



Population and Community Ecology

Changes in Container-Breeding Mosquito Diversity and Abundance Along an Urbanization Gradient are Associated With Dominance of Arboviral Vectors

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Abstract

Environmental conditions associated with urbanization are likely to influence the composition and abundance of mosquito (Diptera, Culicidae) assemblages through effects on juvenile stages, with important consequences for human disease risk. We present six years (2011–2016) of weekly juvenile mosquito data from distributed standardized ovitraps and evaluate how variation in impervious cover and temperature affect the composition and abundance of container-breeding mosquito species in Maryland, USA. Species richness and evenness were lowest at sites with high impervious cover (>60% in 100-m buffer). However, peak diversity was recorded at sites with intermediate impervious cover (28–35%). Four species were observed at all sites, including two recent invasives (*Aedes albopictus* Skuse, *Ae. japonicus* Theobald), an established resident (*Culex pipiens* L), and one native (*Cx. restuans* Theobald). All four are viral vectors in zoonotic or human transmission cycles. Temperature was a positive predictor of weekly larval abundance during the growing season for each species, as well as a positive predictor of rapid pupal development. Despite being observed at all sites, each species responded differently to impervious cover. Abundance of *Ae. albopictus* larvae was positively associated with impervious cover, emphasizing that this medically-important vector not only persists in the warmer, impervious urban landscape but is positively associated with it. Positive temperature effects in our models of larval abundance and pupae occurrence in container habitats suggest that these four vector species are likely to continue to be present and abundant in temperate cities under future temperature scenarios.

Key words: urban, biodiversity, arthropod, virus

Mosquitoes are a diverse and ubiquitous group of insects that require water to develop through juvenile life stages, and most require a vertebrate blood meal to complete their reproductive cycle. While mosquitoes bite a wide range of vertebrates, species that adapt to survive in urban ecosystems are more likely to encounter and bite humans (Munoz et al. 2011, Faraji et al. 2014, Goodman et al. 2018, Cebrian-Camison et al. 2020). Global changes in urban land cover and introductions of invasive species have facilitated novel assemblages of urban-adapted mosquito communities (Thongsripong et al. 2013, Hoshi et al. 2014, Kraemer et al. 2019, Seyfarth et al. 2019, Beaulieu et al. 2020, Camara et al. 2020). Transmission of mosquito-borne pathogens in urban settings has risen in recent decades, including localized outbreaks of dengue, chikungunya, and Zika viruses in temperate cities (Chretien and Linthicum 2007, Lambrechts et al. 2010, Weaver 2013, Campbell

et al. 2015, Delisle et al. 2015, Quam et al. 2015, Tsuda et al. 2016, Ali et al. 2017, Manore et al. 2017, Kraemer et al. 2019, Sukhralia et al. 2019). While mosquito ecology is particularly relevant to spatial and temporal variation in public health risk, these fast-lived organisms also represent a tractable system for examining effects of urbanization on community and population-level dynamics in real-world landscapes.

Urbanization can result in loss of native species in many animal and plant communities (Savard et al. 2000, McKinney 2002, Lepczyk et al. 2008, Thongsripong et al. 2013, Sol et al. 2014), but is also associated with species gains through introduction of non-native species (Lepczyk et al. 2008, Francis and Chadwick 2015, Francis and Chadwick 2017, Gaertner et al. 2017, Evans et al. 2018a, Pearse et al. 2018). High resource availability and/or low predation in urban ecosystems can further support high

population growth for some organisms, including many rodent, weed, and mosquito species (Gardner-Santana et al. 2009, Hoshi et al. 2014, Johnson et al. 2015a). The presence and abundance of mosquito species in any environment is strongly influenced by environmental conditions experienced during juvenile stages (Juliano 2007). Female mosquitoes lay eggs into or near aquatic habitats, and juveniles develop over days to months before emerging as winged adults. Differences in aquatic habitat composition, volume, persistence, and detrital inputs can influence which species will oviposit in a specific site and how likely the eggs are to survive to adulthood (Yee et al. 2012, Li et al. 2014, Townroe and Callaghan 2014, Leisnham et al. 2019, Wilke et al. 2019). Carry-over effects from juvenile life stages can also influence metrics of adult fitness (Lounibos et al. 1993, Reiskind and Lounibos 2009, Alto et al. 2012, Takken et al. 2013, Barreaux et al. 2018, Chandrasegaran et al. 2018) and vector competence (Alto et al. 2008, Westbrook et al. 2010, Muturi and Alto 2011, Dodson et al. 2012, Vantaux et al. 2016, Evans et al. 2018b). In natural ecosystems, different mosquito species oviposit in a wide range of aquatic habitats, including ephemeral pools, ponds, flood zones, and tree holes. In urban ecosystems, mosquito species utilize a wide array of human-made containers for juvenile development (Bartlett-Healy et al. 2012, LaDeau et al. 2013, Little et al. 2017, Wilke et al. 2019) and these curated (or discarded) containers can support the emergence of adult females with easy access to human blood meals.

Urbanization represents a fundamental change in impervious surface cover and heat exchange from the natural environment. Impervious surfaces hold heat more effectively than natural surfaces, affecting the mean and variation of local air temperatures (Buyantuyev and Wu 2010, Imhoff et al. 2010, Ramamurthy and Bou-Zeid 2017). High local temperature can affect evaporation of water in container habitats (Bartlett-Healy et al. 2011) and alter aquatic processes that generate detrital and microbial food resources for juvenile mosquitoes (Gray et al. 2016, Zander et al. 2017). Temperature has been positively but often nonlinearly associated with rates of juvenile development, as well as adult body condition, survival, and fitness of all life stages (Afrane et al. 2005, Delatte et al. 2009, Alto et al. 2014, Ciota et al. 2014, Evans et al. 2019).

