# Sand Fly Vectors of American Cutaneous Leishmaniasis in Brazil

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The eco-epidemiology of Brazilian American cutaneous leishmaniasis (ACL) is a complex of epidemiological chains involving different parasites, vectors, and reservoirs. The transmission of the seven *Leishmania* spp. associated with ACL in Brazil involves different phlebotomine species that are closely associated with the parasite's mammalian reservoirs, which range from Xenathra to rodents to primates, resulting in a variety of transmission cycles in the different geographical regions in the country. However, evidence is also accumulating that indicates that there are geographical clades of the different *Leishmania* species that may be associated with different vectors. *Leishmania* species (*L.* (*Leishmania*) *amazonensis*; *L.* (*Viannia*) *braziliensis*; *L.* (*V.*) *guyanensis*; *L.* (*V.*) *lainsoni*; *L.* (*V.*) *shawi*; *L.* (*V.*) *naiffi*; and *L.* (*V.*) *lindenbergi*) are associated with human cutaneous leishmaniasis. However, other Brazilian parasites of the subfamily Leishmaniinae exist, some of which are found in sand flies (*L.* (*V.*) *utingensis*; *Endotrypanum* spp.), whereas others (*L.* (*Mundinia*) *enriettii*; *Porcisia deanei*) have so far not been recorded in them (the parasite nomenclature follows that published in Espinosa et al. 2016).

Over the years well-defined and accepted criteria, data from field studies and—in some cases—experimental results have led to some species being considered as ACL vectors. In our opinion, some are primary vectors, and we will discuss these first. However, an increasing amount of data, principally from molecular studies, suggest that other sand-fly species may be participating in the cycles, and we will discuss these towards the end of this chapter.

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## *Nyssomyia intermedia* (Lutz & Neiva, 1912)

*Nyssomyia intermedia* was described from specimens collected at Fazenda Ouro Fino in the municipality of Além Paraíba (MG) and also from SP and RJ, where it was found to be abundant in homes. It was one of the first phlebotomine species to be described in the neotropical region (Barretto 1961; Martins et al. 1978; Young and Duncan 1994; Marcondes 1996). The current geographic distribution of *Ny. intermedia* includes Brazil (PA, PI, MA, PE, PR, SC, RS, MG, MS, GO and TO [Fig. 1]), Argentina and Paraguay (Young and Duncan 1994; Marcondes et al. 1997; Rangel and Lainson 2003, 2009).

Recently published projections under climate-change scenarios predict a global decrease in the climatically suitable areas of *Ny. intermedia* in Brazil with a slight expansion in specific areas of the Northeast region for the upcoming decades (McIntyre et al. 2017).

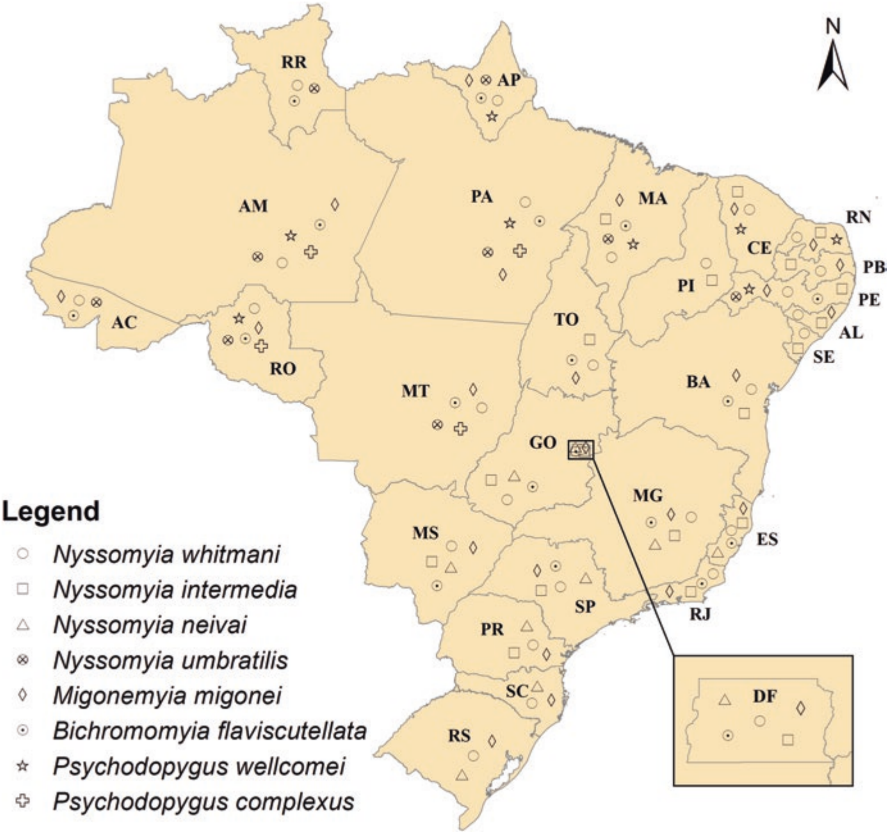

**Fig. 1** Distribution of sand-fly vectors of ACL in Brazil

One year after the suggestion of the transmission of cutaneous leishmaniasis by sand flies in the Old World (Sergent et al. 1921), Aragão (1922, 1927) reported in the city of Rio de Janeiro (locality Águas Férreas, currently Cosme Velho and Santa Tereza) the importance of *Ny. intermedia* in the transmission of *L.* (*V.*) *braziliensis* by inoculating a triturated pool of this sand fly in the nose of a dog and thus experimentally reproducing the disease for the first time on the American continent. Subsequently, Costa Lima (1932) recorded the occurrence of *Ny. intermedia* and *Migonemyia migonei* in the neighbourhoods of Copacabana and Laranjeiras, near the slopes of Corcovado and Santa Teresa hills, in Rio de Janeiro. In 1952, Forattini and Santos found promastigotes (referred to as "leptomonads") in *Ny. intermedia*, like those observed by Aragão (1922).

Forattini (1973) pointed out an irregular seasonal behaviour for this species in observing greater population density during the colder months of the year. However, Rangel et al. (1990) reported the occurrence of the vector throughout the year, and Souza et al. (2003) demonstrated that in Rio de Janeiro, *Ny. intermedia* has high density during the hottest times of the year.

Epidemiological evidences suggest *Ny. intermedia* as a vector of *L.* (*V.*) *braziliensis* in endemic areas in the Southeast, considered the main ACL vector in SP and RJ (Forattini 1953, 1973; Forattini et al. 1976; Araújo Filho et al. 1981; Gomes et al. 1986; Rangel et al. 1986, 1990, 1992, 1999; Meneses et al. 2005; Rangel and Lainson 2009). Pita-Pereira et al. (2005) isolated the parasite from *Ny. intermedia*, captured in a focus of ACL in Jacarepaguá (RJ), and identified it as *L.* (*V.*) *braziliensis*. This reinforced all the ecological and epidemiological evidence regarding this vector. In MG and ES, it shares its vector role with *Ny. whitmani* (Barretto 1943; Falqueto 1995; Mayrink et al. 1979; Aguiar & Soucasaux 1984; Souza-Rocha et al. 2007).

*Ny. intermedia* starts its hematophagous activities at dusk and peaks during the first half of the night. It is abundant inside houses; in peri-domiciliary environments in domestic-animal shelters, such as birds, dogs, equines, and rodents; and in the forest to feed on other wild animals (Forattini 1953, 1973, 1976; Araujo Filho et al. 1981; Rangel et al. 1986; Gomes and Galati 1989; Pirmez et al. 1997; Afonso et al. 2005).

## *Nyssomia neivai* (Pinto, 1926)

This species was described from a sample of males collected in the city of São Paulo at the Butantan Institute. It was considered a synonym of *Ny. intermedia*. Marcondes (1996), however, revalidated *Ny. neivai* as a species after a study of morphological and morphometric characters of specimens collected in Bolivia and the holotypes of both species. The distinction between *Ny. intermedia* and *Ny. neivai* was made possible mainly by morphological differences in the spermathecae (Marcondes 1996; Marcondes and Alexander 2003; Andrade-Filho et al. 2004). The males of the species were not separated by morphology but only by a series of morphometric data

(Marcondes and Borges 2000). According to Andrade-Filho and Brazil (2003), the presence of cryptic species, such as *Ny. intermedia* and *Ny. neivai*, is a result of allopatry, which in the case of these species must have occurred about 250,000 years ago, thus indicating that the separation of species was recent.

*Ny. neivai* occurs in colder and drier regions of Brazil compared with *Ny. intermedia* (Marcondes et al. 1998, Fig. 1). It was suggested as an important vector mainly in the states of the South and Southeast regions. According to McIntyre et al. (2017), the appropriate climatic range of *Ny. neivai* is currently restricted to the South, Southeast, and Central West regions of Brazil, extending to western Bolivia and Paraguay, like *Ny. intermedia*. The investigators predict that *Ny. neivai* will face changes in its climatic range in the future with the Central West region, in particular, becoming less habitable.

The first record of *Ny. neivai* naturally infected by *L.* (*V.*) spp., possibly *L.* (*V.*) *braziliensis*, was described by Marcondes et al. (1999) using PCR techniques of specimens collected in Piçarras (SC). Later, Silva et al. (2008) found a high incidence of *Ny. neivai* in 37 municipalities of PR where 75.6% of all specimens collected were *Ny. neivai*, thus suggesting their possible participation in the disease cycle. This hypothesis gained strength with the encounter of specimens of *Ny. neivai* infected with *L.* (*V.*) spp. in this state by multiplex PCR techniques (Oliveira et al. 2011). Since 2002, autochthonous cases of ACL by *L.* (*V.*) *braziliensis* have been recorded in the outskirts of the city of Porto Alegre (RS), in vegetation areas near streams (Pita-Pereira et al. 2009). Entomological studies revealed a large predominance of *Ny. neivai* in the area of occurrence of the cases (Gonçalves 2003); later, the natural infection by *L.* (*V.*) *spp.* was found in this species by PCR techniques, thus identifying the phlebotomine as a potential vector of *L.* (*V.*) *braziliensis* (Pita-Pereira et al. 2009).

