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Convergent Habitat Segregation of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in Southeastern Brazil and Florida

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ABSTRACT During the rainy season of 2001, the incidence of the dengue vectors *Aedes aegypti* and *Ae. albopictus* was examined in different habitats of two cities (Rio de Janeiro and Nova Iguaçu) in Rio de Janeiro State, Brazil, and in two cities (Palm Beach and Boca Raton) in Florida. Oviposition trap collections were performed in urban, suburban, and rural habitats in both areas. Our hypothesis that the abundances and frequencies of occurrence of *Ae. aegypti* and *Ae. albopictus* are affected in opposite ways by increasing urbanization was only partially supported. City, habitat, and their interaction significantly affected the abundance of both species. Cities with high abundance of *Ae. aegypti* also had a high abundance of *Ae. albopictus*. The two species were most abundant in the cities of Rio de Janeiro state and the lowest in Boca Raton. Habitat had a significant but opposite effect on the abundances of *Ae. aegypti* and *Ae. albopictus*. In general, *Ae. aegypti* was most prevalent in highly urbanized areas and *Ae. albopictus* in rural, suburban, and vegetated urban areas in Rio de Janeiro state and Florida. However, abundances of the two species were similar in most suburban areas. Analyses of frequencies of occurrence showed an unexpected high level of co-occurrence of both species in the same oviposition trap. Despite the different geographical origins of *Ae. albopictus* in Brazil and the United States, the habitats used by this recent invader are remarkably similar in the two countries.

KEY WORDS dengue vectors, abundance, occurrence, Brazil, United States

OCCUPANCY OF ARTIFICIAL CONTAINERS, human facilitated transport, desiccation-resistant eggs, and associations with human habitats enabled two important dengue vectors, *Aedes aegypti* (L.) and *Ae. albopictus* (Skuse), to become cosmopolitan (Lounibos 2002). The present geographic distributions of the two mosquito species overlap in tropical Asia, America, West Africa, and African island nations in the Indian Ocean. Invasions by one or the other of these two species have impacted the distribution and abundance of resident species (Hawley 1988, O'Meara et al. 1995, Galardo 2002, Lounibos 2002).

After its arrival in Asia toward the end of the 19th century (Tabachnick 1991), the increase in abundance of *Ae. aegypti* in many cities was accompanied by a decrease in the abundance of the native *Ae. albopictus* (Rudnick and Hammon 1960, Gilotra et al. 1967, Chan et al. 1971, Ho et al. 1972, Hawley 1988). In contrast, the recent establishment and spread of *Ae. albopictus* (Sprengrer and Wuithiranyagool 1986, Moore 1999) in the United States has been accompa-

nied by a decrease in the range and abundance of *Ae. aegypti*, a resident of the Americas for centuries. *Ae. albopictus* has largely displaced *Ae. aegypti* and became the most abundant mosquito in artificial containers in most of the southeastern United States (O'Meara et al. 1995, Moore 1999). *Ae. aegypti* remains common only in urban centers of the southern United States (Hornby et al. 1994, O'Meara et al. 1995). Simultaneously, *Ae. albopictus* of a different geographic origin (Birungi and Munstermann 2002) invaded, established, and spread in Brazil (R.L.d.O., personal communication, Forattini 1986, Galardo 2002), but little is known of the effects of this invasion on resident mosquitoes.

There are several alternative explanations for the Asian and North American shifts in mosquito distributions after invasions (Barrera 1996). Many workers have assumed that because one species has been replaced by the other in some habitats or whole areas, competitive displacement has occurred (Hawley 1988). Field experiments in both the United States (Juliano 1998) and Brazil (Braks et al. 2003) have shown a strong competitive advantage for *Ae. albopictus* larvae that seems to be independent of population origin or environmental conditions (Braks et al. 2003). Although resource competition among larvae seems to account for the displacement of *Ae. aegypti*

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in some regions of the United States, it does not explain the persistence of *Ae. aegypti* in southern cities, often coexisting with *Ae. albopictus*. Juliano et al. (2002) proposed that local coexistence of the species is possible because warm dry climates favor *Ae. aegypti* by alleviating the effects of competition from *Ae. albopictus* through differential mortality of *Ae. albopictus* eggs. Coexistence of the species observed in tropical Asia might be also caused by this phenomenon. In these regions of sympatry, *Ae. aegypti* and *Ae. albopictus* rarely share identical habitats in southeast Asia (Hawley 1988). There, the former species is more often found in urban habitats where it oviposits indoors (Thavara et al. 2001, Harrington et al. 2001), whereas the latter species is commonly found in less urbanized habitats with more outdoor larval sites (Hawley 1988, Thavara et al. 2001). The displacement of *Ae. albopictus* by *Ae. aegypti* in certain Asian cities was suggested to be caused by destruction of *Ae. albopictus* habitats with a concomitant increase in urban habitat more suitable for *Ae. aegypti* (Chan et al. 1971, Hawley 1988). Fontenille and Rodhain (1989) also suggested that restrictive abiotic factors, more than competition, brought about the spatial segregation of these species on Madagascar. In Asia, *Ae. aegypti* had an overall competitive advantage over *Ae. albopictus* in urban areas and therefore displaced the latter there (Rudnick 1965, Gilotra et al. 1967). The same process, but with a reversal of competitive advantage, might explain the replacement of *Ae. aegypti* by *Ae. albopictus* in North America. Before the *Ae. albopictus* invasion, *Ae. aegypti* occurred in the southeastern United States mainly in containers outdoors, such as in tires and cemetery vases, more suitable for *Ae. albopictus* (O'Meara et al. 1995), probably because of a lower accessibility (caused by screens and air conditioning) and availability of indoor oviposition sites. In Brazil, in contrast to many areas of Asia, most containers positive for *Ae. aegypti* are found outdoors (Neto 1997, Souza-Santos 1999, Pinheiro and Tadei 2002), although this species rests indoors (Barata et al. 2001).

