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ORIGINAL PAPER

Shift in the spatial and temporal distribution of *Aedes taeniorhynchus* following environmental and local developments in St. Johns County, Florida

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Abstract The Anastasia Mosquito Control District (AMCD) of St. Johns County (SJC), St. Augustine, Florida, USA, was formed in 1948 to cover the 27 km^2 of Anastasia Island and control the black salt marsh mosquito, *Aedes taeniorhynchus* (Wiedemann). Today AMCD covers the entirety of SJC (1588 km^2) and *Ae. taeniorhynchus* is still the most abundant mosquito species in the county. Here we present the findings from 16 years' worth of surveillance records of AMCD mosquito populations in conjunction with annual land-use land-cover (LULC) change and climate data to better understand how environmental factors have impacted SJC *Ae. taeniorhynchus* populations in recent history. The statistical regression and geospatial analyses demonstrated the presence of spatial and temporal clusters of *Ae. taeniorhynchus* populations in terms of abundance and distribution. Additionally, *Ae. taeniorhynchus* abundance and distribution were significantly influenced by the annual changes of LULC and climate variables. The linear regression analysis using standard least square and corrected Akaike Information Criterion revealed a migration of mangrove swamps and saltwater marshes that corresponded to a southern shift in the spatial–temporal distribution of *Ae. taeniorhynchus* communities. This was confirmed by the significant change in LULC characteristics between three representative years (2004, 2009, 2014) and the redistribution of *Ae. taeniorhynchus* abundances represented by Moran's I index values. The annual values of four climate variables (average and minimum temperature, mean dew point, and maximum vapor pressure deficit) and three LULC types (mangrove swamps, saltwater pools within saltmarshes, and upland nonforested) significantly predicted annual abundance and redistribution of *Ae. taeniorhynchus*.

Keywords Saltmarsh · Mosquitoes · Climate change · Population dynamics · Land use

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Introduction

Aedes taeniorhynchus (Wiedemann), the black salt marsh mosquito, is one of the major nuisance pests along coastal Florida and serves as one of the most

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abundant mosquito species in St. Johns County (SJC), Florida. This species is not only important because it is an aggressive biter and can emerge in prolific numbers, but it has also been found to be naturally infected with the Everglades, St. Louis encephalitis, West Nile, Venezuelan, Eastern and Western equine encephalitis viruses (Hodapp et al. 1966; Chamberlin et al. 1969; Sudia et al. 1969; Hribar et al. 2003, 2004; Agramonte and Connelly 2014; Barrera et al. 2014). *Ae. taeniorhynchus* has also been reported to fly long distances with reports of up to 32 miles (Harden and Chubb 1960; Provost 1952). Thus, even with oviposition isolated to tidal and brackish areas, these mosquitoes can become a burden in inland areas away from their preferred oviposition habitats.

Historically, the Anastasia Mosquito Control District (AMCD) of SJC was formed in 1948 to cover the 27 km^2 of Anastasia Island, St. Augustine, FL, to control black salt marsh mosquitoes. Today AMCD encompasses the entirety of the county (1588 km^2) which is surrounded by the St. Johns River to the west and the Atlantic Ocean to the east and also includes the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR). The GTMNERR comprises approximately 30,350 ha of undeveloped coastal and estuarine habitats. Over the last 70 years, SJC has grown significantly in population and infrastructure, drastically changing the landscape and opportunities for mosquito-human contact. Even with a large growth in residential and commercial development along the coastline, SJC also experienced an increase in mangrove acreage over the last couple of decades likely due to the reduced occurrence of cold events of air temperature less than − 4° C (Cavanaugh et al. 2014). Due to the changing landscape and environmental conditions, we propose to investigate the last 16 years' worth of AMCD mosquito population data to better understand how environmental factors impact geographic distribution of *Ae. taeniorhynchus* populations.

Methods

Study sites and sampling design

Population density (total number of mosquito/season/locality) of adult host-seeking mosquitoes were monitored by AMCD using Centers for Disease Control and Prevention (CDC) light traps (John W. Hock Company, Gainesville, FL) baited with an octenol lure stick (synthetic semiochemical, Biosensory) at 33 permanent locations in the county during 2004–2014. Out of 33 sampling locations, only 18 were accessible and sampled during 2015–2019. Buffer radii (0.5 and 2.0 km) were used to reflect the uncertainty in trapping location and to demonstrate the probable mosquito flight range around their suitable habitats for blood feeding and oviposition (DeMeillon 1934, Nayar and Sauerman 1973). Traps were placed outdoors at the beginning of March through the first week of December during 2004–2019. Traps were suspended 1 m above the ground surface by a shepherd's hook and operated for 18–20 h using a 6 V battery. Mosquito collections were transported from the field to the AMCD facility for identification to species level using the taxonomic keys of Darsie & Ward (Darsie and Ward 2005).

For data cleaning and preparation, a python script was used to extract consistent sampling locations during the sampling period and the script is available at GitHub (www.github.com). A basic list of addresses and known coordinates, with defined uncertainties in meters, was used to make a master list of all approximate latitude/longitude for each trap locality using a unique identification locality number (Sallam et al. 2016). The uncertainty was used to represent the distance a trap site may have been moved away from the assigned coordinate.

Environmental and climate parameter collection

Climate and environmental variables were collected from various sources as potential predictors of *Ae. taeniorhynchus* spatial and/or temporal distribution (Table 1). The selected climate factors included rainfall, temperature, and vapor pressure in addition to the environmental factors of ocean tide, land-use land-cover (LULC), and elevation above sea level. Data was downloaded at varying resolutions of either county-wide (i.e. one measurement to apply to the entire county study area) or at the level of geographic coordinates of individual trap sites.

County-wide rainfall and temperature readings were downloaded from the Climate Data Online portal available from the National Oceanic and Atmospheric Administration (NOAA). Global monthly and annual summaries of temperature and precipitation were

