OXFORD

Population and Community Ecology

Recent Changes in the Local Distribution of *Aedes aegypti* (Diptera: Culicidae) in South Florida, USA

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Abstract

Disease transmission is directly tied to the spatial distribution of disease vectors. The distribution of *Aedes aegypti* (L.) in the United States has diminished since the introduction of *Aedes albopictus* (Skuse) in the 1980s. However, *Ae. aegypti* persists in some urban areas, particularly in south Florida. The pattern of habitat segregation of these two species is well documented, but the consistency of this phenomenon over time is unknown. To examine the dynamics of the local distributions of these two species, we studied the spatial pattern of *Ae. aegypti* and *Ae. albopictus* over time at a fine landscape scale in Palm Beach County, FL. We compared patterns from 2006–2007 with their distributions in 2013, taking into account abiotic factors of microclimate and land cover. We found evidence for a local shift in *Ae. aegypti* distribution, but could not attribute this to changes in measured abiotic factors. Alternatively, the interaction between *Ae. aegypti* and *Ae. albopictus* that initially resulted *Ae. aegypti* decline may be being attenuated through natural selection. This study confirms the importance of monitoring the changing ranges of these two important vector species.

Key words: mosquito, *Aedes aegypti*, *Aedes albopictus*, population dynamics, interspecific competition

The spatial distribution of *Aedes* (*Stegomyia*) *aegypti* (L.) in the United States has changed significantly over the past 30 yr (O'Meara et al. 1995, Britch et al. 2008). Once widespread in the southern United States, *Ae. aegypti* declined rapidly in range and abundance shortly after the introduction of the Asian tiger mosquito, *Aedes* (*Stegomyia*) *albopictus* (Skuse), during the 1980s (O'Meara et al. 1995, Moore and Mitchell 1997). This pattern of decline after invasion by *Ae. albopictus* is documented in other parts of the world as well, such as in Bermuda (Kaplan et al. 2010) and Mayotte (Bagny Beilhe et al. 2012). Although diminished in range, *Ae. aegypti* has persisted locally (O'Meara et al. 1995, Britch et al. 2008, Reiskind and Lounibos 2013) and currently occurs in the southeastern United States, mostly restricted to urban regions and the Florida Keys. Elsewhere, this species is patchily distributed in urban areas of Texas, Arizona, Louisiana, and California (Gloria-Soria et al. 2014). The range of *Ae. aegypti* is relevant because its vector competence differs from that of *Ae. albopictus*. Therefore, differential vector composition alters arbovirus transmission risk (Simard et al. 2005, Juliano 2010).

Interspecific interactions influence the distribution of *Ae. aegypti* (Braks et al. 2003, Rey et al. 2006, Reiskind and Lounibos 2013) via mechanisms such as larval competition and mating interference. A meta-analysis of lab and field experiments showed that larval *Ae. albopictus* are competitively superior to *Ae. aegypti*, especially when only low quality food sources are available (Juliano 2010). This advantage is context-dependent however, as *Ae. aegypti* suffers less

from interspecific competition when high quality food sources are available (Juliano 2010, Reiskind et al. 2012). Mating interference by *Ae. albopictus* negatively affects *Ae. aegypti* populations. When heterospecific mating occurs, accessory gland products from *Ae. albopictus* males sterilize *Ae. aegypti* females, but the converse of this—*Ae. aegypti* males sterilizing *Ae. albopictus* females—does not occur. This asymmetrical reduction in *Ae. aegypti* fitness is considered to be a driver in the rapid displacement of *Ae. aegypti*, along with larval competition, and may have evolutionary implications for *Ae. aegypti* persistence in the presence of *Ae. albopictus* (Bargielowski and Lounibos 2015).

Aedes aegypti is also influenced by abiotic conditions determined by climate and landscape (Jansen and Beebe 2010). Although the global range of *Ae. aegypti* may be determined by macroclimate (Capinha et al. 2014), microclimate better predicts the heterogeneous distribution of *Ae. aegypti* at a fine scale (Hayden et al. 2010). Climatic conditions directly impact *Ae. aegypti* at different life stages (Christophers 1960, Costanzo et al. 2005, Lounibos et al. 2010, Eisen and Moore 2013), and a combination of rainfall, temperature, and humidity can dictate the suitability of a habitat (Mogi et al. 1996, Reiskind and Lounibos 2013). Rainfall generally increases mosquito abundance by the filling of suitable container habitats (Costanzo et al. 2005, Reiskind and Lounibos 2013, Simoes et al. 2013). *Aedes aegypti* eggs and adults are generally more desiccation tolerant than *Ae. albopictus* (Sota and Mogi 1991, Mogi et al. 1996, Juliano et al. 2002, Reiskind and Lounibos 2009,

Lounibos et al. 2010), which further highlights the importance of temperature and humidity in determining the distribution of the two species.