Recent investigations in the Southeast region suggest that the migration of *Ny. neivai* from forests to residential areas has resulted in the occurrence of ACL cases. However, in a study on the biology of this sand fly in an endemic area in São Paulo, the investigators considered it as having low competence as *Leishmania* vector (Casanova et al. 2009). Studies on the feeding preferences of *Ny. neivai* showed that it is an opportunistic sand fly (feeding on domestic animals such as pigs, dogs, rabbits, and chicken) with few specific host preferences (Dias-Sversutti et al. 2007).

## *Migonemyia migonei* (França, 1920)

The literature suggests that *Mg. migonei* is a sylvatic species found in forests, generally areas of abundant vegetation, occurring less frequently in secondary forests and in capoeiras. However, it is common to observe this phlebotomine inside houses and in domestic animal shelters (Barretto 1943; Forattini 1973; Araújo Filho et al. 1981; Rangel et al. 1986). It is believed that this species has great capacity for adaptation, surviving in degraded areas by man, and approaching impacted environments where it feeds on domestic animals and man, possibly being able to maintain the enzootic cycle of the disease in areas of secondary forest (Ferreira et al. 2001; Queiroz et al. 1994; Rangel and Lainson 2009). It is distributed in Brazil (AP, AC, PA, MA, CE, PB, PE, BA, ES, RJ, SP, PR, SC, RS, MG, MT, Fig. 1), Venezuela, Argentina, Paraguay, Peru, Trinidad, and Tobago (Young and Duncan 1994; Rangel and Lainson 2003).

According to seasonal studies conducted in PE, *Mg. migonei* can be captured during all months of the year; however, other studies have indicated the absence of the vector during the coldest and driest months (Rangel and Lainson 2009; Guimarães et al. 2012).

Its hematophagous activity begins at dusk and advances into the night. According to Nieves and Pimenta (2002), *L.* (*V.*) *braziliensis* infections were observed in *Mg. migonei* females that fed on wild rats, opossums, horses, and males. The first citation of the role of *Mg. migonei* in the ACL-transmission cycle was through the encounter of a species naturally infected by flagellates, probably *Leishmania* promastigotes, in 1941 by Pessoa and Coutinho in São Paulo. Later studies also showed the coincident increase of ACL cases and *Mg. migonei* specimens in SP (Camargo-Neves et al. 2002; Rangel and Lainson 2009). In RJ, the species has been implicated as a probable vector in regions, such as Ilha Grande and Jacarepaguá, where the species has a preference for biting dogs and is associated with the maintenance of canine leishmaniasis in addition to its natural infection with *L.* (*V.*) *braziliensis* in Jacarepaguá (Pita-Pereira et al. 2005; Rangel and Lainson 2009; Gouveia et al. 2012; Carvalho et al. 2014). *Mg. migonei* has also been associated with ACL transmission in MG and ES. In the Northeast region, more precisely in CE, *Mg. migonei* was found to be naturally infected by *L.* (*V.*) *braziliensis* (Azevedo & Rangel 1991, Queiroz et al. 1994). However, this occurred only as a secondary vector of ACL (Rangel and Lainson 2009). Recently molecular studies using PCR techniques identified *Mg. migonei* infected by *L.* (*L.*) *infantum chagasi*, the etiological agent of AVL, in PE and CE (Carvalho et al. 2010; Silva et al. 2014a, b; Rodrigues et al. 2016).

## *Nyssomyia whitmani* (Antunes & Coutinho, 1939)

*N. whitmani* was described by Antunes and Coutinho in 1939 as *Flebotomus whitmani* in honour of Dr. Whitman of the Rockefeller Foundation, which collaborated with the Brazilian government in the Yellow Fever Campaign. The new species was described based on male and female specimens collected in Ilhéus (BA). Until 1939, it was misidentified as *Ny. intermedia*. In Brazil, this species was registered throughout the country except for SC and RS (Fig. 1) and beyond in French Guiana, Paraguay, Peru, and Argentina (Young and Duncan 1994).

The participation of *Ny. whitmani* in the epidemiological chain of ACL is restricted to the Brazilian territory where its first report as a vector was in SP when it was found infected by flagellates, possibly *Leishmania* (Pessôa & Coutinho 1941). It was considered a sylvatic species, although it could be found inside houses that were located within or near the forest. At dusk, it was found biting man and feeding on dogs and was shown to be present in large numbers in chicken houses. Because the localities Barretto (1943) studied were close to deforested areas, he suggested that the high-density population under these circumstances was simply due to the wide variety of blood sources available to this sand fly.

In 1953, Forattini confirmed the presence of *Ny. whitmani* in both the forest and nearby domestic animal shelters in SP. Later (1960) he commented on the fact that although initially dependent on primary forest, this sand fly could now be captured during several months of the year inside houses, peri-domestic pigsties, and banana plantations and that there was no doubt that it was now thriving in a domestic environment. In the same publication, Forattini (1953) believed that although there were reports indicating that *Ny. whitmani* coexists with *Ny. intermedia* in areas recently occupied by man and may outnumber the latter species as the environmental alterations proceed, more detailed information was needed to confirm this suggestion.

In RJ in general, the *Ny. whitmani* population has for some time remained at a low level (Rangel et al. 1986, 1990; Oliveira et al. 1995). Souza et al. (2001) registered this sand fly's presence in the Atlantic Forest and, more importantly, its frequency in residential areas close to the forest. The same investigators recorded both *Ny. intermedia* and *Ny. whitmani* biting man in a peri-domestic habitat close to the forest and noted that the former prevailed in the residential area, whereas the latter was the most frequent of the two insects in the forest. They observed a higher density of *Ny. whitmani* during winter months, whereas *Ny. intermedia* was most abundant during the hotter months of the year (Souza et al. 2002).

The tendency of *Ny. whitmani* to occupy residential areas in MG was discussed by Mayrink et al. (1979) and Passos et al. (1991). It was found feeding on man and domestic animals and thought to possibly be breeding in this habitat. Conversely, it was found in very small numbers in the neighbouring forest.

In Northeast Brazil, in BA, CE and PE, its behaviour has been shown to be like that seen in the Southeast region, namely, highly attracted to man and well adapted to the domiciliary habitat (Barreto et al. 1982; Vexenat et al. 1986; Brandão-Filho et al. 2003). In BA, it was suggested that *Ny. whitmani* might be breeding on cocoa plantations (França et al. 1991).

Regarding seasonality, differences in behaviour have been noted in different regions of Brazil, probably due to differing climatic conditions. In the Southern region, for example, Barretto (1943) noted its presence year-round, whereas in studies in Petrópolis, RJ, it was found in greater numbers during the months of low temperatures in June through August (Souza et al. 2002).

Although the dusk and nocturnal feeding habit of *Ny. whitmani* follows the usual sand-fly pattern (Barretto 1943), it, too, has been shown to be somewhat variable in different regions of Brazil. In the Northeast, Azevedo and Rangel (1991) showed that it can also be captured during the whole of the dawn period, in chicken houses or feeding on equines, with maximum activity from 1–3 am. Souza et al. (2004) noted that in RJ it could be found feeding on man, in the peri-domestic habitat, between 4 and 6 am, and such behaviour was previously recorded by Teodoro et al. (1993) in PR; studies on host preferences of *Ny. whitmani* among domestic animals, made in the same state, showed that this insect is an opportunistic feeder resulting in a wide choice of hosts in the peri-domestic environments of human colonization.

In the primary forest, in several different regions of PA, Lainson et al. (1979) noted that *Ny*. *whitmani* has very different habits from those discussed previously in other regions. It was found to be essentially sylvatic and was captured principally from large tree trunks and in the forest canopy. It was disinclined to bite man and attempts to demonstrate its invasion of houses located very near the forest were completely unsuccessful. Subsequent studies confirmed these observations and led to the conclusion that any divergence from this behaviour is likely to occur only under special conditions (Ready et al. 1986; Lainson 1988; Shaw et al. 1991).

This situation led to the suggestion that *Ny*. *whitmani* might represent a species complex of two or more taxa (Lainson 1988), and this has resulted in several comparative studies on populations of this sand fly from widely different areas of Brazil. Some investigations suggested the existence of at least three different lineages of this sand fly based on biological characters, geographical variations, and morphometric features together with observations on sequences of mitochondrial DNA (Rangel et al. 1996; Ready et al. 1997, 1998). Rangel et al. (1996) made it clear, however, that they did not discard the possibility that the populations they studied—from PA, CE, and BA—could represent a cline. Ishikawa et al. (1999) studied populations from the North, Northeast, Southeast, and the South regions and indicated the existence of a clade from RO within the lineage of forested areas, which included haplotypes of the Amazon and Atlantic forests and Ilhéus (the type locality of *Ny*. *whitmani*). They suggested that their findings did not sustain the hypothesis of a cryptic species complex but rather the occurrence of a recent crossing-over of populations in forested areas.

Margonari et al. (2004) studied populations of *Ny*. *whitmani* from the Northeast and the Southeast of Brazil. They confirmed observations on the similar morphometry of these but presented evidence of two biogeographical "clusters." Later, however, they suggested the existence of a genetic flow between the two lineages.

Regarding the incrimination of *Ny*. *whitmani* as an important vector of ACL, the first suggestion of this was made in 1941, when Pessôa and Coutinho found a specimen from SP infected by flagellates, which were considered possibly to be promastigotes of *Leishmania*: As a result, entomological investigations were intensified in areas of ACL transmission in this region and soon showed that although considered as a sylvatic species, *Ny*. *whitmani* was a highly anthropophilic sand fly with a particularly dense population (Barretto 1943; Forattini 1954).

In Southeastern Brazil, data in the literature suggest the participation of this sand fly in the transmission of ACL in a focus of the disease in Caratinga, MG, and in the mountainous area of Afonso Cláudio (Mayrink et al. 1979; Falqueto 1995), and Souza et al. (2002) considered that it might be sharing the role of a vector of *L*. (*V*.) *braziliensis*, together with *Ny*. *intermedia*, in rural RJ. Recently, the finding of a specimen of *Ny*. *whitmani* infected with a *Leishmania* of the subgenus *Viannia* by PCR analysis, in a region very close to Belo Horizonte, MG, has led to the suggestion that this sand fly could be the vector of cutaneous leishmaniasis in that area (Carvalho et al. 2008).