Table 1 Description of predictor data and data collection sources

Variable	Unit	Download source
Land-use land-cover	m^2	Florida Geographic Data Library
Urban & built-up land		https://www.fgdl.org/metadataexplorer/explorer.jsp [Accessed August 2020]
Agriculture		
Upland nonforested		
Upland forests		
Water		
Wetlands		
Saltmarsh associated		
Temperature	°F	National Oceanic and Atmospheric Administration (NOAA)
Minimum		https://www.ncdc.noaa.gov/cdo-web/
Maximum		[Accessed September 2020]
Mean		PRISM Climate Group
		https://prism.oregonstate.edu/historical/
		[Accessed October 2020]
Precipitation	inches	National Oceanic and Atmospheric Administration (NOAA)
Minimum		https://www.ncdc.noaa.gov/cdo-web/
Maximum		[Accessed September 2020]
Mean		PRISM Climate Group
		https://prism.oregonstate.edu/historical/
		[Accessed October 2020]
Dew point	°F	PRISM Climate Group
Minimum		https://prism.oregonstate.edu/historical/
Maximum		[Accessed October 2020]
Mean		
Vapor pressure deficit	hPa	PRISM Climate Group
Minimum		https://prism.oregonstate.edu/historical/
Maximum		[Accessed October 2020]
Mean		
Full moon cycle	date	NOAA Center for Operational Oceanographic Products and Services
		https://tidesandcurrents.noaa.gov/astronomical.html [Accessed October 2020]
Digital Elevation	ft	WorldClim Global Climate
		http://www.worldclim.org
		[Accessed October 2020]

retrieved from a single station based in a southwestern township of St. Johns County (HASTINGS 4 NE, FL US; GHCND:USC00083874; 29.7652°, − 81.4697°). Georeferenced measurements of precipitation, temperature, dew point, and vapor pressure were later retrieved by inputting the latitude/longitude coordinates of permanent trap sites into the data explorer maintained by the PRISM Climate Group (Parameter-elevation Regressions on Independent Slopes Model). Due to a lack in available tidal amplitude data for SJC, dates of lunar phase cycles were used as indirect proxy values of ocean tide by representing a chronological timing of high tides since full moons (and new moons) are associated with higher tidal amplitude (Rochlin and Morris 2017). Lunar phase data was found at the NOAA Center for Operational Oceanographic Products and Services (CO-OPS).

Land-use land-cover data (LULC)

The distribution of mosquitoes is greatly affected by the availability of blood meal sources, resting places, and oviposition sites (Sallam et al. 2016), thus urban & built-up areas were included as predictors representing the distribution of the human population (Fig. 1). Vegetation provides resting places and sugar meal sources for adult mosquitoes and this variable has been extensively used as a predictor for their occurrence (Andersson and Jaenson 1987; Foster 1995; Gu et al. 2011). Agriculture, upland nonforested, and forested LULC data layers were used as an indicator for vegetation in our study. Surface water and wetlands, which include salt marshes and associated land classes, were also examined as indicators for mosquito oviposition and distribution range (Sallam et al. 2016, 2017a, 2017b). Wetlands and surface water were used as two separate data layers to distinguish between salt marshes and other water bodies that do not provide oviposition habitats.

All LULC data layers of the three most recently available timepoints (2004, 2009, 2014) that fit our historical data timeline (2004–2019) were originally developed by the St. Johns River Water Management District (SJRWMD) and downloaded from the Florida Geographic Data Library. The SJRWMD defines several increasingly detailed levels (1–3) of LULC codes and Level 1 has the broadest descriptions. Here the LULC of SJC was categorized into six major LULC level 1 classes (urban & built-up, agriculture, upland nonforested, upland forests, water, wetlands) in addition to one hybrid category of 'saltmarsh associated' LULC classes. This hybrid LULC class was comprised of three different LULC Level 3 codes that were deemed to be associated with saltmarshes (enclosed saltwater ponds within salt marshes, mangrove swamps, saltmarshes). Other Level 1 LULC categories (barren land and transportation, communication, utilities) were excluded from correlation analyses. Notably, urban & built-up included numerous LULC Level 2 codes for residential (high density, medium density, low density), commercial and services, industrial, institutional, recreational, and extractive. Agriculture covered cropland and pastureland, feeding operations, tree crops, nurseries and vineyards, and specialty farms. Upland nonforested was coded for herbaceous, shrub, bushland, and mixed LULC while upland forests was coded for tree plantations and coniferous or hardwood forests. Water included both moving and static water bodies (reservoirs, streams and waterways, lakes, bays, and estuaries) and wetland contained vegetated, nonvegetated, and mixed wetland. All LULC layers for the years of 2004, 2009, and 2014 were extracted within buffer zones (0.5 km and 2.0 km radii) around the 33 sampling locations using ArcGIS ver. 10.1. The total area of each LULC category within the buffer zone of individual trap sites (n = 33) was retrieved and percent LULC areas were calculated to evaluate the influence of LULC on mosquito abundance within the individual buffer radii (Vander Kelen et al. 2012).

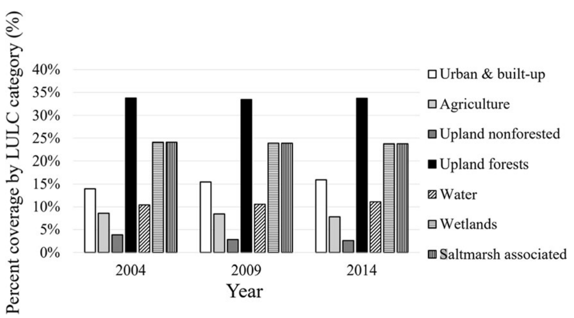

Fig. 1 LULC composition of St. Johns County, Florida during the years 2004, 2009, and 2014. The percent coverage was calculated by totaling the area (m^2) of each LULC category from the entire county and dividing by total area of all classified LULC polygons

Digital elevation model

A digital elevation model measures the rate of changes of elevation, slope, aspect ratio, hill shade, and curvature at surface location. For slope, it is expressed as an angle from 0° (flat) to 90° (high elevation). Aspect ratio indicates the orientation of the slope and eventually this ratio reflects the places of water accumulation and larval mosquito establishment (Gorsevski et al. 2000; Mushinzimana et al. 2006). Aspect ratio ranges from 0° to 360°, however, in this study, aspect ratio was cosine-transformed to represent ranges from + 1 (north-facing slope) to − 1 (south-facing slope) (Nmor et al. 2013). Curvature and hill shade reflect depressions and sunlight intensity on the land surface. The four indicators were generated from a 30 arc-seconds Digital Elevation Model (DEM) data layers and clipped to the study site using the surface spatial analyst tool in Arc tool box of ArcGIS ver. 10.1.

Data analyses

Geospatial distribution analysis

The distribution of *Ae. taeniorhynchus* density was analyzed using spatial statistics tools in ArcGIS ver. 10.1. First, the standard deviational ellipse (SDE) analyses in this package were used to evaluate the spatial distribution pattern of *Ae. taeniorhynchus* density between years. The SDE creates a polygon to summarize the spatial directional distribution which may show dispersion, central tendency, and directional trends. Therefore, SDE was used to map the directional distribution trend of mosquitoes within their flight range. Second, we used Global Moran's I (Anselin and Getis 1992), a correlation coefficient that measured the overall spatial autocorrelation of the 33 consistent sampling locations and *Ae. taeniorhynchus* population density concurrently. Clusters of sites with high mosquito density (High–High) were considered "high-risk areas" whereas clusters of sites with low density (Low–Low) were considered "low-risk sites." The value of Moran's I is measured between − 1 and 1, with the 'Z' score value calculated to test whether the observed clustering or dispersal is significant. Therefore, when the Z score indicates statistical significance, a positive Moran's I indicates a tendency toward clustering while a negative value indicates a tendency toward dispersion. When the Z score value is not significantly different from zero, it is assumed that there is no spatial autocorrelation, and the pattern does not appear to be significantly different from a random distribution. The clustering hypothesis (H_1) was tested for the density of adult mosquito populations. The null hypothesis (H_o) was that there is no spatial clustering of mosquito populations in SJC.

