

# ***Aedes albopictus* (Diptera: Culicidae) on an Invasive Edge: Abundance, Spatial Distribution, and Habitat Usage of Larvae and Pupae Across Urban and Socioeconomic Environmental Gradients**

Talya Shragai and Laura C. Harrington<sup>1</sup> 

Department of Entomology, Cornell University, 3131 Comstock Hall, Ithaca, NY 14853, and <sup>1</sup>Corresponding author, e-mail: [lch27@cornell.edu](mailto:lch27@cornell.edu)

Subject Editor: Dr. Gabriel Hamer

Received 1 July 2018; Editorial decision 28 October 2018

## **Abstract**

The Asian tiger mosquito [*Aedes albopictus* (Skuse)] is an invasive species of public health importance that is currently expanding its range in the Northeast United States. Effective *Ae. albopictus* control depends on a thorough understanding of factors influencing their abundance, spatial distribution, and habitat preference. We conducted a series of container surveys for *Ae. albopictus* larvae/pupae over 2 yr across nine sites in neighborhoods along its invasive range in southern New York. Selected sites represented a gradient of percent impervious surface and median household income. Two hypotheses were tested: 1) *Ae. albopictus* larval/pupal abundance increases and spatial distribution becomes less clustered as site-level median income decreases and percent impervious surface increases because of increased larval habitat quality and availability; and 2) container-level characteristics are predictive of *Ae. albopictus* larval/pupal infestation across a range of sites. In 2016, neither median household income nor impervious surface predicted *Ae. albopictus* abundance. In 2017, sites with greater impervious surface were more heavily infested by some measures. In both years, *Ae. albopictus* larval/pupal spatial distribution as measured by K-function was more clustered in with greater median household income. Most container characteristics were either not predictive of *Ae. albopictus* or varied between years. Based on the variability of predictive container characteristics, we conclude that identification of key containers is not useful in this region. However, *Ae. albopictus* can be nonhomogenously distributed or abundant based on income level and impervious surface. Improved control of immatures should consider these regional predictors of *Ae. albopictus* populations.

**Keywords:** container survey, urbanization, socioeconomic status, Asian tiger mosquito

In the 30 years since its introduction into Texas, the Asian tiger mosquito [*Aedes albopictus* (Skuse)] has rapidly moved into the eastern United States. *Aedes albopictus* is now invading southern New York State and has become a serious health concern. The public is at high risk of exposure to *Ae. albopictus*, because this mosquito readily and aggressively bites humans, adults host-seek diurnally, and females oviposit in peridomestic habitat (Hawley 1988, Koehler and Castner 1997). In addition to being a serious biting pest, *Ae. albopictus* transmits at least 20 viral pathogens including dengue, chikungunya, West Nile, and Zika viruses, making it a potential risk to public health (Paupy et al. 2009a). Because most regional control of *Ae. albopictus* focuses on immature mosquitoes, it is of particular importance to study larval and pupal ecology. To monitor and control immatures of this species, we need a thorough understanding of their abundance and distribution across the region.

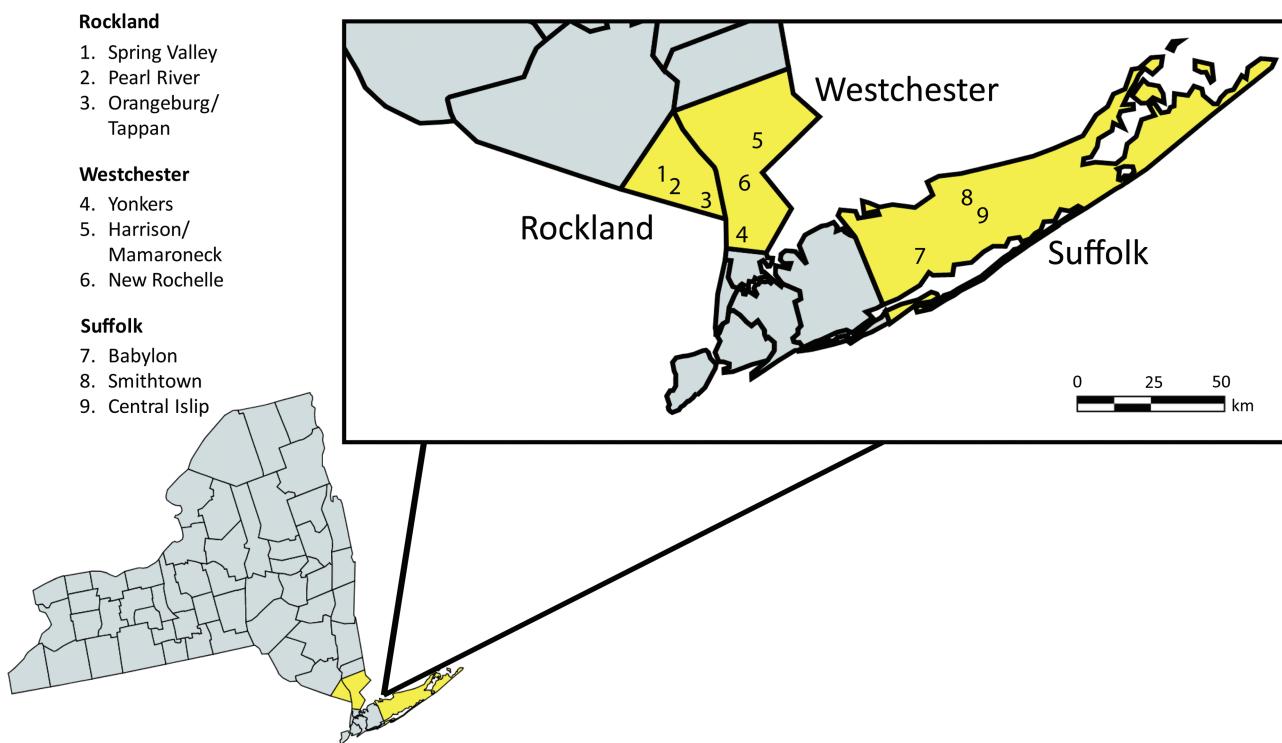
*Aedes albopictus* larval and pupal abundance depends on environmental context. Impervious surface and socioeconomic status are two important environmental measures that affect mosquito habitat quality through variation in ambient temperature or availability of resting and oviposition sites (Alirol et al. 2011, Little et al. 2017, Murdock et al. 2017). While most studies of the related urban mosquito *Ae. aegypti* agree that abundance increases with increasing impervious surface (Landau and van Leeuwen 2012, Rubio et al. 2013, De Azevedo et al. 2018) and there is some evidence that larval habitat increases with decreasing socioeconomic status (De Azevedo et al. 2018, Walker et al. 2018), this is less clear for *Ae. albopictus*. A few studies have compared a limited number of sites of variable levels of urbanization, a measure closely related to impervious surface, but have produced conflicting results. Comparisons of *Ae. albopictus* density have demonstrated that they can be the most abundant in suburban (Barker

et al. 2003, Tsuda et al. 2006), urban (Bagny et al. 2009, Beilhe et al. 2012, Li et al. 2014), and rural (Hornby et al. 1994, Braks et al. 2003a, Honório et al. 2009) environments. In part, these studies are hard to compare because urbanization has been defined multiple ways; using a more specific measure such as impervious surface can help hone in on precise aspects of the environment. From similarly conflicting studies of socioeconomic status, surveys of limited numbers of sites of different incomes have found that adults (Unlu et al. 2011) and pupae (LaDreau et al. 2013) are more abundant in sites of lower income, whereas other studies have found that larvae and adults are more abundant in high income sites (Becker et al. 2014) or that there was no variation in density by income (Dowling et al. 2013). A key limitation of all these studies is that all were conducted on a limited number of sites of contrasting landscapes instead of those representing a full gradient of either impervious surface or income, without which it is impossible to analyze using a regression and therefore difficult to detect true landscape-level patterns.

Just as it is important to study abundance by environmental variables, understanding the spatial distribution of larval positive containers across the landscape can serve as an important basis for effective action against immature life stages. The related species *Ae. aegypti* has been shown to cluster both at the immature and adult stage (Getis et al. 2003). If abatement programs can identify where containers are most likely to be clustered into hotspots, those locations may be targeted for more efficient control. However, only one author to date has analyzed the spatial structure of *Ae. albopictus* immature stages, identifying clustering above an expected random distribution of pupae in residential North Carolina neighborhoods (Richards et al. 2006, 2008). Again these studies were conducted in four similar neighborhoods rather than across an environmental gradient, and it is unknown if this pattern holds in variable environments.