In the South, *Ny. whitmani* was also considered as a possible vector of ACL in PR, whereas in the northern part of this state a natural infection with *L.* (*V.*) *braziliensis* found in one specimen and the insect's high population density clearly emphasized this sand fly's medical importance (Luz et al. 2000; Teodoro et al. 2003).

In all areas of ACL in Northeast Brazil, this same species of sand fly is considered as an important vector of the disease based on the finding of specimens infected by *L.* (*V.*) *braziliensis* in the area of Três Braços, BA (Hoch et al. 1986; Ryan et al. 1990). The sand fly's predominance in houses and the peri-domestic habitats in general prompted these investigators to suggest the development of a purely domestic cycle of transmission by *Ny. whitmani*. In Ilhéus, BA, the type locality of this sand fly, its fondness for human blood, and its high population density in the domestic habitat led to the same conclusion (Azevedo and Rangel 1991). In the Serra de Baturité, CE, a parasite of the subgenus *Viannia* and others positively identified as *L.* (*V.*) *braziliensis* were found in dissected *Ny. whitmani* (Azevedo et al. 1990; Queiróz et al. 1994) and, once again, these findings—together with population density in the peri-domestic habitat—indicated this fly as the local vector of ACL due to this parasite. Gil et al. (2003) registered *Ny. whitmani* as the second most prolific sand fly in captures made in the central area of RO, stressed its preferential arboreal habits, and recorded the presence of unidentified trypanosomatid parasites in some specimens.

In the municipalities of Rio Branco, Bujari, and Xapuri, AC, a study of sand-fly fauna and the potential vectors of ACL showed that *Ny. whitmani* was the most abundant species with its spatial distribution coinciding with proven transmission sites of *L.* (*V.*) *braziliensis*: it was therefore suggested that this sand fly was a probable vector of this parasite in that region (Azevedo 2008).

The state of Tocantins (TO) has suffered environmental impacts resulting in ecological changes due to the construction of hydroelectric plants, agricultural activities, and the establishment of new settlement areas, and the increasingly high incidence of ACL in this region has probably been due to these activities. *Ny. whitmani* is found in most of the endemic municipalities especially in areas that have been degraded by man (Vilela et al. 2008). In the Central West region, some studies conducted in areas that suffered environmental changes due to human activities have suggested *Ny. whitmani* as an important vector of *L.* (*V.*) *braziliensis* (Galati et al. 1996; Dorval et al. 2009).

This sand fly is one of the principal ACL vectors in Brazil having been recorded in large numbers of endemic areas (Costa et al. 2007) and in association with a wide vegetation diversity. Environmental and climatic changes most probably account for the spread of ACL in Brazil in recent years (Shaw 2007), and *Ny. whitmani* adapts readily to new environments, such as degraded areas, in association with domestic animals and man in rural and peri-urban areas (Costa et al. 2007; Shaw 2008). Peterson and Shaw's (2003) ecological niche modelling of ACL vectors predicted that climate warming would favour the adaptation of *Ny. whitmani* to new areas as well as its geographical expansion within Brazil.

The very different behaviour of *Ny. whitmani* in the primary forest in PA, North Brazil, has already been discussed, and until now this sand fly has not been associated with ACL due to *L.* (*V.*) *braziliensis* in this region. The suggestion was made, however, that promastigotes of a member of the subgenus *Viannia* found in this sand fly in Monte Dourado, PA—an area of ACL due to *L.* (*V.*) *guyanensis*— were probably those of this parasite and that *Ny. whitmani* was participating in its transmission together with the principal vector, *Ny. umbratilis* (Lainson et al. 1981b). The parasite was not identified at the time, and in view of later isolations of *L.* (*V.*) *shawi* from *Ny. whitmani* in another area of primary forest in PA (Lainson et al. 1989), it was suggested that the parasite of *Ny. whitmani* in Monte Dourado, PA, was also *L.* (*V.*) *shawi* (Rangel et al. 1996, Lainson & Shaw 1998). However, the Monte Dourado *Ny. whitmani* infections were recently typed (de Souza et al. 2017) and proved to be *L.* (*V.*) *guyanensis*. Therefore, we conclude that in the Brazilian Guiana Shield *Ny. whitmani* participates in the transmission of *L.* (*V.*) *guyanensis* as previously suggested (Lainson et al. 1981b).

The comment by Lainson (1988), based on years of entomological observations in areas of primary forest in PA by workers in the Instituto Evandro Chagas (i.e. that in Amazonia *Ny. whitmani* is "seldom observed biting man, and never in large numbers") conflicts with the frequency of human *L.* (*V.*) *shawi* infections. One explanation could be that other anthropophilic sand flies are involved in the transmission of *L.* (*V.*) *shawi* with *Ny. whitmani* merely maintaining the enzootic in wild animals. However, Campbell-Lendrum et al. (1999) observed no significant difference in the anthropophily of *Ny. whitmani* from North Brazil and *Ny. whitmani* sensu stricto from other areas in Brazil. The Instituto Evandro Chagas team's observations were made in primary forest biomes, in which it was either absent (de Souza et al. 1996; Ward et al. 1973b) or present in small numbers (de Souza et al. 2016, 2017). Those of Campbell-Lendrum et al. (1999) were performed in a "patch of degraded primary forest" in an area of extensive deforestation. Another study (Donalisio et al. 2012) clearly showed a highly significant difference between the sizes of populations in forested and peri-domiciliary areas of PE. A simple explanation for the apparently conflicting opinions in relation to the anthropophily of Amazonian *Ny. whitmani* populations is variations in population densities related to environmental conditions. The fact that fewer flies are attracted to men in different areas is perhaps not because of difference in their anthropophily rather but differences in populations sizes.

## *Bichromomyia flaviscutellata* (Mangabeira, 1942)

In their various field trips in Brazil, Mangabeira and collaborators captured approximately 17,000 specimens of sand flies representing 57 different species and with 35 of them being new to science. Among the latter was Mangabeira's description of *Bi. flaviscutellata*, which was based only on male insects and collected in the locality of Aurá close to Belém, PA. Later, Sherlock and Carneiro (1962) described the female of the species after the establishment of a laboratory colony of this sand fly from BA. It must be stressed, however, that the taxonomic status of the material from BA has been questioned (Young and Duncan 1994). The specific name of this sand fly was probably chosen in view of the double colouration of the shield where the scutelum is clear and the remainder of the structure a dark brown (Latin *flavus* = golden; yellow + *scutu* = shield).

*Bi. flaviscutellata* has an extensive geographical distribution (Fig. 1) and can be found in very different habitats such as primary forest, secondary or copse-like vegetation, and lowland *várzea* forest, which during half of the year is subject to various degrees of flooding. Ready et al. (1983) showed that together with the various rodents and marsupials on which it feeds, it rapidly adapts to plantations of introduced trees, such as *Pinus* and *Gmelina*, and it is occasionally captured in the peridomestic habitat of houses located near forest (Lainson et al. 1994). The distribution and population ecology of *Bi. flaviscutellata* are also influenced by climate, particularly by seasonal precipitation (Shaw and Lainson 1972; Ready et al. 1983). Projections from climate-change scenarios suggest an expansion of climatically suitable areas for *Bi. flaviscutellata* in the Southeast and South regions of Brazil in the future (Carvalho et al. 2015). Given continuous environmental and climatic changes, there are modifications in the behaviour of some sand-fly vectors of leishmaniasis, and in the Brazilian *Cerrado* of Central Brazil (extensive, flat areas of low, fire-resistant trees, small palms, and thorny bushes), it is possible to note the spread of *Bi. flaviscutellata* found in association with domestic-animal shelters and the presence of new cases of anergid diffuse cutaneous leishmaniasis (ADCL) (Vilela et al. 2008, 2011; Shaw 2008; Nunes et al. 2008; Queiroz et al. 2012; Brito et al. 2014).

*Bi. flaviscutellata* is a low-flying sand fly that is essentially nocturnal in its biting habits and highly attracted to rodents but not greatly attracted to man (Lainson and Shaw 1968; Shaw and Lainson 1968; Shaw et al. 1972; Gomes 1994; Vilela et al. 2006, 2007). This is fortunate because it is the proven vector of *Leishmania* (*L.) amazonensis*, which, in addition to being an agent of single-lesion cutaneous leishmaniasis, is also the cause of ADCL in individuals with a faulty immunological system. ADCL is highly disfiguring and cured with difficulty. In Brazil, human cases of ADCL were notified in North, Northeast, Central West, and Southeast regions (Costa et al. 2009). In 2007 the first autochthonous human case of ADCL from RJ was notified in the municipality of Paraty (Azeredo-Coutinho et al. 2007). Despite the records of *Bi. flaviscutellata* in the neighbouring municipality of Angra dos Reis (Araújo Filho et al. 1981; Carvalho et al. 2013), the vector remains to be detected in Paraty even after 3 years of monthly sand-fly captures in the region (Vieira et al. 2015). *Bi. flaviscutellata* was not detected in Paraty probably because animal-baited Disney traps were not yet used. This has proven to be the best capture method for zoophilic sand flies such as *Bi. flaviscutellata* (Shaw & Lainson 1968; Dorval et al. 2007, 2009, 2010).

In 1963, Lainson paid a visit to the Instituto Evandro Chagas in Belém, PA, and during a demonstration of the animal-trapping programme of the Rockefeller Virus Laboratory discussed the unique opportunity this held for the examination of these animals for evidence of *Leishmania* infections: ACL was a considerable public health problem in the Amazon Region of Brazil. The director of the programme, the late Dr. Otis Causey, was impressed with the similarity of cutaneous lesions he had seen on the tails of wild rodents and those caused by *Leishmania* (*L.) mexicana* on the tails of forest rodents in Belize, Central America (Lainson and Strangways-Dixon 1964). He promised to look more closely at the next ones he saw and within a few days presented Lainson with a stained smear of a lesion on the tail of the rodent *Oryzomys capito*, which was rich in amastigotes. At first it was thought that the parasite was *L.* (*V.*) *braziliensis* (Guimarães & Costa 1966), but after subsequent study of the parasite it was given the name of *Leishmania mexicana amazonensis* (Lainson & Shaw 1972) and later amended to *Leishmania* (*L.) amazonensis* (Lainson & Shaw 1987).

