de Janeiro and Rio Grande do Norte States (Aguiar et al., 1987; Ximenes et al., 1999).

Previous studies have revealed that urbanization and peri-urbanization in the Amazon region has led to an increase in the incidence of cutaneous leishmaniasis disease and the frequency of sand fly vectors. Paes (1991) observed *Nyssomyia umbratilis* (Ward & Frahia) in the peridomicile of households in a Manaus city neighborhood. Feitosa and Castellón (2004) showed that 70% of sand flies captured near houses in Manaus were anthropofilic. Barbosa et al. (2008) also observed sand fly species in forests and peridomiciliary areas near a peri-urban community in Manaus City. Arias and Freitas (1982) and Guerra et al. (2007) captured sand fly vector species infected with *Leishmania* near residences in urban and peri-urban locations in Manaus; they also caught opossums *Didelphis marsupialis* (Linnaeus) infected with *Leishmania*. The presence of both vectors and reservoirs in areas close to human populations has led to an increase in the incidence of disease; these changes in transmission patterns could result in a serious threat to public health (Guerra et al., 2007; Paes, 1991).

Thus, we evaluated the anthropic impact of deforestation and human population density on the diversity and abundance of sand flies in a rural settlement in the Rio Pardo Community, Presidente Figueiredo Municipality, Amazonas State, Brazil.

2. Materials and methods

2.1. Study area

This study was conducted in the rural settlement of Rio Pardo (~1°48′ S 60°19′ W), located in the municipality of Presidente Figueiredo (Fig. 1), State of Amazonas, Brazil. The settlement was created in 1996 by the Brazilian National Institute of Colonization and Agrarian Reform (INCRA). It has approximately 700 inhabitants. Agriculture, cattle breeding, and vegetable extraction are the main economic activities (Gonçalves et al., 2012). In 2002, approximately 95% of its total area—about 28,000 hectares—was composed of preserved forest. From 1996–2002, the rate of deforestation was estimated to be about 150 ha/year, while land was developed for agricultural and community use at a rate of about 220 ha/year (Vilela, 2003). Previous studies have detected the presence of