Another strategy to better target monitoring and control of immature urban mosquitoes is to identify the most heavily exploited and highly productive container categories (key containers) in order to focus limited resources. Although this can be successful for *Ae. aegypti* (Maciel-de-Freitas and Lourenco-de-Oliveira 2011), studies of *Ae. albopictus* have produced unclear results (Maciel-de-Freitas and Lourenco-de-Oliveira 2011, Bartlett-Healy et al. 2012, Unlu et al. 2013). To this end, we attempted to complement existing studies to establish what, if any, container characteristics predict the presence of *Ae. albopictus* larvae and pupae.

To address these gaps and inconsistencies, we measured abundance, spatial distribution, and container habitat characteristics of *Ae. albopictus* larvae/pupae in sites representing full environmental ranges for southern New York State (Westchester, Rockland, and Suffolk counties). We conducted two consecutive years of container surveys across the northern invasive range of *Ae. albopictus* to identify trends in abundance and spatial patterns of larval/pupal habitat across gradients of socioeconomic demographics (as measured by household median income at the residential block level) and percent impervious surface. Although survey date range was longer in the first year, all data were analyzed within the same date range for comparisons between the two sampling years. We tested the following hypotheses: 1) because increased impervious surface and lower socioeconomic status can be associated with greater and more widespread larval habitat availability, as impervious surface increases and as socioeconomic status decreases, *Ae. albopictus* larval/pupal abundance will increase and spatial distribution will become less clustered; and 2) container-level characteristics that have been previously identified as important such as the type of container and placement of container in shaded areas will predict infestation with *Ae. albopictus* larvae/pupae.



**Fig. 1.** A map of the nine survey sites in Rockland, Westchester, and Suffolk counties, New York. Each shaded county indicates a surveyed county and each number indicates a single survey site.

## Methods

### Site Selection

Surveys were conducted in nine sites along the established range of *Ae. albopictus* invasion in Rockland, Suffolk, and Westchester counties (2017; Fig. 1). Three sites covering 0.1–0.15 km<sup>2</sup> in each of the three counties were selected in consultation with county health department personnel.

The three counties we selected encompass a range of income levels (Min = \$12,875, Q<sub>1</sub> = \$67,135, Q<sub>2</sub> = \$90,604, Q<sub>3</sub> = \$117,762, and Max = \$250,001) and impervious surface (mean = 31.93%, SD = 25.56). We selected nine sites within our three counties that represented as full and even spread of the ranges as possible that also were 1) classified as residential by the county, 2) already identified as positive for *Ae. albopictus*, 3) dense enough for surveys to be feasibly conducted on foot, and 4) determined as safe by the county health department. Data from the 2011 National Land Cover Database (2011) were used to select residential sites that covered a range of percent impervious surface and data from the 2015 United States Census were consulted to select sites that covered a range of socio-economic strata as measured by median household income. Our sample size of sites was comparable sizes used in other ecological studies measuring changes across landscape gradients (Cox et al. 2007, Grab et al. 2018).

### Larval Surveys

#### 2016 Surveys

Data from continuous days were defined as a survey period. Twelve container survey periods were conducted from 28 April to 17 October 2016. Surveys were conducted every other week for 3–5 d, apart from September and October, when sampling was conducted once per month for 2 d.

Sites were divided into blocks. Each house on every block was approached; if we gained permission from the homeowner, a survey was performed. This process was conducted until our target number (40 houses per site) was reached. For several sites, every block was surveyed without reaching the target number. In this case, adjacent blocks were randomly selected and added to the study site until 40 houses were surveyed. This process was randomized by assigning all blocks adjacent to the study site a number and using a random number generator to select one.

After obtaining permission from homeowners through door-to-door interviews, teams of two to three trained field personnel surveyed the outdoor areas of each house. Teams identified all water-holding containers suitable for larval development (as defined by ability to hold at least 2 ml of water) and recorded water volume, water temperature, container category and material, degree of shading, presence of live and dead plant material, and estimated number of mosquito larvae. Container category and container material were each divided into commonly found types. For container category, this included bucket, planter, sheeting, tarp, trash, tire, bird bath, piping/tubing, and toy. Container materials included plastic, metal, rubber, ceramic, stone/cement, and natural. Both category and material also included an ‘other’ option for containers that did not fit into one of the above types. When a container was classified as ‘other’, the exact container category and/or material was specified. Degree of shading was divided into fully shaded, partially shaded, and no shade and was based on shading received throughout the day. The number of larvae was scored as 0, 1, 2, 3, or 4, with scores indicating an estimated 0, 1–25, 26–50, 51–100, or >100 larvae, respectively.

If larvae and/or pupae were present, the water was gently stirred with a plastic turkey baster. If there were <25 larvae, all larvae in the

container were collected. If >25 larvae were present, a subsample of 25 was collected. All samples were collected with plastic transfer pipettes and placed in a 50-ml tube with ~20 ml of container water.

#### 2017 Surveys

In the second year, three survey periods were conducted from 21 July to 13 August 2017 within the peak activity period identified in 2016. Because the date range for 2017 differed from 2016, we only compared the 2 yr for data taken within the same dates.

Survey periods were conducted for 3 d each. Within each site, we first attempted to survey each house that was previously surveyed in 2016, with the goal of surveying at least 20 houses per site. Each house surveyed in 2016 was approached up to three times, once per survey period. If by the last survey period all houses had already been approached three times and our goal had not been reached, we randomly approached new houses until we had surveyed a total of at least 20. House selection was randomized by assigning each block within a site a number, using a random number generator to select one, and approaching each house on that block in sequence from lowest address to highest address number. All other survey procedures were the same as for 2016 (described above).

### Mosquito Identification

Because of the high numbers of collected larvae/pupae and relative time needed to identify each individual larva, we chose to rear all collected larvae/pupae to eclosion and only then classified adults to species. Different species are known to have different survival rates in shared containers (Braks et al. 2004); to ensure that we were not biasing numbers toward any one species or underestimating numbers, we counted all collected larvae and all identified adults from each container to calculate mortality rate. On average, mortality rate was 9%, and any container with >15% mortality was excluded from any analysis for estimated total numbers. Mosquito larvae and pupae in 50-ml tubes were transferred within 24 h to a plastic 710-ml food storage container. Collected water was supplemented with dechlorinated tap water and one Hikari Gold Cichlid food pellet, mean weight = 0.1781 g (Hikari, Himeji, Japan). Containers of mosquitoes were held at 23°C until eclosion. Newly eclosed adults were removed daily with an aspirator and stored at –20 °C in plastic Petri dishes lined with filter paper. All adults from each container were identified to species using published keys (Andreadis et al. 2005).

### Data Analysis

To enable comparisons between years, for all analyses comparing 2016 and 2017, data were restricted to the same date range. All data analyses were conducted using R (R Core Team, Version 3.3.1).

### Site Metrics

Median household income and percent impervious surface for each site was calculated using ArcMap 10 GIS (ESRI, Redlands, CA) to layer polygons of our survey sites against corresponding polygons generated from the American Community Survey Median Income Block Group map (2015) and the National Land Cover Database (2011). For median income, if a site spanned multiple block groups, the mean median income weighted by area was calculated. For percent impervious surface, a 150 ml buffer was drawn around each house surveyed. This buffer size was chosen to correspond to a biologically relevant average dispersal distance for *Ae. albopictus* (Niebylski and Craig 1994, Honório et al. 2003, Marini et al. 2010, Medeiros et al. 2017). The mean percent impervious surface was determined within each buffer, and then the mean of all buffers within a site was

calculated. To see the median household income and percent impervious surface for each site, see [Supp Table I \(online only\)](#).