Inverse distance weighted interpolation

An interpolation method was chosen to increase the spatial resolution of *Ae. taeniorhynchus* population hotspots across different surveillance seasons. Inverse distance weighting (IDW) is one of the simplest interpolation techniques and estimates the value at an unsampled location based on the observed values at neighboring sites and the geographical distance between unsampled and sampled neighbor locations (Allen and Shellito 2008). All IDW maps were created with ArcMaps ver. 10.7.1 under default parameters (variable distance, twelve minimum neighbors). The input values were the total seasonal mosquito count (each year 2004–2019) at the geocoded locations of traps that were consistently active during the entire time frame (n = 18).

Statistical analysis

First, we examined the statistical distribution and data normality of mosquito abundance and covariates using normal quantile plots and goodness of fit tests using the Shapiro–Wilk W statistic. Second, abundances at individual trap sites were log10(n + 1) transformed to achieve a more normalized distribution. We then used a standard least squares (SLS) and corrected Akaike Information Criterion values (AICc) in a regression analysis to evaluate the response of *Aedes* abundance to LULC characteristics (percent buffer coverage by each LULC class), DEM, and annual values of climate variables for the years 2004, 2009, and 2014. For non-spatial analyses, classical Pearson's correlation analysis was used to test the association between: year of sampling vs total monthly averaged mosquito abundance, year of sampling vs total annual averaged mosquito abundance for each trap site, and year of sampling vs total annual averaged mosquito abundance. All statistical analyses were conducted using R statistical packages ver. 3.3.

Results

Geospatial distribution analysis

We found spatial clustering of *Ae. taeniorhyncus* abundance during 2004 (Moran's I = 0.24, Z-score = 3.1, $p = 0.00$), 2009 (Moran's I = 0.50, Z-score = 5.8, $p = 0.00$), and 2014 (Moran's I = 0.25, Z-score = 3.6, $p = 0.00$). The SDE analysis and SDE polygon maps for 2004, 2009, and 2014 demonstrated that areas under risk of higher *Ae. taeniorhyncus* abundances were similarly clustered in the mid- and north- eastern regions of SJC and bounded within a range of 8 km from the Atlantic coast (Fig. 2). The areas of risk bounded by SDE polygons and the corresponding percentages of total county land area

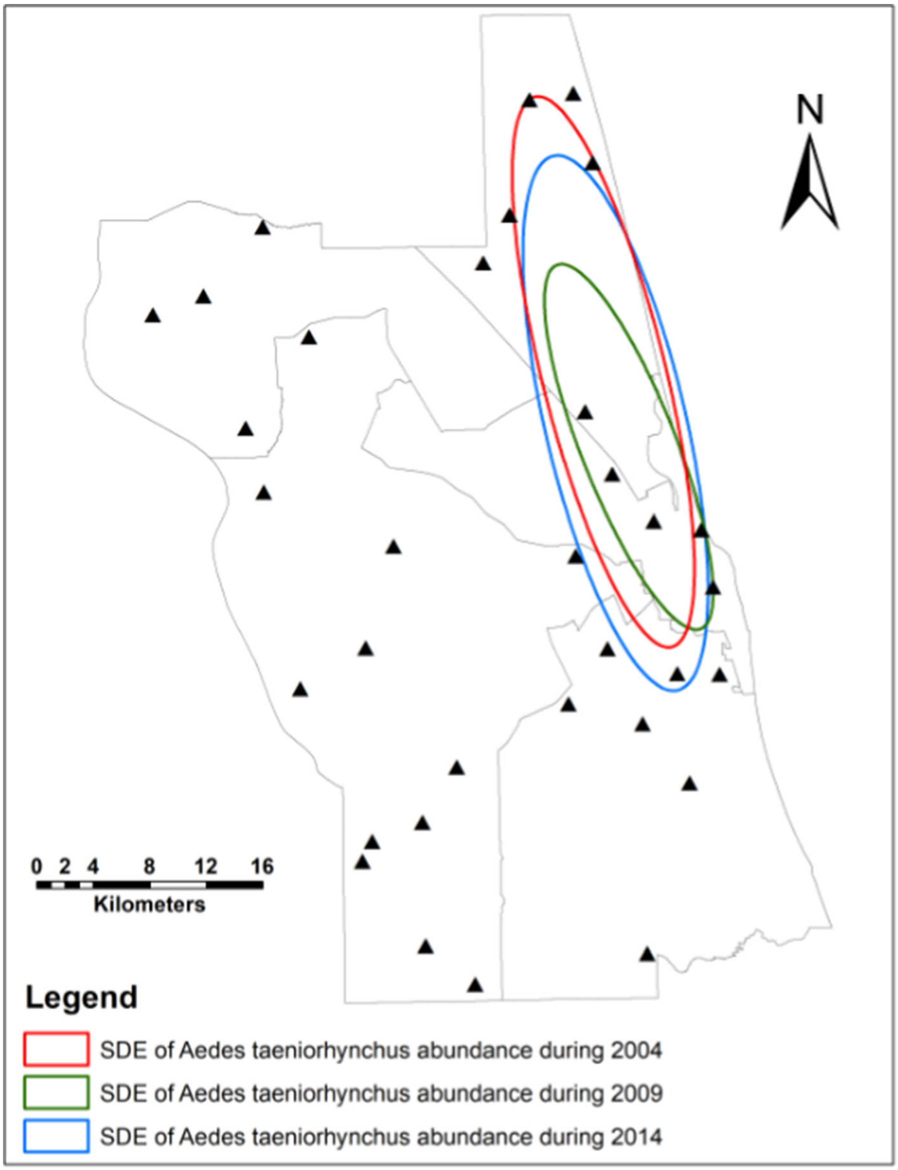

Fig. 2 Standard Deviational Ellipse (SDE) polygons showing trap sites and *Aedes taeniorhynchus* abundances collected in St. Johns County, Florida during 2004, 2009, and 2014

fluctuated between the three years to cover 319.16 km^2 (20.10%) during 2004, 169.53 km^2 (10.68%) during 2009, and 351.75 km^2 (22.15%) during 2014. Accordingly, the clustering hypothesis (H_1) for the spatial distribution of *Ae. taeniorhynchus* was accepted.