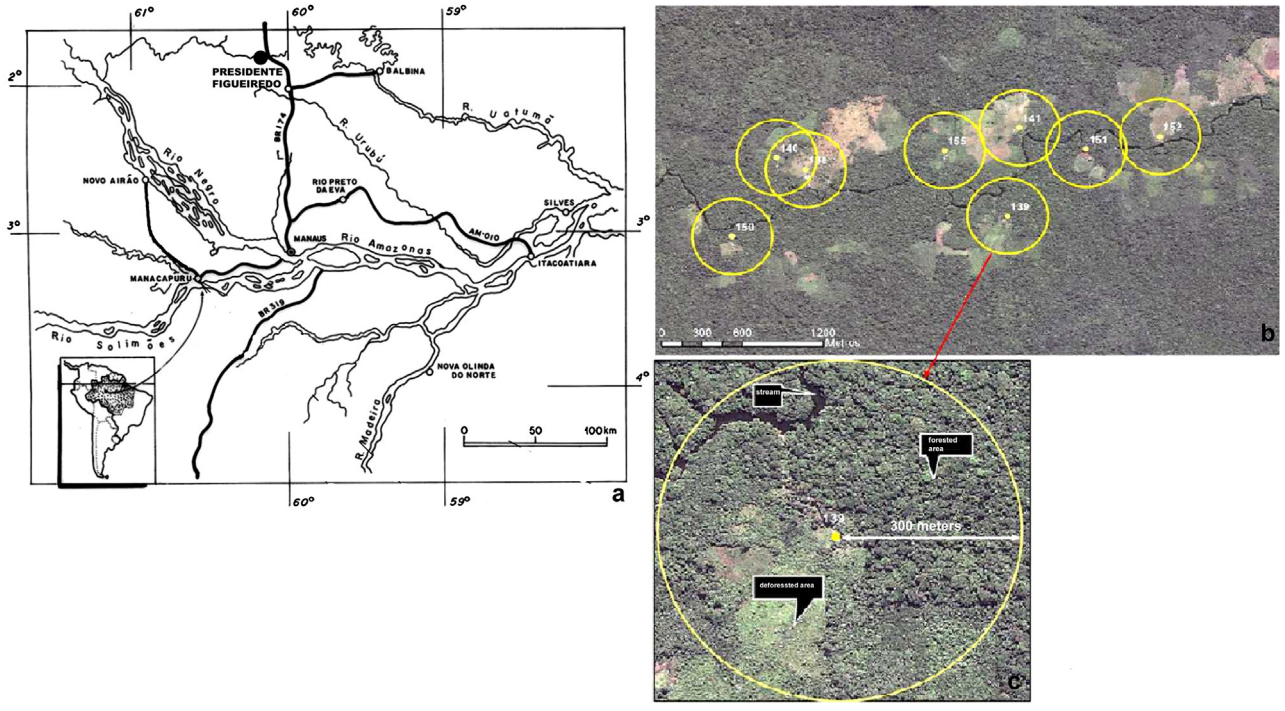

Fig. 1. Central Amazon map showing: (a) location of Presidente Figueiredo Municipality (source: modified from Chagas et al. (2006)); (b) the rural settlement of Rio Pardo showing, in circles, some of the selected areas for field collection of phlebotomine sand flies, (c) each field collection area was defined as a household within a radius of 300 m.

parasites that cause leishmaniases in 47% of the dwellings, and at least one case of the disease has been reported (Soares, 2010).

2.2. Sample design

To calculate the human population density and forest cover associated with households, a buffer zone with a radius of 300 m was established for each household. This radius is arbitrary, but we assumed that the dispersal radius of Amazonian sand flies is similar to the dispersal radius registered for sand flies from other Neotropical rain forests—usually 200 m or less (Alexander, 1987; Casanova et al., 2005; Chaniotis and Correa, 1974; Galati et al., 2009).

Forest cover data was computed from satellite images (PRODES®, 1 m × 1 m, August 2008), and the degree of forest cover was taken to be the percentage of area without forest cover in the household buffer zone. The extent of forest cover was drawn manually on the IKONOS image, and its deforestation percentage was calculated using the PRODES program (INPE, 2008); percentages ranged from 0 to 99%. We considered buffer zones with low forest cover to be those deforested by 43% or more.

Questionnaires and field research were used to systematically gather detailed socio-economic information about the settlers and the characteristics of their households (Ethical committee: Brazilian National Ethics Committee Board—CONEP 384/07).

For each household, human population density was calculated as the number of permanent inhabitants in the household plus the number of inhabitants living within the 300 m buffer zone; human population density varied from 0 to 63 persons. We considered buffer zones with a high population density to be those inhabited by 15 persons or more.

Settlement households were grouped into four categories: (G1) high population density and low forest cover; (G2) low population density and low forest cover; (G3) high population density and high forest cover; (G4) low population density and high forest cover. Six households were randomly chosen from each category, giving a total of 24 sampling points. During random selection, when two households had overlapping buffers, one household was discarded and another was chosen from the set.

2.3. Sand fly collections

Sand fly capture was performed over two periods: September–November 2009 and June–August 2010. These are both intermediary periods that fall between rainy and dry seasons. Capture was performed on four consecutive nights per month. Five Centers for Disease Control (CDC) light traps were installed in each household, and six households were sampled per day. The CDC light traps were installed 150 cm above the ground in five different environments within the household buffer zone: forest, forest edge, peridomicile, fruit garden, and successional vegetation habitats. The traps were kept in place from 5:00 p.m. to 6:00 a.m. A total of 30 CDC traps per day were installed in all habitats. Collected sand flies were identified according to the identification keys proposed by Young and Duncan (1994) and the genera are named following the nomenclature proposed by Galati (2003).

2.4. Data analyses

Sand fly abundance was calculated as the total number of flies per category (human population/forest cover). To compare the phlebotomine abundance among the different categories and different environments, Kruskal–Wallis and a posteriori Student–Newman–Keuls tests were used. The Shannon–Wiener index was used to evaluate diversity (H') between categories. The Jaccard index (CCJ) was used for similarity measurement and the Pielou index (J') was used to evaluate equitability between categories. Individual-based rarefaction curves were used to estimate species richness (S sp), and 95% confidence intervals (CIs) were calculated (Gotelli and Colwell, 2001). Both S sp. and the number of species observed in a sample (S obs) were graphically compared among categories. The Shannon diversity index (H') reflects two basic attributes: the number and the equitability of species. The Pielou index (J') allows the distribution of individuals among existing species to be represented as a value ranging from 0 (least uniform) to 1 (maximum uniformity). Richness was calculated as the number of observed species (Magurran, 2005).