In Florida, *Ae. aegypti* predominates in highly urbanized areas yet is relatively rare in rural areas (O'Meara et al. 1995, Braks et al. 2003, Rey et al. 2006, Reiskind and Lounibos 2013). Similarly, the spatial pattern of *Ae. aegypti* was associated with urban variables in Buenos Aires, Argentina, and in Ribeirao Preto, Brazil (Carbajo et al. 2006, Summers 2011). When considering landscape, geographic scale is an important factor as microhabitats may enable *Ae. aegypti* presence within inhospitable landscapes. For example, in a largely arid Arizona desert, *Ae. aegypti* was positively associated with highly vegetated areas (Hayden et al. 2010), as might be expected because vegetation provides shade, regulates humidity, and provides allochthonous inputs that nourish container habitats (Vezzani et al. 2005, Barrera et al. 2006).

The persistence of *Ae. aegypti* in the United States is worrisome because hot urban habitats suitable for *Ae. aegypti* are expected to double or triple within the next 50 yr due to urban sprawl and climate change (Terando et al. 2014). It is possible the incomplete displacement of *Ae. aegypti* is a transient phase, and eventually *Ae. aegypti* will become extirpated from areas in sympatry with *Ae. albopictus* (Paupy et al. 2010). Alternatively, stable coexistence with *Ae. albopictus*, or even an expansion of *Ae. aegypti* distributions may be possible. Such an expansion could be due to resource availability (Juliano 2010), spatio-temporal heterogeneity in competitive congener distributions (Mogi et al. 1996, Juliano et al. 2002, Lounibos et al. 2010, Reiskind and Lounibos 2013, Fader and Juliano 2014), a reduction in interspecific competition through natural selection (Bargielowski et al. 2013), or climatic changes that favor *Ae. aegypti*.

We assessed *Ae. aegypti* persistence and recrudescence by comparing *Ae. aegypti* and *Ae. albopictus* distribution data from 2006, 2007, and 2013 across a 45- by 15-km landscape in Palm Beach County, FL, where the two species have co-occurred since at least the early 1990s (Moore and Mitchell 1997). Palm Beach County encompasses a longitudinal landscape gradient from the heavily urbanized coastline to rural inland Florida, as well as temperature and humidity gradients (Reiskind and Lounibos 2013). We evaluated the changes in *Ae. aegypti* distributions in this region of south Florida by comparing patterns between years, taking into account microclimate, biotic, and landscape variations.

Materials and Methods

Site Selection

We monitored *Ae. aegypti* and *Ae. albopictus* in Palm Beach County, FL, at sites previously sampled in 2006 and 2007 by Reiskind and Lounibos (2013). The sites were located along six longitudinal 15-km long transects that extended westward from the east Florida coastline; each transect contained five sites located at 0, 1, 3, 8, and 15 km from the coast (Fig. 1). By collecting from previously sampled sites using the same methods over the same time period, we were able to compare relative population changes over time.

Mosquito Collection and Rearing

Over a 6-wk period from May to July 2013, three oviposition traps at each site collected mosquito eggs and larvae using the same methods described by Reiskind and Lounibos (2013). GPS coordinates for each trap were recorded using a Trimble Juno 3B Handheld computer running Esri ArcPAD 10.1 software with 5 m accuracy (Trimble Navigation Ltd., Sunnyvale, CA; Esri, Redlands, CA). Eggs and residual aquatic fractions were collected, and traps were rebaited weekly (Reiskind and Lounibos 2013). Traps were kept in the same location the entirety of the study unless they were found to be missing or destroyed (1.48% of all traps were lost or destroyed). When this occurred, replacement traps were relocated in close proximity to the original trap (<10 m).

An iButton data logger (Maxim Corp., Dallas, TX) was attached to the underside of one trap at each site and recorded temperature and humidity readings every 10 min for at least three weeks over the 6-wk period. The proportion of traps containing water was recorded for each site during trap servicing—this metric reflected rainfall at each site.

Eggs and aquatic fractions were transported to the laboratory on the day of collection, and eggs were dried overnight, counted, and then hatched the following day. Mosquito eggs and larvae were reared in food grade plastic containers (700 ml total volume, Instawares.com, Kennesaw, GA) with high quality rearing medium consisting of 200 ml tap water, 100 ml leaf infusion, 0.03 g Brewer's yeast, and 0.03 g powdered freeze-dried egg yolk or Bacto TC lactalbumin (BD Biosciences, San Jose, CA). Pupae were identified to species using a dissecting microscope and, although uncommon, if larvae died before pupation they were identified at the larval stage. Pupae were transferred to vented 50-ml conical tubes, allowed to eclose, and then were freeze-killed and preserved in 80–100% ethanol.