In contrast to Asia and North America, there are only a few reports for Brazil on spatial relationships and habitat segregation between the recently introduced *Ae. albopictus* and *Ae. aegypti*. Most information comes from surveys by the national health department (Fundação Nacional de Saúde [FUNASA]), which typically report presence-absence only (Alves et al. 1991, Galardo 2002), rather than abundance. In Brazil, information on the habitat distribution of these species is vital for control efforts directed at reduction of dengue vectors. More generally, our understanding of habitat distributions of these species would be improved if we could determine whether patterns of distribution and co-occurrence observed in any area could be generalized to other areas where these species occur. Hence, comparison of habitat distributions of *Ae. aegypti* and *Ae. albopictus*, determined using the same methods in different regions, is vital for both basic and practical reasons.

Our main objective is to quantify and to compare how habitat, broadly defined based on human land use, is related to the abundances and frequencies of occurrence and co-occurrence of *Ae. aegypti* and *Ae. albopictus* in two areas of the Americas, Rio de Janeiro and Florida, that were independently colonized by these species. The mosquito population was monitored by means of oviposition trap collections instead of larval surveys of naturally occurring containers, because the former has been proven to be more efficient for monitoring abundances of *Ae. aegypti* (Rawlins et al. 1998, Braga et al. 2000) and *Ae. albopictus* (Marques et al. 1993) in the Americas. Our descriptions of habitat use are a step toward understanding the mechanisms used by these species for habitat selection. Based on the literature available, we hypothesize that the abundances and frequencies of occurrence of *Ae. aegypti* in the oviposition traps are positively correlated with increasing urbanization (defined by high population density, high building coverage, scarcity of nonhuman hosts and low vegetation coverage), whereas the abundances and frequencies of occurrence of *Ae. albopictus* are adversely affected by urbanization. Further, we hypothesize that the total numbers of *Ae. aegypti* collected in the oviposition traps are affected by region and are lower in Florida than in Rio de Janeiro state. This latter hypothesis is based on the higher standard of living in Florida, where most inhabitants live in air conditioned houses.

Materials and Methods

Study Areas

Surveys in southeastern Brazil (Fig. 1) were performed in two cities of Rio de Janeiro State, Nova Iguaçu (22°45'S; 43°27'W) and Rio de Janeiro (22°55'S; 43° 12'W), where endemic dengue transmission occurs, mostly during the rainy season from December until April (Nogueira et al. 1999, Honório and Lourenço-de-Oliveira 2001). Nova Iguaçu is a city belonging to the greater metropolitan area of Rio de Janeiro and comprises an area of 933 km², with an average human population density of 981.1 inhabitants/km² and mean annual minimum and maximum temperatures of 15 and 36°C, respectively (Instituto Brasileiro de Geografia e Estatístico 2002). Rio de Janeiro city comprises 1,261 km², with an average population density of 4,645.4 inhabitants /km² (Instituto Brasileiro de Geografia e Estatístico 2002).

Florida, in the southeastern United States (Fig. 1), has a rainy season from June until October. The survey was performed in two cities in Palm Beach county, Boca Raton (26°21'S; 80°06'W) and West Palm Beach (26°41'S; 80°07'W), where *Ae. aegypti* still persists despite the invasion of *Ae. albopictus*. The mean annual minimum and maximum temperatures are 18 and 30°C, respectively. The city of Boca Raton has an area of 72.3 km², with 1,033.2 inhabitants/km², and Palm Beach has an area of 90.2 km² and 1,200.3 inhabitants/km² (U.S. Census Bureau 2002).

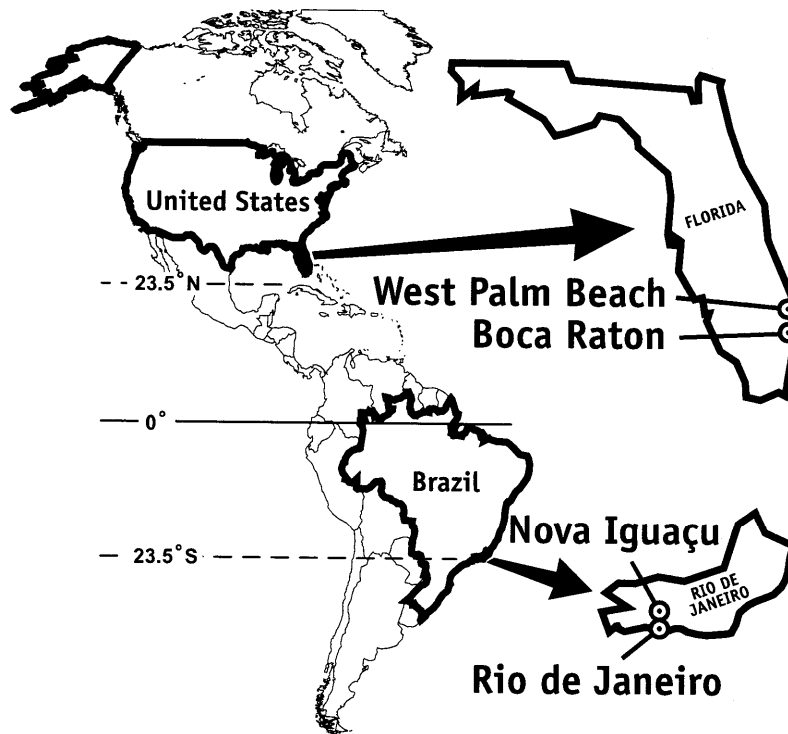


Fig. 1. Study areas where oviposition trap collections were performed.

