

Spatial-Temporal Population Dynamics of Male and Female *Aedes Albopictus* at a Local Scale in Medellín, Colombia

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Research

Keywords: *Aedes albopictus*, *Aedes aegypti*, Population ecology, Male-female distribution

Posted Date: March 13th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-300583/v1>

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Abstract

Background: Diseases transmitted by invasive *Aedes aegypti* and *Aedes albopictus* mosquitoes are major public health issues in the tropics and subtropics. Understanding the ecology of mosquito vectors is essential for the development of effective disease mitigation programs and will allow for accurate predictions of vector occurrence and abundance. Studies that examine mosquito population dynamics are typically focused on female presence or total adult captures without discriminating the temporal and spatial distribution of both sexes.

Methods: We collected immature and adult mosquitoes twice monthly during a two-year period (2018 – 2019) in the Medellín Botanical Garden (Medellín, Colombia) and assessed: 1) the relationship between climatic variables/vegetation coverage and adult captures, 2) the temporal and spatial distribution of *Ae. aegypti* and *Ae. albopictus* during the study period, 3) the temporal and spatial distribution of *Ae. albopictus* males and females, and 4) the correlation of male and female size in relation to climatic variables and vegetation coverage.

Results: We show that *Ae. albopictus* was the predominant species in the park during the study period. Adult captures were positively correlated with precipitation and relative humidity, and inversely correlated with temperature and wind speed. Spatial analysis showed that *Ae. aegypti* and *Ae. albopictus* were distributed at different locations within the surveilled area. Moreover, we observed a spatial misalignment of *Ae. albopictus* males and females—the majority of males were located in the high vegetation coverage sites and the females in the medium vegetation coverage sites.

Conclusions: Our work elucidates the differential dynamics of *Ae. albopictus* males and females, which is pivotal to develop accurate surveillance and the successful establishment of vector control programs based on the disruption of insect reproduction.

Background

Aedes aegypti and *Ae. albopictus* mosquitoes are invasive species responsible for the dissemination of viruses that adversely affect human health, including the dengue [1], Zika [2] and chikungunya viruses [3]. Both species are present throughout the tropics and sub-tropics, and their populations often co-occur in the same habitats [4]. *Aedes albopictus* is further distributed in more temperate regions due to the ability of this species to tolerate low temperatures, diapause during winter months, and lay eggs that are resistant to desiccation [5–8]. Both *Aedes aegypti* and *Ae. albopictus* have successfully colonized urban- and peri-urban environments and are anthropophilic [9, 10]. As territory habitable by *Aedes* continues to expand [11, 12], the incidence of diseases disseminated by these vectors is expected to increase, as has been previously observed [13, 14].

In Colombia, diseases spread by *Ae. aegypti* and *Ae. albopictus* are continuing public health concerns [15, 16]. For example, more than 23 million Colombians—nearly half the country’s population—live in areas and dengue epidemics occur every 3–4 years [16–18]. In

Medellín, Colombia's second largest city, *Ae. aegypti* was the predominant species until 2011, when the presence of *Ae. albopictus* was first detected [19]. Since that time, *Ae. albopictus* populations have been established in several areas of Medellín (Secretaria de Salud Medellín, unpublished data). Overlapping ecological niches of these two species can result in the competitive displacement of *Ae. aegypti* by *Ae. albopictus* or the stabilization and co-existence of both species [20, 21].

As *Ae. aegypti* and *Ae. albopictus* differ in their human biting behaviors [22] as well as their disease transmission abilities [3], factors that influence vector abundance can alter disease transmission rates. Additionally, interactions between *Ae. albopictus* and *Ae. aegypti* populations has implications for mosquito control programs that introduce transgenic [23] or *Wolbachia*-infected [24] *Ae. aegypti* into the field. Beginning in 2017 in Medellín, the World Mosquito Program (WMP) began releasing *Wolbachia*-infected *Ae. aegypti* males and females to replace native populations [25], as artificial infection of *Ae. aegypti* females by *Wolbachia* blocks transmission of some viruses [26, 27]. The continued invasion of Medellín by *Ae. albopictus* is likely to influence the successful implementation of this program. Understanding the population dynamics of *Ae. albopictus* where control programs are implemented may identify factors that influence the establishment of *Wolbachia*-infected *Ae. aegypti* in areas where *Ae. albopictus* populations exist. Further, elucidation of the spatial dynamics of *Aedes* males and females will aid control programs that exclusively release males [23, 28]. To date, most emphasis has been placed on examining *Ae. aegypti* population dynamics, but little information regarding *Ae. albopictus* has been reported.