Subsampling

Collected eggs and larvae were subsampled in two ways due to logistical constraints. First, one of three traps was selected for rearing and species identification from every site per week. Only traps containing eggs were considered for selection. If only one of the three traps contained eggs, that trap was selected. If two or three traps contained eggs, a random integer generator was used to randomly select one of the traps. All mosquito larvae collected in aquatic fractions of traps were reared to the fourth-instar or pupal stage for species identifications, but only larvae corresponding to selected traps during subsampling were included in the analysis. Mortality during rearing was assessed by comparing egg counts with mosquito yields and by attempting to vacuum-induce hatch a subset of unhatched eggs; the pattern of mortality appeared to be random.

Second, a maximum of 30 eggs were subsampled from selected traps. This was achieved by cutting paper strips into sections and haphazardly choosing 30 eggs by section for rearing. Only 16 of 162 traps had >30 eggs and required subsampling. Although this procedure sacrificed the identification to species of every egg laid, the proportion of *Ae. aegypti* relative to *Ae. albopictus* at each site is the focus of this study and was accurately measured using this method. Further, the proportion of each species was used to account for nonidentified mosquitoes to estimate abundance based on egg counts (Lozano-Fuentes et al. 2014).

Incorporation of GIS data

Areas within 100 m of collection sites were classified by land cover type (Fig. 1). Esri ArcMap 10.2.2 software (Esri, Redlands, CA) was used to digitize land cover using high-resolution orthoimagery for the years 2006 (0.5 m pixel resolution, USGS, 2006, USGS Earth Explorer) and 2013 (0.3 m pixel resolution, Palm Beach County Information System Services, 2013, Palm Beach County GIS Database); orthoimagery was not available for 2007. The
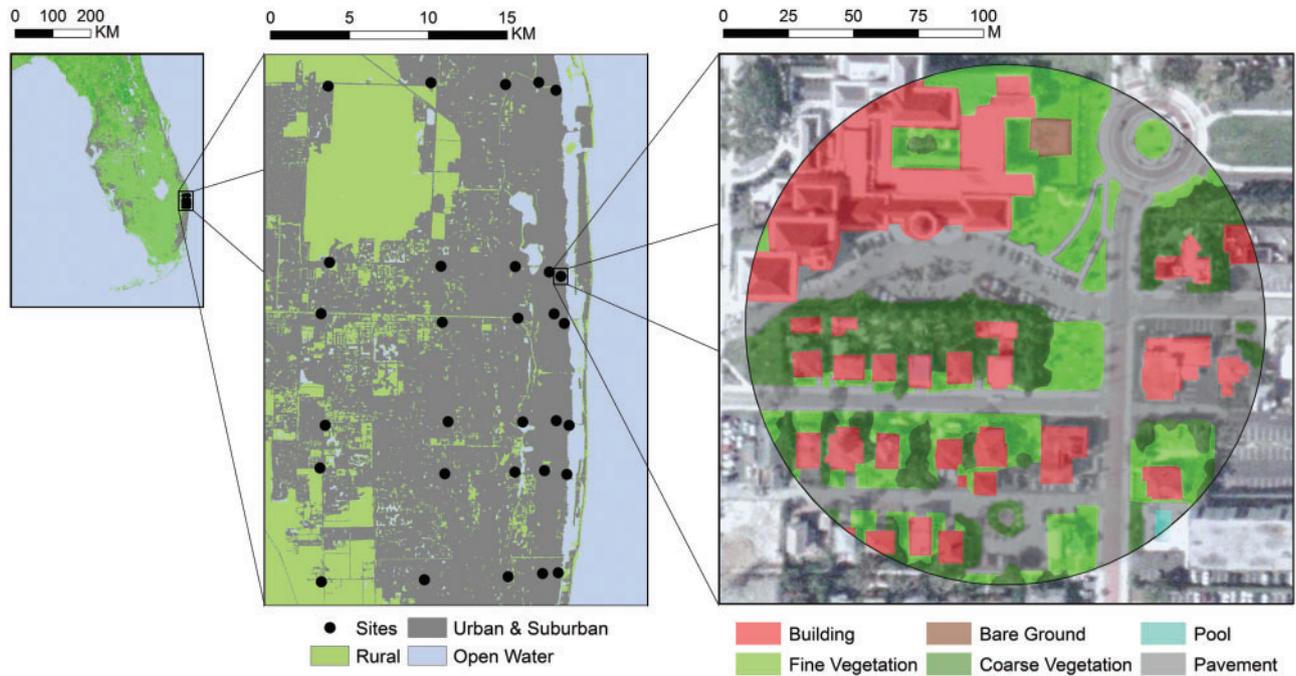
Fig. 1. Collection sites in Palm Beach County, FL. Site locations within Florida are shown in the left panel as black circles. The center panel shows site locations within Palm Beach County as black circles, and indicates generalized land cover (urban and suburban, rural, open water). The right panel shows a single site with its associated land cover classifications (building, fine vegetation, bare ground, coarse vegetation, pool, and pavement) (Online figure in color).