Inverse distance weighted interpolation

Hotspots of *Ae. taeniorhynchus* did not follow a consistent seasonal distribution and there were several contractions and expansions of the hotspot focal points over the 2004–2019 timeline (Fig. 3), similar to the SDE results. Overall, this species was most commonly collected at trap sites located along the mid- to northeastern coast of SJC and was rarely collected in the western region, especially lacking in the northwest corner of the county. There was also a noticeable absence on the southern coast for the majority of years. Even so, the seasonal hotspots of population density

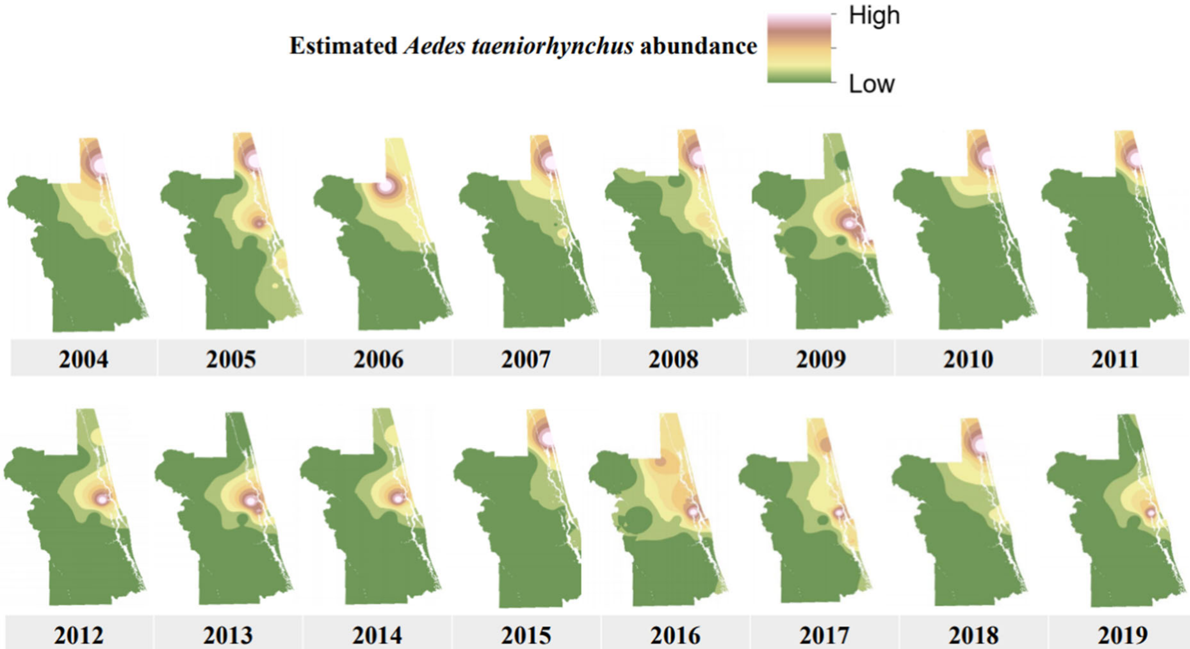

Fig. 3 Spatio-temporal hotspot distribution (2004–2019) with total seasonal mosquito count collected at traps sites that were permanently active 2004–2019 (n = 18). The legend displays the estimated mosquito density using an equal interval symbology color scale, low to high. Individual seasonal maps do not share a quantitatively standardized scale, hotspots are relative only to the county-wide trap counts for that single season

did appear to have gradually shifted southward along the coast.

Spatial–temporal differences in *Ae. taeniorhynchus* abundances

The peak of *Ae. taeniorhynchus* population abundances showed a cyclic pattern during the first 15 days of every month, especially during June-October. This pattern reflected a delayed response of *Ae. taeniorhynchus* abundances at least 15–30 days after a complete full moon cycle. (Fig. 4). The total annual averaged *Ae. taeniorhynchus* abundance (mosquitoes/trap no./year) in 2011 was the highest (156.72 ± 147.19) during June–August, whereas in 2013 was the lowest (4.5 ± 2.7). The log transformation of total *Ae. taeniorhynchus* abundances maintained normal distribution of the data. The log transformation also reduced the variances between data records for each locality, especially with short mosquito seasons in specific years such as in 2011.

Pearson's correlation analysis using log-transformed *Ae. taeniorhynchus* abundances showed a significant difference between the three years 2004, 2007, and 2013 (Fig. 5). The recorded annual averaged *Ae. taeniorhynchus* abundances of the years 2004 (29.28 ± 12) and 2007 (38.06 ± 19.9) were significantly higher than those collected during 2013 (4.5 ± 2.69) ($t = 1.96$, $p = 0.03$). Total annual averaged abundances (total mosquitoes/trap night/locality) showed no significant differences between trap sites for each year. The monthly averaged abundances of *Ae. taeniorhynchus* populations showed variations between years. Monthly averaged abundances in June–August during 2011 were significantly higher than other collection months for all years except 2010, 2012, 2015, and 2017 ($t = 1.96$, $p < 0.05$). *Ae. taeniorhynchus* abundances were significantly reduced during September and October compared to June–August. However, *Ae. taeniorhynchus* abundance during September and October was significantly highest in 2016 ($t = 1.96$, $p < 0.05$) and 2017 ($t = 1.97$, $p < 0.01$) compared to other years. *Ae. taeniorhynchus* abundances collected during March–May and November were the lowest compared to the other months. However, *Ae. taeniorhynchus* abundances collected during these months were significantly high only in 2008 ($t = 1.98$, $p < 0.05$), 2012