Survey

By means of oviposition traps, immature stages of *Ae. aegypti* and *Ae. albopictus* were collected in different habitats of Rio de Janeiro city (RJ) and Nova Iguaçu (NI) from 8 to 29 March 2001, and in Palm Beach (PB) and Boca Raton (BR) from 19 September to 10 October 2001. Slum, urban, suburban, rural, and edge of forest habitats were identified in the Brazilian sites. We did not find comparable slum and forest edges in Florida, hence only urban, suburban, and rural areas were surveyed here. The selection of the survey sites in the four areas was based on knowledge of neighborhoods obtained from the local health au-

thorities (FUNASA) in Rio de Janeiro and Palm Beach County mosquito control authorities in Florida. The parameters used for the characterization of the habitats were population density, number of houses, level of sanitation, vegetation coverage, and presence of nonhuman hosts (Table 1). Only the population density per neighborhood was quantified (Table 1B). For the survey, 10 houses were arbitrarily chosen per habitat, but always separated by at least 2 houses, and two oviposition traps were placed outdoors in shady sites near each house. The oviposition trap consisted of a black plastic jar (400 ml) containing 270 ml tap water and 30 ml of a 10% by weight aqueous hay infusion

Table 1. Habitat characterization by four qualitative parameters of urbanization (a) and quantified population density (b)

a. Habitat characteristics				
Habitat characteristics	Number of houses	Level of sanitation	Vegetation coverage	Presence of non-human hosts
Slum ^a	High	poor	low	moderate
Urban		good		few
Suburban	↓	good	↑	few
Rural		moderate		many
Forest edge ^a	low	moderate	high	many
b. Population density				
Population density	Rio de Janeiro ^b	Nova Iguaçu ^b	Palm Beach ^c	Boca Raton ^c
Slum ^a	30,800.7	8,227.0	—	—
Urban	13,003.3	12,166.8	3,610.6	1,958.1
Suburban	291.7	5,982.8	797.3	1,456.9
Rural	161.8	312.3	91.6	962.1
Forest edge ^a	378.1	180.1	—	—

^a Slum and forest edge are not included in the survey in Florida.

^b Source = Instituto Brasileiro Geografia e Estatística (2002).

^c Source = U.S. Census Bureau (2002).

(incubated for 7 d). A wooden oviposition paddle (2 by 12 cm), with its rough side facing the center, was secured to the jar with a large paperclip. Once a week for 3 consecutive wk, all *Aedes* larvae were collected in plastic bags (whirl-pack; Nasco, Fort Atkinson, WI), paddles were collected and replaced, and the hay infusion solution was refreshed. Larvae were identified and counted in the laboratory within 1 wk of collection (field hatch). Paddles collected were stored at 25–27°C and >80% RH. Within 2 mo after the collection, they were immersed in water, and the emerging larvae were reared to fourth instar, identified, and counted (laboratory hatch).

Data Collection and Analyses

Abundance. Numbers of larvae that hatched in the field and laboratory were summed by species over the 3 wk of the survey (the sample unit). To satisfy requirements of normality, the summed numbers of each species were log-transformed before analyses. The log-transformed numbers of each species (*aeg*, *alb*) were used in three separate multivariate analyses of variance (MANOVA) with habitat and city as fixed effects (SAS Institute 1989, Scheiner 2001). Data from both Rio de Janeiro and Florida were first analyzed together for urban, suburban, and rural habitats present in both states. Separate MANOVAs were run for slum, urban, suburban, rural, and forest habitats in Rio de Janeiro and for urban, suburban, and rural habitats in Florida.

Each MANOVA tested for differences in the variables *aeg* and *alb* caused by city, habitat, and city \times habitat interaction. We determined which of the variables contributed the most to significant MANOVA effects using standardized canonical coefficients as described by Scheiner (2001). Standardized canonical coefficients are scaled eigenvectors (analogous to a least-squares regression of multivariate means) that quantify the relative contribution of each dependent variable to the multivariate effect and the relationship among the dependent variables (positive or negative) (Scheiner 2001). Significant interactions were further analyzed by bivariate (Scheiner 2001) pairwise contrasts of habitat effects within a city (e.g., urban versus rural areas within Nova Iguaçu) using the Dunn-Sidak method for multiple comparisons, with experimentwise $\alpha = 0.05$ (Sokal and Rohlf 1995). Significant main effects were further analyzed by univariate contrasts of pairs of main effect means (Dunn-Sidak method with experimentwise $\alpha = 0.05$, Sokal and Rohlf 1995). However, this analysis of main effects contributed little information and is therefore omitted in the interest of brevity.