3. Results

A total of 3074 phlebotomine sand flies were collected, including 1163 females (37.8%) and 1911 males (62.2%), belonging to 13 genera and 52 species (Table 1). The most abundant genus was *Nyssomyia* (Barretto), with six species and 1659 individuals (54.0%), followed by *Psychodopygus* (Mangabeira), with seven species and 313 individuals (10.2%), and *Evandromyia* (Mangabeira), with seven species and 198 individuals (6.4%). The least-represented genus was *Lutzomyia* (França), with four species and five individuals (0.2%), followed by *Trichopygomyia* (Barretto), with one species and 11 individuals (0.3%).

The most abundant species was *Nyssomyia antunesi* (Coutinho) (1090 individuals; 35.4%), found particularly in environments with peridomestic henhouses. The next most abundant species were *Nyssomyia umbratilis* (Ward and Fraiha) (389 individuals; 12.6%), *Micropygomyia rorotaensis* (Young and Porter) (194; 6.3%), and *Trichophoromyia ubiquitalis* (Mangabeira) (164; 5.3%) (Table 1). Other species found in lower abundance totalled 1237 individuals (40.2%). Only one specimen each was collected for the species *Lutzomyia flabellata* (Young and Arias), *Micropygomyia chassigneti* (Floch and Abonnenc), *Lutzomyia gomezi* (Nitzulescu), *Lutzomyia sherlocki* (Martins, Silva and Falcão), *Nyssomyia richardwardi* (Ready and Fraiha), *Sciopemyia pennyi* (Arias and Freitas), and *Trichophoromyia gibba* (Young and Arias).

The highest levels of sand fly richness and abundance were found in G3 (high population density and high forest cover), with 1136 sand flies distributed among 43 species, followed by G1 (high population density and low forest cover), with 758 individuals in 39 species. In G1, *N. antunesi*, *T. eurypyga* and *N. umbratilis* were the most abundant. In G4 (low population density and high forest cover), 586 individuals and 34 species were observed, while in G2 (low population density and low forest cover), 594 individuals and 37 species were observed. In G4, the most representative species were *N. antunesi*, *N. umbratilis*, and *T. ubiquitalis*; while in G2, *N. antunesi* was the most abundant species followed by *N. umbratilis* (Table 1).

There was no significant difference in the abundance of phlebotomine populations among the four categories ($H = 4.10$, df = 3, $p = 0.249$). Species diversity was highest in G3 ($H' = 1.20$) and lowest in G4 ($H' = 0.75$). The values of H' showed the following gradient: G3 > G2 > G1 > G4. The equitability (J') index for G2 and G3 was greater than in the others (Table 2), indicating that phlebotomine individuals are more equitably distributed among different species in these categories.

Observed richness (S obs) differed among landscape types. According to rarefaction estimates, similar levels of richness were observed in G1, G2 and G4, with 95% CIs overlapping among these categories, and higher richness in G4 (Tables 1 and 2, and Fig. 2).

The environment with the highest abundance of species was peridomicile, with 1330 sand flies; followed by forest (1069 individuals), forest edge (511), fruit garden (113), and successional vegetation (51) (Table 3). These environments differed significantly in the number of sand fly individuals ($H = 40.14$, df = 4, $p < 0.0001$).

Table 1
CDC light trap collected species and abundance of sand flies from Rio Pardo rural settlement, Presidente Figueiredo Municipality, Amazonas State, collected from September–November 2009 and June–August 2010.