However, impervious surfaces in cities are associated with habitat modification beyond effects on local temperature. For example, impervious land cover is often correlated with low forest or vegetation cover (Bigsby et al. 2014, Saverino et al. 2021). Residential neighborhoods with high impervious surface and low vegetation cover are often lower-income communities that often receive lower municipal investment in infrastructure maintenance and garbage removal (Schwarz et al. 2015, Biehler et al. 2018), exacerbating neighborhood differences in detrital resources and management of discarded containers. Thus, impervious surface can be associated both with the availability of physical mosquito habitat and the temperature profile experienced by juvenile and adult mosquitoes (Little et al. 2017, Evans et al. 2019, Wimberly et al. 2020).

While many studies have examined how changes in temperature and detrital resources influence competitive outcomes or development of container-breeding mosquitoes in controlled experiments, few have assessed how mosquito assemblages change along a real urbanizing gradient with naturally experienced temperature and impervious cover changes (Chaves et al. 2011, Zahouli et al. 2016, Zahouli et al. 2017, Evans et al. 2019) and fewer still extend across multiple years. This study leverages a six-year dataset of weekly abundances of mosquito larvae and pupae in standardized container traps to explore container-breeding assemblages vary with local-scale impervious surface cover and microhabitat-scale temperature.

We further assess how variation in land cover and temperature predict larval abundance for the four most frequently observed species: two *Culex* species known to amplify West Nile virus cycles in the region (*Cx. pipiens* and *Cx. restuans*) and two invasive species (*Ae. albopictus* and *Ae. japonicus*) introduced to the region in the 1980's and 1990's, respectively.

Methods

Study sites (Fig. 1) include a subset of stream-adjacent sampling sites along an urbanization gradient from forested Baltimore County to Baltimore City (MD) that were first established by researchers at the Baltimore Ecosystem Study (<https://baltimoreecosystemstudy.org>). Four sites are in the Gwynns Falls Watershed, including (1) Glyndon (GFGL), (2) Gwynnbrook (GFGB), and (3) Villa Nova (GFVN), which are located in the suburban headwaters with intermediate human density (1,000–2,000 people per km²). The fourth site in the Gwynns Falls Watershed is (4) Carroll Park (GFCP), located at a green infrastructure site near the confluence with the harbor in Baltimore City. Additional sites are in similar-sized watersheds adjacent to Gwynns Falls and are also associated with BES riparian sampling locations, including two sites with low residential development (human density < 500 per km²): (5) Pond Branch (ORPB), a forested reference site, and (6) Baisman Run (ORBR), a site at the edge of a forest with low-density residential development. We also included (7) Rognel Heights (RGHT), another intermediate human density site and (8) Maidens Choice (MAWI), a second green infrastructure site located outside Baltimore City. Three sites not associated with BES riparian sampling locations were added for mosquito work specifically, located in community gardens in high human density (>2,500 people per km²) neighborhoods in West Baltimore City: (9) Fulton Street Community Garden (FSCG), (10) Harlem Park Community Garden (HPCG), and the (11) Sunflower Village Garden (SFCG). Four sites that span the full urbanization gradient were sampled in all six years, including FSCG, GFCP, GFVN, and OROX (Table 1). Human densities in Table 1 are based on 2017 American Community Survey values at the block group level. Since several sites were on the border of two block groups, the proportion the 100-meter radius that came from of each block group was calculated and population density per square kilometer of each partial block group was multiplied by the proportion within the buffer and then summed.

Data Collection

Standardized container traps are often used in complex landscapes in order to estimate composition and relative abundance of species likely to oviposit in container habitats (Day 2016, Manica et al. 2017). The ovitraps that were used in this study were 800 mL black, plastic cups, lined with brown seed germination paper and filled with 350 mL of Timothy hay-infused water. Three ovitraps were deployed at least 1 meter apart at each site and were re-sampled weekly between May and September in each year of the study. All ovitraps were placed in shade with at least 1-m clearance of overhanging vegetation. Additionally, iButton (Maxim Integrated Products, DS1922L-F5#) data loggers were deployed in 2011 through 2015, secured with gray duct-tape to the underside of one ovitrap at each site, to record temperature every hour. The hourly temperature records were averaged to a weekly mean temperature for each site for analyses presented here. The mean annual temperature measured across the four sites visited in the five years with iButton records (2011–2015) ranged from a season average 19.58 (0.77)°C at the forested OROX site to 23.89 (1.66)°C at the urban FSCG site. The season average temperature across the sites in each of