With the knowledge that rodents were important reservoir hosts of the parasite, rodent-baited Disney traps were used to capture sand flies attracted to them. By far the greatest number trapped were *Bi. flaviscutellata*, and dissection of these revealed 8 of 2706 to be heavily infected with promastigotes, which proved to be those of *L.* (*L.*) *amazonensis* (Lainson & Shaw 1968): During this and continuing studies, a total of 45 heavily infected *Bi. flaviscutellata* were recorded in 7498 females dissected, and on no occasion was the parasite encountered in other species of sand flies from the same area.

Finally, *L.* (*L.*) *amazonensis* was experimentally transmitted from hamster to hamster by the bite of *Bi. flaviscutellata* (Ward et al. 1977). This species was replaced in the upper reaches of the Amazon River in the Rondônia and Amazonia states by *Bi. olmeca nociva* and *Bi. reducta*. Infections of *L.* (*L.*) *amazonensis* have been found in both, and it seems likely that these two species are its vector in these areas.

## ***Nyssomyia umbratilis* (Ward & Fraiha, 1977)**

During a study of the epidemiology of cutaneous leishmaniasis in Surinam in 1966, Wijers and Linger recorded flagellate infections in a tree-trunk inhabiting sand fly, which they referred to as *Phlebotomus anduzei* (syn. *Ny. anduzei*). It was thought to be the most likely vector of "bosch yaws," or *pian-bois*, due to *L.* (*V.*) *guyanensis*, but their attempts to infect hamsters with the flagellates failed, and the parasite remained unidentified.

Lainson et al. (1976) worked in the primary forest of Monte Dourado (Jari), PA, Brazil, north of the Amazon River, where approximately 300 cases of ACL due to *L.* (*V.*) *guyanensis* were recorded, in 1 year, in men working on deforestation. They recorded massive infections with *L.* (*V.*) *guyanensis* in 4 of 55 specimens of a sand fly considered, at the time, to be *Ny. anduzei* and isolated the parasite after the intradermal inoculation of hamsters. Suspicions were aroused during these studies, however, that the vector was not in fact *Ny. anduzei*, and subsequent morphological studies showed that it was a closely related and morphologically very similar sand fly that was new to science.

Ward and Fraiha (1977) described the new sand fly as *Ny. umbratilis* from 10 females collected during the work in Monte Dourado, PA, and an intense study of its behaviour was initiated in the same area (Lainson et al. 1979). It was found that although sand-fly species of the subgenus *Psychodopygus* predominated at ground level, *Ny*. *umbratilis* was extremely abundant in the forest canopy but descended to ground level, presumably to oviposit, by way of the tree-trunks, on which it could be collected in great numbers in the early morning. In studies conducted in RO, in the area of Samuel Ecological Station; however, it was noted that *Ny*. *umbratilis* predominated in the canopy (Azevedo et al. 1993). In Monte Dourado, PA, it was noted that *Ny*. *umbratilis* flies off the tree-trunks when disturbed by man's activities and attacks the nearest person. In the same study, *L*. (*V*.) *guyanensis* was isolated from 16 more specimens of *Ny*. *umbratilis* and, of 77 sand flies attacking 2 men collecting from the tree trunks, 72 (92.5%) proved to be *Ny*. *umbratilis*. Some idea of the efficiency of this sand fly in the transmission of ACL in the Monte Dourado, PA, area may be gained by the fact that the 2 men developed a total of 13 leishmanial lesions due to *L*. (*V*.) *guyanensis* on their arms, probably providing the most conclusive incrimination of a vector of ACL ever obtained.

The explanation of this great number of infected sand flies on tree trunks came with the detection of *L*. (*V*.) *guyanensis* in 27 of 59 specimens of the sloth *Choloepus didactylus* in the Monte Dourado area, PA (Lainson et al. 1981a, b). This animal spends most of its time in the forest canopy and has thus become the principal mammalian reservoir host of the parasite. Because the animal may remain in the same tree for a considerable time, there is a gradual build-up of infected *Ny*. *umbratilis* on a given tree. This sand fly's similar role as a vector of *L*. (*V*.) *guyanensis*, as well as its common presence in the forest canopy and on large tree-trunks at ground level, has been recorded in some other areas of the Amazon region of Brazil (Arias and Freitas 1977a, 1978) and in French Guiana (Le Pont and Pajot 1980). Infection of an undoubted specimen of *Ny*. *anduzei* with a parasite having development consistent with that of members of the subgenus *Viannia* has been reported in Manaus (AM) (Arias and Freitas 1977b). However, this sand fly can, at most, now be considered only as a possible secondary vector of *L*. (*V*.) *guyanensis* and is probably of low importance with regard to the transmission of ACL to man.

Ready et al. (1986) performed a detailed study of the ecology of *Ny*. *umbratilis* in the region of Monte Dourado, PA. It is highly anthropophilic and presumably becomes infected after feeding at night, particularly on the two-toed sloth *Choloepus didactylus*, but also on other arboreal animals such as the ant-eater *Tamandua tetradactyla*. In Manaus, AM, precipitin tests on blood in naturally fed *Ny*. *umbratilis* showed that 66% of them had fed on sloths (Christensen et al. 1982). In a later evaluation with the same method, *Ny*. *umbratilis* females captured in a non-flooded upland forest in Manaus fed predominantly on rodents (34%) followed by dogs (19%), sloths (18%), humans (16%) and chickens (13%) (Nery et al. 2004). In addition to its nocturnal feeding habits, however, this sand fly clearly will feed in the early daylight hours if disturbed from its resting place on tree trunks. It is recorded biting man in the dry season and, particularly, directly after the rainy season.

Areas of high ACL prevalence due to *L*. (*V*.) *guyanensis* may be found in communities located in or very close to primary forest, and this has led to the erroneous impression that *Ny*. *umbratilis* is undergoing the process of adapting to a peri-domestic habitat. However, no consistent data exist proving that this is true, and any transmission in this environment is almost certainly due to sand flies that have been attracted to a residential area, from nearby primary forest, by the lights of the houses. Esterre et al. (1986) discussed the acquisition of ACL due to *L.* (*V.*) *guyanensis* in persons living in a small village within forest in French Guyana and came to the same conclusion: When the forest was cleared to about 400–500 m around the village, all peri-domestic transmission ceased. Guerra et al. (2007) discussed this situation in Manaus, AM, and were clearly of the opinion that the eco-epidemiology of ACL there is the same as that recorded in Monte Dourado, PA. In other forested areas on the outskirts of Manaus, however, *Ny. umbratilis* was considered to be present in equal numbers in both the forest and in the peri-domestic habitat (Barbosa et al. 2008).

Observations exist suggesting that *Ny. umbratilis* is a vector of *L.* (*V.*) *guyanensis* in the state of Bolivar, Venezuela (Feliciangeli et al. 1985), possibly indicating an expansion of the Brazilian zoonotic cycle.

Rangel et al. (1998) isolated *L.* (*V.*) *braziliensis* from patients with ACL in Peixoto de Azevedo (MT), and Azevedo et al. (2002) noted that one of the most abundant and highly anthropophilic sand fly in the same area was, morphologically, *Ny. umbratilis*. In addition, they confirmed observations made by workers in the Instituto Evandro Chagas, Belém, PA (Ward et al., 1976) that the population of this sand fly, south of the Amazonas River, behaved very differently from that studied north of the river (Monte Dourado, PA). Although abundant in the forest canopy, it was not found to accumulate on tree trunks at ground level. It was this marked behavioural difference that led Lainson (1988) to suggest that perhaps the populations of *Ny. umbratilis* north and south of the Amazonas River were not identical and, since that time, the taxonomic status of *Ny. umbratilis* started to attract special attention.

Azevedo et al. (2002) studied the morphology and the morphometric characters of the head, thorax, and abdomen of populations of the insect from Brazil (in AP, PA, AM, and MT) and Venezuela (state of Bolivar). They found that analysis of the morphological characters could not separate the populations but that the quantitative characters (morphometry) showed that 77% of these separated the Venezuelan population from the Brazilian ones. The analysis did not, however, supply evidence of heterogeneity among the populations from Brazil, but later studies on *Ny. umbratilis* populations from Brazil and Venezuela suggest the existence of three different populations, which are separated by the geographical barriers of the *planalto* of RR and the two rivers, Negro and Amazon; One is in Venezuela and the other two in Brazil (north and south of the Amazon River (Azevedo 2008)).

The same investigator recorded 52 different species of sand flies in the municipalities of Rio Branco, Xapuri and Bujari, AC (17 being a new record for that state); *Ny. umbratilis* was abundant in the forest canopy in close association with the major reservoir of *L.* (*V.*) *guyanensis*, the sloth *C. didactylus*; and Tojal da Silva et al. (2006) recorded the presence of ACL due to *L.* (*V.*) *guyanensis* in the municipality of Rio Branco. These observations lead Azevedo et al. (2005, 2008) to conclude there is, in fact, a transmission cycle of this parasite south of the Amazonas River involving *Ny. umbratilis*. More recent sand-fly captures in urban and peri-urban Rio Branco did not detect *Ny. umbratilis*, but the other ACL vectors—*Ny. whitmani*, *Ny. antunesi*, and *Bi. flaviscutellata*—were present (Araújo-Pereira et al. 2014).

A biological analysis under laboratory conditions compared *Ny. umbratilis* populations from Manaus and Manacapuru (left and right sides of the Negro River, respectively) and showed differences in their life cycle, fecundity, fertility, adult longevity, and emergence. These differences suggested that some divergence of intrinsic biological features evolved because of their geographical isolation by the Negro River (Justiniano et al. 2004). Further phylogenetic analyses based on mitochondrial DNA detected two distinct lineages in *Ny. umbratilis* populations of opposite sides of the Amazon and Negro rivers, thus reinforcing the thought that these rivers may be acting as effective barriers, preventing gene flow between them (Scarpassa and Alencar 2012).

In PE, where most ACL cases are caused by *L.* (*V.*) *braziliensis* and transmitted by *Ny. whitmani* (Brandão-Filho et al. 1999), studies conducted at a forest reserve in Recife detected *Ny. umbratilis* at very high frequencies (96.5%) and biting rates (≤333.3 flies/person-hour) (Balbino et al. 2001, 2005). Phylogenetic analysis based on wing morphometry and the period clock gene concluded that the Recife population of *Ny. umbratilis* is significantly closer to the Rio Preto da Eva population (north of the Amazon River, AM) and that both populations are genetically distant from Manacapuru (south of Amazon River, AM) (Souza Freitas et al. 2015, 2016).