Species	G1	G2	G3	G4	Total	% Total
Brumptomyia brumpti (Larrousse)	1	1	8	2	12	0.39
Bichromomyia flaviscutellata (Mangabeira)	21	27	16	12	76	2.47
Bichromomyia olmeca nociva (Young & Arias)	4	2	21	2	29	0.94
Bichromomyia reducta (Feliciangeli, Ramirez Pérez & Ramirez)	8	2	2		12	0.39
Evandromyia inpai (Young & Arias)	2	5	25		32	1.04
Evandromyia monstruosa (Floch & Abonnenc)	10	30	9	2	51	1.66
Evandromyia pinotti (Damasceno & Arouk)	1	6	1		8	0.26
Evandromyia saulensis (Floch & Abonnenc)	2		1		3	0.10
Evandromyia sericea (Floch & Abonnenc)	5		4	5	14	0.46
Evandromyia walkeri (Newstead)	13	16	54	3	86	2.80
Evandromyia williamsi (Damasceno, Causey & Arouk)	2	1		1	4	0.13
Lutzomyia flabellata (Martins & Silva)		1			1	0.03
Lutzomyia baityi (Damasceno, Causey & Arouk)	2				2	0.07
Lutzomyia gomezi (Nitzulescu)			1		1	0.03
Lutzomyia sherlocki (Martins, Silva & Falcão)		1			1	0.03
Micropygomyia chassigneti (Floch & Abonnenc)	1				1	0.03
Micropygomyia micropyga (Mangabeira)	6	15	5	3	29	0.94
Micropygomyia pilosa (Damasceno & Causey)	1	1			2	0.07
Micropygomyia rorotaensis (Floch & Abonnenc)	13	45	124	12	194	6.31
Nyssomyia anduzei (Rozeboom)	36	60	74	2	172	5.60
Nyssomyia antunesi (Coutinho)	381	118	243	348	1090	35.46
Nyssomyia richardwardi (Ready & Fraiha)			1		1	0.03
Nyssomyia shawi (Fraiha, Ward & Ready)			3	1	4	0.13
Nyssomyia umbratilis (Ward & Fraiha)	47	74	201	67	389	12.65
Nyssomyia yuilli yuilli (Young & Porter)	1		1	1	3	0.10
Pressatia choti (Floch & Abonnenc)	1	1	22	1	25	0.81
Pressatia triachanta (Mangabeira)	2			2	4	0.13
Pressatia trispinosa (Mangabeira)	5	4	11	2	22	0.72
Psathyromyia abonnenci (Floch & Chassignet)	1			1	2	0.07
Psathyromyia aragaoi (Costa Lima)	3	5	12	3	23	0.75
Psathyromyia cuzquena (Martins, Llanos & Silva)			2		2	0.07
Psathyromyia dreisbachi (Causey & Damasceno)	11	5	9	2	27	0.88
Psathyromyia inflata (Floch & Abonnenc)			2		2	0.07
Psathyromyia lutziana (Costa Lima)	1	4	5	1	11	0.36
Psathyromyia punctigeniculata (Floch & Abonnenc)	5	3	13	3	24	0.78
Psathyromyia scaffi (Damasceno & Arouk)	4	3	2	1	10	0.33
Psychodopygus amazonensis (Root)	7	30	42	3	82	2.67
Psychodopygus carrerai carrerai (Barreto)		1	7		8	0.26
Psychodopygus chagasi (Costa Lima)	18	9	16	5	48	1.56
Psychodopygus claustrei (Abonnenc, Léger & Fauran)	3	20	31	3	57	1.85
Psychodopygus davisi (Root)	9	28	57	3	97	3.16
Psychodopygus hirsutus (Mangabeira)			2		2	0.07
Psychodopygus squamiventris squamiventris (Lutz & Neiva)	4	2	9	4	19	0.62
Sciopemyia nematoducta (Young & Arias)	9	17	8	5	39	1.27
Sciopemyia pennyi (Arias & Freitas)			1		1	0.03
Sciopemyia sordellii (Shannon & Del Ponte)	15	10	1	10	36	1.17
Trichophoromyia eurypyga (Martins, Falcão & Silva)	61	25	21	5	112	3.64
Trichophoromyia gibba (Young & Arias)		1			1	0.03
Trichophoromyia ubiquitalis (Mangabeira)	39	15	43	67	164	5.34
Trichopygomyia trichopyga (Floch & Abonnenc)		1	10		11	0.36
Viannamyia furcata (Mangabeira)	3	5	9	3	20	0.65
Viannamyia tuberculata (Mangabeira)			7	1	8	0.26
Total	758	594	1136	586	3074	100

G1 = high population density and low forest cover, G2 = low population density and low forest cover, G3 = high population density and high forest cover, G4 = low population density and high forest cover.

Table 2
Species of sand flies from Rio Pardo, Presidente Figueiredo, Amazonas State, collected with CDC light trap from September–November 2009 and June–August 2010. Sample number (N), events number (n), total individuals (TI), Shannon & Wiener index (H'), and Pielou equitability (J') for categories of households.