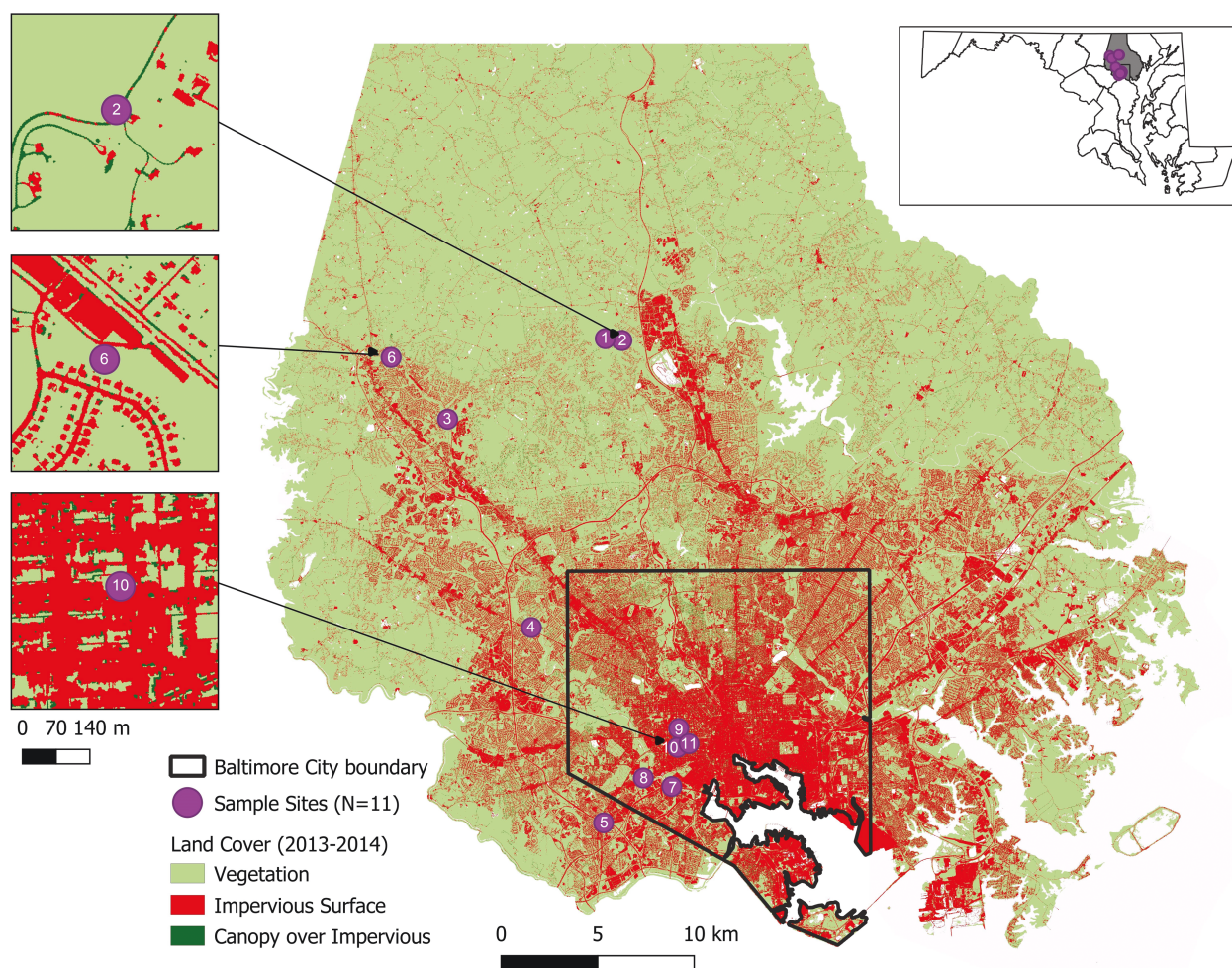


Fig. 1. Map of Baltimore City and County with eleven study sites. Enlarged land cover maps are shown for three sites representing high, intermediate and low impervious cover sites.

Table 1. Site sampling descriptions with species diversity metrics calculated across years

Site		Years Sampled	Impervious Surface	Shannon Diversity Index	Evenness	Species #	Human Density (per Km ²)
1	ORPB	2011–2013 & 2015–2016	0.00	1.20	0.58	8	188.83
2	OROX		2011–2016	0.09	1.22	0.53	9
3	GFGB	2011–2014	0.17	1.18	0.54	8	1,523.14
4	GFVN	2011–2016	0.28	1.48	0.62	10	1,020.77
5	RGHT	2011–2014	0.34	1.48	0.76	7	1,856.56
6	GFGL	2011–2013	0.35	1.45	0.70	8	1,021.42
7	GFCP	2011–2016	0.48	1.18	0.54	9	2,574.02
8	MAWI	2011–2014	0.50	1.20	0.55	8	323.74
9	HPCG	2014–2016	0.63	0.62	0.35	6	4,100.20
10	FSCG	2011–2016	0.76	0.78	0.38	6	7,089.09
11	SFCG	2014–2016	0.82	1.05	0.54	6	2,890.23

Bold-face denotes sites with greatest Shannon Diversity and evenness scores. Impervious surface (proportion cover) and human density are estimated for the 100-m radius of the centre ovitrap at each site.

the five years ranged from a low of 20.38 (1.182)°C in 2014 to 22.91 (2.90)°C in 2012.

Ovitrap were replaced weekly and returned to the lab where all juvenile mosquitoes were removed, identified to species, and counted. All pupae present when traps were collected from the field were counted. Germination papers were dried for 24 h

before re-submerging in water for up to 5 d to allow egg and larvae maturation. Larvae used in analyses here are the summed total of those present when cups were collected from the field and those present after 5 d of maturation in the lab. All specimens were subsequently identified to species or genus and enumerated.

In 2011, existing habitat with standing water present in the immediate vicinity of each ovitrap (10-m radius) was surveyed for larval presence. This included a tree hole at ORBR and standing pooled water at GFCP and GFGB. In each case, water was homogenized and up to three 350ml samples were examined. All existing habitat was dry at the time of sampling after June 30, 2011 and no additional larvae were found after this date. Discarded containers that appeared within 10 meters of our ovitraps during the study were removed. Land cover data for each site was compiled from a 1-meter spatial resolution dataset from 2014 created by the Chesapeake Bay High-Resolution Land Cover Project (www.chesapeakeconservancy.org/conservation-innovation-center/land-cover-data-project/). At each site, we created a 100-meter buffer to represent the minimum mean dispersal distance reported for mosquito species observed in the region (Niebylski and Craig 1994, Guerra et al. 2014). Landscape attributes and surface cover within the buffers were extracted using the Zonal Tabulate Area tool in ArcMap 10.8.1. As expected, significant correlation between vegetation and impervious cover was detected (Pearson's product moment: -0.99 , $P < 2.2e-16$) and we elected to focus analyses on variation in impervious surface cover only.