classification system used was modified from the Anderson Land Cover Classification System (Anderson et al. 1976) and included eight land cover types: building or structure, pavement, bare ground, fine vegetation, coarse vegetation, freshwater, saltwater, and swimming pool. Classifications were determined on the basis of visual interpretation of satellite data and ground-truth verification. Using this method, fine scale changes in landscape from 2006 to 2013 were quantified in such a way that land cover types could be included in statistical analyses as possible explanatory factors for spatial variation between species.

Statistics

Sites were compared by distance from the coast (0, 1, 3, 8, 15 km), and each transect was treated as a replicate. Abiotic variables including temperature, relative humidity (RH), and site wetness were examined for the 6-wk sampling period. The daily minimum, average, and maximum temperature and RH at each distance from the coast were calculated. The percentage of wet containers at each distance from the coast was calculated by dividing the total number of wet containers at each distance by the total number of containers recovered. Esri ArcMap 10.2.2 software was used to calculate the area of each land cover type at every site. Temperature, RH, site wetness, and land cover type were analyzed with linear regressions as a function of distance from the coast (JMP Pro 11.2, 2014). Paired *t*-tests were used to compare between sampling periods the temperature, RH, and land cover types at each distance (JMP Pro 11.2, 2014).

The total numbers of *Ae. aegypti* and *Ae. albopictus* eggs for each distance from the coast for the entire sampling period were calculated, as well as weekly *Ae. aegypti* abundance (Supp. Fig. 1 [online only]). Egg abundances and the proportions of *Ae. aegypti* were analyzed with linear regressions as a function of distance from the coast. Paired *t*-tests were used to compare between sampling periods the abundances of both species at each distance (JMP Pro 11.2, 2014).

Data from 2006 and 2007 were summarized for time periods that overlapped with 2013 sampling (two weeks in 2006, and six weeks in 2007). For 2006 and 2007, only 11–15 of the 30 sites had associated environmental data, so linear regression equations were used to estimate missing temperature and RH variables for all sites (Reiskind and Lounibos 2013). The yearly proportions of *Ae. aegypti* for each distance from the coast were compared between sampling periods with a generalized linear mixed model logistic regression (PROC GLIMMIX, SAS 10.3 Institute, 2014). The proportion of *Ae. aegypti* served as the dependent variable and was analyzed using a binomial distribution and a logit link function. Distance, year, and the interaction of distance and year were modeled as independent variables, and site was modeled as a random effect (Lozano-Fuentes et al. 2014).