#### Site-level degree of infestation

The degree of *Ae. albopictus* larval/pupal infestation for each site was analyzed as total positive containers per containers surveyed, total positive containers per 100 houses surveyed, and total estimated quantity of *Ae. albopictus* per site. This measure of total estimated quantity was taken to account for container productivity. To calculate estimated quantity, we multiplied the proportion of mosquitoes from a positive container sample identified as *Ae. albopictus* by the score indicating the estimated number of total larvae in the original container (1–4). For example, if 50% of the sample was identified as *Ae. albopictus* and the original container was given a score of 3 (50–100 larvae/pupae), the score for the estimated quantity of *Ae. albopictus* in the container was calculated to be 1.5. These scores were then summed for each site. The scores were used rather than the absolute numbers so as not to bias toward either end of the estimated range.

A linear mixed effects model was used to predict abundance by median household income and percent impervious surface. Percent positive containers, positive containers per 100 houses surveyed, and total estimated number were used as our dependent variables measuring abundance. Site-level impervious surface, household median income, year, the interaction between impervious surface and year, and the interaction between household median income and year were used as our fixed variables. Site was included as a random effect. In the regression of percent positive containers and positive containers per 100 houses surveyed, there was an outlying observation. We conducted the analysis with and without the outlier and reported both results.

#### Site-level spatial distribution analysis

Spatial distribution at the site level was analyzed for both *Ae. albopictus*-positive containers and estimated number of *Ae. albopictus*. All spatial analyses were performed using the spatsat and splanes packages in R ([Baddeley and Turner 2005](#), [Rowlingson et al. 2013](#)).

To address the degree to which *Ae. albopictus*-positive containers were clustered within each of the nine sites, we used a modification of a bivariate K-function ([Baddeley 2008](#)), following the methods of [Getis et al \(2003\)](#). This point pattern analysis assigns a binary value (presence/absence of *Ae. albopictus* larvae) to each container in a site and determines whether the spatial distribution of positive containers is random, dispersed, or clustered. First, the function assigns a K-value at each spatial scale from zero to the total area of the site for the entire site (For an example of output of K-values across multiple scales for a single site, see [Supp Fig. 1C \(online only\)](#)). A complete random distribution is typically then used as the control, and the greater above random the observed value of K, the greater the degree of clustering. However, because homeowner availability and permission resulted in a nonrandom and incomplete distribution of houses surveyed within each site area (for an example of nonrandom house distribution, see [Supp Fig. 1A \(online only\)](#)), rather than use a complete random distribution of containers as the control, we calculated random clustering within the spatial structure of the homes surveyed in each site. For each site, we ran 1,000 permutations of random container distributions among the spatial structure of the houses we surveyed, using the same number of positive containers as in our sampling data for each permutation (for an example of a single permutation at one site, see [Supp Fig. 1B \(online only\)](#)). The mean was taken of these permutations and used as our control function. We then calculated the degree of clustering at each site by comparing the observed distribution to

our calculated control function – the greater the positive difference between the observed distribution and the calculated control function, the greater the degree of clustering ([Supp Fig. 1C \(online only\)](#)).

We next tested whether the degree of spatial clustering was predicted by either percent impervious surface or household median income using a general linear model, which requires a single continuous response variable for each site. We reduced our output from the full range of spatial scales to the degree of clustering at 150 m to produce a single K-value at a single scale for each site. Then, we calculated the difference between the observed K-value and our generated control function at that single scale. We chose 150 m because this is the established average flight range of adult *Ae. albopictus* and it was the most pronounced scale at which clustering occurred across sites.

To address the degree to which estimated quantity of *Ae. albopictus* immatures were clustered within a site, we used a marked correlation function, again following the methods of [Getis et al. \(2003\)](#). This method was performed because we were measuring a continuous variable (number of immature *Ae. albopictus*) rather than a categorical variable (positive/negative container). Like our analysis of *Ae. albopictus* presence/absence, we generated a theoretical random distribution of *Ae. albopictus* larvae using 200 simulation envelopes against which we compared observed *Ae. albopictus* distributions within the observed spatial structure of homes visited. For further explanation of the analysis, see [Supp Fig. 2 \(online only\)](#). From these distributions, clustering was again calculated at 150 m using the same method as for positive containers to represent the effect size of clustering for each site.

A multiple linear regression was performed to test if our two independent variables, median household income and percent impervious surface, predicted our response variables, the clustering index of positive containers, and estimated number of *Ae. albopictus*.

#### Container-level analysis

This analysis was carried out at the container level. A generalized linear mixed effects model using a binomial distribution with address, site, and county as nested random effects was performed to compare our response variable – the presence or absence of *Ae. albopictus* – to all container predictor variables (container category, container material, water temperature, water volume, degree of shading, presence of dead and/or live plants, and sampling date). This model was fit using the lme4 package in R ([Bates et al. 2014](#)). We tested each individual predictor with a likelihood ratio test comparing the full model to a reduced model omitting that variable. We then performed post hoc pairwise comparisons using the lsmeans package in R ([Lenth 2016](#)).

Water volume was highly skewed toward low-volume containers and was log transformed for the analysis. We confirmed that our sample size was adequate to detect differences by running a power analysis for a multiple regression with six predictors, an anticipated effect size of  $f^2$  of 0.15, statistical power of 0.8, and probability of 0.05.

## Results

### Residential Field Sites

For our study, median household income was ranged from \$42,071 (Yonkers) to \$154,759 (Orangeburg-Tappan). Mean impervious surface ranged from 9.12% (Orangeburg-Tappan) and 61.17% (Yonkers) (see [SuppMaterial \(online only\)](#)). Low levels of multicollinearity were present in our two site-level measures (variance inflation factor = 1.47 for median household income, 1.82 for mean impervious surface).

**Table 1.** Counts of survey results by site, 2016 (A) and 2017 (B)

Site	Houses surveyed	Containers surveyed	Larvae positive containers	<i>Aedes albopictus</i> positive containers	Percent of containers <i>Ae. albopictus</i> positive	<i>Aedes albopictus</i> positive containers per 100 houses surveyed
(A) 2016						
Babylon	43 (23)	235 (110)	44 (22)	16 (14)	0.068 (0.127)	37.21 (60.87)
Central Islip	40 (16)	222 (95)	61 (25)	21 (14)	0.095 (0.147)	52.50 (87.50)
Harrison-Mamaroneck	45 (13)	190 (38)	58 (9)	9 (3)	0.047 (0.079)	20.00 (21.74)
New Rochelle	46 (26)	195 (82)	50 (31)	18 (15)	0.092 (0.183)	39.13 (57.69)
Orangetburg-Tappan	59 (37)	260 (184)	54 (39)	16 (16)	0.062 (0.087)	27.11 (43.24)
Pearl River	48 (21)	148 (67)	35 (21)	11 (6)	0.074 (0.090)	22.92 (28.57)
Smithtown	42 (24)	150 (80)	34 (18)	12 (10)	0.080 (0.125)	28.57 (41.67)
Spring Valley	45 (29)	210 (107)	62 (39)	16 (15)	0.076 (0.140)	35.56 (45.83)
Yonkers	45 (23)	210 (89)	29 (16)	13 (9)	0.062 (0.101)	28.89 (39.13)
Total	412 (212)	1820 (852)	436 (229)	132 (102)	0.073 (0.120)	
(B) 2017						
Babylon	29	120	42	35	0.29	120.69
Central Islip	26	141	48	42	0.30	150.00
Harrison-Mamaroneck	20	80	45	36	0.45*	175.00*
New Rochelle	27	88	26	23	0.26	88.46
Orangetburg-Tappan	25	80	27	16	0.20	64.00
Pearl River	31	87	30	20	0.23	64.52
Smithtown	28	101	29	24	0.24	85.71
Spring Valley	26	65	26	19	0.29	73.08
Yonkers	30	92	34	28	0.30	93.33
Total	242	854	316	243	0.28	
*Outlying value						*Outlying value

For 2016, the results for the full date range of surveys are shown first, and the results for surveys restricted to the 2017 survey dates for comparison between the 2 yr are shown afterward in parentheses.

### Numbers of Houses and Containers Surveyed

In 2016, across the full sampling date range, we surveyed 412 houses and 1,820 containers. In total, 436 containers (23.95%) had mosquito larvae; 132 (7.30%) were *Ae. albopictus* positive (Table 1A). When the results are restricted to the same period as the 2017 surveys, we surveyed 212 houses and 852 containers. About 229 (26.88%) of those containers were larvae/pupae positive, and 102 (12.00%) contained *Ae. albopictus* (Table 1A). Other species collected were *Aedes japonicus*, *Aedes triseriatus*, *Culex pipiens/restuans* (Diptera: Culicidae), and *Anopheles punctipennis* (Diptera: Culicidae). The distribution of estimated *Ae. albopictus* per positive container was bimodal; most containers had 1–25 larvae/pupae, few had 25–80 larvae/pupae, and slightly more had >80 larvae/pupae.