Molecular taxonomy studies based on a barcode region of mitochondrial DNA of *Ny. umbratilis* and *Ny. anduzei* from different regions of the Amazon clearly separated both species. However, the barcode region did not have enough power to separate the two lineages of *Ny. umbratilis* from opposite sides of the Amazon River, likely reflecting incipient species that have not yet reached the status of distinct species (Scarpassa and Alencar 2013).

*Ny. umbratilis* has so far not been associated with the transmission of ACL south of the Amazon River, but its behaviour is markedly different from that of the populations from regions located north of the river. One key behavioural difference is the failure of the southern *Ny. umbratilis* populations to concentrate at the base of trees. A parasite isolated from *Ny. umbratilis* captured in Peixoto de Azevedo, MT, proved to be *L.* (*V.*) *braziliensis* and not *L.* (*V.*) *guyanensis* (Azevedo et al. 2002). This raises the question as to its possible participation in the transmission *L.* (*V.*) *braziliensis*. In addition, *L.* (*V.*) *guyanensis* is replaced in the Amazonian forest south of the river by its sister species, *L.* (*V.*) *shawi*, where it is transmitted by *Ny. whitmani*.

## *Psychodopygus wellcomei* (Fraiha, Shaw & Lainson, 1971)

In 1968, the Meridional Mining Company, undertaking mineral exploration in PA, requested the Instituto Evandro Chagas to investigate an alarming number of men acquiring ACL due to *L.* (*V.*) *braziliensis* whilst working on road construction through primary forest in the Serra dos Carajás. It required only a few days for one particular sand fly to become highly suspected as the vector due to its avid feeding on man.

It proved to be a previously undescribed sand fly, which was named *Ps. wellcomei* in honour of Sir Henry Wellcome, founder of the Wellcome Trust, London, who was to sponsor the Institute's leishmaniasis programme for nearly 40 further years.

Ward et al. (1973a) made a study of sand flies captured during a 2-month period (December and January) using human bait, rodent-baited Disney traps, and aspiration from tree trunks, all at ground level, and captures with CDC light traps on platforms built in the trees at 5 and 11 m above the forest floor. A total of 23 different species were caught, and approximately 65% of all the sand flies captured while biting man were *Ps. wellcomei*. Heavy promastigote infections were encountered in three specimens of this sand fly, and the parasite was isolated in culture and the skin of hamsters; subsequent studies showed it to be *L.* (*V.*) *braziliensis*. Finally, Ryan et al. (1987a) performed experimental transmission of the parasite to hamsters by placing the animals in cages with large numbers of newly caught sand flies. All fed flies were separately maintained in glass vials until they had oviposited, at which time they were dissected to detect promastigotes and the eggs of all infected specimens maintained in order to rear males for positive identification. This was necessary because the females of *Ps. wellcomei* are morphologically indistinguishable from those of a sympatric species, *Ps. complexus,* whereas the males have distinctly different morphology.

*Ps. wellcomei* is an essentially sylvatic and highly anthropophilic species (Ward et al. 1973a; Wilkes et al. 1984). In addition, Ward et al. (1973b) found that 25.5% of all sand flies attracted to rodent-baited traps were of this species: This, and the fact that this sand fly has a vertical flight-range of only 1–2 m above ground level, led to their suggestion that the sylvatic hosts of *Ps. wellcomei* are terrestrial animals, the most highly suspected being rodents and marsupials (Lainson et al. 1973). The isolation of parasites with the biological characters of *L.* (*V.*) *braziliensis* from the rodents *Oryzomys concolor*, *O. capito*, *O. nigripes*, *Akodon arviculoides*, *Proechimys* spp., *Rattus*, and *Rhipidomys leucodactylus*—and the opossum *Didelphis marsupialis* in Brazil—tended to support this view (Lainson and Shaw 1970, 1979; Forattini et al. 1972; Forattini 1973; Lainson et al. 1981b; Rocha et al. 1988). Finally, a more definitive identification of this parasite from the Brazilian rodents *Bolomys lasiurus* and *R. rattus* was obtained by multi-locus enzyme electrophoresis (Brandão-Filho et al. 2003).

Regarding its behaviour and seasonality, *Ps. wellcomei* is most abundant during the rainy season (November–April) and enters into diapause during the dryer months when it is rarely encountered. The same seasonal pattern was observed in more recent studies in areas out of the Amazon Region, in RN, where *Ps. wellcomei* only occurs in months with greater rainfall and lower temperatures (Pinheiro et al. 2013, 2016a, b). Limiting forest work to the dryer months can therefore greatly reduce the risk of acquiring ACL in areas where this sand fly is found. The great importance of *Ps. wellcomei* as a vector of *L.* (*V.*) *braziliensis* is due to its tendency to not only feed at night but also during broad daylight, particularly in cloudy weather. The number of infected females captured during the day was, in fact, found to be greater than that obtained during the night suggesting that transmission is actually most frequent during the day (Wilkes et al. 1984).

The presence of *Ps. wellcomei* has been recorded in other areas out of the Amazon Region such as in forest of the Serra de Baturité, CE (Ready et al. 1983; Azevedo and Rangel 1991). The former investigators suggested that sand flies recorded as *Ps. squamiventris* by Lucena (1953) in Guaramiranga, CE, were possibly *Ps. wellcomei* because the females of the two species are morphologically very similar.

In the Serra de Baturité area, CE, Queiroz et al. (1994) detected flagellates in *Ps. wellcomei* (infection rate 0.05%), but unfortunately the parasites were not identified. *Ps. wellcomei* was also captured in MA, but it was classified as an accessory species (Pereira Filho et al. 2015) because the local main vector of *L.* (*V.*) *braziliensis* is probably *Ny. whitmani* (Rebêlo et al. 2010; Azevedo et al. 2011; Campos et al. 2013).

Other areas of *Ps. wellcomei* recorded outside the Amazon include RN and PE. Despite the recent additional evidence of its high anthropophily in Nísia Floresta, RN (Pinheiro et al. 2016a), the importance of *Ps. wellcomei* as a vector of ACL in Northeast Brazil still must be confirmed. Although *Ps. wellcomei* has been found in the Atlantic Rainforest region of PE, again there is so far no association of this species with local ACL in that region (Andrade et al. 2005; Silva and Vasconcelos 2005).

## *Psychodopygus complexus* (Mangabeira, 1941)

This sand fly was described by Mangabeira from a single male, captured in the municipality of Abaetetuba, PA, in 1938, by members of the Commission of Studies of American Visceral Leishmaniasis. Like *Ps. wellcomei*, the females are highly anthropophilic, although they seem not to share that sand-fly's daytime biting habits.

The females of *Ps. complexus* and *Ps. wellcomei* are morphologically indistinguishable, although the males are easily identified by the structure of the external genitalia. Ready et al. (1991), however, used DNA probes to distinguish the two species and showed that a fragment of DNA highly repetitive for *Ps. wellcomei* was not detected in either sex of *Ps. complexus*.

In Serra dos Carajás, PA, the two species share the same forest habitat, which at first created difficulties in pinpointing the principal vector of *L.* (*V.*) *braziliensis* in that area and required the rearing of males from the eggs of infected females to obtain the all-important males. In a transect running from high up on the range of hills down to the lowland forest, Ready et al. (1984) showed that the predominant species at the higher altitude (≥700 m above sea level) was *Ps. wellcomei* and that this predominance was slowly reversed with decreasing altitude until *Ps*. *complexus* predominated, in large numbers, in the forest at the foot of the hills (200 m) and *Ps*. *wellcomei* was completely absent at ≤150 m. Because ACL due to *L*. (*V*.) *braziliensis* is commonly found in the latter lowland forest in various regions of PA, this is a clear indication that vectors other than *Ps*. *wellcomei* are involved (Shaw et al. 1987). In later studies in Paragominas, where *Ps*. *wellcomei* is uncommon, several infected females of the *squamiventris* group were found and, because all the males captured proved to be *Ps*. *complexus*, it was considered sufficient evidence to incriminate this sand fly as the vector of *L*. (*V*.) *braziliensis* in that region (de Souza et al., 1996).

Azevedo et al. (2002) showed that *Ps*. *complexus* represented 8.2% of all captured sand flies in an area of ACL transmission in Peixoto de Azevedo, MT, although the participation of this species as a vector in this region has yet to be established.

In a military-training area of the Atlantic Forest in Pernambuco, Andrade et al. (2005) found flagellates characteristic of *Leishmania* during dissections of *Ps*. *complexus* females, but species typing could not be done due to contamination of the cultures. Because *Ps*. *complexus* predominated (87%) during periods of military activities that were followed by records of human cases of ACL, the investigators considered *Ps*. *complexus* as the principal suspected vector involved in the local transmission of ACL (Andrade et al. 2005).

In the municipality of Guaraí, Tocantins, *Ps*. *complexus* was the prevalent sand-fly species in the rural environment associated with human settlements and in captures with Shannon traps, thus confirming its anthropophilic behaviour (Vilela et al. 2013). Additionally, a multiplex PCR analysis of pooled dissected females detected natural infections by *L*. (*V*.) *braziliensis*, which lead the investigators to conclude that although *Ny*. *whitmani* is thought of as the most important ACL vector in TO, *Ps*. *complexus* may also play an important role in the transmission cycle of ACL in rural settlement areas of Guaraí (Vilela et al. 2013). Recent studies in the same municipality found positive correlations between *Ps*. *complexus* abundance and precipitation, which further supports its potential role as a *L*. (*V*.) *braziliensis* vector during the rainy season (Godoy et al. 2017).

## *Psychodopygus ayrozai* (Barretto & Coutinho, 1940)

This species has an extensive geographical distribution in Brazil that encompasses the North, Northeast, Central, Southeast, and South regions (AM, RO, RR, PA, BA, PE, MT, MG, RJ) (Aguiar and Medeiros 2003). However, its level of anthropophily appears to vary in different regions.