Results

Spatial Variation of Abiotic Variables

In 2013, temperature, RH, and four land cover types varied significantly with distance from the coast. Average daily temperature decreased with distance from the coast (Fig. 2A, $R^2 = 0.2475$, $F_{1,28} = 9.2076$, $P = 0.0052$). The average parameter estimate for the linear coefficient of distance from the coast for temperature is $-0.0861°C$ (range: $-0.1144°C$ to $-0.0577°C$), meaning that for each kilometer west from the coast, temperature decreased by ~0.086°C, or about 1.3°C across each longitudinal transect. Minimum daily temperature also decreased with distance from the coast ($R^2 = 0.4395$, $F_{1,28} = 21.9586$, $P < 0.0001$), but maximum daily temperature did not ($R^2 = 0.0599$, $F_{1,28} = 1.785$, $P = 0.1923$). Temperature parameter estimates are similar to parameter estimates for 2006 and 2007 (range: $-0.0705°C$ to $0.1475°C$, Reiskind and Lounibos 2013). Temperature was significantly cooler in 2007 and 2013 than in 2006 at 15 km from the coast by a mean difference of 0.468°C and 0.865° C, respectively (Paired *t*-test, 2007,
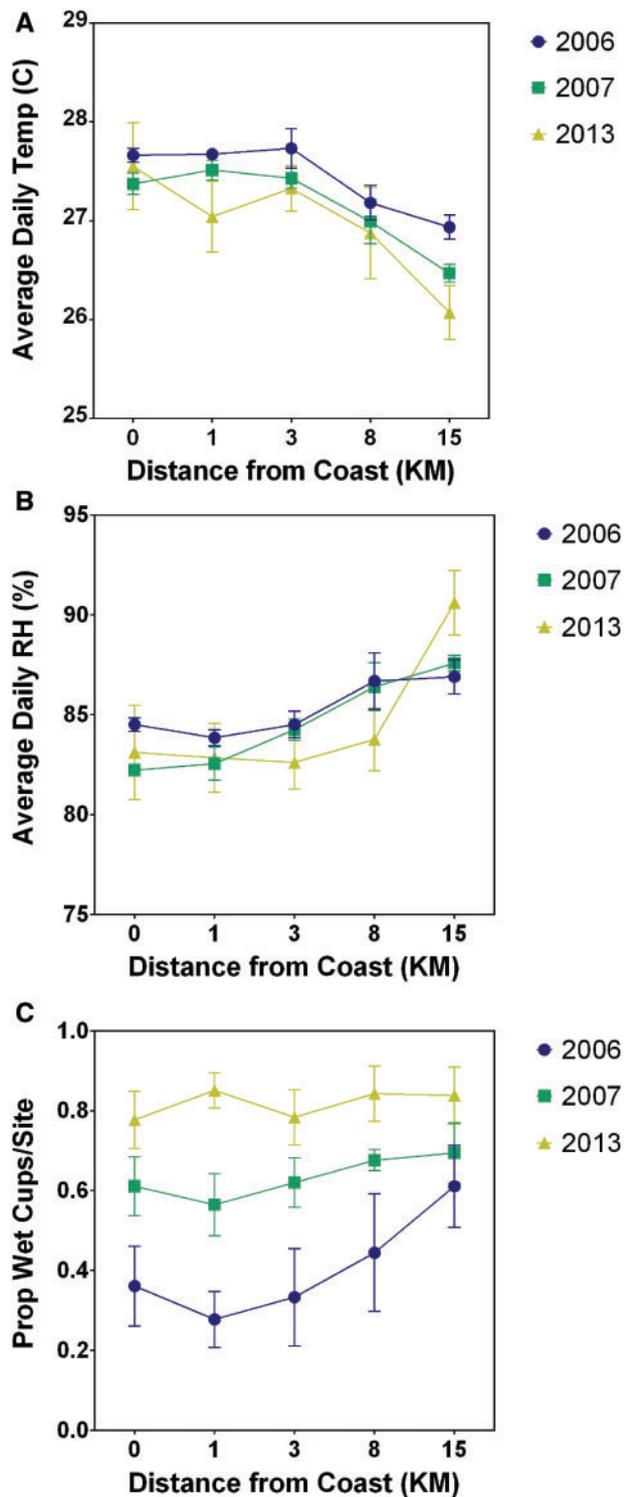
Fig. 2. (**A**) Average daily temperature (°C), (**B**) average daily relative humidity (%), and (**C**) average proportion of wet oviposition traps per site for 2006 (blue), 2007 (green), and 2013 (yellow). Each error bar is constructed using 1 standard error from the mean (Online figure in color).

for RH was 0.4963% (range: 0.3552% to 0.6374%), meaning that for each kilometer west from the coast, humidity increased by ~0.5%, or about 7.5% across each transect. Maximum daily RH also significantly increased with distance from the coast ($R^2 = 0.3158$, $F_{1,28} = 12.9212$, $P = 0.0012$), but minimum daily RH did not ($R^2 = 0.0916$, $F_{1,28} = 2.8224$, $P = 0.1041$). These parameter estimates are similar to parameter estimates for 2006 and 2007 (range: 0.2529% to 0.5533%, Reiskind and Lounibos 2013) and show the same positive trend. No significant differences in average daily RH were detected between 2013, 2006, or 2007. Percent site wetness did not decrease with distance from the coast in 2013 (Fig 2C, $R^2 = 0.0099$, $F_{1,28} = 0.2798$, $P = 0.0601$).