In 2017, we surveyed 242 houses and 854 containers and found a much higher proportion of containers positive both for mosquitoes and for *Ae. albopictus*. About 210 of houses surveyed (82.64%) were previously surveyed in 2016, and 32 were only surveyed in 2017. About 316 containers were larvae/pupae positive (37.00%) and 243 were *Ae. albopictus* positive (28.45%; Table 1B). Other species collected were *Ae. japonicus*, *Ae. triseriatus*, *Cx. pipiens/restuans*, *Toxorhynchites rutilus* (Diptera: Culicidae), and *An. punctipennis*. The numbers of *Ae. albopictus* per positive container followed the same distribution as in 2016.

### Site-Level Degree of Infestation by Impervious Surface and Household Median Income

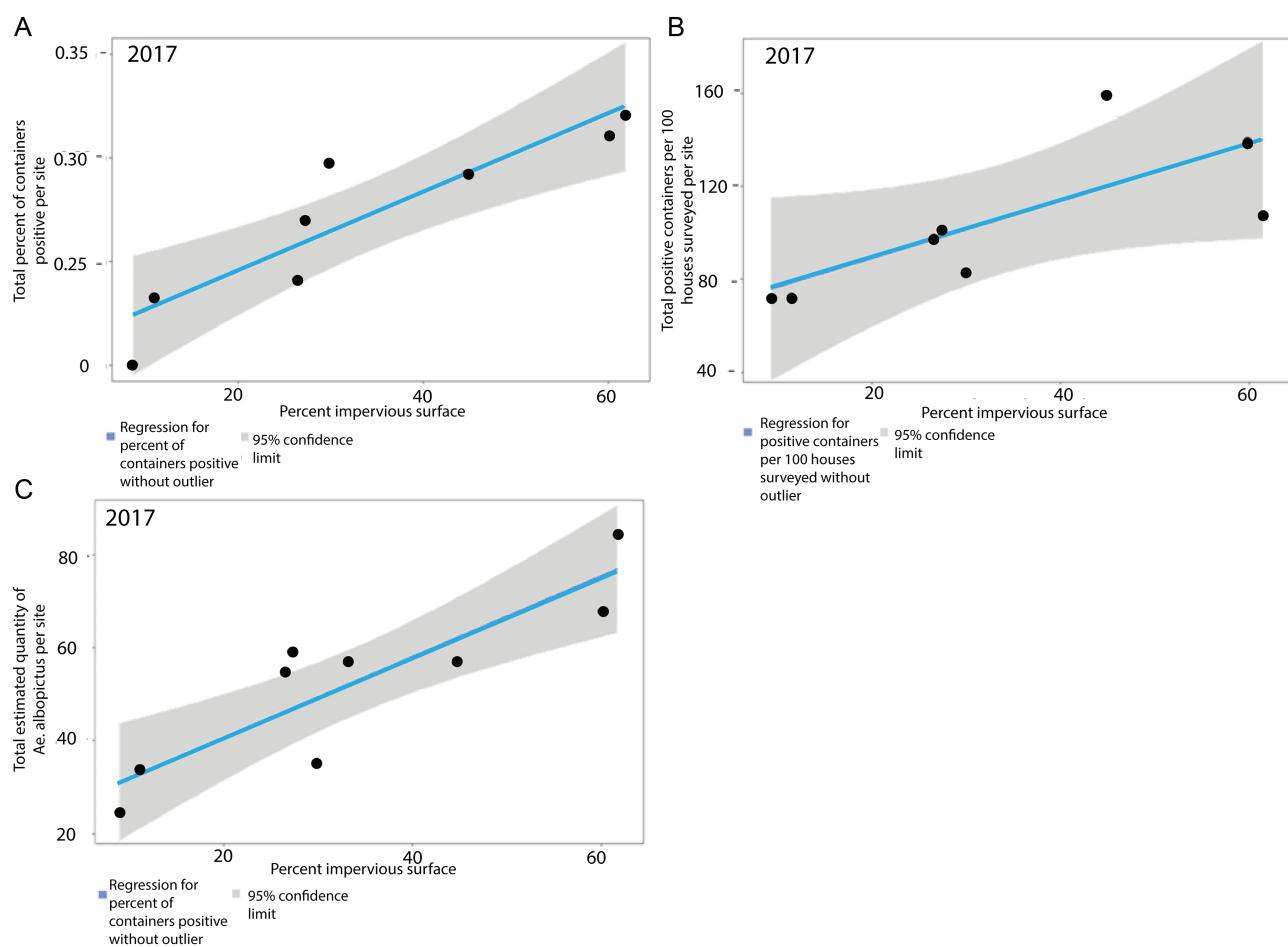
*Aedes albopictus* larval/pupal abundance as measured by percent positive containers and by positive containers per 100 houses surveyed had one outlying observation; when this outlier was removed, there was a significant interaction between year and impervious

surface for both measures ( $\beta = 0.00124$ ,  $P = 0.0401$ ;  $\beta = 0.674$ ,  $P = 0.0412$ ). For 2017, greater impervious surface led to higher percent positive containers and positive containers per 100 houses surveyed (Fig. 2A and B, Table 2). For 2016, impervious surface had no effect on either measure. When the outlier was retained, the percent of containers positive and the positive containers per 100 houses surveyed were not significantly predicted by site-level impervious surface ( $\beta = 0.00136$ ,  $P = 0.367$ ;  $\beta = 1.17$ ,  $P = 0.251$ ). When *Ae. albopictus* larval/pupal abundance was measured by total estimated abundance, there was once again a significant interaction between year and impervious surface ( $\beta = 0.700$ ,  $P = 0.0287$ ); in 2017, sites of higher impervious surface had higher total estimated abundance (Fig. 2C, Table 2), but there was no effect for 2016.

Median household income was not a predictor of *Ae. albopictus* larval/pupal estimated total abundance, nor was there any significant interaction by year ( $\beta = 0.145$ ,  $P = 0.621$ ;  $\beta = 7.18e-07$ ,  $P = 0.621$ ). Median household income was also not predictive of the percent of *Ae. albopictus*-positive containers in each site or the number of containers per 100 houses surveyed and there was not a significant interaction by year for either measure (percent positive containers:  $\beta = 0.00155$ ,  $P = 0.405$ ;  $\beta = 7.67e-07$ ,  $P = 0.405$  and positive containers per 100 houses surveyed:  $\beta = -0.145$ ,  $P = 0.595$ ;  $\beta = 0.0300$ ,  $P = 0.830$ ).

### Spatial Distribution by Impervious Surface and Household Median Income

We analyzed distribution of *Ae. albopictus*-positive aquatic habitat by median household income and impervious surface and found that while impervious surface did not predict abundance, income did predict spatial distribution of *Ae. albopictus* larvae/pupae.



**Fig. 2.** Increasing percent impervious surface predicted abundance of *Ae. albopictus*. In 2017, increasing percent impervious surface predicted both the number of *Ae. albopictus* (A) percent positive containers, (B) positive container per 100 houses surveyed, and (C) total estimated quantity of *Ae. albopictus* in each site.