In the present study, we evaluated the spatial, temporal and population dynamics of male and female *Ae. aegypti* and *Ae. albopictus* adults in the Medellín Botanical Garden (Medellín, Antioquia, Colombia), an area with high vegetation and human intervened environments representing several micro-ecosystems, which makes it an excellent open-field laboratory to test hypotheses on mosquito habitat use and competition. During the study period, *Ae. albopictus* was the predominant species, accounting for ~ 95% of adult captures. Spatial analysis of captured adults identified areas in the Botanical Garden with significant associations and disassociations between *Ae. aegypti* and *Ae. albopictus*. When we examined *Ae. albopictus* exclusively, we found that males and females differed in their distributions around the park, and we observed seasonal variation in the distribution patterns of *Ae. albopictus* males and females. Vegetation coverage had a significant influence on *Ae. albopictus* captures, with most adults collected in areas with high vegetation. Vegetation coverage also influenced capture of *Ae. albopictus* males and females differently: males were primarily captured in areas with high vegetation coverage, while females were evenly distributed in areas with high, medium and low vegetation coverage. Our results show that factors favoring *Ae. albopictus* populations are present in the Medellín Botanical Garden, and that male and female *Ae. albopictus* have unique distribution patterns that are at least partially influenced by vegetation coverage.

Methods

This study was conducted in the Jardín Botánico de Medellín (Medellín Botanical Garden; Fig. 1) that has an area of 14 ha and is located near the city center ($6^{\circ}16'25''N$ and $75^{\circ}33'47''W$). At 1400 m above sea level, the Medellín Botanical Garden has a subtropical semi-humid climate with vegetation consisting of tropical flora like palms, bromeliads, orchids, ferns, and cycads. The garden is home to various species of birds, small mammals (cats, monkeys and squirrels) and reptiles. The area immediately around the garden consists of residential housing, businesses and other public spaces (a park, a museum and a university), and is adjacent to the city metro line. The Medellín Botanical Garden receives an estimated 130,000 people each month.

Mosquito Collection

Larvae and adult mosquitoes were collected from January 2018 to December 2019 (Fig. 1). Sampling was conducted every two weeks in the late morning (9am-12pm). Adult collections were made at 19 locations within the park (Fig. 1D) employing both human landing catch and sweep nets to capture adults; four researchers remained at each sampling site for 5 min. Captured adults were aspirated into 50 ml conical tubes and labeled with the collection site identification code. Larvae were collected at four different locations within the park (Fig. 1D); when present, 20-100ml of water from natural containers (e.g., tree holes) was collected, depending on the volume available. Adult mosquitoes were brought to the laboratory for species and sex identification based on morphological characteristics. Wings of adult captures were measured as in [29] to estimate body size. Larvae from each collection site were transferred to 500 ml containers with 100 mL dH_2O and given a pinch of fish food (Tetramin) until pupation. Pupae were transferred to 5 ml tubes and the species and sex of each specimen was determined upon eclosion.

Spatial analysis of *Aedes* mosquitoes

We examined differences in adult captures and larvae collected per site per year using a linear mixed model (LMM) with site and year as fixed variables, and the month of collection as a random variable in the model. For males and females at each site we used a Generalized linear mixed model (GLMM) with a binomial distribution using each sex over the total captures as the response variable, and site and year as fixed variables. Spatial distribution of adult counts was assessed through the Spatial Analysis by Distance Indices (SADIE) methodology [30, 31]. SADIE calculates overall aggregation through D , the minimum distance to achieve regularity for the counts in the dataset. The quotient of D and the mean minimum total distance to regularity of thousands of permutations of the dataset yields an overall aggregation index denoted as I_a , and a p -value for significance with a null hypothesis of randomness (denoted as P_a). When $I_a > 1$, counts are considered aggregated, otherwise this is an indication of regularity. We were interested in detecting patches of consistently high counts relative to the surrounding locations. SADIE provides local indices of clustering, v_i for patches and v_j for gaps, depending if they are above or below ($v_i > 1$ or $v_j < -1$), or well above or well below the expectation ($v_i > 1.5$ or $v_j < -1.5$),

respectively. These cluster values are then used to calculate neighborhoods of high counts (V_i) or low counts (V_j).

We also tested spatial associations between *Ae. albopictus* males and females and adult *Ae. albopictus* and *Ae. aegypti* using the spatial association test provided by SADIE [32], which tests the significance of the association (or disassociation) between two sets of count data, and detects locations where such association is statistically significant. The overall spatial association between two datasets, X , is given by the local index x_k . If there is presence of either a patch or a gap for the two data, it represents a positive association at the local scale. On the other hand, a negative association, or disassociation, represents a patch for one data and a gap for the other in the same location. Significance of X was assessed by comparing the value obtained from the data with the quantiles derived from X_{rand} , the overall index values of 4000 permutations of the two datasets.