Data Analysis

All statistical summaries, plots, and model analyses were conducted using the open-source R software, version 4.0.2 (R Core team, 2020). The Shannon Diversity Index (H) and Pielou's measure of species evenness ($J = H/\ln(S)$) values were calculated for each site using the package "vegan" (Oksanen et al., 2019). While year-to-year variation in species presence at each site are evident, as noted in Table 2, the current study combines observations across all years in which a site was sampled to calculate a single richness and evenness metric for each site. Site-year specific diversity metrics were calculated for the four sites sampled in all six years (Supp. Fig. 1), although they are not analyzed in the current study. Generalized linear mixed effects models (GLMMs) were fit to observed counts for each of the four focal species separately using the LME4 package in R (Bates et al. 2015). We used the Akaike Information Criterion (AIC) to compare models (Burnham and Anderson 2002) to a base model that included a fixed effect for week-of-the-year and random effect terms for location and year to account for dependencies within these groups. We then evaluated inclusion of a fixed year effect (annual trend) for each species. The annual trend effect only reduced the

AIC score for the model fit to *Ae. japonicus* observations, and we've therefore included it as part of a base model only for this species. We next added either a covariate for mean weekly temperature or for site-level impervious surface cover to the base model for each species and finally evaluated a full model that included both weekly temperature and site-level impervious cover together. Because local air temperature and impervious land cover are known to be correlated, the intent of this full model was to examine how temperature variability (across sites and weeks) explains larval abundance when site-level differences in impervious surface cover are also included, assuming that resulting land cover effects are indicative of some mechanism other than temperature. The mean and variance of predicted values for the best fit (lowest AIC score, Supp. Table S1) model for each species were calculated and compared to observed metrics in order to assess assumptions about error distribution. The initial Poisson assumption did not sufficiently capture the variation present in observations of *Ae. japonicus* or either *Culex* species. Model fit and selection for these species was conducted using a negative binomial error distribution, which fits a variance parameter separate from the mean. Predictors of pupae presence were evaluated using the same model selection protocols as for species abundances but with a binomial error distribution.

Results

Eleven mosquito species were observed over the course of our study (Table 2), with a maximum of ten species found at any one site. Shannon diversity indices were highest at sites with intermediate (28–35%) impervious cover and lowest at two of the most urban sites with high impervious cover (>60%) and high human population density (Table 1). These differences reflect variation in site-level evenness scores (Table 1). While evenness scores close to 1 indicate similar abundances among all species observed at a given site, evenness at our sites ranged from 0.3 to 0.74 and like Shannon diversity, was greatest at sites with intermediate levels (28–35%) of impervious cover. Despite having the highest impervious surface cover and identical species richness, evenness was higher at the community garden site (SFCG) relative to the two other urban sites and thus, so was Shannon diversity (Table 1). The 32 larvae sampled from two standing pools of water at GFCP and GFGB in 2011 were predominantly *Cx. territans* Walker (86%) and 4 were *Anopheles punctipennis* Say. While *Cx. territans* was also observed in our standardized container habitat at these sites, *An. punctipennis* was not.

Orthopodomyia signifera Coquillett, *Toxorhynchites rutilus septentrionalis* Dyar and Knab, *Ae. aegypti* Linnaeus, and *Aedes cinereus* Meigen were the least frequently observed species over the course of the study. *Ae. cinereus* (33 larvae in 2011) and *Orth. signifera* (20 larvae in 2012) were observed in a single year. Both were recorded at GFVN and nearly 100% (19) of the *Orth. signifera* larvae were observed at the forested site, OROX. Thirty-nine *Toxo. septentrionalis* larvae were recorded from all sites except for the three high-density residential community garden locations. A total of 76 *Ae. aegypti* larvae were recorded at five sites (OROX (5), MAWI (20), GFVN (20), GFGB (20), and GFCP (11)), and 75 of these were observed in a single year (2011), when species identifications were confirmed by multiple researchers. Just three species were recorded when the mean weekly temperature exceeded 28°C (*Ae. albopictus*, *Aedes triseriatus* Say, *Cx. pipiens*), and three (*Ae. albopictus*, *Ae. japonicus*, *Cx. restuans*) were sampled only when weekly mean temperatures were less than 15°C (Fig. 2). There was no temperature record for the one week in 2011 when *Ae. cinereus* were collected.

Table 2. List of species observed across the 11 site, 6 year study

Species	Sites (#)	Years (#)	Mean(se)
<i>Ae. aegypti</i>	5	2	0.08 (0.12)
<i>Ae. albopictus</i>	11	6	15.90 (0.05)
<i>Ae. cinereus</i>	1	1	0.035(1.07)
<i>Ae. japonicus</i>	11	6	6.17 (0.05)
<i>Ae. triseriatus</i>	9	5	0.84 (0.03)
<i>Cx. pipiens</i>	11	6	3.28 (0.09)
<i>Cx. restuans</i>	11	6	6.97 (0.09)
<i>Cx. salinarius</i> (Coquillett)	8	3	0.39 (0.13)
<i>Cx. territans</i>	8	4	0.30 (0.10)
<i>Orth. signifera</i>	2	1	0.02 (0.31)
<i>Tox. Septentrionalis</i>	7	6	0.04 (0.01)

Means show relative densities per trap calculated from all weeks at a site and in a year when the species was recorded in at least one ovitrap. The number of unique sites and years with observations are shown for each species. Bold text signifies species observed each year in all sites.