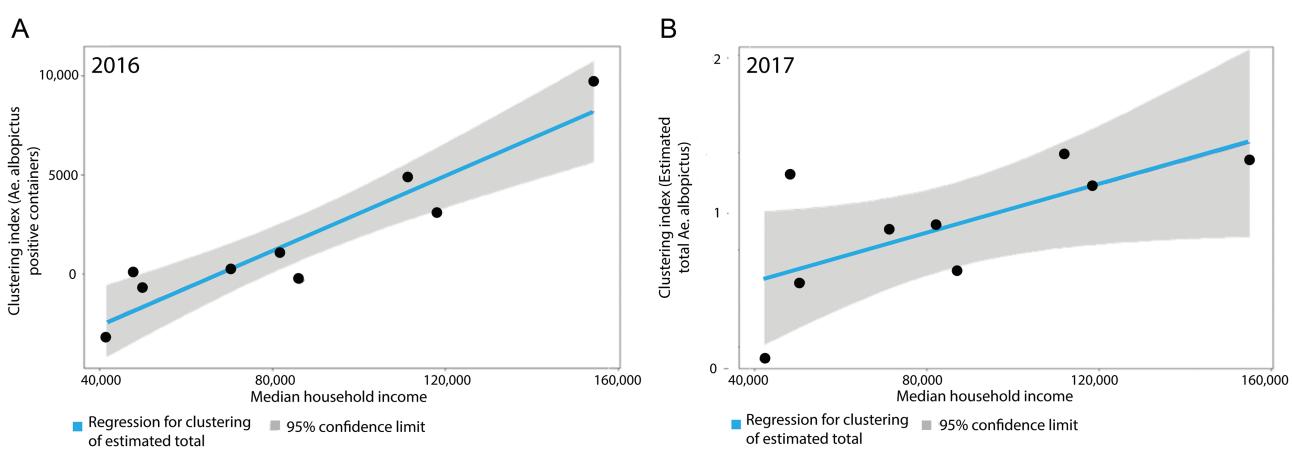
Distribution was significantly predicted by median income at a scale of 150 m. When the dependent variable was the degree of clustering of positive containers for each site, the results of the multiple regression indicated that the predictors explained 66.15% of the variance ( $R^2 = 0.661$ ,  $F_{(5, 12)} = 3.94$ ,  $P = 0.0132$ ). The clustering of *Ae. albopictus*-positive containers was predicted by income with higher degree of clustering of positive containers and estimated number of *Ae. albopictus* in higher income sites ( $\beta = 8.87 \times 10^{-8}$ ,  $P = 0.0177$ ). This effect was stronger in 2016 than 2017, with a significant interaction between year and income ( $\beta = -1.073$ ,  $P = 0.0366$ ; Fig. 3A). When the dependent variable was the degree of clustering of estimated quantity of *Ae. albopictus* for each site, the predictors explained 44.14% of the variance ( $R^2 = 0.441$ ,  $F_{(5, 12)} = 5.53$ ,  $P = 0.0510$ ). There was a borderline significant interaction between year and income ( $\beta = 0.0106$ ,  $P = 0.0510$ ). For 2017, greater income surface led to greater clustering of estimated quantity of *Ae. albopictus* (Fig. 3B). For 2016, income had no effect. *Aedes albopictus* larval distribution, as measured by both positive containers ( $\beta = -6.32 \times 10^{-8}$ ,  $P = 0.346$ ) and estimated number ( $\beta = 0.0188$ ,  $P = 0.494$ ), was not related to impervious surface in either year.

#### Positive Container Variables

We looked for container measurements that predicted the presence of *Ae. albopictus* in order to identify variables that could focus future control efforts. Together these data show that, while there were significant variables in both years, the significant measurements varied from 2016 to 2017.

In 2016, water temperature, shading, and plants were significant predictors of positive containers, whereas container category, container material, and water volume were not significant predictors (Table 3). *Aedes albopictus* were more likely to be found in containers with dead plants over no plants (coeff. =  $-1.927$ , SE =  $0.343$ ,  $z$ -value =  $-5.616$ ,  $P < 0.0001$ ) and with dead plants over live plants (coeff. =  $-2.283$ , SE =  $0.845$ ,  $z$ -value =  $-2.702$ ,  $P = 0.00689$ ). In addition, they were more likely to be found in containers in full shade over those with no shade (coeff. =  $-2.114$ , SE =  $0.838$ ,  $z$ -value =  $-2.521$ ,  $P = 0.0117$ ) or partial shade (coeff. =  $-0.649$ , SE =  $0.291$ ,  $z$ -value =  $-2.232$ ,  $P = 0.0256$ ). Increasing water temperature increased the likelihood of a container being *Ae. albopictus* positive (coeff. =  $0.119$ , SE =  $0.0531$ ,  $z$ -value =  $2.248$ ,  $P = 0.0246$ ).

When number of positive containers was analyzed by container characteristics for 2017, water temperature, container category, water volume, and plants were significant predictors of *Ae. albopictus* presence (Table 3). In contrast to 2016, two container categories – planters and piping/tubing – significantly predicted the presence of *Ae. albopictus* (coeff. =  $0.871$ , SE =  $0.354$ ,  $z$ -value =  $2.461$ ,  $P = 0.0139$ ; coeff. =  $1.0690$ , SE =  $0.466$ ,  $z$ -value =  $2.293$ ,  $P = 0.0219$ ), increasing water volume increased the likelihood of a container being positive (coeff. =  $0.237$ , SE =  $0.0476$ ,  $z$ -value =  $4.974$ ,  $P < 0.0001$ ), increasing water temperature decreased the likelihood of a container being *Ae. albopictus* positive (coeff. =  $-0.0597$ , SE =  $0.0302$ ,  $z$ -value =  $-1.976$ ,  $P = 0.0481$ ) and shading was not significant. Similarly, as in 2016, *Ae. albopictus* were more likely to be found in containers with dead



**Fig. 3.** Median household income predicted greater clustering of *Ae. albopictus*. (A) In 2016 positive containers were more highly clustered in sites with higher median household income and (B) in 2017 estimated quantity of *Ae. albopictus* were more highly clustered in sites with higher median household income.

**Table 2.** Site-level predictors of *Ae. albopictus* abundance by three measures

Coefficient	Percent pos. containers		Pos. containers per 100 houses surveyed		Estimated quantity of <i>Ae. albopictus</i>	
	Estimates (CI)	P	Estimates (CI)	P	Estimates (CI)	P
Intercept	0.16 (0.09 to 0.22)	0.003	52.18 (-6.78 to 111.13)	0.192	20.44 (-2.26 to 43.13)	0.164
Year	0.11 (0.01 to 0.20)	0.113	16.96 (-11.59 to 45.50)	0.373	-2.60 (-34.69 to 29.50)	0.896
Impervious surface	-0.00 (-0.00 to 0.00)	0.859	0.22 (-0.63 to 1.07)	0.683	-0.00 (-0.33 to 0.32)	0.984
Income	-0.42 (-0.91 to 0.06)	0.180	-144.74 (-571.06 to 281.59)	0.595	-58.48 (-222.59 to 105.63)	0.569
Year by impervious surface	0.00124 (-0.08 to 0.002)	0.040	0.67 (0.27 to 1.08)	0.041	0.70 (0.24 to 1.16)	0.029
Year by income	-0.08 (-0.77 to 0.61)	0.858	29.58 (-185.40 to 244.56)	0.830	71.69 (-160.40 to 303.78)	0.621
<b>Random Effects</b>						
$\sigma^2$	0.00		56.00		76.67	
$\tau_{00}$	0.00		461.39		0.00	
ICC	0.08		0.89		0.00	
Observations	17		17		18	
Marginal R <sup>2</sup> /conditional R <sup>2</sup>	0.906/0.913		0.579/0.954		NA	

plants over no plants (coeff. = -0.986, SE = 0.217, z-value = -4.550,  $P < 0.0001$ ), with dead plants over live plants (coeff. = -1.875, SE = 0.590, z-value = -3.180,  $P = 0.00147$ ), and container material was not significant.

## Discussion

Our study describes the abundance and distribution of *Ae. albopictus* larvae and pupae along impervious surface and socioeconomic gradients on a northern border of its invasive range. Uniquely, we covered a full spectrum of sites along landscape gradients with unprecedented scope and coverage for the Northeast region. Our first hypothesis, that increasing site-level impervious surface and decreasing household median income would predict higher abundance and less clustered distribution of *Ae. albopictus* larval habitat because of increased quality and availability of larval habitat was partially supported. Our second hypothesis that *Ae. albopictus*-positive larval habitat would be predicted by container characteristics that have been previously identified as important, such as shading or container type, was not consistently supported enough to be useful for targeted mosquito control. These results contribute to our knowledge of how landscape shapes *Ae. albopictus* distribution and abundance and identifies container characteristics related to the presence of this species.