Categories	N	n	TI	H'	J'	S obs	S sp
G1	30	4	758	0.99	0.62	39	37.4 (±1.3)
G2	30	4	594	1.18	0.75	37	36.6 (±0.57)
G3	30	4	1136	1.20	0.73	43	38.3 (±1.65)
G4	30	4	586	0.75	0.51	34	29.7 (±0.5)

S obs, observed species; S sp, estimated species; G1, high population density and low forest cover; G2, low population density and low forest cover; G3, high population density and high forest cover; G4, low population density and high forest cover.

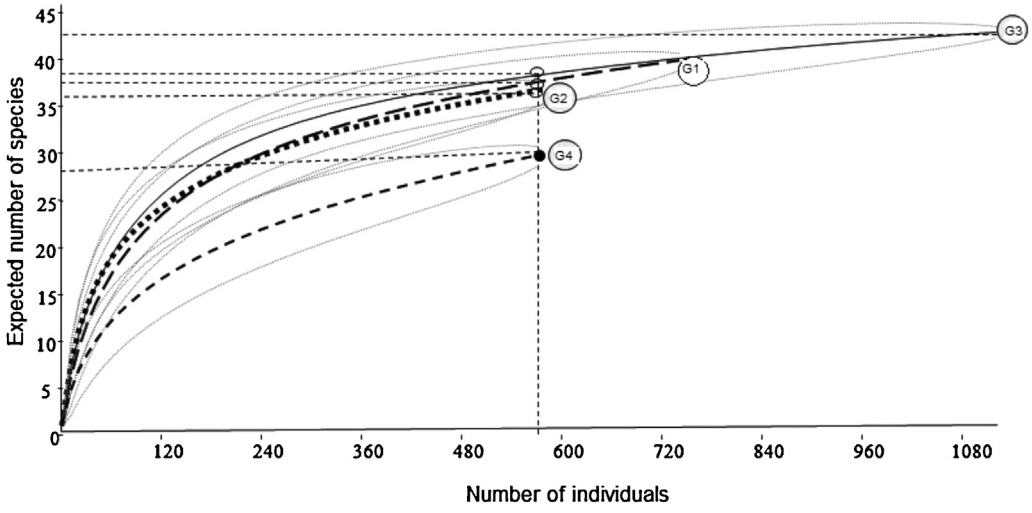

Fig. 2. Rarefaction curves representing species richness of sand flies in four categories (G1, G2, G3, and G4—black solid lines) and 95% CI (gray line) in Rio Pardo, Presidente Figueiredo, Amazonas. Number of species observed (S obs) is the number of species sampled in each category. Species richness (S sp) (estimated the number of species in each category considering equal sample size) was considered to be the number of individuals in the category with the lowest abundance of sandflies (●). The open and closed circles (●, ○) indicate S sp and the letters (G1, G2, G3, and G4) represent S obs. G1, high population density and low forest cover, G2, low population density and low forest cover, G3, high population density and high forest cover, G4, low population density and high forest cover. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A posteriori paired tests showed significant differences between the forest and all other environments, with the exception of the peridomicile ($p < 0.05$). The peridomicile environment was significantly different from the successional vegetation and fruit garden environments ($p < 0.05$) (Fig. 3).

The greatest richness of sand fly species was observed in the forest environment, where 43 species were captured. This was followed by forest edge (41), and the peridomicile (33). The successional vegetation and fruit garden environments showed the lowest richness of species, with 13 and 25 species captured respectively. We found seven vector species of *Leishmania* distributed in all environments, including the peridomicile (Table 3).

4. Discussion

Forty-nine percent of the sand fly fauna in Brazil exists in the state of Amazonas. As of 2013, 113 species had been recorded; of these, 67 are present in Manaus and nearby municipalities (Alves et al., 2012; Castellón, 2009; Galati, 2003; Oliveira et al., 2013; Young and Duncan, 1994). In this study, we collected 52 sand fly species distributed in forest interior, forest edge, fruit garden, successional vegetation, and peridomiciliary habitats in the rural settlement of Rio Pardo. In different areas of primary forest near Manaus Arias and Freitas (1982), Castellón et al. (1994) and Dias-Lima et al. (2002) found 50, 57, and 41 sand flies species, respectively. As expected, phlebotomine fauna is as diverse in Rio Pardo as it is in other areas of the State.