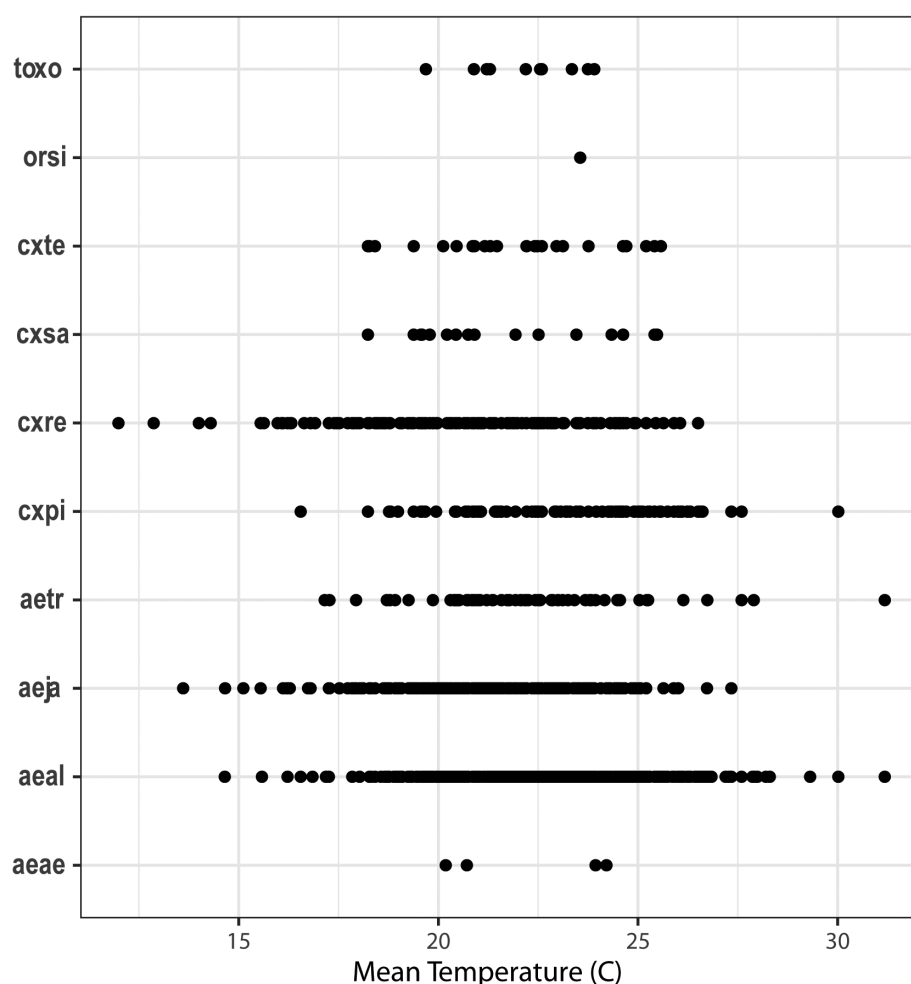


Fig. 2. Distribution of species observations by mean weekly temperature (°C). Species are identified by first two letters each of Genus and Species name (see full names in Table 2).

Four species (*Ae. albopictus*, *Ae. japonicus*, *Cx. pipiens*, and *Cx. restuans*) were present at all eleven sites and in each year of sampling. These four species were also observed at greater densities than other species (Table 2). *Aedes albopictus* and *Cx. pipiens* larvae were most abundant at sites with high impervious cover, while *Ae. japonicus* and *Cx. restuans* generally declined with impervious cover (Fig. 3). *Aedes albopictus* was the most abundant species recorded at sites with >40% impervious cover, while *Cx. restuans* was the most abundant at the two forested sites with <10% impervious cover (OROX and ORPR). *Culex pipiens* abundance was low across the impervious gradient except for at the one site with >80% impervious cover (Fig. 3). *Culex restuans*, *Ae. albopictus*, and *Ae. japonicus* abundances were all relatively high (> average 10 larvae per trap-week) at sites with 30–40% impervious cover (Fig. 3).

No pupae were present at the time of collection when mean weekly temperatures were below 19 °C, and most pupae were recorded when weekly temperature means were above 23°C (Fig. 4). Consistently, temperature was the best predictor of pupae presence ($\Delta AIC < 2$, coef 0.329, $z = 5.014$, $p = 5.07e-07$).

Parameter estimates and summary statistics for the species-specific abundance models with the lowest AIC scores are shown in Table 3, while AIC values for all models fit are provided in Supp. Table S1. The delta-AIC (ΔAIC) value for each of the models in Table 3 was more than two points lower than all other models

with two exceptions where values were equal or differed by 1, as explained below.

Abundance of *Ae. albopictus* larvae in container traps was positively predicted by week-of-year, consistent with greater abundances later in the season (positive effect of Week, Table 3). Mean temperature during the week that ovitraps were deployed was an important addition to the base model with $\Delta AIC = -3723$, although adding impervious surface cover alone did not improve model fit (Supp. Table S1). Including both temperature and land cover did not improve AIC score over a model with temperature alone; although the impervious cover effect was still significantly different from zero. In this full model, both mean weekly temperature at the ovitrap location and proportion impervious surface cover in the 100-m radius buffer were positively associated with abundance of *Ae. albopictus* larvae (Table 3).

Abundance of *Ae. japonicus* larvae increased across the years of our study, indicative of population establishment (Year effect, Table 3). Week-of-year was a negative predictor of *Ae. japonicus* abundances (negative effect of Week). The addition of weekly temperature to the base model improved model fit (Supp. Table S1). Including impervious cover also improved model fit over the base model although ΔAIC was lower than for the temperature-only model (Supp. Table S1). Abundance of *Ae. japonicus* larvae was positively predicted by temperature but negatively associated with impervious cover (Table 3).