## Variation Year to Year

We found the percent containers positive for *Ae. albopictus* dramatically increased from the first to second year of this study. Although surveys for 2016 were conducted over an entire season of adult activity and those in 2017 were completed over 3 wk, this trend held even when comparing data from the same period in both years. For data within the same date range for both years, the proportion of containers positive for any mosquito was greater in 2017 than in 2016. However, the percent rise in the number of *Ae. albopictus*-positive containers was larger than for mosquito-positive containers overall. This suggests that *Ae. albopictus* did not just increase because mosquito populations increased, but that they were more successful than other container species. There is no obvious connection to weather; while we would expect that a hotter and wetter weather would predict greater mosquito abundance, using data from the NOAA, Northeast Regional Climate Center at Cornell University, 2017, was both slightly cooler and slightly drier than 2016 ([Supp Fig. 3 \[online only\]](#)). The variation we observed over just 2 yr is not sufficient to identify long-term patterns, but it highlights the necessity of systematic surveillance to track long-term population trends over time and more clearly pinpoint the factors driving changes.

**Table 3.** Container variables predictive of the presence of *Ae. albopictus* in 2016 and 2017

Coefficient	2016		2017	
	Odds ratios (CI)	P	Odds ratios (CI)	P
Intercept	0.07 (0.01–0.30)	0.001	1.39 (0.27–7.22)	0.692
Water temp	1.08 (1.02–1.13)	0.005	0.94 (0.89–1.00)	0.048
Water volume	1.07 (0.97–1.18)	0.169	1.27 (1.16–1.39)	<0.001
Container material				
Metal	0.92 (0.32–2.36)	0.875	1.11 (0.58–2.09)	0.759
Rubber	4.40 (0.69–39.13)	0.135	1.50 (0.24–12.38)	0.674
Ceramic	1.40 (0.37–4.63)	0.594	0.55 (0.19–1.55)	0.270
Stone	1.62 (0.38–6.43)	0.495	1.37 (0.40–4.88)	0.616
Other	0.99 (0.20–3.74)	0.991	2.56 (0.58–13.84)	0.231
Container type				
Planter	2.03 (0.77–5.19)	0.142	2.39 (1.20–4.84)	0.014
Tarp	1.60 (0.51–4.69)	0.400	3.43 (0.83–17.54)	0.102
Sheeting	0.76 (0.19–2.44)	0.660	0.54 (0.11–2.11)	0.403
Tire	0.30 (0.03–2.08)	0.255	0.85 (0.10–5.25)	0.871
Trash	0.47 (0.13–1.36)	0.197	1.41 (0.66–3.00)	0.374
Toy	0.87 (0.35–1.99)	0.754	0.68 (0.30–1.48)	0.337
Bird bath	0.28 (0.03–1.51)	0.180	0.63 (0.19–1.93)	0.431
Piping/tubing	1.65 (0.32–7.00)	0.515	2.91 (1.17–7.37)	0.022
Other	0.60 (0.28–1.23)	0.179	0.76 (0.42–1.36)	0.358
Degree of shading				
No shading	0.22 (0.06–0.62)	0.009	0.56 (0.29–1.06)	0.077
Partial shading	0.65 (0.41–1.05)	0.077	0.87 (0.57–1.33)	0.533
Organic material				
Live plants	0.22 (0.05–0.72)	0.024	0.15 (0.04–0.46)	0.001
Live and dead plants	1.20 (0.38–3.49)	0.745	0.61 (0.30–1.22)	0.161
No plants	0.18 (0.10–0.32)	<0.001	0.37 (0.24–0.57)	<0.001
Observations	554		529	
Cox and Snell's R <sup>2</sup> /Nagelkerke's R <sup>2</sup>	0.142/0.221		0.160/0.215	

### Site-Level Degree of Infestation by Impervious Surface and Household Median Income

We found differences between 2016 and 2017 in the effect of impervious surface on mosquito abundance; no relationship was found in 2016 and, by some measures, *Ae. albopictus* were more abundant in sites of greater impervious surface in 2017. Impervious surface is an important environmental factor for urban container breeding mosquitoes like *Ae. albopictus*. Densely covered areas with concrete and asphalt can create heat islands and increase the availability of habitat (Murdock et al. 2017). It is possible that sites with greater impervious surface are of greater quality and can support larger *Ae. albopictus* populations or sustain faster population growth. It may be that in 2016 other factors limited population size regardless of impervious surface and abundance was not high enough to detect any patterns across sites, but in 2017 better conditions allowed populations to grow, and they grew larger in the higher-quality, high impervious surface sites. However, the percent of containers positive for *Ae. albopictus* was only significantly predicted by impervious surface when one outlying site was removed, and it is unclear how this trend would hold when analyzed over a greater number of sites. This further highlights the needs for more comprehensive surveys over a larger range and number of sites than was within the scope of this study.

Our results do not support the current literature which typically portrays *Ae. albopictus* as a suburban or rural species, especially in locations where their range overlaps with *Ae. aegypti* (Braks et al. 2003b, Rey et al. 2006, Reiskind and Lounibos 2013). At least in southern New York, which is free of *Ae. aegypti*, our results demonstrate that *Ae. albopictus* populations can be higher in sites of high impervious surface. This discrepancy may stem from the fact that

little research has been conducted on *Ae. albopictus* across its diverse and wide geographic range, and our results suggest caution when extrapolating results from one region to another.

We did not see a relationship between household median income and overall *Ae. albopictus* abundance. Socioeconomic status using median income as a measure has been correlated with *Ae. albopictus* infestation. For example, Becker et al. (2014) and LaDeau et al. (2013) reported different infestation levels between sites of varied socioeconomic status; however, ours is the first study conducted with sufficient sites along a socioeconomic gradient to have enough statistical power to analyze income as a causative factor. Beyond larval counts, one previous study found more ‘disused containers’ (containers not in use or regularly dumped or treated by residents) in low-income sites and a higher likelihood of *Ae. albopictus* occurrence in these disused containers; concluding that lower-income neighborhoods are at greater risk for high *Ae. albopictus* abundance (Dowling et al. 2013). In our study, we did not detect differences in abundance by household median income, nor did we see any clear relationship between income and average number of suitable oviposition containers per site. Although we did not use the used/disused metric of Dowling et al. (2013), we also did not find that container category and material was a consistent predictor of *Ae. albopictus* infestation. Altogether, our results reinforce that control campaigns should equally target sites across income groups.

### Spatial Distribution by Household Median Income and Impervious Surface

However, household median income did explain spatial distribution of larvae/pupae, with *Ae. albopictus*-positive containers more clustered in

higher-income sites in 2016 and overall abundance more clustered in 2017. These results may be connected to the distribution of the containers themselves, which were more clustered in higher income sites. *Ae. albopictus* are considered poor dispersers with an average flight distance of 50–200 m (Marini et al. 2010), so even distribution of containers in low-income neighborhoods may facilitate more even dispersal of gravid females across the landscape. In contrast, in high-income neighborhoods, *Ae. albopictus* movement may be restricted to 'islands' of clustered oviposition habitat. This is supported by a study of residential populations in North Carolina that examined the spatial distribution of *Ae. albopictus*-positive containers: they showed that pupal 'hot spots' in a suburban neighborhood were aggregated around homes with large numbers of potential oviposition containers (Richards et al. 2006). While control campaigns should cover neighborhoods across the socioeconomic spectrum, the specific strategy could be tailored based on income level. It should be noted that while our sites did represent a gradient of socioeconomic level, *Ae. albopictus* populations thrive in US cities outside of the ranges represented here, and it is unknown how these patterns would hold in those locations. However, given our results, targeted control of *Ae. albopictus* hot spots may be more efficient in high-income sites and widespread control more effective in low-income sites.

In contrast to our results for household income, impervious surface was not a driver of spatial distribution in any year by any measure.

### Container-Level Predictors

Even between two consecutive years of surveys within the same sites or primarily the same houses, all but one of our container characteristic measures failed to consistently predict *Ae. albopictus* larvae from 2016 to 2017. While the presence of dead organic material in container water positively predicted the presence of *Ae. albopictus* in both years, all the other significant factors were either unique to 1 yr or predictive in opposite directions between years. This is even true for measures like water volume or shading that have been linked to *Ae. albopictus* infestation in the past (Delatte et al. 2008, Unlu et al. 2013). We argue that, at least for the Northeast US region, oviposition behavior or survival postoviposition is highly dependent on environmental factors that vary year-to-year. As a result, focusing on certain containers is an inviable strategy. It may be more useful instead to identify landscape or climatological features that consistently determine *Ae. albopictus* population dynamics to target response.