Land cover types varied longitudinally (Supp. Table 1 [online only]). Areas of buildings and pavement declined with distance from the coast ($R^2 = 0.1424$, $F_{1,28} = 4.6476$, $P = 0.0398$; $R^2 = 0.1454$, $F_{1,28} = 4.7637$, $P = 0.0376$, respectively), while freshwater bodies and coarse vegetation areas increased with distance from the coast ($R^2 = 0.1780$, $F_{1,28} = 6.0622$, $P = 0.0202$; $R^2 = 0.2809$, $F_{1,28} = 10.9364$, $P = 0.0026$, respectively). The parameter estimate for buildings was -0.564%, meaning that for each kilometer the percentage of building land cover decreased by 0.56%, or ~8.4% across each transect. The parameter estimate of pavement was -1.1201%, meaning the percentage of pavement land cover decreased ~16.8% across each transect. Parameter estimates indicate the area of freshwater (parameter estimate = 0.381%) increased by ~5.7% across transects, and coarse vegetation (parameter estimate = 1.343%) increased by ~20.1%. Buildings and pavement are typically associated with urban areas, as coarse vegetation and freshwater bodies are associated with rural areas. Bare soil, saltwater bodies, pools, and fine vegetation did not show significant relationships with distance from the coast. No significant differences were detected between 2006 and 2013 for any land cover types at any distance from the coast, except for a significant decrease in bare ground at 15 km (Paired *t*-test, $t = -2.412$, df = 5, $P = 0.0304$). This difference can be attributed to a transition from a construction site in 2006 to fine vegetation in 2013 at a single study site.

Spatial Patterns of Mosquito Abundance

Aedes aegypti predominated in coastal, urban environments, while *Ae. albopictus* was more abundant in inland, rural environments during the 2013 collection period, as observed for 2006–2007 by Reiskind and Lounibos (2013; Fig. 3). In 2013, there were significant differences between *Ae. aegypti* and *Ae. albopictus* total abundance at 0, 1, and 15 km (Paired *t*-test, 0 km, $t = -4.412$, df = 5, $P = 0.0069$; 1 km, $t = -4.221$, df = 5, $P = 0.0083$; 15 km, $t = 6.167$, df = 5, $P = 0.0016$), and no significant differences at 3 and 8 km from the coast (Paired *t*-test, 3 km, $t = -0.803$, df = 5, $P = 0.4585$; 8 km, $t = -0.083$, df = 5, $P = 0.937$). The proportion of *Ae. aegypti* decreased with distance from the coast ($R^2 = 0.622$, df = 29, $P < 0.0001$), on which scale egg abundance increased ($R^2 = 0.303$, df = 29, $P < 0.0016$).

Spatio-Temporal Changes in Mosquito Distributions

Our study supports a distributional shift in *Ae. aegypti* proportions inland from the coast (Fig. 4). The generalized linear mixed model logistic regression model showed that the interaction between distance and year significantly affected the proportion of *Ae. aegypti* collected (Table 1). The proportion of *Ae. aegypti* was significantly higher at 3 and 8 km in 2013 compared with 2006 and 2007 ($P < 0.0001$ for both years). At 1 km, the proportion of *Ae. aegypti* was higher in 2007 compared with 2013 ($P < 0.0001$).
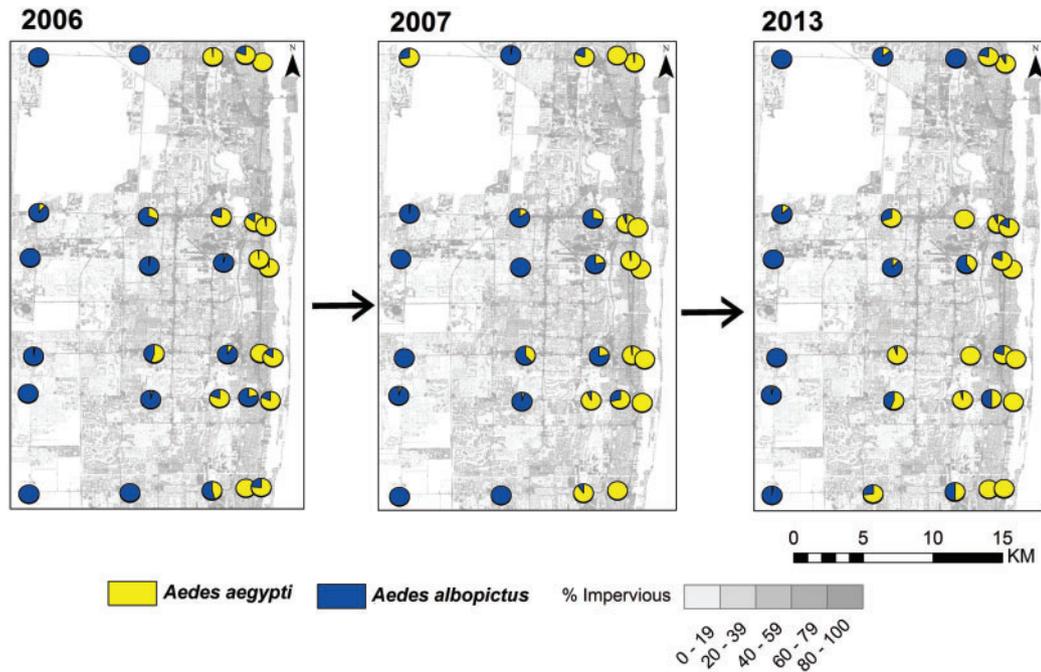
$t = -9.4821$, df = 5, $P = 0.0001$; 2013, $t = -4.0458$, df = 5, $P = 0.0099$). No other significant differences in average daily temperature were detected between 2013 and 2006 or 2007.