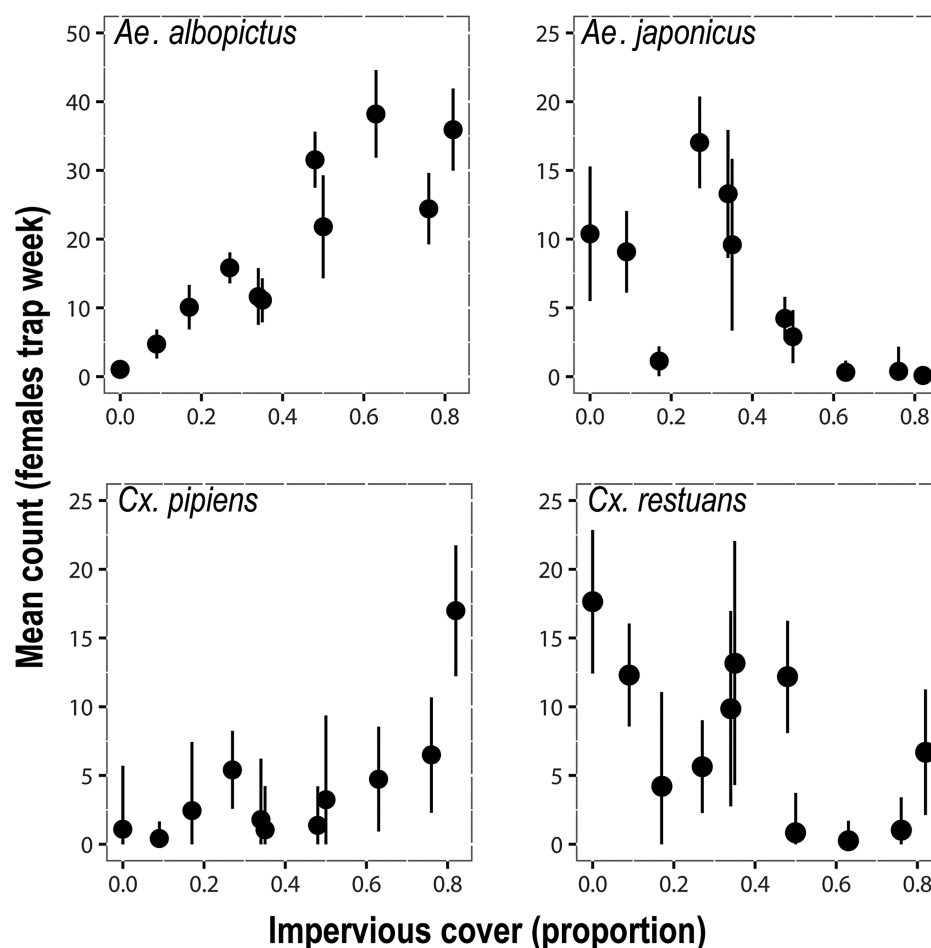


Fig. 3. Larval abundance (per trap week) for each site plotted against site-level proportion impervious cover within a 100-meter radii buffer.

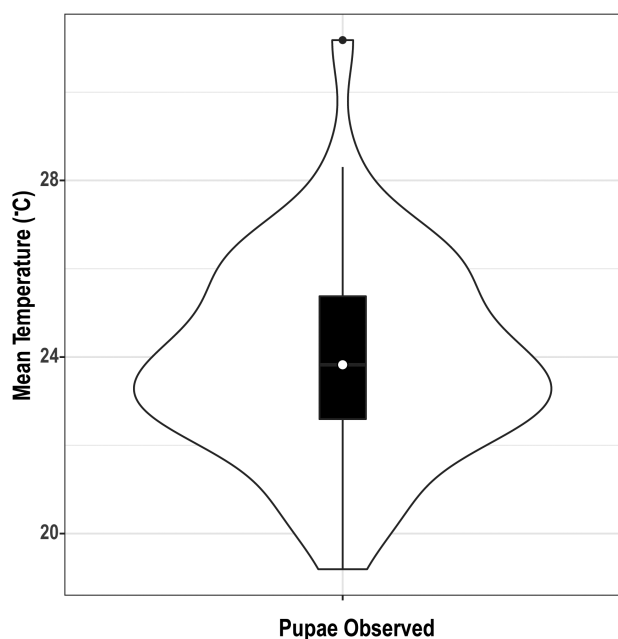


Fig. 4. Distribution (symmetrical) showing frequency of pupa occurrence after 1-week deployment by mean weekly temperature (°C).

The temperature-only model was the best fit to *Cx. pipiens* larval abundances (Supp. Table S1). Both week-of-year and temperature were positive predictors of *Cx. pipiens* larval abundance. However, the best-fit model generated predicted values that were not well correlated with observed values (Table 3). Unexplained variance associated with the year of collections was much greater than the estimated site-level variance, suggesting high unexplained year-to-year variability in observed *Cx. pipiens* abundance (Table 3).

The model that included both weekly temperature and land cover resulted in the lowest AIC score for *Cx. restuans* larval abundance, although the Δ AIC between this full model and one with land cover alone was small (Supp. Table S1). Both week-of-year and impervious surface were negative predictors of *Cx. restuans* larval abundance, although temperature effects were positive (Table 3).

Discussion

Understanding how urbanization influences biodiversity is a critical research goal in ecology, as is understanding how changes in species diversity can affect human health risk (Keesing et al. 2006, Johnson et al. 2015c, Ziter 2016). Here we investigated the composition and relative abundances of container-breeding mosquito assemblages across an urbanization gradient in the eastern United States. We recorded eleven species overall and as may be expected, diversity was lowest at sites with high impervious surface cover, a predominant

Table 3. Model results by species

Parameters	<i>Ae. albopictus</i>			<i>Ae. japonicus</i>			<i>Cx. pipiens</i>			<i>Cx. restuans</i>		
	coef (se)	Z	p	coef (se)	Z	p	coef (se)	Z	p	coef (se)	Z	p
Intercept	1.57 (0.38)	4.1	<0.001	3.21 (1.18)	2.7	0.007	-1.19 (1.24)	-1.6	0.12	5.10 (1.08)	4.7	<0.001
Year	na	na	na	0.61 (0.25)	2.5	0.013	na	na	na	na	na	na
Week	0.02 (0.002)	8	<0.001	-0.16 (0.03)	-5.9	<0.001	0.08 (0.04)	1.9	0.05	-0.13 (0.07)	-4.8	<0.001
Temp	0.23 (0.004)	55.4	<0.001	0.25 (0.05)	4.7	<0.001	0.42 (0.09)	4.4	<0.001	0.13 (0.07)	1.9	0.058
Impervious	1.70 (0.83)	2.4	0.041	-7.66 (1.80)	-4.3	<0.001	na	na	na	-5.17 (1.6)	-3.2	0.001
random effect	year: 0.57, site: 0.48			year: 0.74, site: 1.95			year: 0.99, site: 0.45			year: 2.38, site: 1.28		
Cor (Pred,Obs)	0.597			0.44			0.16			0.41		
Observed mean	19.16 (var=833.84)			6.75 (var=268)			4.08 (var=161)			7.64 (var=346)		
Predicted mean	19.16 (var=351)			7.48 (var=146)			5.85 (var=148)			9.61 (var=278)		