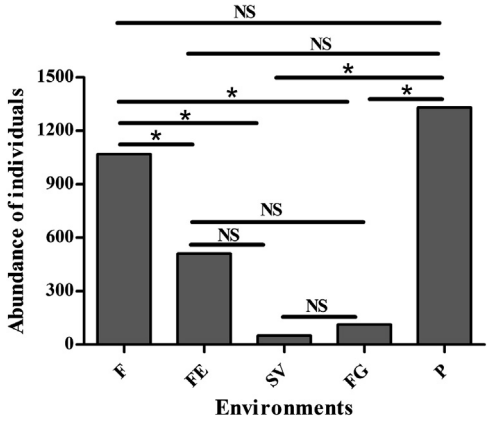

Fig. 3. Abundance of sand flies collected by CDC light traps in forest (F), forest edge (FE), peridomicile (P), successional vegetation (SV) and fruit garden (FG) environments in the settlement of Rio Pardo, Presidente Figueiredo Municipality, Amazonas State, Brazil. * Significant difference after a Kruskal–Wallis test followed by Student–Newman–Keuls test ($p < 0.05$).

The most abundant species found in the study were *N. antunesi*, *N. umbratilis*, *M. rorotaensis*, *N. anduzei* and *T. ubiquitalis*. All of these species are of medical importance, except for *M. rorotaensis*, which may transmit trypanosomes to some lizards (Lainson and Shaw, 1979; Tesh et al., 1971). Pessoa et al. (2007) found a high rate of flagellate infection in this species. In Rio Pardo, *N. antunesi* was the most abundant species in every category studied (Table 1), and was particularly abundant in peridomicile environments (Table 3). In Pará State, *Nyssomyia antunesi* is related to the transmission of *Leishmania* (*Viannia*) *lindenbergi* (Silveira, Ishikawa and de Souza). Previous studies in disturbed areas of Pará State indicate that this species is dominant in domestic animal shelters, and that it exhibits a high degree of adaptability to fragmented environments (Rangel and Lainson, 2009; Silveira et al., 1991).

The species *N. umbratilis* is the main vector of *L.* (*V.*) *guyanensis* (Floch) in the Amazon region (Arias and Freitas, 1977). This species was found primarily in forest environments, but it was also found in peridomicile and fruit garden environments, which indicates close contact between this species and humans outside the forest. Paes (1991), Feitosa and Castellón (2006) and Feitosa et al. (2012) found similar circumstances in peridomicile areas in Manaus and Santarém, both Amazonian Municipalities. *N. anduzei* is found in the same environments as *N. umbratilis*, and is also associated with the transmission of *L.* (*V.*) *guyanensis*.

Freitas et al. (2002) studied the sand fly fauna in a small rural settlement in Amapá State: *N. umbratilis* was the most abundant species at all capture sites, and a high number of individuals were infected with flagellates. During collections in Rio Pardo, this species was the second most abundant, being most frequent in forest environments followed by the forest edge; however, *N. umbratilis* was also found in fruit and vegetable gardens,

Table 3
Sand fly species abundance in forest, forest edge, peridomicile, successional forest and fruit garden from Rio Pardo rural settlement, Presidente Figueiredo Municipality, Amazonas State, collected during September–November 2009 and June–August 2010 by CDC light trap.