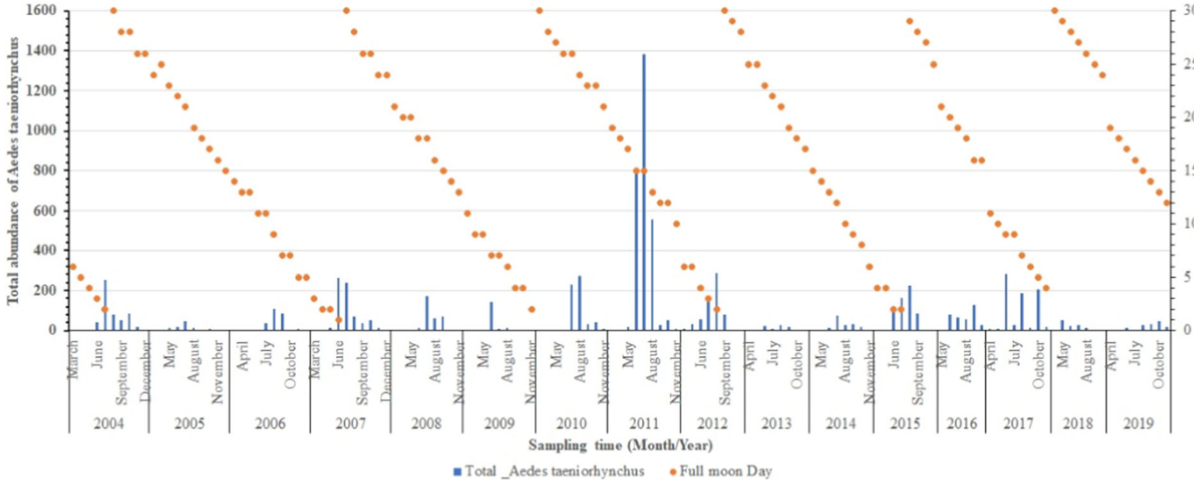

Fig. 4 Total monthly *Aedes taeniorhynchus* abundances and lunar cycles (day) collected in St. Johns County during 2004–2019

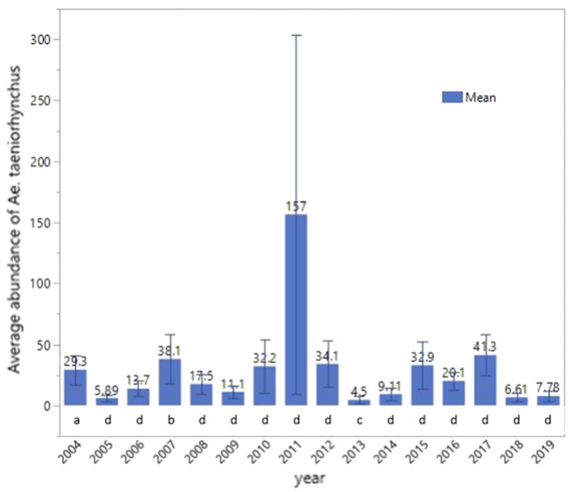

Fig. 5 Total annual averaged *Aedes taeniorhynchus* abundances (± SE) collected in St. Johns County during 2004–2019. Letters (a, b, c, d) underneath each bar indicate whether or not there was a significant difference in log transformed *Ae. taeniorhynchus* abundances between years; years with same letter are not significantly different from one another

(t = 1.99, $p < 0.05$), 2017 (t = 1.97, $p < 0.05$), and 2018 (t = 1.97, $p < 0.05$) compared to other years.

Environmental and LULC predictors

The regression analysis showed the migration of mangrove swamps (Fig. 6) and saltwater marshes that corresponded to a southern shift in the spatial–temporal distribution of *Ae. taeniorhynchus* communities. The increase in percent areas of mangrove swamp land cover in 2014 resulted in the redistribution of *Ae. taeniorhynchus* abundances (t = 1.35, β = 0.13, $p < 0.05$). Application of county-wide measurements of precipitation and temperature in correlation tests did not produce significant results. With georeferenced climatic measurements, the increase in annual minimum temperature (57.86–63.45 °F) (t = 4.56, β = 1.44, $p < 0.01$), mean dew point (58.05–60.73 °F) (t = 4.12, β = 1.10, $p < 0.01$), and maximum vapor pressure deficit (12.51–17.31 hPa) (t = 4.5, β = 1.00, $p < 0.01$) were significantly associated with high *Ae. taeniorhynchus* abundance. Annual mean temperature and two LULC categories, upland nonforested and enclosed saltwater ponds within saltmarshes, were negatively associated with *Ae. taeniorhynchus* abundance.

LULC and DEM

Regarding LULC coverage of the entire St. Johns County, there were increases in the total area (m^2) from 2004 to 2014 with the Level 1 LULC categories of water and urban & built-up (Table 2). Comparatively, the broad categories of agriculture and upland nonforested largely decreased, with smaller decreases in upland forests and wetlands. The hybrid salt marsh associated category also decreased from 2004 to 2019, however, while the two Level 3 codes for saltmarshes and enclosed saltwater pools contributed to the overall decline, the subclass mangrove swamps had instead

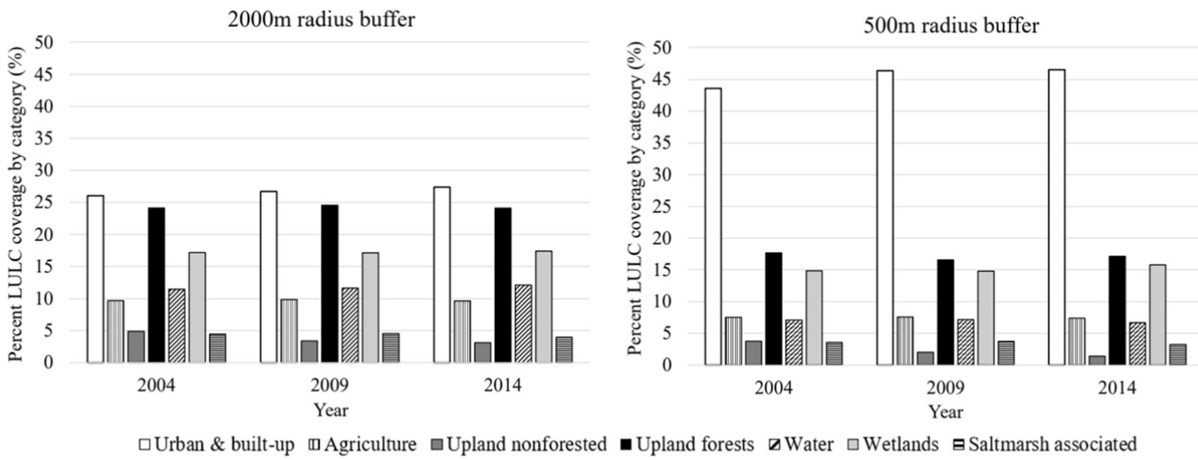

Fig. 6 Spatial distribution of mangrove swamps during 2004, 2009, and 2014 showing the expansion and re-distribution of their geographic extent

significantly increased in total coverage area (Table 3).

The LULC proportions around trap sites were similar to overall county proportions aside from a higher presence of urban & built-up (Table 2). There were also similar trends of rising and/or declining LULC percent coverage across the 0.5 km and 2.0 km radii buffers. These patterns were for the majority consistent between the two buffer sizes however the category of water did show an equivocal direction of change. The percent coverage of individual LULC categories also changed drastically from 0.5 to 2.0 km (Fig. 7). As the buffer radii increased, urban & built-up remained the primary LULC category although the proportions of other categories became more pronounced. Similar to the county trend, the total area of salt marsh associated land decreased in the buffers around trap sites, specifically due to decreases in saltwater marshes and enclosed saltwater pools while mangrove swamps expanded farther into the buffer zones (Table 3). Spatial maps revealed that mangrove swamps particularly increased in the buffer zones of four traps located on the mid-eastern coast of the county, while the decreases in saltwater marshes were less localized.