Correlation between predicted and observed counts, as well as mean and variance of observed and predicted counts are provided for each model. The model for *Aedes albopictus* assumes a Poisson error distribution, while the other three models use Negative Binomial distributions. Variances (unexplained by main covariate effects) associated with within-site and within-year sampling structure are shown for each model.

condition of urbanization. Impervious surfaces have direct impact on local temperatures but are also associated with structural changes in habitat conditions, including reduced vegetation cover. Vegetation is an important food resource for larval and adult mosquito stages, and trees in particular can be an important structural habitat that influences fine-scale habitat temperature and humidity. Despite both increased temperature and reduced vegetation resources, we still observed six mosquito species even at our site with 80% impervious surface cover. The residential landscapes in our study are heterogeneous in land cover and condition, with differences in abandoned infrastructure and vegetation management even between adjacent city blocks (e.g., Little et al. 2017). Many of the species observed at our most urban sites may have dispersed there from beyond the 100-meter radius of our study buffer, which is just large enough to capture roughly half of any adjacent blocks. Dispersal of *Culex* species, for example, can be more than a kilometer while *Ae. albopictus* dispersal capacity may be closer to a maximum 100-m (Niebylski and Craig 1994, Marini et al. 2010, Ciota et al. 2012, Hamer et al. 2014). Previous work in Baltimore demonstrated a positive and predictive association between juvenile and adult *Ae. albopictus* but not *Culex* species at the scale of a city block (Bodner et al. 2019), further supporting the idea that differences in dispersal distances among species may complicate alignment of local conditions with larval abundance. It is also important to note that our standardized ovitraps at the three most highly impervious sites were placed in community gardens, and although impervious cover in the buffer was high, there was very little impervious cover within the immediate vicinity (~5-m) where traps were located. The fact that SFCG (Sunflower Village in Franklin Square) had higher species evenness relative to other sites with > 60% impervious cover could reflect greater area and habitat heterogeneity at this site, which was established in 2012 and extends across several parcel lots. While both vegetables and flowers are grown on the two other sites, SFCG is maintained as a community park with tree canopy, flower beds, and a rain garden.

Understanding when and why changes in mosquito community composition occur is important because it can indicate shifts in the presence or abundance of specific vector species capable of transmitting pathogens to humans or domestic animals (Allan et al. 2009, Chaves et al. 2011, LaDeau et al. 2015, Beaulieu et al. 2019, Beaulieu et al. 2020, Camara et al. 2020). In this study, we recorded a loss of species diversity at the most urban sites that resulted in mosquito assemblages dominated by four species, each of which has demonstrated competence for maintaining zoonotic (Molaei et al. 2006) or human (Vega-Rua et al. 2013, Westby et al. 2015, Vanlandingham et al. 2016) arboviral transmission cycles. The highest species richness and evenness was recorded at sites with intermediate impervious cover (28–35%), consistent with patterns observed for other taxonomic groups and in a range of ecosystems (e.g., (Kershaw and Mallik 2013, Callaghan et al. 2019, Tocco et al. 2020, Orta-Pineda et al. 2021)). One of the species that was found only at intermediate impervious cover sites was *Ae. aegypti*, which has low probability of overwinter survival in the study region (although see (Lima et al. 2016)) and we hypothesize that it may have been introduced locally each year that it was observed. This species oviposits eggs that can survive on dry surfaces, facilitating its dispersal (Lounibos 2002, Juliano and Lounibos 2005). The GFVN site, where this species was observed at the highest densities, is located near a mechanic shop where rubber tires were often observed.

We found that species richness was greatest at sites with intermediate impervious cover and intermediate human population density (Table 1), where habitat heterogeneity may be expected to be relatively high. Habitat heterogeneity and high vegetation cover have

previously been associated with mosquito densities and species richness in urban settings (Diuk-Wasser et al. 2006, Chaves et al. 2011, Ferraguti et al. 2016, Little et al. 2017, Akhtar et al. 2019, Yang et al. 2019). The most species rich sites in our study were also associated with riparian sampling locations, and riparian vegetation corridors are important pathways for species introductions or dispersal in the urban landscape (Aronson et al. 2017). The standardized container traps used in our study can be effective tools for assessing the relative abundance of the subset of species likely to oviposit in water-holding containers, including tree holes, bromeliads, and human-made structures, but they are likely to underestimate the species richness of the entire mosquito community due to differences in oviposition habitat use (Reiskind and Wilson 2004, Juliano 2007, Day 2016, Zahouli et al. 2016). For example, we found *An. punctipennis* in a stream overflow pool adjacent to our traps in 2011, but did not recover this species in the standardized container traps. This design limitation is likely to have the greatest impact on species richness estimates at the forest sites where pervious ground and vegetation cover represent greater habitat heterogeneity (Zahouli et al. 2016).