Average daily RH increased with distance from the coast (Fig. 2B, $R^2 = 0.3065$, $F_{1,28} = 12.3749$, $P = 0.0015$). The average parameter estimate for the linear coefficient of distance from the coast

Fig. 3. Proportion of *Ae. aegypti* and *Ae. albopictus* in 2006, 2007, and 2013. Each pie chart represents a collection site. Yellow represents *Ae. aegypti* and blue represents *Ae. albopictus.* Base map data sources include the National Land Cover Database and the U.S. Census Bureau (Online figure in color).
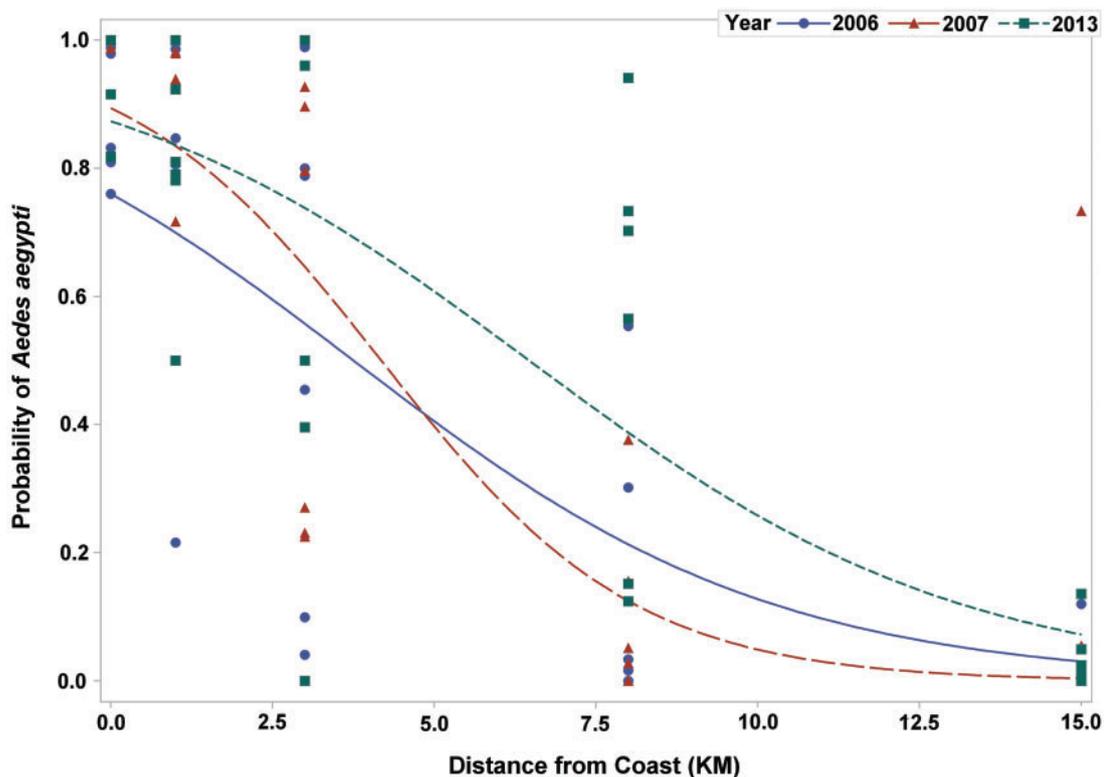

Fig. 4. Generalized linear mixed model logistic regression results. The proportion of *Ae. aegypti* served as the dependent variable and was analyzed using a binomial distribution and a logit link function. Distance, year, and the interaction of distance and year were modeled as independent variables, and site was modeled as a random effect. Lines represent the modeled logistic of the probability of *Ae. aegypti* as a function of distance for each year (Online figure in color).