*Psychodopygus ayrozai* is anthropophilic in the more mountainous area in Atlantic Forest of Southeast Brazil (Aguiar and Soucasaux 1984), and its seasonality is associated with the hot and humid months decreasing in frequency during the colder and dryer months of the year. Studies in the Serra dos Órgãos, Rio de Janeiro state, showed that its feeding activity begins at dusk, extending until 12 pm, and that feeding occurred preferentially at ground level (Aguiar and Soucasaux 1984). In the Atlantic Forest of Paraná state, studies indicated it as one of dominant species whose population density fluctuated with temperature and rainfall indices (Marcondes et al. 2001).

*Psychodopygus ayrozai* has been implicated as a vector of *L.* (*V.*) *naiffi* in the Amazon Region, especially in PA (Lainson and Shaw 1998; Rangel and Lainson 2009). In fact, human *L.* (*V.*) *naiffi* cases are infrequent, probably because *Ps. ayrozai* does not reveal itself as anthropophilic sand-fly species in this region (Lainson and Shaw 1998; Rangel and Lainson 2009). Specimens of this phlebotomine have also been found in *L.* (*V.*) *naiffi* in AP and RO (de Souza et al. 2017; Arias et al. 1985).

In recent studies carried out in TO, in the Cerrado *biome*, *Ps. ayrozai*, which was first recorded in TO, was found with natural infection by *L.* (*V.*) *braziliensis*. These infections occurred in settlements in rural areas in the municipality of Guaraí, an endemic area for ACL with a local transmission profile related to environmental impacts by different purposes. However, the species was not among the most frequent in the study, and the investigators suggest that it may not play a secondary role in local epidemiology (Vilela et al. 2013).

## *Pintomyia fischeri* (Pinto, 1926)

This species was described based on specimens from SP with its occurrence in secondary forested areas from many municipalities (Barretto 1943). Because it could be found close to domestic-animal shelters, it was suggested that it was adapting to a domiciliary environment (Barretto 1943). Currently, the species has its distribution mainly in the states of the South and Southeast regions of Brazil (SC, RS, PR, SP, RJ, MG, ES, MS, MT, and GO) (Aguiar and Medeiros 2003).

Discussion of the epidemiological importance of *Pi. fischeri* began when it was recorded in peri-domestic habitats of São Paulo state where ACL occurred (Forattini 1953). In addition, in MG and SC it was found in endemic ACL areas (Alexander et al. 2002; Marcondes et al. 2005). A study conducted from 1986 to 1995 again found this sand fly in the domiciliary habitat in areas with ACL of SP cases (Camargo-Neves et al. 2002).

Even though it had not found naturally infected with a *Leishmania* sp., there were strong grounds for considering it to be a potential vector. It is highly anthropophilic, and its spatial distribution coincides with reports of human ACL cases in deforested areas, Lainson (1983) suggested that this sand fly could be maintaining transmission of *L.* (*V.*) *braziliensis* among wild animals in forest fragments.

Recently its importance as a vector of *L.* (*V.*) *braziliensis* was reinforced with records of natural infections in females captured in endemic ACL areas of ES

(Rocha et al. 2010). In another study (Pita-Pereira et al. 2011), in the periphery of Porto Alegre (RS), where human cases of *L.* (*V.*) *braziliensis* have occurred, *L.* (*Viannia)* sp. was found infected. This result led the investigators to suggest that it was participating as an ACL vector in the region. In the metropolitan area of Greater Sao Paulo, cases of ACL are sporadic and are associated with fragments of the Atlantic rain forest. In the latter, both within the forest and outside in peridomiciliary ecotopes *Pi.* f*ischeri* was the dominant species (Moschin et al. 2013). It is interesting to note that neither *Ny. intermedia* nor *Ny. neivai* were found in this habitat but that *Mg. migonei* was present in smaller numbers.

All the previously cited literature reinforces the importance of *Pi. fischeri* in the eco-epidemiology of ACL in Southeast and Southern Brazil, particularly in forested habitats.

## *Lutzomyia gomezi* (Nitzulescu 1931)

This species was described from female sand flies captured in San Cristobal, Tachira state, Venezuela. The male of this species was described from Panama by Rozeboom in 1940 as *Phlebotomus suis*, which was synonymized by Fairchild and Hertig (1948).

In Brazil, this sand fly has been recorded mainly in Northern regions, but it has also been recorded in the Northeast and Central regions (AC, AP, AM, RO, RR, PA, MA, GO, MT, and BA) (Young and Duncan 1994; Aguiar and Medeiros 2003).

Although in northern Brazil, specimens of *Lu. gomezi* were found infected with promastigotes, suggested as being a *Leishmania* sp., belonging to the subgenus *L.* (*Viannia)*, this was not confirmed (Rangel and Lainson 2009).

Historically, this phlebotomine has been associated with *L.* (*V.*) *panamensis* transmission in some South American countries without any evidence of transmission of *Leishmania* spp. in Brazil. However, recently, a natural infection of *L.* (*V.*) *shawi* was found in *Lu. gomezi* captured in Amazonian forest of PA (de Souza et al. 2016). The investigators suggest that this phlebotomine may participate in ACL eco-epidemiology, especially because of its arboreal habits, which is where the mammalian reservoirs of *L.* (*V.*) *shawi* occur.

## *Other vectors*

We consider that the species discussed previously (*Bichromomyia flaviscutellata, Lutzomyia gomezi, Ny. intermedia, Ny. whitmani, Ny. neivai, Ny. umbratilis, Migonemyia migonei*, *Pintomyia fischeri, Psychodopygus wellcomei, Ps. complexus,* and *Ps. ayrozai*) are primary ACL vectors. However, others exist based on either epidemiological or parasitological evidence, or both, that may be playing roles in ACL transmission.

*Trichophoromyia ubiquitalis*, the only known vector of *L.* (*V.*) *lainsoni* (Silveira et al. 1991) but an *L.* (*L.*) *amazonensis* infection, was recorded by molecular methods in flies from Lábrea (AM) (Silva et al. 2014b). This sand fly is found in the Brazilian Amazonian forests and is anthropophilic being taken off man in larger numbers where the population is higher. Shannon-trap catches are considered to reflect anthropophily because a man catches the flies as they alight on the traps' surface. In forests, south of the Amazon River, PA, it ranked 16th of 68 species of the females in Shannon-trap catches, but it ranked 3rd in abundance when light-trap catches were included in the calculations (de Souza et al. 2016). In the Brazilian Guiana Shield forest of AP in Shannon-trap catches, it ranked sixth and also sixth when light-trap catches were included in the calculation (de Souza et al. 2017). These figures reflect moderate levels of anthropophily. It is interesting to note that in both places the proportion of males to females in Shannon-trap catches was almost equal (e.g. 21 of 23 in the PA catches and 31 of 36 in those from AP), thus suggesting no great differences in population sizes despite considerable ecological differences reflected by the dominant anthropophilic species in PA being *Ps. complexus/wellcomei* and in AP *Ny umbratilis*. In CDC catches in Lábrea (AM), it was the second most common species (Silva et al. 2014b). Its constant presence in relatively high numbers is consistent with the number of *L.* (*V.*) *lainsoni* ACL cases in forested regions and it being considered this parasite's principal vector.

Evidence exists that *Ps. davisi* participates in the transmission of *L.* (*V.*) *braziliensis* (Grimaldi et al. 1991), but there is stronger evidence for that of *L.* (*V.*) *naiffi* (Gil et al. 2003; de Souza et al. 2016). This sand fly has an extensive distribution throughout Amazonia and in pockets of the Atlantic rainforest. Infections of *L.* (*V.*) *naiffi* have been found in *Ps. davisi* in RO (Gil et al. 2003) and PA (de Souza et al. 2016). It was the dominant species in RO and ranked fifth in the PA study, but consecrated anthropophilic species—such as the *complexus/wellcomei* group and *Ny. umbratilis*—were present in large numbers. However, in the RO study area, *L.* (*V.*) *braziliensis* was the most common parasite, and no cases of human cases of *L.* (*V.*) *naiffi* were detected (Shaw et al. 2007). A possible explanation is that *L.*(*V.*) *naiffi* infections in man are mild and thus go unnoticed.

Another highly anthropophilic species is *Ps. squamiventris*, which occurs in the AM, AP, RR, and regions of PA north of the Amazon River (Ready et al. 1982). Its level of anthropophily is reflected by the fact that 4 times the number of females were captured in Shannon traps than in ground-level CDC traps (de Souza et al. 2017). Infections of *L.* (*V.*) *naiffi* have been found in specimens captured in AM, AP, and PA (Grimaldi et al. 1991; de Souza et al. 2017; Naiff et al. 1991). It has also been found infected with *L.* (*V.*) *braziliensis*, and a natural infection was transmitted experimentally to a hamster (Ryan et al. 1987b). Given its avidity for man, as well as the fact that it has been found infected with two *Leishmania* (*Vianna*) must be considered a highly probable ACL vector.

Records exist in the literature of infections in wild-caught Brazilian phlebotomines that were not identified to the species level. The first was that of Pessôa and Pestana (1940), who found flagellates in *Mg. migonei* and suggested that they were probably *L.* (*V.*) *braziliensis*. Such findings should not be ignored nor forgotten because they are strong circumstantial evidence for the possible role of a species in ACL transmission that needs confirmation. In some cases, subsequent identifications indicate what they most probably were. An example of this are studies (Ryan et al. 1987a) performed more than 30 years ago in the Serra das Carajás. Flagellates were found in 114 of 11,586 phlebotomines, and many identified as "*Leishmania braziliensis* subspecies" were found in *Lu. gomezi, Ny. richardwardi, Ny. shawi, Ny. whitmani, Th. ubiquitalis, Ps. hirsutus,* and *Ps. "wellcomei."* Worthy of mention is 11 infections occurring in *Th. ubiquitalis*. They were almost certainly *L.* (*V.*) *lainsoni* because this species was later identified in this same sand-fly species (Silveira et al. 1991), and this adds weight to the importance of this species as the primary vector of this parasite. *Ps. hirsutus* had also been found infected with *Leishmania* (*Vianna*) in Rio de Janeiro (Rangel et al. 1985), but we do not know what the parasites were. *L.* (*V.*) *shawi* was described in arboreal mammals captured in the Carajás, and it seems quite likely that the infections in the three *Nyssomyia* species belong to this species, but this needs confirmation. In addition to the above-mentioned infections, others have been recorded by different investigators in *Lu. renei, Ny. umbratilis, Pintomyia pessoai, Psathyromyia aragaoi, Pa. dendrophyla*, *Psychodopygus amazonensis, Ps. claustrei*, *Ps. davisi*, and *Ps. paraensis*. The *Leishmania* species were not identified; however, based on epidemiological and molecular data they probably belonged to an ACL *Leishmania* species.