### Limitations and General Conclusions

Although our multiyear, multisite study is one of the largest conducted to date for *Ae. albopictus* in the Northeast region, we still cannot make conclusions about long-term seasonal or subregional trends in our key drivers of interest. Larval surveys are labor intensive, limiting the number of households that can be covered even with multiple survey teams, and are difficult to conduct over a large region for multiple years or even months. Thorough sampling of the landscape is difficult. Within our sites, we were unable to access all homes, and it is unknown if those that gave us access were biased toward or against those with more or fewer containers. Although we made every effort to locate all water-holding containers in each property, including notoriously cryptic habitat such as gutters and corrugated drain pipes, *Ae. albopictus* infest inaccessible and hidden habitat, meaning we likely were not able to locate all containers. Our sample size was robust enough to meet the goals of this study despite these limitations, with sufficient power to detect significant factors for all measures.

We stress that the results of our larval survey do not necessarily correlate to adult *Ae. albopictus* abundance; variable survivorship to adulthood can result in significant decoupling between larval and

adult population sizes, at least for *Ae. aegypti* (Tun-Lin et al. 1996). This means that no conclusions can be drawn to quantify biting risk or to recommend control that targets adult populations. These results can only be used to make recommendations regarding control targeting immature stages, such as dumping or treating containers.

In the long term, more research is necessary to address these limitations: a systematic, region-wide approach studying larvae, pupae, and adults will be essential to allow us to gain a clear understanding of *Ae. albopictus* ecology and population dynamics. Unfortunately, current funding for county and regional programs in the Northeast United States that conduct mosquito surveillance is insufficient to perform wide-scale sampling. Most counties currently rely on lower resource-input adult trapping, which is only effective over a short range and therefore a poor tool for tracking *Ae. albopictus*.

General comparisons between studies conducted to date are hampered by a lack of standardization and identifying biologically meaningful differences among studies with methodological differences is therefore difficult. Discrepancies in resources between counties compound this issue – adjacent counties with wide gaps in funding produce incomparable data sets, hindering comparisons across space. We cannot stress enough the importance of greater communication and standardization between groups with similar objectives to ease and enhance the interpretation of collected data.

*Aedes albopictus* vectors are notorious for their high level of plasticity and ability for rapid local adaptation, meaning that real ecological differences can exist between populations from different proximate environments (Paupy et al. 2009b). Control of this important vector can be improved by tailoring efforts based on localized studies, saving time, money, and human effort. Existing mosquito surveillance and control strategies in the Northeast are not designed to target this species and distribution data are inconsistent or incomplete. More standardized studies covering a sufficiently large numbers of sites along landscape gradients are required to identify causative measures of ecological differences. This is particularly important in southern New York, because it represents a northern boundary of *Ae. albopictus* expanding range.

### Supplementary Data

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

### Acknowledgments

We are grateful for the assistance of Amy Isenberg (Rockland County), Scott Campbell and Brian Gibbons (Suffolk County), and John Ruggiero (Westchester County) for their advice on sampling locations. We appreciate the statistical consulting of Erika Mudrak and Patrick Sullivan and the technical assistance of Tamsin Smith, Jody Gangloff-Kaufman, the Harrington laboratory group, and The Louis Calder Center. We thank Maria Diuk-Wasser, Courtney Murdock, Scott McArt and Katja Poveda for reviewing early drafts of the manuscript. We are also grateful for our funding, in part from the Cornell University Extension and Outreach (EOA) Fellowship awarded to TS, in part from the National Institute of Food and Agriculture (NIFA), U.S. Department of Agriculture, Hatch Project under 2017-18-160, and in part by the Centers for Disease Control and Prevention (U01 CK000509).

### References Cited

- 2011. National land cover database. USGS Multi-resolution Land Characteristics Consortium, US Department of Interior, US Geological Survey. <https://www.mrlc.gov/contact.php> (accessed 7 July 2017).
- 2015. American community survey. United States Census Bureau. "B19013 Median Household Income in the Past 12 Months." 2007–2011 American Community Survey. US Census Bureau's American Community Survey Office, 2013.