The digital elevation data layers for these suitable habitats within the SDE were found to be within 0–27 m above water level (Fig. 8). The elevation range showed insignificant variation between the three years. The wetland, in general, and specifically the mangrove swamps were concentrated within the same elevation range that predicted the geographic extent of *Ae. taeniorhynchus* abundances.

Discussion

We identified a clustered distribution and change in the geographic extent for *Ae. teaniorhynchus* abundances using a combination of available LULC, climatic variables, DEM (0–27 m), lunar cycle dates, and our own mosquito data during the 2004, 2009, and 2014 surveillance seasons. The migration of mangrove salt marshes between the three years, demonstrated by the expansion of mangrove distribution and the increase in percent LULC area from 2009 to 2014, was found to result in redistribution of *Ae. taeniorhynchus* abundances. The redistribution and expansion of mangrove salt marshes during 2014 is basically attributed to developmental projects in SJC, especially the coastal restorations conducted over the last decade (SJC TDC 2015). These coastal restoration projects showed not only changes to the vegetation with colonization by saltmarsh and mangroves (intended) but also increased oviposition sites available to *Ae. taeniorhynchus* and possibly other saltmarsh mosquito species (unintended) (Lewis and Gilmore 2007). Our findings were consistent with similar studies in Australia, which highlighted the impact of restoration projects in creating or enhancing mosquito habitats that cause nuisance or health issues (Lawler et al. 2007; Turner and Streever 1999). Moreover,

Table 2 Percent coverage by Level 1 LULC: The percent coverage (%) of each LULC Level 1 category was calculated by totaling the area (m^2) of each LULC category from the entire St. Johns County or across all 0.5 km or 2.0 km buffer zones surrounding traps active 2004–2014 (n = 18). This total was divided by total area of classified polygons within county borders or total area within the buffer zones (not excluding areas where buffer zones overlapped)

		St. Johns County				Buffer = 2000 m				Buffer = 500 m			
Description	LULC L1 Code	Percent coverage (%)			Change in total area (m^2) 2004–2014	Percent coverage (%)			Change in total area (m^2) 2004–2014	Percent coverage (%)			Change in total area (m^2) 2004–2014
		2004	2009	2014		2004	2009	2014		2004	2009	2014	
Urban & built-up	1000	13.96	15.46	15.94	14.13%	26.06	26.72	27.41	5.19%	43.62	46.37	46.52	6.67%
Agriculture	2000	8.59	8.44	7.80	− 9.19%	9.70	9.87	9.66	− 0.43%	7.54	7.60	7.41	− 1.70%
Upland nonforested	3000	3.86	2.83	2.62	− 32.24%	4.87	3.37	3.09	− 36.54%	3.76	2.00	1.38	− 63.30%
Upland forests	4000	33.78	33.46	33.75	− 0.10%	24.13	24.56	24.12	− 0.05%	17.66	16.55	17.12	− 3.01%
Water	5000	10.43	10.57	11.10	6.40%	11.44	11.61	12.08	5.58%	7.10	7.18	6.69	− 5.69%
Wetlands	6000	24.09	23.88	23.75	− 1.85%	17.17	17.13	17.40	1.35%	14.82	14.77	15.77	6.35%
Salt march associated	5430	3.81	3.83	3.35	− 11.94%	4.44	4.51	3.95	− 11.16%	3.56	3.73	3.23	− 9.16%
	6120												
	6420												

Table 3 Percent coverage by saltmarsh associated LULC: The percent coverage (%) of each LULC Level 3 category included in the "Saltmarsh associated" Level 1 LULC category

		St. Johns County				Buffer = 2000 m				Buffer = 500 m			
Description	LULC L3 Code	Percent coverage (%)			Change in total area (m^2) 2004–2014	Percent coverage (%)			Change in total area (m^2) 2004–2014	Percent coverage (%)			Change in total area (m^2) 2004–2014
		2004	2009	2014		2004	2009	2014		2004	2009	2014	
Enclosed saltwater ponds within a salt marsh	5430	0.03	0.03	0.01	− 48.23%	0.03	0.03	0.02	− 26.93%	0.10	0.10	0.03	− 67.24%
Mangrove swamp	6120	0.03	0.04	0.15	407.68%	0.03	0.05	0.19	559.37%	0.00	0.00	0.18	
Saltwater marshes	6420	3.75	3.77	3.19	− 14.96%	4.38	4.43	3.26	− 15.32%	3.46	3.63	3.02	− 12.70%