Table 1 lists infections of *L.* (*L.*) *amazonensis* in species of *Nyssomyia* and *Trichophoromyia* captured in forests and in *Lutzomyia, Martinsmyia*, and *Nyssomyia* species captured in peri-domestic habitats. *L.* (*V.*) *braziliensis* has been documented in *Evandromyia, Martinsmyia, Micropygomyia*, and *Psychodopygus* species obtained from sylvatic habitats as well as a smaller number near human dwellings. Similarly, infections of *L.* (*V.*) *guyanensis* have been recorded in species of *Martinsmyia* and *Micropygomyia* from forests. The question is this: What do these infections mean in relation to ACL transmission? They may or may not be participating in enzootic or zoonotic ACL cycles, but future studies are needed to answer these questions. The finding of infections using molecular methods in pools of flies must be viewed with caution. It does not mean that the species in question should immediately be considered as a vector. Was blood present? Where were the parasites located? How many were there? Were metacyclic forms present? These are just a few questions, some of which are only answered by viewing the dissected insect's gut. A technique used extensively in the past that can lead to the parasite's isolation. For many years, epidemiological data favored the one parasite/vector hypothesis. However, depending on the *Leishmania* species, recent parasitological results now suggest a more complex situation where one species may be the dominant vector with other species being involved in enzootic and zoonotic ACL transmission.

**Table 1** A list of sand fly species implicated in the transmission of American cutaneous leishmaniasis found in sylvatic and peridomestic environments in Brazil

| *Leishmania* species | Sand flies implicated as vectors* or potential vectors in the sylvatic habitat | Sand flies implicated as vectors* or potential vectors in the peridomestic habitat |
|---|---|---|
| *L. (L.) amazonensis* | *Bichromomyia flaviscutellata* #* | *Bichromomyia flaviscutellata* |
| | *Bichromomyia olmeca nociva* #* | |
| | *Bichromomyia reducta* #* | |
| | | *Lutzomyia longipalpis* |
| | | *Martinsmyia minasensis* |
| | | *Nyssomyia intermedia* |
| | *Nyssomyia umbratilis* | |
| | *Nyssomyia yuilli* | |
| | *Trichophoromyia ubiquitalis* | |
| *L. (V.) braziliensis* | *Evandromyia apurinan* | |
| | *Evandromyia edwardsi* | |
| | *Evandromyia lenti* | *Evandromyia lenti* |
| | *Martinsmyia minasensis* | |
| | *Micropygomyia capixaba* | |
| | | *Micropygomyia ferreirana* |
| | *Micropygomyia peresi* | |
| | *Migonemyia migonei* #* | *Migonemyia migonei** |
| | *Nyssomyia intermedia* #* | *Nyssomyia intermedia** |
| | *Nyssomyia neivai* #* | *Nyssomyia neivai** |
| | *Nyssomyia whitmani* #* | *Nyssomyia whitmani** |
| | *Pintomyia fischeri* #* | *Pintomyia fischeri** |
| | *Psychodopygus carrerai* | |
| | *Psychodopygus complexus* #* | |
| | *Psychodopygus davisi* | |
| | *Psychodopygus squamiventris* # | |
| | *Psychodopygus wellcomei* #* | |
| *L. (V.) guyanensis* | *Martinsmyia minasensis* | |
| | *Micropygomyia goiana* | |
| | *Nyssomyia anduzei* # | |
| | *Nyssomyia umbratilis* #* | |
| *L. (V.) naiffi* | *Nyssomyia anduzei* # | |
| | *Psychodopygus ayrozai* #* | |
| | *Psychodopygus davisi* #* | |
| | *Psychodopygus hirsutus* # | |
| | *Psychodopygus paraensis* # | |
| | *Psychodopygus squamiventris* # | |
| *L. (V.) lainsoni* | *Trichophoromyia ubiquitalis* #* | |
| *L. (V.) shawi* | *Lutzomyia gomezi* # | |
| | *Nyssomyia* whitmani #* | *Nyssomyia whitmani** |
| *L. (V.) utingensis* | *Viannamyia tuberculata* #* | |

Species marked with a hash (#) denotes identifications based on isolated parasites. Species not marked with an asterisk (*) are only potential vectors as they have been found infected by molecular methods with the respective *Leishmania* species

## *Impacts of Environmental and Climatic Changes*

Global human population is facing the impacts of centuries of constant changes in natural environments. Climate change is happening now and impacts in the dynamics of infectious diseases are not only expected but can already be noticed (IPCC 2014; Woodward et al. 2014). Vector-borne diseases are particularly susceptible to environmental and climatic changes because their occurrence depends on the ecological balance between different species in complex transmission cycles (Walsh et al. 1993; Patz et al. 2000; McMichael 2004). Leishmaniases are among the vector-borne diseases most affected by this *ecological chaos* driven by human actions (Shaw 2008), and one of the expected impacts is the expansion of its geographical distribution (Ashford 2000; Dujardin 2006; WHO 2010).

Sand flies are affected by climate, especially by precipitation, humidity, and temperature. These variables influence their distribution, metabolism, and interactions with *Leishmania* (Ready 2008; WHO 2010; Hlavacova et al. 2013). One of the expected impacts of climate change in the eco-epidemiology of leishmaniasis is the expansion of the geographical distribution of its vectors (Peterson and Shaw 2003; González et al. 2010; Moo-Llanes et al. 2013; Carvalho et al. 2015; McIntyre et al. 2017). Given the wide latitudinal range of Brazil, regional climates play a major role in delimiting the distribution of species. Most projections under climate-change scenarios agree that disease vectors should find climatic conditions favourable to their geographic expansions towards higher latitudes in the upcoming decades (Carvalho et al. 2017).

In Brazil, the concept of leishmaniases as a sylvatic zoonosis is restricted to the Amazon Forest, Atlantic Forest fragments, and parts of Cerrado. A new transmission profile has emerged driven mostly by human-made environmental changes. In past decades, human migration of different origins and purposes resulted in major deforestation and unplanned settlements. These changes favour the dispersion of sylvatic animals (some *Leishmania* reservoir hosts) and sand flies (especially those species with eclectic feeding habits) to peri-domestic areas where new transmission cycles may establish close to human dwellings (Rangel 1995; Rangel and Lainson 2009; Costa et al. 2007).

Brazil is currently facing an increasing geographical expansion of ACL, which can probably be explained by the growing environmental changes, which in turn affect vector behaviour (Rangel et al. 2014). Some ACL-vector species have been showing evidences of adaptation to man-modified environments by establishing in peri-domestic areas, even in outskirts of large cities (Brasil 2007; Rangel and Lainson 2009). In this case, two sand-fly species are particularly good examples in different eco-epidemiological situations: *Ny. whitmani* and *Bi. flaviscutellata*. However, there are records of other species (see Table 1) that have been found in or near human dwellings that may be playing secondary or even primary roles in ACL-transmission cycles.

Because of its extensive geographical distribution and its association with two ACL parasites (*L.* (*V.*) *braziliensis* and *L.* (*V.*) *shawi*), *Ny. whitmani* is currently considered the most important ACL vector in Brazil, especially in impacted areas. This sand-fly species was found in several localities associated with the exploitation of natural environments and deforestation caused by the construction of roads, hydroelectric power plants, human settlements, wood extraction, agricultural activities, military training, and ecotourism. These epidemiological patterns occur throughout Brazil and together are considered to be responsible for the geographical expansion of ACL in the country.

Peterson and Shaw (2003) published the first projections of future potential distributions of Brazilian leishmaniasis vectors under climate-change scenarios. The investigators concluded that the ACL vectors *Ny. whitmani*, *Ny. intermedia*, and *Mg. migonei* should expand their distributions by the middle of the twenty-first century in different directions, most notably southwards, with *Ny. whitmani* showing the most dramatic range changes (Peterson and Shaw 2003). More recent projections of the potential distribution of *Ny. whitmani* reinforce the trends described by Peterson and Shaw (2003) and indicate a greater area of expansion of climate suitability in the North region (Costa et al., 2018, Fig. 2). Although climate-change scenarios show

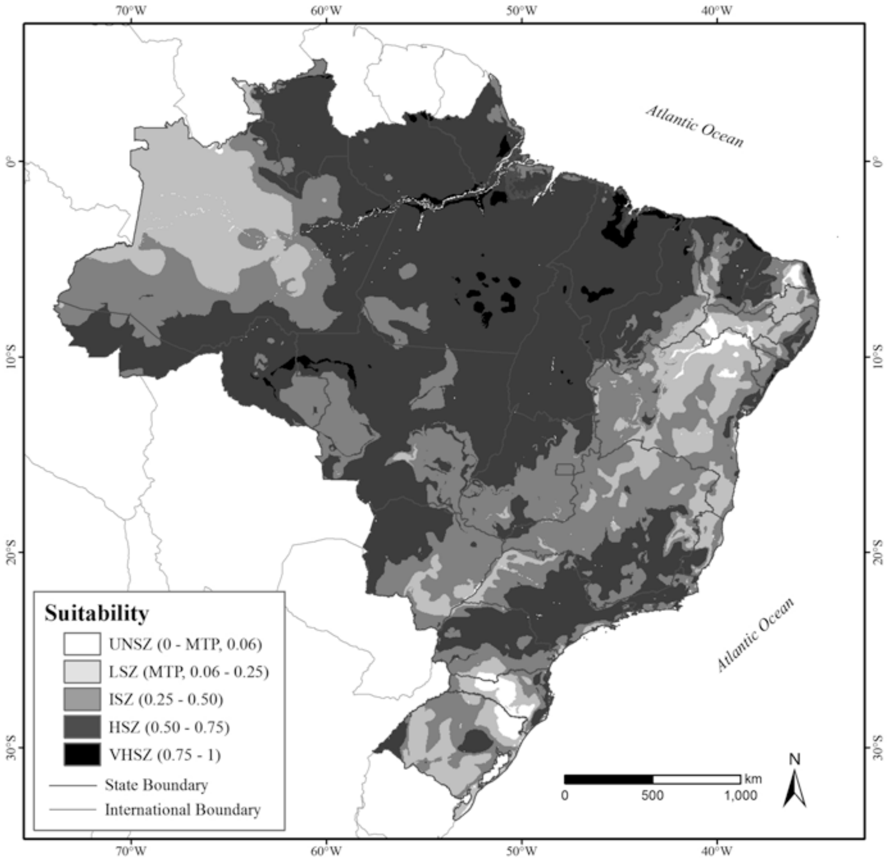

**Fig. 2** Climatic suitability of *Ny. whitmani* under a "business as usual" climate-change scenario (average for years 2041–2060). UNSZ unsuitable zone, LSZ low-suitability zone, ISZ intermediate-suitability zone, HSZ high-suitability zone, VHSZ very high-suitability zone