Species	Environments					
	F	FE	P	SV	FG	Total
Bumptomyia brumpti	5	2	3	2	0	12
Bichromomyia flaviscutellata[a]	48	17	9	0	2	76
Bichromomyia olmeca nociva[a]	10	6	13	0	0	29
Bichromomyia reducta	7	2	3	0	0	12
Evandromyia inpai	26	5	1	0	0	32
Evandromyia monstruosa	42	7	2	0	0	51
Evandromyia pinotti	7	0	1	0	0	8
Evandromyia saulensis	1	2	0	0	0	3
Evandromyia sericea	6	3	4	0	1	14
Evandromyia walkeri	19	9	47	3	8	86
Evandromyia williamsi	1	1	0	0	2	4
Lutzomyia flabellata	1	0	0	0	0	1
Lutzomyia baityi	0	0	2	0	0	2
Lutzomyia gomezi	0	1	0	0	0	1
Lutzomyia sherlocki	1	0	0	0	0	1
Micropygomyia chassigneti	0	0	1	0	0	1
Micropygomyia micropyga	8	2	10	2	7	29
Micropygomyia pilosa	2	0	0	0	0	2
Micropygomyia rorotaensis	72	39	60	16	7	194
Nyssomyia anduzei[a]	88	53	23	7	1	172
Nyssomyia antunesi[a]	130	52	890	6	12	1090
Nyssomyia richardwardi	0	1	0	0	0	1
Nyssomyia shawi	1	2	0	0	1	4
Nyssomyia umbratilis[a]	225	108	38	6	12	389
Nyssomyia yuilli yuilli	0	3	0	0	0	3
Pressatia choti	19	5	1	0	0	25
Pressatia triachanta	4	0	0	0	0	4
Pressatia trispinosa	21	1	0	0	0	22
Psathyromyia abonnenci	1	0	1	0	0	2
Psathyromyia aragaoi	15	3	2	0	3	23
Psathyromyia cuzquena	0	2	0	0	0	2
Psathyromyia dreisbachi	9	2	14	0	2	27
Psathyromyia inflata	1	1	0	0	0	2
Psathyromyia lutziana	2	8	0	0	1	11
Psathyromyia punctigeniculata	17	2	3	0	2	24
Psathyromyia scaffi	3	4	2	0	1	10
Psychodopygus amazonensis[a]	47	26	4	0	5	82
Psychodopygus carrerai carrerai	5	2	0	0	1	8
Psychodopygus chagasi	18	17	4	0	9	48
Psychodopygus claustrei	49	7	0	0	1	57
Psychodopygus davisi[a]	43	47	2	0	5	97
Psychodopygus hirsutus	0	2	0	0	0	2
Psychodopygus squamiventris squamiventris	3	11	5	0	0	19
Sciopemyia nematoducta	19	9	9	1	1	39
Sciopemyia pennyi	0	0	0	1	0	1
Sciopemyia sordellii	17	3	12	1	3	36
Trichophoromyia eurypyga	45	26	30	2	9	112
Trichophoromyia gibba	1	0	0	0	0	1
Trichophoromyia ubiquitalis[a]	15	16	114	3	16	164
Trichopygomyia trichopyga	7	1	1	1	1	11
Viannamyia furcata	8	1	11	0	0	20
Viannamyia tuberculata	0	0	8	0	0	8
Total	1069	511	1330	51	113	3074

F, forest; FE, forest edge; P, peridomicile; SF, successional vegetation; FG, fruit garden.
[a] Vector *species Leishmania* sp.

successional vegetation, and in peridomiciliary areas. The presence of this species in peridomicile and garden environments suggests that vectors and humans are in close contact, and it highlights the risk that the transmission of CL may occur close to dwellings—not just in forested areas. In Manaus, Brazil, Paes (1991) found *N. umbratilis* not only in the forest and outdoors, but also inside occupied dwellings in neighborhoods on the periphery of the city.

In Pará State, the species *T. ubiquitalis* is related to the transmission of CL cases caused by *L.* (*V.*) *lainsoni* (Silveira, Shaw, Braga, and Ishikawa) (Silveira et al., 1991). Despite the low anthropophily of this sand fly species in natural environments, this species can bite humans under laboratory conditions (Rangel and Lainson, 2009; Rebêlo and Oliveira-Pereira, 2001; Silveira et al., 1991). In Rio Pardo, this species was the fifth-most abundant, found mainly in peridomestic environments.

The highest index diversity was observed in environments with high population density and high forest cover (G3), and environments with low population density and low forest cover (G2). Low values on the Shannon & Wiener index (H') were due to the abundance of five predominant species: *N. antunesi*, *N. umbratilis*, *M. rorotaensis*, *N. anduzei*, and *T. ubiquitalis*; these species were found in every category studied. Other species were found in low numbers. The H' and Pielou equitability (J') indices in G4 were influenced by the presence of a single predominant species (*Ny. antunesi*); while in G3, a number of species shared predominance. Similar indices of sand fly diversity in the Amazon region were observed

in Acre (Azevedo et al., 2008) and in the Amazonas States (Gomes et al., 2013).