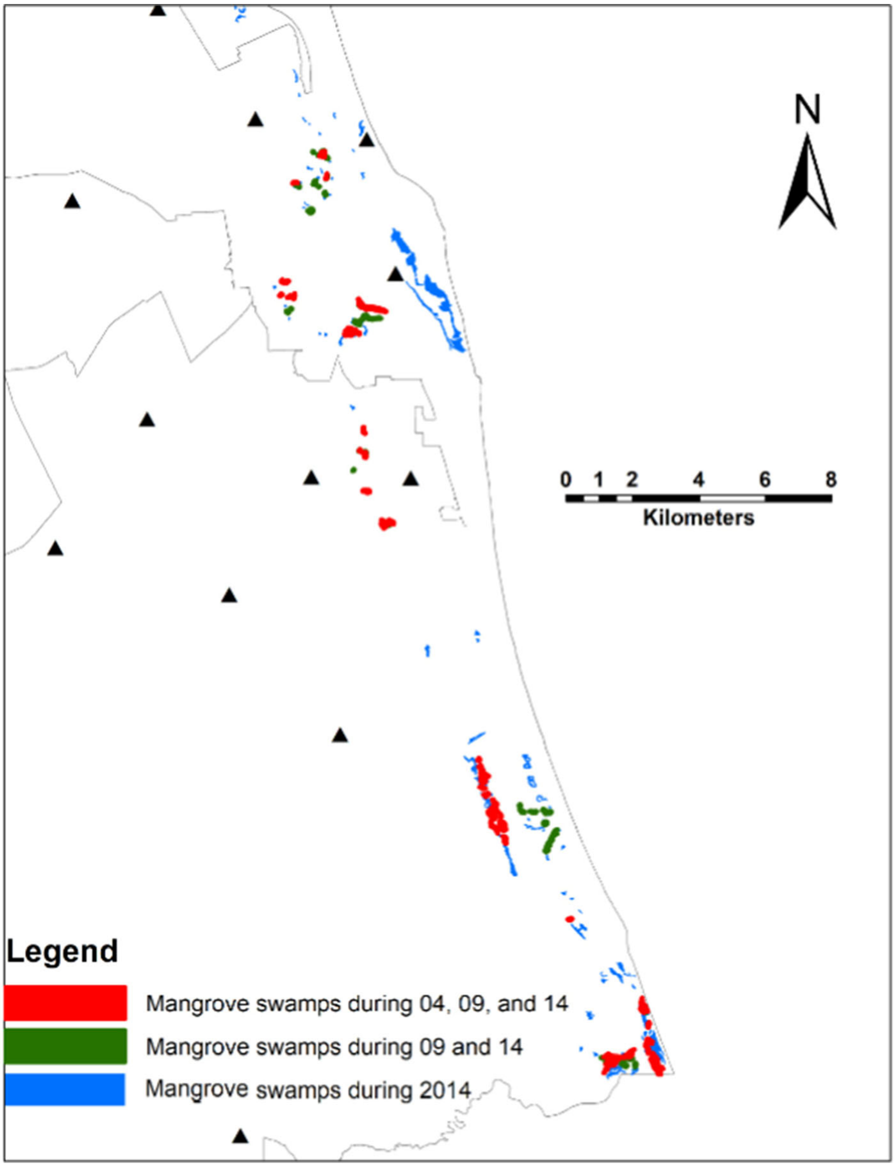

Fig. 7 LULC composition within the buffer zones (radii 0.5 km or 2.0 km) around trap sites that were permanently active 2004–2014 (n = 33). The total area (m^2) of each LULC category compiled across all trap sites was divided by the total area compiled from the 33 buffer zones at each radius size

Lewis and Gilmore (2007) provided a very useful review of mangrove restoration in Florida's east coast wetlands that had been impounded for mosquito control. They suggested strategies for restoration of fish habitats but did not discuss the potential to unintentionally restore the mosquito populations that led to impoundment in the first place.

Similar studies highlighted that the population dynamics and seasonality of *Ae. taeniorhynchus* around mangrove habitats in the Caribbean were in response to landscape features, with mosquitoes favoring low lying marshland compared to agricultural, urban, and rainforest areas (Ritchie 1992; Barrera et al. 2014; Agramonte and Connelly 2014). Although *Ae. taeniorhynchus* was collected from other landscapes (urban, agricultural, rainforest), it was speculated that adult mosquitoes were being blown into novel habitats during tropical storms, which may

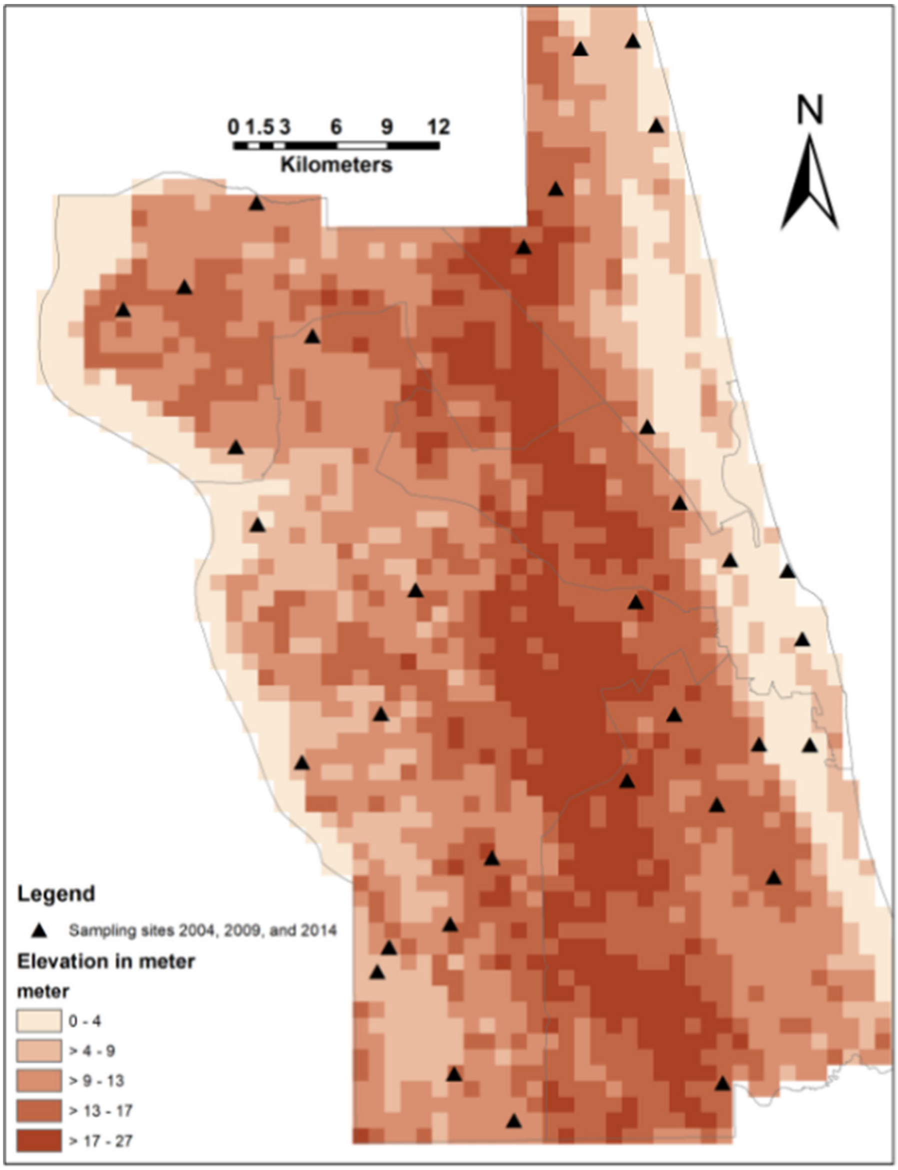

Fig. 8 Digital Elevation Model (DEM) within St. Johns County boundaries showing elevation gradient at different sampling sites

have provided transient oviposition/development habitats for *Ae. taeniorhynchus*. Vegetation parameters have been highlighted in previous studies as potential indicators for salt marsh mosquitoes such as *Ae. vigilax* (Skuse) in Australia (Kurucz et al. 2009). The low–high lying mangrove salt marshes were defined as potential suitable habitats for *Ae. vigilax*, especially in areas with high tides and increased precipitation rates (Whelan 2007). Additionally, other vegetation of relatively low height and density, such as occurs in grassy brackish ponds, were found to be suitable for saltmarsh mosquitoes (Reynolds 1961; Sinclair 1976; Strickman 1982; Dale et al. 2013).