Frequency. The frequencies of occurrence of the two species in the different habitats were examined by maximum likelihood categorical analyses using the SAS CATMOD procedure (SAS Institute 1989). The following questions were addressed. (1) What are the frequencies of occurrence of *Ae. albopictus* and *Ae. aegypti* in oviposition traps and are they independent of habitat and city? (2) What are the frequencies of

Table 2. MANOVA results for the abundance of *Aedes* mosquitoes in three habitats of Rio de Janeiro State and Florida (I) and in all five habitats in just Rio de Janeiro state (II) and three habitats in just Florida (III)

Analysis	Source	df	Pillai's trace	P
I Rio de Janeiro State and Florida	City	3	0.58	0.0001
	Habitat	2	0.72	0.0001
	City \times habitat	6	0.45	0.0001
	Error	108		
II Rio de Janeiro State	City	1	0.15	0.0011
	Habitat	4	0.95	0.0001
	City \times habitat	4	0.41	0.0001
	Error	86		
III Florida	City	1	0.48	0.0001
	Habitat	2	0.93	0.0001
	City \times habitat	2	0.16	0.0569
	Error	54		

co-occurrence of the two species in oviposition traps and are they independent of habitat and city? For both questions, we also tested for habitat \times city interactions, which would indicate whether the pattern of dependence on habitat is, in turn, dependent on which city is being considered. We categorized the individual species distribution by presence versus absence in an oviposition trap during the 3 wk of the survey. The two species' joint distribution was categorized by co-occurrence or not in an oviposition trap during the 3 wk of the survey. The analyses were performed separately for the states of Rio de Janeiro and Florida. The strategy was to test a full model (habitat, city, and habitat \times city interaction), and if the interaction was not significant or if the resulting parameters were undefined, the reduced model (habitat and city) was tested.

Results

General

A total of 97.2% of all oviposition traps in Brazil (581/600) and 98.5% in the United States (353/360) were recovered. A total of 21,685 mosquitoes was collected and identified from Rio de Janeiro and 4,914 from Florida. *Ae. aegypti* accounted for 45.5% in Rio de Janeiro and 60.9% in Florida of the total *Aedes* identified and the remainder was *Ae. albopictus*. For *Ae. aegypti*, larvae that hatched in the field comprised 27.7 and 36.9% of the total immatures identified (field and laboratory hatch) in Rio de Janeiro and Florida, respectively. For *Ae. albopictus*, larvae that hatched in the field comprised 15.8 and 35.5% of the total immatures identified in Rio de Janeiro and Florida, respectively.

Abundance

Combined Analyses: Three Habitats in Four Cities. MANOVA indicated significant effects of city, habitat, and city \times habitat interaction on the abundances of *Aedes* mosquitoes (Table 2). Standardized canonical coefficients (SCC) showed that *aeg* contributed more

Table 3. Standard Canonical Coefficients of bivariate pairwise contrasts of three habitats within cities of Florida and Rio de Janeiro state collections

Rio de Janeiro	Variable	SCC		
		urban ^a	suburban	rural ^b
urban	<i>aeg</i>		1.02 ^b	1.35
	<i>alb</i>		0.88 ^b	-0.40
suburban	<i>aeg</i>	-0.39		1.41
	<i>alb</i>	1.03		-0.09
rural	<i>aeg</i>	1.16	1.26 ^a	
	<i>alb</i>	-0.87	-0.60 ^a	

Florida	Variable	SCC		
		urban ^c	suburban	rural ^d
urban	<i>aeg</i>		1.39 ^d	1.36
	<i>alb</i>		0.13 ^d	-0.39
suburban	<i>aeg</i>	1.37		-0.02
	<i>alb</i>	-0.35		1.18
rural	<i>aeg</i>	1.27	-0.82 ^c	
	<i>alb</i>	-0.61	1.01 ^c	

Significant bivariate pairwise contrasts (with probability associated with Pillai's trace value <0.05) are highlighted in bold.

- ^a RJ.
- ^b NI.
- ^c PB.
- ^d BR.

to the differences among the city × habitat combinations ($SCC_{aeg} = 1.20$, $SCC_{alb} = 0.55$). Bivariate pairwise contrasts between habitats within a city showed that all but two contrasts (NI/urban versus NI/suburban and BR/suburban versus BR/rural) were significant (Table 3). Of all significant contrasts, all but one pair of SCCs (BR/urban versus BR/suburban) had opposite signs, indicating a general negative

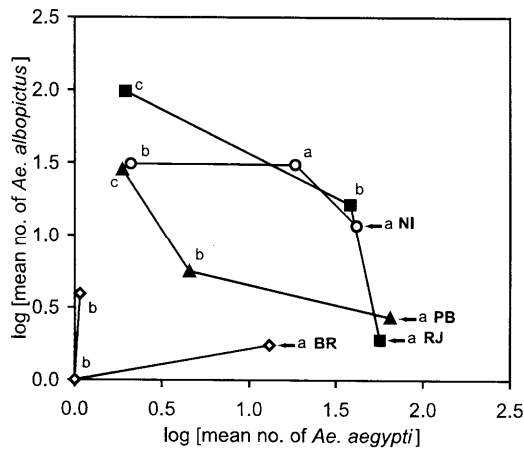


Fig. 2. Least squares means of the log-transformed mean number of *Ae. aegypti* and *Ae. albopictus* from Florida and Rio de Janeiro collections by habitat within Rio de Janeiro (RJ), Nova Iguaçu (NI), Palm Beach (PB), and Boca Raton (BR). The data points of the different habitats within a city are connected with a line starting from urban (arrow) through suburban to rural habitat. Within a city, different letters denote bivariate means that are significantly different from one another by multivariate pair-wise comparisons (Scheiner 2001). For sake of clarity, the SEs of least square means of *Ae. aegypti* (SE = 0.16) and *Ae. albopictus* (SE = 0.11) are omitted.