Discussion

We found that the distributional patterns of *Ae. aegypti* and *Ae. albopictus* in Palm Beach County, FL, were similar to those described by Reiskind and Lounibos (2013). *Aedes aegypti* predominated at and near the urbanized coast, while *Ae. albopictus* was more abundant inland, with the greatest overlap in distributions of two species at 3 and 8 km (Reiskind and Lounibos 2013). Most notably, we found the distribution of *Ae. aegypti* had expanded

Table 1. Generalized linear mixed model logistic regression results

Type III tests of fixed effects

Effect	Num df	Den df	*F* value	$Pr > F$
Distance	4	49	20.40	<0.0001
Year	2	49	75.22	<0.0001
Distance × Year	8	49	41.41	<0.0001

The proportion of *Ae. aegypti* served as the dependent variable and was analyzed using a binomial distribution and a logit link function. Distance, year, and the interaction of distance and year were modeled as independent variables, and site was modeled as a random effect.

inland since 2006–2007. While overall relative species abundances were similar in 2013 to 2006–2007, we detected a significant increase in the proportion of *Ae. aegypti* at 8 km from the coast.

Historically, *Ae. aegypti* was less geographically restricted and occurred across both urban and rural areas in south Florida (O'Meara et al. 1995). Today, *Ae. aegypti* is generally restricted to urban areas. Urban areas are a niche to which *Ae. albopictus* is less well adapted, and may act as a refuge for *Ae. aegypti* populations (Braks et al. 2003). These urban refugia could sustain *Ae. aegypti* populations, which may then recolonize wider areas either when conditions improve or when competition is overcome through natural selection (Hylander et al. 2015). However, these small and isolated populations may also be more susceptible to genetic drift, inbreeding, and stochastic events resulting in extinction. There is evidence *Ae. aegypti* populations in contact with *Ae. albopictus* are adapting to avoid competitive mating interference (Bargielowski et al. 2013). Bargielowski and Lounibos (2015) demonstrated rapid behavioral adaptations of naïve *Ae. aegypti* females to avoid heterospecific matings with *Ae. albopictus* males over only 1–3 generations in the laboratory. If *Ae. albopictus* populations exclude *Ae. aegypti* geographically through mating interference, and *Ae. aegypti* adapts to avoid heterospecific mating, this behavioral adaptation may facilitate the observed local expansion of *Ae. aegypti* in Palm Beach County.

It is also possible that local microclimates have changed in a way that now supports *Ae. aegypti* populations further inland. Land cover classifications confirmed a longitudinal urban–rural gradient across the total study area, and data loggers recorded temperature and RH gradients. Temperature and impermeable surfaces, including buildings and pavement, decreased with distance from the coast, while coarse vegetation, freshwater bodies, and humidity increased. These habitat qualities correspond to what is already known about either species' habitat preferences (O'Meara et al. 1995, Braks et al. 2003, Reiskind and Lounibos 2013, Leisnham et al. 2014); the two species spatially segregate based, in part, on climatic conditions and condition specific interspecific competition (Costanzo et al. 2005, Leisnham et al. 2014). *Aedes aegypti* tolerate dry conditions better than *Ae. albopictus* as eggs and adults (Sota and Mogi 1991, Mogi et al. 1996, Reiskind and Lounibos 2009, Lounibos et al. 2010), and *Ae. albopictus* is generally the superior larval competitor under wet conditions (Juliano et al. 2002, Costanzo et al. 2005). Leisnham et al. (2014) also found spatial partitioning in Tampa, FL, consistent with habitat segregation and condition-specific competition. However, our measurements of temperature, humidity, and site wetness did not significantly change over time at 8 km distance from the coast, and land cover changed little between 2006 and 2013. Although microclimatic and land cover variables do not explain this change independently, subtle changes in environmental variables

working in tandem could have influenced the spread of *Ae. aegypti*. It is also possible that the relative abundances and geographic distributions of either species fluctuate at random, that random processes yield ranges that wax and wane, and that this pattern cannot be ascribed to competition, competitive evolution, land use, or climate. Only long-term datasets, which are rare, could truly assess a shift in local range relative to a normal level invariation. Unrecorded variables, such as changes in host density and pesticide treatment regimes, also have the potential to influence distributions.

We sought to document and determine whether local *Ae. aegypti* distributions have decreased, increased, or remained stable in recent history. Though it is compelling to speculate on the mechanisms that may explain an increase in *Ae. aegypti*, further study is needed to understand the patterns observed. Intensive sampling every 5 to 7 yr of the same area using the same methods will build a robust dataset that tracks field populations of *Ae. aegypti* and *Ae. albopictus* over time. Landscape genetic analyses can inform whether *Ae. albopictus* acts as a biological barrier to *Ae. aegypti* and can potentially identify a molecular basis for the behavioral adaptations of *Ae. aegypti* observed in the laboratory. Furthermore, larger-scale monitoring of *Ae. aegypti* populations, informed by historical datasets (e.g., O'Meara et al. 1995), may also provide evidence for changes in the ecology of this vector in the southern United States.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

Acknowledgments

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