The impacts of coastal restoration efforts, one of many developmental projects completed or currently ongoing in SJC, on the presence of suitable habitats for larval mosquitoes have been either undetermined or neglected in recent studies. Despite a growing body of science supporting coastal restoration, few studies have addressed the impact of these restoration efforts on other non-target ecological systems, particularly in cases where restoration efforts were sustained for long periods (i.e. several years to decades) (DeAngelis et al. 2020). A few example studies conducted in Tampa Bay, FL, discussed the impact of population growth, urban development, and marine restoration projects on emergent tidal wetlands (mangroves, salt marshes, salt barrens) and their negative effect on coastal wetlands and seagrass bed health (Fehring 1986; Lewis and Robison 1995; TBEPCC 2017; Lewis and Estevez 2020). Marine ecological systems and the specifics of the ecological restoration in coastal areas were not the focus of our study. Rather, we focused on the geographic extent and abundance of black salt marsh mosquitoes and their response to the environmental changes resulting from continuous developmental projects in SJC.

Unsurprisingly, the geographic distribution of *Ae. taeniorhynchus* abundances was concentrated along the coastal areas of St. Johns County and highlighted suitable saltmarsh habitats for their immature development and blood meal preference. However, no previous literature was available to demonstrate their geographic extent away from the coast or to characterize their landscape/climate thresholds using empirical data. The SDE polygons showed high abundances of *Ae. taeniorhynchus* clustered as far as 8 km away from the coast within the generated distribution polygons. A lowlands elevation has previously been shown to be an indicator for both the impoundment of wetlands (Ferrigno and Jobbins 1968; Swamy et al. 2002) and for adult female oviposition and larval development (Gorsevski et al. 2000; Rogers and Randolph 2000; Mushinzimana et al. 2006; Sallam et al. 2013). Other studies used elevation as a precursor for mosquito oviposition/developmental habitats by delineating soil–water gravitational potential energy (Moore et al. 1993), surface water flow velocity, drainage and accumulation of water (Gorsevski et al. 2000; Warren et al. 2004), and surface and underground water movement within drainage channels and throughout the landscape. Other DEM parameters such as slope and hill shade were used as promising remote sensing data that reflect areas with surface water accumulation (Nmor et al. 2013). Hill shade was used in previous studies as a predicting precursor for water suitable habitats of malaria vectors in Africa (Nmor et al. 2013).

The annual values of four climate variables (average and minimum temperature, mean dew point, and maximum vapor pressure deficit) significantly predicted *Ae. taeniorhynchus* abundances and distribution between years. Temperature has been highlighted in previous studies as a predicting variable for mosquito larval development and adult survival (Lord and Day 2001; Sallam et al. 2013). Although temperature is important to boost the development rate of mosquito immature stages, it is also the key predictor for increased evaporation rate of mosquito oviposition/development sites, especially at transient water bodies in lowlands after high tides or rainfall. Surprisingly, our analysis did not show any association between the precipitation rates and seasonality or abundance of *Ae. taeniorhynchus*. This might be attributed to the collinearity demonstrated in our regression analyses between data layers of precipitation and dew point and vapor pressure deficit. It is also possible that the exclusion of direct tide level data as an environmental parameter may have confounded analyses and/or masked any significance. The impact of increased annual precipitation rate on high abundances of *Ae. taeniorhynchus* was demonstrated in other studies (DeGaetano 2005; Dieng et al. 2012; Reisen et al. 2008; De Little et al. 2009; Asigau and Parker 2018). Interestingly and unlike our findings, precipitation had a strong effect on seasonality and relative abundance of *Ae. taeniorhynchus* in Valentine et al (2020). Although excess rain may fatally drain larvae away from their habitats and cause an instant decrease in adult mosquito populations (DeGaetano 2005; Dieng et al. 2012), a seasonal increase in precipitation increases the abundance and persistence of larval habitats resulting in higher densities (Reisen et al. 2008, De Little et al. 2009, Sallam et al. 2013, 2016, 2017a, 2017b, Asigau and Parker 2018, Hopperstad et al. 2020). In similar studies, relative humidity precursors have been shown to have important positive effects on the abundance (Asigau and Parker 2018; Evans et al. 2019; Bayoh 2001), lifespan (Bayoh 2001; Hylton 1969), activity, and questing behaviors of adult mosquitoes (Rowley et al. 1968, Okech et al. 2004), and are thus a consideration to include in future study models.

Important limitations of this study include shortcomings in meaningful data. Firstly, we were not able to measure mosquito abundance in relation to a direct index of tidal amplitude, i.e. tide height measurements from certified coastal stations. Use of a lunar phase proxy variable that was applied on a county-wide level also prevented fine-scale resolution of the likely heterogeneous effect of tide on traps from nearby tidal regions along the SJC coastline. Secondly, the heterogeneous nature of environmental conditions across microhabitats is another key consideration in regards to mosquito species distribution (Hopperstad and Reiskind 2016). Initial analyses with county-level measurements of precipitation and temperature failed to achieve sufficient resolution and significance but this limitation was overcome by retrieving interpolated historical values of georeferenced coordinates from the PRISM network database. LULC data was fortunately available at a very fine spatial resolution; however, the most recently updated dataset is from 2014/2015 and we were unable to analyze the ecological impacts of the large increases in population and development growth of SLC over the last five years.

Conclusion

Our results show that in SJC, AMCD's targeted surveillance program and operational efforts to control *Ae. taeniorhynchus* populations should be directed towards newly established oviposition/development sites in mangrove swamps in the central and southern areas during late dry and early wet seasons (April–July). Our study provides a more comprehensive spatio-temporal distribution of black salt marsh mosquitoes in response to LULC and climate. Our findings are just one of the ongoing studies in SJC that highlights the impact of landscape-climate interactions on mosquito communities. We conclude that urban expansion and large-scale development projects in SJC, especially coastal restorations, have led to the development of new suitable habitats for *Ae. taeniorhynchus* and thus a expansion in *Ae. taeniorhynchus* population distribution. Although we did not directly focus on the coastal restorations themselves, the expansion of mangrove swamps from 2004 to 2014 and the significant influence on black salt marsh mosquito abundance, in addition to similarities with previous literature, demonstrated a likely parallel impact by such coastal development projects in SJC. A separate rigorous study should be directed to study the extent of novel mosquito oviposition/development habitats that are created as a consequence of coastal restorations. The findings from this study are essential for designing targeted surveillance and control efforts of mosquito communities in SJC by delineating the spatio-temporal thresholds for mosquito abundances and distribution.

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Authors' contributions WAQ and RDX conceptualized the manuscript. MRS and MFS contributed significantly to data compilation, organization, and performed all analyses and data interpretation. WAQ, JRW, MRS, YZ, MFS, and RDX contributed to writing the paper.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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