Many studies have demonstrated positive effects of temperature on rates of mosquito development, although the association is often nonlinear (Dohm et al. 2002, DeGaetano 2005, Delatte et al. 2009, Dodson et al. 2012, Gray 2013, Ciota et al. 2014, Murdock et al. 2017, Evans et al. 2018b). However, warming associated with urban heat island effects or future climate changes will likely have a positive influence on mosquito growth rates and survival in higher latitude (or high elevation) regions (Francis and Chadwick 2015, Paaimeans et al. 2009, Jia et al. 2017). While it is beyond the scope of this study to infer how temperature influences species presence, species richness was reduced when mean weekly temperatures were below 15°C or greater than 28°C (Fig. 2). We further found that temperature was an important and positive predictor of weekly juvenile abundances for each of the four most commonly observed species (Table 3). Likewise, the development of pupae in less than a week was positively predicted by temperature, suggesting warming temperatures could allow for greater potential survival and emergence of biting adults.

We observed four mosquito species in all years and at all sites, although each was differentially associated with impervious cover and temperature variables (Table 3). *Aedes albopictus* and *Ae. japonicus* are both native to Asia and were introduced through trade routes to the United States in the 1980's and 1990's, respectively (Juliano and Lounibos 2005, Fonseca et al. 2010). Both species are now found in container habitats across the mid-Atlantic United States (Bartlett-Healy et al. 2012, Dowling et al. 2013), although *Ae. japonicus* population establishment is favored in northern states (Bevins 2007, Kaufman and Fonseca 2014) where *Ae. albopictus* remains less abundant (Kraemer et al. 2019, Kache et al. 2020). Both species are competent vectors of several zoonotic pathogens, including West Nile virus (Sardelis and Turell 2001, Turell et al. 2001, Sardelis et al. 2003), and both are likely to bite humans when present in human-dominated landscapes (Niebylski et al. 1994, Richards et al. 2006, Molaei et al. 2009, Sawabe et al. 2010, Valerio et al. 2010, Munoz et al. 2011, Farjana and Tuno 2013, Faraji et al. 2014, Anderson et al. 2018, Goodman et al. 2018). *Ae. albopictus* has been implicated as the primary vector of dengue virus transmission in temperate cities such as Tokyo, Japan (Kutsuna et al. 2015, Tsuda et al. 2016) and of chikungunya viral outbreaks in temperate regions of Italy (Rezsa et al. 2007). *Ae. albopictus* was first detected in Baltimore City in 1987 (Hawley et al. 1987), and our study demonstrates that while it has successfully established across the region, it remains predominantly focused in urban locations with high impervious cover. This is consistent with recent findings outside St. Louis, MO (Westby et al. 2021). The two most frequently observed

Culex species are predominant vectors of West Nile virus in the north-eastern U.S. *Culex pipiens* is the primary vector of West Nile virus to humans (Turell et al. 2005, Anderson and Main 2006, Molaei et al. 2006, Hamer et al. 2009), while native *Cx. restuans* feeds on birds and is an important zoonotic amplification vector of WNV (Sardelis et al. 2001, Molaei et al. 2006, Johnson et al. 2015b). These *Culex* species overlap across the sites in our study, although consistent with expectations for an ornithophilic feeder, *Cx. restuans* was most abundant earlier in the season and at sites with low impervious cover. Larval densities in container traps were lower at forest sites compared to urban sites across species (e.g., Fig. 4). While this could be due to the use of alternative oviposition and development habitats in these sites, our limited examination of surrounding habitat in 2011, including ephemeral pools, did not recover any of the four most common species, although *Cx. restuans* was sampled from ephemeral pools within the 100-meter buffer at our forest sites as part of another study (LaDeau unpublished data). The relatively low predictive power of the best-fit models for *Cx. pipiens* abundance may also be indicative of longer dispersal capabilities of *Culex* species relative to *Ae. albopictus* (Ciota et al. 2012, Guerra et al. 2014, Hamer et al. 2014), which may contribute to misalignment of habitat within our 100-m radius buffer. Likewise, the sampling design in this work does not allow for inference on interspecific interactions that might influence egg and juvenile survival during the week prior to our sampling. Several studies however, demonstrate that species interactions can have strong impact on juvenile presence and abundance in container habitats. For example, larval *Ae. aegypti* growth and survival was negatively impacted by *Ae. albopictus* presence in container habitats (Juliano 1998), and the presence of predatory *Toxo. rutilus septentrionalis* juveniles enhanced competitive outcomes and increased juvenile density of *Ae. triseriatus* when *Ae. albopictus* was present (Johnson and Sukhdeo 2013). Likewise, although *Ae. albopictus* is often the dominant competitor in controlled lab conditions (Costanzo et al. 2005), species like *Cx. pipiens* can persist locally by utilizing a wider range of habitat types (Carrieri et al. 2003, Dowling et al. 2013, Parker et al. 2020, Leisnham et al. 2021), while other species may escape competition through temporal partitioning mechanisms (Leisnham and Juliano 2009, Leisnham et al. 2014). Results from our study are consistent with both spatial and temporal resource partitioning as a strategy for maintaining species diversity in this landscape.

Conclusion

The composition of juvenile mosquito assemblages is influenced by changes in land cover and local temperature along an urbanization gradient, with greatest diversity occurring at sites with intermediate impervious surface cover. Both evenness and richness were lowest in the high-density residential neighborhoods with greatest impervious cover, although larval densities of invasive species and pupae development rate were high at these sites. Four medically-important vector species were observed across all sites, including two invasive *Aedes* species and two *Culex* species. While each of these species may employ different strategies to maintain population presence across the full urbanization gradient studied here, higher weekly temperatures during the growing season were consistently associated with greater abundances of larvae and more rapid development of pupae. This study contributes to the understanding of ways in which vegetation cover and temperature related to urbanization can alter composition of mosquito assemblages, as well as potential human exposure to medically-important vector species. Results from this work suggest that mosquito species, like *Ae. albopictus*, are likely to continue to benefit from urbanization and warming in temperate latitudes, with important implications for human disease risk.

Supplementary Data

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

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