Table 4. Standard Canonical Coefficients of bivariate pairwise contrasts of the five habitats within cities of Rio de Janeiro state, Rio de Janeiro (RJ) and Nova Iguaçu (NI)

Rio de Janeiro	Variable	SCC				
		slum ^a	urban	suburban	rural	forest ^b
slum	<i>aeg</i>		0.44 ^b	-0.17 ^b	-0.82 ^b	-0.85
	<i>alb</i>		1.14 ^b	1.14 ^b	1.15 ^b	1.12
urban	<i>aeg</i>	1.18		-0.86 ^b	1.51 ^b	1.18
	<i>alb</i>	0.03		1.11 ^b	-0.65 ^b	-0.53
suburban	<i>aeg</i>	-0.21	-0.39 ^a		1.21 ^b	1.19
	<i>alb</i>	1.34	1.16 ^a		-0.26 ^b	-0.01
rural	<i>aeg</i>	-0.8	1.03 ^a	1.26 ^a		-0.50
	<i>alb</i>	1.18	-0.87 ^a	-0.6 ^a		1.31
forest edge	<i>aeg</i>	-0.16	-0.25 ^a	-0.19 ^a	1.21 ^a	
	<i>alb</i>	1.34	1.35 ^a	1.35 ^a	-0.31 ^a	

Significant bivariate pairwise contrasts (with probability associated with Pillai's trace value <0.05) are highlighted in bold.

- ^a RJ.
- ^b NI.

relationship between *aeg* and *alb* among habitat within a city (Table 3; Fig. 2). In Nova Iguaçu, *Ae. aegypti* was abundant in urban and suburban areas and *Ae. albopictus* was abundant in all three habitat types; mosquito abundances in urban and suburban area of NI were not significantly different (Fig. 2; Table 3). In Boca Raton, no significant difference was found between the rural and suburban mosquito abundances because of their absence from suburban oviposition traps and low abundance (*alb*) and absence (*aeg*) from rural oviposition traps (Fig. 2). In both Rio de Janeiro and Palm Beach, all three habitats differed significantly in *Aedes* abundances (Fig. 2), with *Ae. albopictus* more abundant in rural oviposition traps, *Ae. aegypti* more abundant in urban oviposition traps, and both species moderately abundant in suburban oviposition traps (Fig. 2; Table 3). The magnitudes of the SCCs showed that *aeg* and *alb* contributed nearly equally to the differences among cities ($SCC_{aeg} = 0.89$, $SCC_{alb} = 0.86$, data not shown). The common sign of these SCCs indicates that cities with high abundances of *Ae. aegypti*, also had high abundances of *Ae. albopictus*. *Aedes* mosquitoes were most abundant in the two cities in the state of Rio de Janeiro and the lowest in Boca Raton (Fig. 2). For the habitat main effect, the magnitudes of SCC showed that *aeg* contributed more to the differences among cities than *Ae. albopictus* ($SCC_{aeg} = 1.24$, $SCC_{alb} = -0.64$). The opposite sign of these SCCs indicated a negative relationship between numbers of *aeg* and *alb*, meaning that in habitats where *Ae. aegypti* was abundant, *Ae. albopictus* was rare and vice versa (Fig. 2).

Rio de Janeiro State: Five Habitats in Two Cities. MANOVA indicated significant effects of city, habitat, and city × habitat interaction on the abundance of *Aedes* mosquitoes (Table 2). The magnitude of SCCs showed that *alb* contributed more to the differences among the city × habitat combinations ($SCC_{aeg} = 0.57$, $SCC_{alb} = 1.04$). Bivariate pairwise contrasts between habitats within a city showed that all but two contrasts (RJ/slum versus RJ/urban, and NI/forest versus NI/rural) were significant. Unlike the analysis

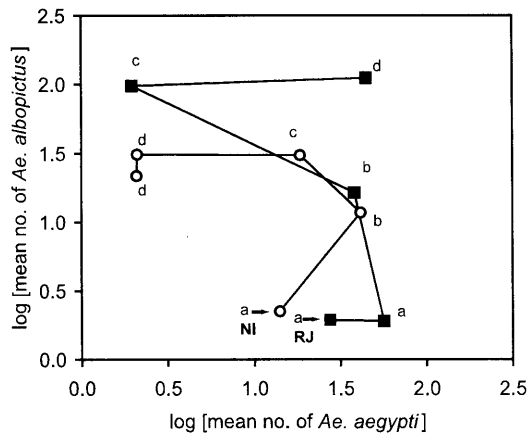


Fig. 3. Least squares means of the log-transformed mean number of *Ae. aegypti* and *Ae. albopictus* from five habitats within Rio de Janeiro (RJ) and Nova Iguaçu (NI). The data points of the different habitats within a city are connected with a line, starting from slum (arrow) and ending with forest edge (see Table 3). Within a city, different letters denote bivariate means that are significantly different from one another by multivariate pairwise comparisons (Scheiner 2001). For sake of clarity, the SEs of least square means of *Ae. aegypti* (SE = 0.13) and *Ae. albopictus* (SE = 0.11) are omitted.