- Alirol, E., L. Getaz, B. Stoll, F. Chappuis, and L. Loutan. 2011. Urbanisation and infectious diseases in a globalised world. Lancet. Infect. Dis. 11: 131–141.
- Andreadis, T. G., M. C. Thomas, and J. J. Shepard. 2005. Identification guide to the mosquitoes of Connecticut. Connecticut Agricultural Experiment Station, New Haven, CT.
- Baddeley, A. 2008. Analysing spatial point patterns in R. Technical report, CSIRO, 2010. Version 4. <https://research.csiro.au/software/r-workshop-notes>.
- Baddeley, A., and R. Turner. 2005. Spatstat: an R package for analyzing spatial point patterns. J. Statist. Softw. 12: 1–42.
- Bagny, L., H. Delatte, N. Elissa, S. Quilici, and D. Fontenille. 2009. *Aedes* (Diptera: Culicidae) vectors of arboviruses in Mayotte (Indian Ocean): distribution area and larval habitats. J. Med. Entomol. 46: 198–207.
- Barker, C. M., S. L. Paulson, S. Cantrell, and B. S. Davis. 2003. Habitat preferences and phenology of *Ochlerotatus triseriatus* and *Aedes albopictus* (Diptera: Culicidae) in southwestern Virginia. J. Med. Entomol. 40: 403–410.
- Bartlett-Healy, K., I. Unlu, P. Obenauer, T. Hughes, S. Healy, T. Crepeau, A. Farajollahi, B. Kesavaraju, D. Fonseca, G. Schoeler, et al. 2012. Larval mosquito habitat utilization and community dynamics of *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae). J. Med. Entomol. 49: 813–824.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.7. 1: 1–23.
- Becker, B., P. T. Leisnham, and S. L. LaDau. 2014. A tale of two city blocks: differences in immature and adult mosquito abundances between socio-economically different urban blocks in Baltimore (Maryland, USA). Int. J. Environ. Res. Public Health. 11: 3256–3270.
- Beilhe, L. B., S. Arnoux, H. Delatte, G. Lajoie, and D. Fontenille. 2012. Spread of invasive *Aedes albopictus* and decline of resident *Aedes aegypti* in urban areas of Mayotte 2007–2010. Biological Invasions 14: 1623–1633.
- Braks, M. A., N. A. Honório, R. Lourenço-De-Oliveira, S. A. Juliano, and L. P. Loumibos. 2003a. Convergent habitat segregation of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in southeastern Brazil and Florida. J. Med. Entomol. 40: 785–794.
- Braks, M. A., N. A. Honório, R. Lourenço-De-Oliveira, S. A. Juliano, and L. P. Loumibos. 2003b. Convergent habitat segregation of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in southeastern Brazil and Florida. J. Med. Entomol. 40: 785–794.
- Braks, M. A. H., N. A. Honorio, L. P. Loumibos, R. Lourenco-De-Oliveira, and S. A. Juliano. 2004. Interspecific competition between two invasive species of container mosquitoes, *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae), in Brazil. Ann. Entomol. Soc. Am. 97: 130–139.
- Cox, J., M. E. Grillet, O. M. Ramos, M. Amador, and R. Barrera. 2007. Habitat segregation of dengue vectors along an urban environmental gradient. Am. J. Trop. Med. Hyg. 76: 820–826.
- De Azevedo, T. S., B. P. Bourke, R. Piovezan, and M. A. M. Sallum. 2018. The influence of urban heat islands and socioeconomic factors on the spatial distribution of *Aedes aegypti* larval habitats. Geospat. Health. 13: 623.
- Delatte, H., J. S. Dehecq, J. Thiria, C. Domerg, C. Paupy, and D. Fontenille. 2008. Geographic distribution and developmental sites of *Aedes albopictus* (Diptera: Culicidae) during a Chikungunya epidemic event. Vector Borne Zoonotic Dis. 8: 25–34.
- Dowling, Z., S. L. Ladeau, P. Armbruster, D. Biebler, and P. T. Leisnham. 2013. Socioeconomic status affects mosquito (Diptera: Culicidae) larval habitat type availability and infestation level. J. Med. Entomol. 50: 764–772.
- Getis, A., A. C. Morrison, K. Gray, and T. W. Scott. 2003. Characteristics of the spatial pattern of the dengue vector, *Aedes aegypti*, in Iquitos, Peru. Am. J. Trop. Med. Hyg. 69: 494–505.
- Grab, H., B. Danforth, K. Poveda, and G. Loeb. 2018. Landscape simplification reduces classical biological control and crop yield. Ecol. Appl. 28: 348–355.
- Hawley, W. A. 1988. The biology of *Aedes albopictus*. J. Am. Mosq. Control Assoc. Suppl. 1: 1–39.
- Honório, N. A., W. D. C. Silva, P. J. Leite, J. M. Gonçalves, L. P. Loumibos, and R. Lourenço-de-Oliveira. 2003. Dispersal of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in an urban endemic dengue area in the State of Rio de Janeiro, Brazil. Memórias do Instituto Oswaldo Cruz 98: 191–198.
- Honório, N. A., M. G. Castro, F. S. Barros, M. D. E. A. Magalhães, and P. C. Sabroza. 2009. The spatial distribution of *Aedes aegypti* and *Aedes albopictus* in a transition zone, Rio de Janeiro, Brazil. Cad. Saude Publica. 25: 1203–1214.
- Hornby, J. A., D. E. Moore, and T. W. Miller, Jr. 1994. *Aedes albopictus* distribution, abundance, and colonization in Lee County, Florida, and its effect on *Aedes aegypti*. J. Am. Mosq. Control Assoc. 10: 397–402.
- Koehler, P. G., and J. Castner. 1997. Bloodsucking insects. University of Florida Cooperative Extension Service, Institute of Food and Agriculture Sciences, EDIS, Gainesville, FL.
- LaDau, S. L., P. T. Leisnham, D. Biebler, and D. Bodner. 2013. Higher mosquito production in low-income neighborhoods of Baltimore and Washington, DC: understanding ecological drivers and mosquito-borne disease risk in temperate cities. Int. J. Environ. Res. Public Health. 10: 1505–1526.
- Landau, K. I., and W. J. van Leeuwen. 2012. Fine scale spatial urban land cover factors associated with adult mosquito abundance and risk in Tucson, Arizona. J. Vector Ecol. 37: 407–418.
- Lenth, R. V. 2016. Least-squares means: the R package lsmeans. J. Statist. Softw. 69: 1–33.
- Li, Y., F. Kamara, G. Zhou, S. Puthiyakunnon, C. Li, Y. Liu, Y. Zhou, L. Yao, G. Yan, and X. G. Chen. 2014. Urbanization increases *Aedes albopictus* larval habitats and accelerates mosquito development and survivorship. Plos Negl. Trop. Dis. 8: e3301.
- Little, E., D. Biebler, P. T. Leisnham, R. Jordan, S. Wilson, and S. L. LaDau. 2017. Socio-ecological mechanisms supporting high densities of *Aedes albopictus* (Diptera: Culicidae) in Baltimore, MD. J. Med. Entomol. 54: 1183–1192.
- Maciel-de-Freitas, R., and R. Lourenço-de-Oliveira. 2011. Does targeting key-containers effectively reduce *Aedes aegypti* population density? Trop. Med. Int. Health. 16: 965–973.
- Marini, F., B. Caputo, M. Pombi, G. Tarsitani, and A. della Torre. 2010. Study of *Aedes albopictus* dispersal in Rome, Italy, using sticky traps in mark-release-recapture experiments. Med. Vet. Entomol. 24: 361–368.
- Medeiros, M. C., E. C. Boothe, E. B. Roark, and G. L. Hamer. 2017. Dispersal of male and female *Culex quinquefasciatus* and *Aedes albopictus* mosquitoes using stable isotope enrichment. Plos Negl. Trop. Dis. 11: e0005347.
- Murdock, C. C., M. V. Evans, T. D. McClanahan, K. L. Miazgowicz, and B. Tesla. 2017. Fine-scale variation in microclimate across an urban landscape shapes variation in mosquito population dynamics and the potential of *Aedes albopictus* to transmit arboviral disease. Plos Negl. Trop. Dis. 11: e0005640.
- Niebylski, M. L., and G. B. Craig, Jr. 1994. Dispersal and survival of *Aedes albopictus* at a scrap tire yard in Missouri. J. Am. Mosq. Control Assoc. 10: 339–343.
- Paupy, C., H. Delatte, L. Bagny, V. Corbel, and D. Fontenille. 2009a. *Aedes albopictus*, an arbovirus vector: from the darkness to the light. Microbes Infect. 11: 1177–1185.
- Paupy, C., H. Delatte, L. Bagny, V. Corbel, and D. Fontenille. 2009b. *Aedes albopictus*, an arbovirus vector: from the darkness to the light. Microbes Infect. 11: 1177–1185.
- Reiskind, M. H., and L. P. Loumibos. 2013. Spatial and temporal patterns of abundance of *Aedes aegypti* L. (*Stegomyia aegypti*) and *Aedes albopictus* (Skuse) [*Stegomyia albopictus* (Skuse)] in southern Florida. Med. Vet. Entomol. 27: 421–429.
- Rey, J. R., N. Nishimura, B. Wagner, M. A. Braks, S. M. O'Connell, and L. P. Loumibos. 2006. Habitat segregation of mosquito arbovirus vectors in south Florida. J. Med. Entomol. 43: 1134–1141.
- Richards, S. L., C. S. Apperson, S. K. Ghosh, H. M. Cheshire, and B. C. Zeichner. 2006. Spatial analysis of *Aedes albopictus* (Diptera: Culicidae) oviposition in suburban neighborhoods of a Piedmont community in North Carolina. J. Med. Entomol. 43: 976–989.
- Richards, S. L., S. K. Ghosh, B. C. Zeichner, and C. S. Apperson. 2008. Impact of source reduction on the spatial distribution of larvae and pupae of *Aedes albopictus* (Diptera: Culicidae) in suburban

- neighborhoods of a Piedmont community in North Carolina. *J. Med. Entomol.* 45: 617–628.
- Rowlingson, B., P. Diggle, R. Bivand, G. Petris, and S. Eglen. 2013. Splancs: spatial and space-time point pattern analysis. R package version: 2.01–33. <http://www2.uaem.mx/r-mirror/web/packages/splancs/splancs.pdf>
- Rubio, A., M. V. Cardo, A. E. Carbajo, and D. Vezzani. 2013. Imperviousness as a predictor for infestation levels of container-breeding mosquitoes in a focus of dengue and Saint Louis encephalitis in Argentina. *Acta Trop.* 128: 680–685.
- The New York State Department of Health (ed.). 2017. NYSDOH statewide mosquito borne disease activity report. [https://www.health.ny.gov/diseases/west\\_nile\\_virus/](https://www.health.ny.gov/diseases/west_nile_virus/)
- Tsuda, Y., W. Suwonkerd, S. Chawprom, S. Prajakwong, and M. Takagi. 2006. Different spatial distribution of *Aedes aegypti* and *Aedes albopictus* along an urban-rural gradient and the relating environmental factors examined in three villages in northern Thailand. *J. Am. Mosq. Control Assoc.* 22: 222–228.
- Tun-Lin, W., B. H. Kay, A. Barnes, and S. Forsyth. 1996. Critical examination of *Aedes aegypti* indices: correlations with abundance. *Am. J. Trop. Med. Hyg.* 54: 543–547.
- Unlu, I., A. Farajollahi, S. P. Healy, T. Crepeau, K. Bartlett-Healy, E. Williges, D. Strickman, G. G. Clark, R. Gaugler, and D. M. Fonseca. 2011. Area-wide management of *Aedes albopictus*: choice of study sites based on geo-spatial characteristics, socioeconomic factors and mosquito populations. *Pest Manag. Sci.* 67: 965–974.
- Unlu, I., A. Farajollahi, D. Strickman, and D. M. Fonseca. 2013. Crouching tiger, hidden trouble: urban sources of *Aedes albopictus* (Diptera: Culicidae) refractory to source-reduction. *Plos One.* 8: e77999.
- Walker, K. R., D. Williamson, Y. Carrière, P. A. Reyes-Castro, S. Haenchen, M. H. Hayden, E. Jeffrey Gutierrez, and K. C. Ernst. 2018. Socioeconomic and human behavioral factors associated with *Aedes aegypti* (Diptera: Culicidae) immature habitat in Tucson, AZ. *J. Med. Entomol.* 55: 955–963.