Despite the importance of forest cover for maintaining sand fly populations, areas with a high human population contain more sources of food (humans, domestic animals, wild animals attracted by food, agriculture, and trash). In addition, the accumulation of substrates can facilitate immature stages of sand fly development. Our observations also suggest that various species of sand fly have an adaptive tendency to colonize or invade new habitats in deforested and anthropically modified environments. This trend was previously reported by Valderrama et al. (2011) in Panama, who also observed higher sand fly abundance in areas of forest fragmentation.

Saraiva et al. (2008) compared sand fly fauna between the banks of Rio das Velhas, in Minas Gerais State, Brazil. They reported higher species diversity in marginal regions with a high human population density. In the area studied, as in many other rural settlements recently cleared and colonized, the sanitary conditions were inadequate and organic residues had accumulated, creating conditions that can attract rodents and marsupials. The possible infection of these animals with *Leishmania* spp., and the joint presence of sand fly vectors and humans could combine to trigger the local emergence or outbreak of infectious disease (Galati et al., 2003; Legriffon et al., 2012; Saraiva et al., 2008). A similar phenomenon was observed in periurban areas of Manaus city, where *D. marsupialis* was found to be infected with flagellates (Arias and Naiff, 1981; Guerra et al., 2007).

The adjacent peridomicile environment showed the greatest species abundance. According to Campbell-Lendrum et al. (2001), Jimenez et al. (2000), and Ximenes et al. (1999), sand flies can be attracted by environmental changes associated with the construction of new houses, and by the presence of farms with poultry, cattle, pigs, and horses. This is particularly true when forests or forest fragments are nearby. Landscape modifications can change the distribution patterns of sand fly species and influence the dynamics of parasite transmission, by creating differential access to reservoirs and hosts (Campbell-Lendrum et al., 2000; Chaves, 2011; Neitzke-Abreu et al., 2012). For example, in a focus of canine visceral leishmaniasis—in an urban area of the Bonito municipality, Mato Grosso do Sul State—*L. longipalpis* (Lutz and Neiva) was found to be most predominant in anthropogenic environments containing henhouses and pigsties (Nunes et al., 2008).

In a rural area where visceral leishmaniasis has been registered, animal shelters offered a peridomicile environment favorable for maintaining *L. longipalpis* populations (Galati et al., 2003). Legriffon et al. (2012) observed a decrease in sand fly abundance after some of the animal shelters were cleaned and reorganized, and after shelters were moved away from households. This reinforces the idea that animal shelters can serve as resting areas, breeding sites, and blood meal sources for sand fly populations.

Despite differences in degrees of deforestation and human population density, most sand flies species were found in all categories. Although the number of observed species varied slightly among categories—G1 (39 species), G2 (37), G3 (43), and G4 (34)—rarefaction estimates showed that these categories did not differ in species richness. The only exception was G3 (high population density and high forest cover), which had the highest Species observed (S obs) and Species expected (S sp). These results suggest that sand fly diversity and richness are generally higher in modified environments. These results differ from those of Fernandez et al. (2012) in Argentina, where degraded environments show lower species richness. The fact that similar numbers of species were observed in all four categories, suggests that most sand fly species adapt readily to different environmental conditions, including those found in peridomiciliary areas. This adaptability increases the chance of contact between vectors and humans, thereby increasing the risk of leishmaniasis transmission.

The results of this study show that both forest cover and human population density affect sand fly diversity and abundance. These effects may be amplified when both factors are conjoined. Low forest cover can reduce sand fly numbers, but high human population density can produce environmental conditions favorable for maintaining the life cycles of several sand fly species that are adaptable to these environments. Pessoa et al. (2007) observed a decrease in the abundance of sand flies after the timber harvest in Itacoatiara, Amazonas. Despite this reduction in the number of sand flies, females with flagellates were still found after the harvest. Torres (2005) studied sand fly fauna in Amazonian forest fragments and noted that the populations remained diversified in fragments of different sizes, and that infected vectors persist in fragments up to one hectare in size.

We hypothesize that some species of sand flies tend toward synanthropization due to the increased availability of food, and of locations for rest and oviposition. In settled areas, the presence of domestic animals and the circulation of wild animals provide the vector with a source of food that enables its adaptation to new environments. This changes the dynamics of parasite transmission, and is therefore an important epidemiological factor.

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