of three habitats (Table 4), the contrast NI/urban versus NI/suburban was significant in this analysis (Table 4). Of all significant contrasts, all but one pair of SCCs (NI/slum versus NI/urban) had opposite signs indicating a general negative relationship between the abundances of the two species (Table 4). *Ae. aegypti* predominated in the slum areas of both cities (Fig. 3). In Rio de Janeiro city, *Aedes* abundance in the slum area was not significantly different from that in the urban area (Fig. 3). Unlike Nova Iguaçu, high numbers of both *Ae. albopictus* and *Ae. aegypti* were found at the edge of the forest of Rio de Janeiro (Fig. 3). The SCC values showed that *aeg* contributed almost exclusively to the city main effect ($SCC_{aeg} =$

1.19, $SCC_{alb} = 0.00$) with more *Ae. aegypti* collected in Rio de Janeiro city than in Nova Iguaçu and similar *Ae. albopictus* abundance in both cities (data not shown). For the habitat main effect, the magnitudes of SCC showed that *alb* contributed more to the differences ($SCC_{aeg} = -0.80$, $SCC_{alb} = 1.16$).

Florida: Three Habitats in Two Cities. MANOVA indicated significant city and habitat effects and a marginally nonsignificant city \times habitat interaction effect on the abundances of the two species of *Aedes* (Table 2). The SCC magnitudes showed that *aeg* contributed somewhat more than *alb* to the differences between cities ($SCC_{aeg} = 1.01$, $SCC_{alb} = 0.78$). For the habitat effect, the magnitudes of SCC showed that *aeg* contributed more to the differences than *alb* did ($SCC_{aeg} = 1.34$, $SCC_{alb} = -0.38$). SCCs of bivariate pairwise comparisons are not shown for Florida separately because they were similar to those already shown in Table 3.

Frequency

Rio de Janeiro State. *Aedes albopictus* was relatively rare in the slums of both cities and urban area of Rio de Janeiro city, but nearly ubiquitous in other habitats across both cities. *Ae. aegypti* was relatively rare in rural areas of both cities and at the edge of the forest of Nova Iguaçu (Table 5). For *Ae. albopictus*, the full model fit poorly with two redundant, nonestimable, parameters. For *Ae. aegypti*, the full model fit better and yielded nonsignificant habitat \times city interaction, indicating that the frequency of occurrence of *Ae. aegypti* across habitats was independent of which city was considered. For both species, the reduced model (i.e., without the interaction) was run (Table 6). For both *Ae. albopictus* and *Ae. aegypti*, there was a significant habitat effect ($P < 0.001$) but no significant city effect. For both species, the likelihood ratio was significant, indicating significant lacks of fit, but that is unlikely to change the conclusion that occurrence

Table 5. The frequency of occurrence of *Ae. albopictus* and *Ae. aegypti* in traps (20 traps per habitat) during the three weeks of the survey per habitat and percentage of total number of traps in Rio de Janeiro city (N = 100) and Nova Iguaçu (N = 100), West Palm Beach (N = 60) and Boca Raton (N = 60)

Habitat	Rio de Janeiro city			Nova Iguaçu		
	<i>alb</i> only ^a	<i>aeg</i> only ^b	Co-oc ^c	<i>alb</i> only ^a	<i>aeg</i> only ^b	Co-oc ^c
slum	0	11	8	0	8	8
urban	1	11	8	1	0	18
suburban	1	0	19	3	1	16
rural	13	0	7	9	1	9
forest edge	1	0	19	9	0	10
percentage	16	22	61	22	10	61
Habitat	West Palm Beach			Boca Raton		
	<i>alb</i> only ^a	<i>aeg</i> only ^b	Co-oc ^c	<i>alb</i> only ^a	<i>aeg</i> only ^b	Co-oc ^c
urban	0	10	10	1	11	6
suburban	4	2	9	0	0	0
rural	9	1	10	6	0	2
percentage	22	22	48	12	18	13

^a *alb* only = number of traps yielding only *Ae. albopictus*.

^b *aeg* only = number of traps yielding only *Ae. aegypti*.

^c Co-oc = number of traps yielding both *Ae. albopictus* and *Ae. aegypti*.

Table 6. CATMOD results for the frequency of occurrence of *Ae. albopictus* and *Ae. aegypti* and their co-occurrence all five habitats in Rio de Janeiro state and in three habitats in Florida

Source	Rio de Janeiro state			Florida			
	df	Chi square	P	df	Chi square	P	
<i>Ae. albopictus</i>	Intercept	1	41.27	0.0001	1	0.17	0.6821
	City	1	1.63	0.2017	1	24.34	0.0001
	Habitat	4	38.72	0.0001	2	10.83	0.0044
	Likelihood ratio	4	17.45	0.0016	2	13.74	0.0001
<i>Ae. aegypti</i>	Intercept	1	46.37	0.0001	1	0.25	0.6167
	City	1	3.28	0.0699	1	16.22	0.0001
	Habitat	4	30.01	0.0001	2	27.46	0.0001
	Likelihood ratio	4	10.64	0.0310	2	2.53	0.2838
Co-occurrence	Intercept	1	11.03	0.0009	1	19.43	0.0001
	City	1	0	1.0000	1	14.69	0.0001
	Habitat	4	25.82	0.0001	2	4.25	0.1197
	City* habitat	4	17.87	0.0013	—	—	—
	Likelihood ratio	0	—	—	2	5.76	0.0563

depended on habitat. For co-occurrence of the two species in the same oviposition trap, there was a significant habitat effect and a significant interaction, indicating that the distribution of co-occurrence across habitats was not the same for Rio de Janeiro and Nova Iguaçu (Table 6). Co-occurrence of *Ae. albopictus* and *Ae. aegypti* in the same oviposition trap was most frequent in the suburban areas of both cities and in the urban area of Nova Iguaçu and the edge of the forest of Rio de Janeiro city. For Rio de Janeiro and Nova Iguaçu pooled, the two species co-occurred in the majority (61%) of the oviposition traps (Table 5).