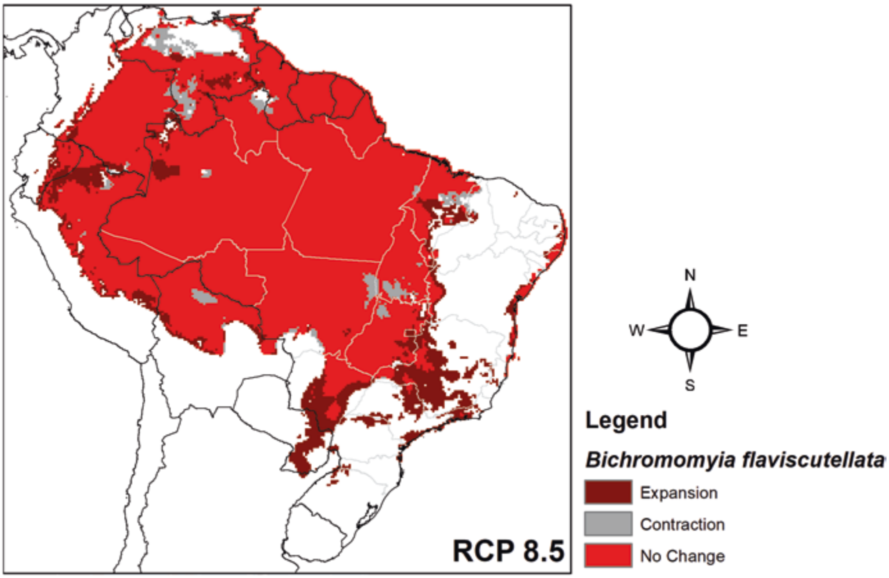

**Fig. 3** Climatic suitability of *Bi. flaviscutellata* under a "business as usual" climate-change scenario (average for years 2041–2060). Dark red represent areas that will only become suitable in the future; light red areas are currently suitable and will remain suitable in the future; grey areas are currently suitable but will become unsuitable in the future. RCP representative concentration pathway

that the Amazon Region will become progressively drier (Joetzjer et al. 2013), the updated results state that *Ny. whitmani* will remain present in the region and should expand its area of climate suitability in the future (Costa et al. 2018).

The presence of *Bi. flaviscutellata* in peri-domestic areas, especially in the Cerrado biome, confirms the process of ruralisation of an *L.* (*L.*) *amazonensis* transmission cycle that was previously considered to be strictly sylvatic. Future projections under climate-change scenarios indicate that *Bi. flaviscutellata* might also expand its distribution beyond its current range limits in the Amazon and the Cerrado southwards into the Southeast and South regions (Carvalho et al. 2015, Fig. 3). Human cases of ADCL in Southeast Brazil are currently rare (Costa et al. 2009; Azeredo-Coutinho et al. 2007), although the disease seems to be gradually expanding its occurrence southwards. If the vector reaches these climatically suitable areas and its dispersion is followed by competent hosts and parasites, these can become ADCL-risk areas, especially because these are the most populated areas within the species' range. The possibility of this enzootic cycle to be maintained in secondary forests and even become peri-domestic was previously discussed (Lainson et al. 1994). This could be happening, in part, because of the adaptation process of the vector to man-modified environments. At first, it would be logical to think that a strictly sylvatic cycle would disappear with the deforestation of primary forests (Campbell-Lendrum et al. 2001), but the *L.* (*L.*) *amazonensis* cycle shows evidences of occurrence in secondary forests and peri-domestic areas, where the vector could be dispersing to domestic-animal shelters (Rangel and Lainson 2009).

The closely related species *Ny. intermedia* and *Ny. neivai* were treated as *Ny. intermedia* sensu lato by Peterson and Shaw (2003), who concluded that its distribution might expand southwards. A recent study reviewed the projections for both species separately, demonstrating that it is only *Ny. neivai* that should expand southwards, whereas *Ny. intermedia* might show some discrete expansions in the Northeast region (McIntyre et al. 2017, Figs. 4 and 5).

Climate change poses new challenges to the control of leishmaniasis. In addition to the long-term effects on the geographic distribution of vectors, interannual fluctuations of climate phenomena, such as the El Niño, might impact the seasonality of the sand flies and leishmaniasis (Franke et al. 2002; Chaves and Pascual 2006; Cardenas et al. 2006, 2008). Further studies are needed about the effects of climate in sand-fly densities including long-term monitoring of natural populations and climate variability. Such studies should also include spatial and temporal variations in leishmaniasis. Results from climate-based models must be validated with robust external data before they can effectively be applied in programs of the surveillance and control of leishmaniasis.

Considering the great challenge that is controlling ACL, a disease with complex epidemiology directly associated with environmental changes, studies that aim to characterize and monitor its spatial and temporal trends can support the epidemiological and entomological surveillance actions of health departments. These studies can help to identify receptive areas for new ACL outbreaks and population groups at higher risk of infection so that control actions can be better planned and more effective.

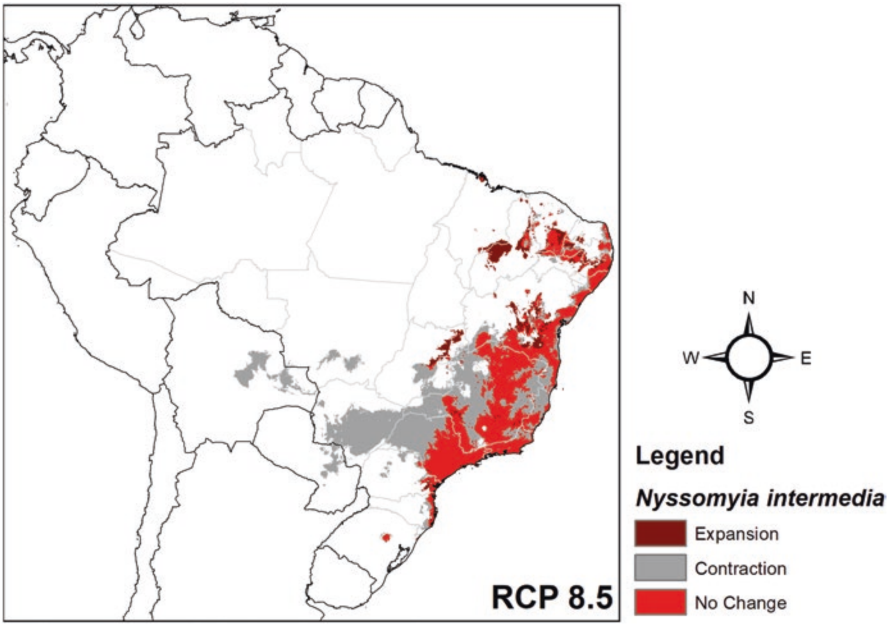

**Fig. 4** Climatic suitability of *Ny. intermedia* under a "business as usual" climate-change scenario (average for years 2041–2060). Dark red represent areas that will only become suitable in the future; light red areas are currently suitable and will remain suitable in the future; grey areas are currently suitable but will become unsuitable in the future. RCP representative concentration pathway

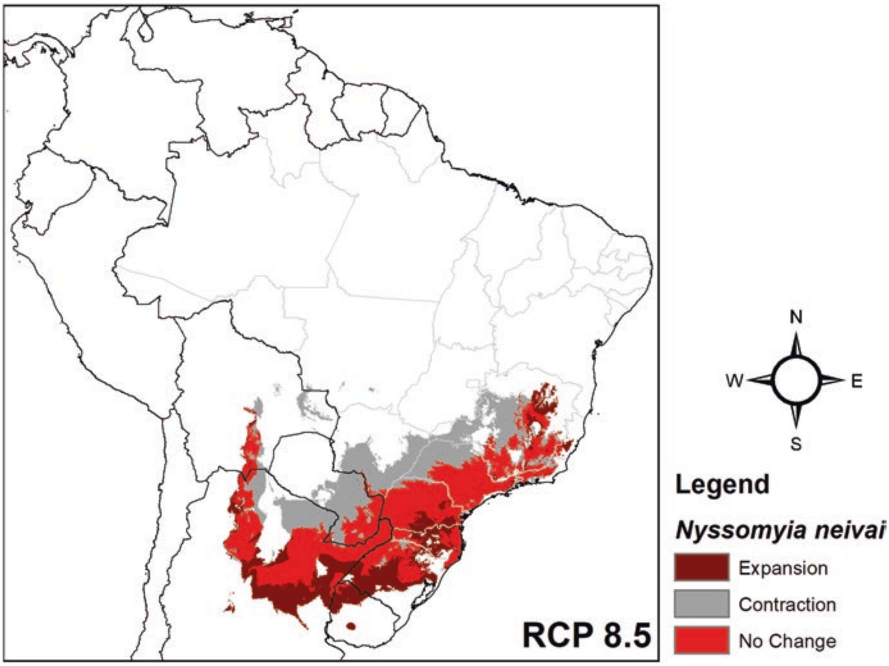

**Fig. 5** Climatic suitability of *Ny. neivai* under a "business as usual" climate-change scenario (average for years 2041–2060). Dark red represent areas that will only become suitable in the future; light red areas are currently suitable and will remain suitable in the future; grey areas are currently suitable but will become unsuitable in the future. RCP: representative concentration pathway

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