Contour maps of local association were constructed by IDW interpolation across the entire sampling region.

Critical values for the contour maps were derived from the quantiles obtained in the permutations. Values of x_k that were $> 85\%$ of X_{rand} were considered significantly associated; those $< 85\%$ of X_{rand} were considered significantly disassociated. To correct for spatial autocorrelation, critical values were multiplied by an inflation factor derived from the method of [33], after a second-order polynomial detrend [34].

Vegetation coverage analysis

We evaluated the correlation of adult male and female *Ae. albopictus* captures with the vegetation coverage within the park. We characterized vegetation coverage of the collection sites using the %Cover application (Public Interest Enterprises, Newcastle, Australia); photographs of each collection site were taken 1 m above the ground. Sites were classified into five categories: very high ($\geq 90\%$), high ($\geq 80\%$), medium ($\geq 70\%$), low ($\geq 60\%$) and very low ($\geq 40\%$) (Table S1). The selection of the sites was intended to represent different ecological settings, ranging from sites near buildings, squares with few plants or trees, and sites with a high density of bushes, plants and trees (sites are described in Table S1). For the statistical analysis, we used the five established vegetation categories as the fixed variable in a LMM, total captures per vegetation classification as a random variable, and the number of males, females and total *Ae. albopictus* as the response variable. Mean comparison was carried out through a Tukey-test.

Temporal analysis of Aedes mosquitoes and correlation with environmental variables

Differences in captures were analyzed per month per year using a LMM, with site as a random factor in the model. Adult and larvae captures were correlated with precipitation, temperature, wind speed, humidity and atmospheric pressure per month. Measurements for these variables during the study period were obtained from the environmental station located in the Botanical Garden maintained by the Sistema de Alerta Temprana de Medellín y el Valle de Aburrá (SIATA; Early alert system of Medellín and the Aburrá

Valley). Data from the environmental station is taken each minute; we used monthly averages for the purpose for this study (Table S2).

Wing Size analysis

We used different LMMs to analyze the wing sizes of captured adults. We first evaluated the overall differences between the sexes and species using each as a fixed variable; captures per month per site were used as a random factor in the model. We next analyzed the change in wing sizes using month and year as fixed variables and captures per site as a random factor in the model. To analyze wing size distribution within the park we used site and year as fixed variables and captures per month as a random factor in the model. We also analyzed the distribution of size across the five vegetation categories (see above). Finally, we developed a LMM of wing size as a function of each assessed environmental variable assessed (precipitation average, maximum and minimum temperature, wind speed and atmospheric pressure; Table S2).

Results

***Aedes albopictus* the predominant species in the Medellín Botanical Garden**

From January 2018 – December 2019, adult and premature mosquitoes were collected every two weeks in the Medellín Botanical Garden. At four sites that had consistent water reservoirs (Fig. 1D), we collected 7376 larvae (5591 of which survived to adulthood). *Aedes albopictus* was the predominant species collected, accounting for 86.1% of the total larvae, followed by *Culex* spp. (13.9%) and *Ae. aegypti* (5.8%) (Table 1). Slightly more male larvae were collected, although both sexes were found in similar proportions (Table 1). Adults were captured at 19 different sites (Fig. 1D); 1398 adults were captured in total. *Aedes albopictus* was the predominant species (94.6%) followed by *Ae. aegypti* (4.2%). *Culex* spp. adults were rarely captured (0.14%). We were unable to identify 1.07% of the adults (Table 1). More adult males (of each *Aedes* species) were collected overall (Table 1).

Spatial distribution of *Aedes aegypti* and *Aedes albopictus* in the Medellín Botanical Garden

Because collection sites were variable (i.e., differences in vegetation, canopy cover, proximity to buildings; Table S1), we examined the spatial distribution of *Ae. aegypti* and *Ae. albopictus* within the park and determined exclusion or association sites of both populations. We found significant differences in the yearly average of larvae collected at each collection site between 2018 and 2019 (LMM: DF = 3, F = 5.7, $p = 0.041$; Figure S1A, B). The majority of larvae was collected at bamboo posts and tree holes: sites 9 and 14 (44% and 38% of the total larvae, respectively) in 2018, and at sites 12 and 14 (31.96% and 53.84%) in 2019. Regarding *Aedes* species, most *Ae. aegypti* larvae was collected at site 9 (69%) in 2018, and at sites 9 and 14 (39% and 38.5%, respectively) in 2019; most *Ae. albopictus* larvae was collected at sites 9 and 14 (42.9% and 40%) in 2018, and at sites 12 and 14 (57.8% and 37.6%) in 2019 (Figure S1A, B).