Florida. *Aedes albopictus* was much more likely to occur in rural areas than in urban or suburban areas (Table 5). However, the data were very heterogeneous between the cities: the frequency of occurrence was much higher in West Palm Beach than in Boca Raton. The complete absence of *Aedes* in suburban areas of Boca Raton (Table 5) renders the Florida data harder to interpret. *Ae. aegypti* was nearly ubiquitous in the urban areas and rare or absent in the suburban and rural areas (Table 5). For both species, the full model fit poorly (significant likelihood ratio, data not shown). For *Ae. albopictus*, the reduced model yielded significant habitat and city effects, and a significant likelihood ratio (Table 6). For *Ae. aegypti*, the reduced model fit well and yielded significant habitat and city effects (Table 6). Although the full model for co-occurrence did not fit well, the reduced model yielded a significant city effect but a nonsignificant habitat effect (Table 6). For West Palm Beach, the two species co-occurred in 48% of the oviposition traps, whereas they co-occurred in only 13% of oviposition traps in Boca Raton (Table 5).

Discussion

The results show that *Ae. albopictus* has not replaced *Ae. aegypti* in the surveyed areas of southeastern Brazil and Florida since its introduction in the mid-1980s. During the rainy season of 2001, both species were common in the four areas sampled, and their abundances were positively correlated across cities but negatively correlated across habitats. Total densities

of these species in the oviposition traps, rather than only that of *Ae. aegypti*, as we hypothesized, were lower in Florida than in Rio de Janeiro state. We believe that this difference is probably because of the lower availability of artificial containers and lower accessibility of hosts in the United States, where waste management and air conditioning are more prevalent. Because of the short-term nature of our survey, possible seasonal differences among the parameters measured are not revealed.

The results clearly support our hypothesis that habitat affects the abundance of *Ae. aegypti* and *Ae. albopictus* in different ways. In our survey, *Ae. aegypti* predominated in highly urbanized habitats, *Ae. albopictus* in more rural areas, and the two species co-occurred in the suburban areas where mosquitoes were found. The significant interaction between city and habitat effects indicated city-specific habitat patterns for these species. The absence of *Aedes* mosquitoes in the suburban area of Boca Raton was most likely a result of mosquito control activity and the scarcity of suitable containers in this neighborhood. When considering the analyses of Rio de Janeiro state separately, *Ae. aegypti* was abundant in not only slum, urban, and suburban areas, but also at the forest edge in the city of Rio de Janeiro. This forest is situated in the middle of a densely populated urban area, which may be the sources of *Ae. aegypti* at its edges. Although *Aedes* mosquito abundances in the urban and suburban area in Nova Iguaçu were not significantly different in the combined analyses, they were in the separate analyses of the Brazilian state. In the latter, mosquito abundances of the urban and slum areas were also significantly different in Nova Iguaçu, but not in Rio de Janeiro. This was because of an unexpectedly high abundance of *Ae. albopictus* in the urban area of Nova Iguaçu, which apparently shares features with suburban areas where both *Ae. aegypti* and *Ae. albopictus* thrive. Co-occurrence of these species has also been reported in highly urbanized areas of Thailand (Yap 1975, Yap and Thiruvengadam 1979) and in rural areas of Vietnam (Kay et al. 2002).

In general, *Ae. albopictus* became most prevalent after invasions of Rio de Janeiro state and Florida in

rural, suburban, and vegetated urban habitats. In the native range of this species in southern Asia similar patterns are suggested to be caused by noncompetitive factors (Hawley 1988). Typically, in Asia, urbanized areas are suggested to favor *Ae. aegypti* because it prefers to oviposit, to rest, to bite humans indoors, and to not require sugar feeding (Harrington et al. 2001), and rural areas to favor *Ae. albopictus* because it prefers to oviposit, to rest, and to bite hosts outdoors (Hawley 1988). However, for noncompetitive spatial segregation, the reverse statement should also be true: *Ae. albopictus* should either avoid urbanized areas, or those areas should yield low population growth, and *Ae. aegypti* should avoid rural areas, or those areas should yield low population growth. Although in many tropical urban areas, outdoor oviposition sites, in the form of trash containers, for *Ae. albopictus* are present, vegetation providing nectar sources for sugar feeding or resting sites might be scarce. Nguyen et al. (1974) mentioned the presence of vegetation as an important determining factor for the presence of *Ae. albopictus* in Vietnam, but they often encountered *Ae. albopictus* in urban areas with vegetation and in suburban and rural areas, but not in highly urbanized areas without vegetation. In Brazil, rural areas do not seem to be avoided by *Ae. aegypti*, because access to indoor breeding and biting sites is similar to the urban areas. In Rio de Janeiro State, the majority of all houses sampled did not have air conditioning and therefore had open windows through which mosquitoes had access to indoor habitats independent of the outdoor habitat. Furthermore, we sampled mosquitoes only at residences, and therefore, human hosts were present at all sites, including rural and edges of forest areas. However, in Florida, the large majority of houses in the suburban and rural areas did have air conditioning, whereas the majority of houses in the urban areas sampled did not, and therefore, rural areas would be indeed expected to hinder, and the urban areas to favor, *Ae. aegypti*. However, this interpretation does not explain how *Ae. aegypti* persists in suburban areas. Presumably, when denied access to humans, *Ae. aegypti* must seek other hosts (Reiter et al. 2003).

In the United States, *Ae. albopictus* is the superior larval competitor where these *Aedes* species are mainly encountered in tire piles and cemetery vases outdoors (O'Meara et al. 1995, Juliano 1998). We hypothesize that in rural areas of Rio de Janeiro state, *Ae. aegypti* is uncommon because *Ae. albopictus* outcompetes it during the larval stage. Braks et al. (2003) suggested that the latter species is the superior larval competitor where leaf litter provides the limiting nutrient resource base. Juliano et al. (2002) proposed that persistence of *Ae. aegypti* in parts of South Florida resulted from site-specific abiotic conditions during the dry season, which favor egg survival of *Ae. aegypti* over *Ae. albopictus*, thereby affecting the outcome of larval competition. Coexistence of the two species seems to be possible when the local environment favors a nonaquatic stage of one species and larval competition favors the other. We suggest that the interaction of habitat characteristics with weather,

desiccation resistance of adults and eggs, adult habitat preference, blood-meal choice, and larval competition determine the relative abundance of *Aedes* mosquito species. Urbanization is generally associated with decreased vegetation and increased human density, structures, and pollution (McIntyre 2000). Unfortunately, most authors do not quantify environmental characteristics, and many do not even give a qualitative account (Hawley 1988). In our study, we investigated distribution patterns in two disjunct countries where different geographic populations of *Ae. albopictus* established and spread contemporaneously. Despite the differences between southeastern Brazil and Florida with respect to the origins of invasive populations (Birungi and Munstermann 2002), climate, vegetation type and coverage, and socioeconomic conditions, the spatial segregation of the two species showed striking similarities.

Aside from the similarities of habitat segregation patterns in all four cities, there is a prominent difference between Rio de Janeiro and Florida. When comparing four cities and three habitats, there is a striking difference in the patterns of *Aedes* abundances in the suburban area with respect to rural and urban areas. The urban-suburban-rural curve is concave in both cities in Florida, whereas it is convex in both cities of Rio de Janeiro state. This suggests that the suburban areas in Florida are less favorable for both *Ae. albopictus* and *Ae. aegypti* than rural and urban areas, respectively, whereas in Rio de Janeiro, suburban areas are more favorable for both species.

Spatial segregation has been invoked to explain coexistence of *Ae. aegypti* and *Ae. albopictus* in various regions (Chan et al. 1971, Hawley 1988, Black et al. 1989, Barrera 1996). In Singapore, Chan et al. (1971) found that only 7% of the larval development sites held larvae of both *Ae. aegypti* and *Ae. albopictus*. In contrast, in the present survey, 61% of the oviposition traps collected in Rio de Janeiro city and Nova Iguaçu and 46% in Palm Beach yielded both species. Part of the discrepancy might be because of the fact that we categorized the individual species distribution by presence versus absence in an oviposition trap during the 3 consecutive wk of the survey to eliminate zero catches of individual weeks from the analyses, which artificially inflates the co-occurrence values. Although Chan et al. (1971) surveyed larvae in natural occurring containers, whereas we collected predominantly eggs, the difference in interspecific co-occurrence between studies is unlikely to be because of larval competition. *Ae. albopictus* has been shown to be a superior larval competitor to *Ae. aegypti* (Juliano 1998, Braks et al. 2003) independent of the local habitat (S.A.J., unpublished data). As mentioned earlier, local habitat characteristics seem to influence the nonaquatic stages (adults and eggs) of these mosquito species (Juliano et al. 2002). Co-occurrence data differ between Rio de Janeiro state and Florida: in Brazil, co-occurrence is habitat-dependent, whereas in Florida, co-occurrence is city-dependent. The latter pattern results from very low co-occurrence frequency in Boca Raton. Although, co-occurrence is definitely not random or

homogeneously distributed, habitat segregation is clearly more evident in species abundance than in frequency of species occurrence. In addition, *Ae. albopictus* occurs in 77, 83, and 72% and *Ae. aegypti* in 81, 71, and 55% of all oviposition traps of Rio de Janeiro city, Nova Iguaçu, and Palm Beach, respectively. In these areas, the two species encounter each other extensively, which probably results in competition among larvae (Juliano et al. 2002). This study has shown that conclusions on the spatial distribution of these species depends on the parameters measured, whether abundance or frequency of occurrence. Few other studies also report both the abundances and high co-occurrences of these two species in the same larval containers (Yap and Thiruvengadam 1979, Schultz 1989, Dutta et al. 1998, Pesina et al. 2001). Most reports present only one or the two parameters, which can lead to wrong or incomplete conclusions and consequences for control. Presence/absence records, for example, could hamper health officials attempts to predict dengue risk because dengue transmission is suggested to be dependent on *Ae. aegypti* abundance (Focks et al. 1995). However, the fact that both mosquitoes occur in (nearly) all habitats implies that a shift in mosquito relative densities can take place instantly on habitat change because there is no lag time for invasion of a mosquito species. Where there is rapid urbanization, *Ae. aegypti* will flourish, and consequently, dengue risk may rise rapidly. Both measures of abundance and frequency are important to understand underlying mechanisms of spatial distribution of *Ae. aegypti* and *Ae. albopictus* and have practical implications for vector control.

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