In our adult collections, no significant differences were observed between the yearly average of each site (Figure S1C, D), although we observed significant differences in

population sizes between sites (LMM: $F = 6.802$, $DF = 18$, $p < 0.001$; Fig. 2A, B; Figure S1C, D). *Aedes aegypti* individuals were captured at eleven sites (Figure S1C, D), with most individuals captured at sites 4, 5, and 9 (Fig. 2A, Figure S1C, D; Table S3). *Aedes albopictus* were collected at all 19 sites; more than 60% were collected at sites 4, 5, 7, 10 and 14 (Fig. 2B, Figure S1C, D; Table S3).

We next characterized the spatial aggregation of individuals of each species, and the spatial association between *Ae. aegypti* and *Ae. albopictus* using SADIE [30, 31]. The overall index of aggregation was $I_a = 1.15$ ($P_a = 0.20$) and $I_a = 1.06$ ($P_a = 0.33$) for *Ae. aegypti* and *Ae. Albopictus*, respectively, which suggests an overall moderate patchiness of both species across the sampled region that is not significantly different from a random pattern. However, we identified individual sites where populations aggregate, forming significant patches and gaps for each species (Fig. 2C, D). This departure of overall aggregation (I_a) from local indices (v_j) may be a result of small sample sizes or edge effects (i.e., large or small counts consistently around the sampling area)—as in our case—when local indices are more powerful at detecting nonrandom distributions [35, 36].

We observed *Ae. aegypti* aggregations at five sites and a patch with significantly above-average density at site 4 ($v_j > 1.5$; Fig. 2C). There were nine areas with low densities or gaps, while sites 14, 15 and 17 had a significantly below-average densities (Fig. 2C). A different local pattern was found for *Ae. albopictus*: we found aggregations at seven sites with a significantly above-average cluster at site 11 ($v_j > 1.5$; Fig. 2D). There were eight sites with low density and a gap at site 17 ($v_j = -1.5$; Fig. 2D). Spatial association between *Ae. albopictus* and *Ae. aegypti* was significant at sites 4 and 5 ($p < 0.05$; Fig. 2E), where both species aggregate and the majority of adults were captured (Fig. 2A, B; Figure S1C, D; Table S3). Significant local disassociations of *Ae. aegypti* and *Ae. albopictus* were found at sites 9, 11 and 14 ($p < 0.05$; Fig. 2E); only *Ae. aegypti* was aggregated at site 9 and only *Ae. albopictus* was aggregated at sites 11 and 14. Although we observed co-existence and exclusion locally, we did not observe significant disassociation ($p = 0.5844$) or association ($p = 0.415$) for the overall population across the study area.

Spatial distribution of male and female *Aedes albopictus* in the Medellín Botanical Garden

As we collected more *Ae. albopictus* males than females during this study (58.4% vs. 41.6%; Table 1), we examined *Ae. albopictus* male and female distribution within the park to identify areas where they aggregate or disperse. The average proportion of males and females collected at each site did not significantly differ between 2018 and 2019 (GLMM: $DF = 18$, $F = 0.654$, $p = 0.1$; Figure S2). However, we observed significant differences of the average male-female proportions between sites (GLMM: $F = 2.7041$, $DF = 18$, $p < 0.001$; Fig. 3A, B). The largest proportion of males were collected at sites 4 and 5 (Fig. 3A; Figure S2), two sites with a high vegetation density (Fig. 1, Table S1). Females had higher proportions at sites 10 and 14 (Fig. 3A, B), sites with low and high vegetation, respectively.

The overall distribution of males and females was moderately patchy, but not significantly different from what is expected by chance (Males: $I_a = 0.9$, $P_a = 0.63$; Females $I_a = 1.18$, $P_a = 0.157$). Locally, however,

with a high density of females at site 15 ($v_i > 1.5$; Fig. 3D). Both sexes had low densities at seven sites. However, sites 2, 10 and 19 were occupied by females but not by males. Significant gaps for females were found at sites 16 and 17 ($v_i < -1.5$; Fig. 3D). We found that both sexes were significantly associated across the sampled area ($p = 0.016$). Significant local associations were observed at sites 5, 7 and 11 (Fig. 3E), where high numbers of both males and females were recorded (Fig. 3A, B). Site 17 also had a significant local association, due to concomitant small counts of both sexes (Fig. 3C, D).

We further analyzed the spatial distribution of males and females during the dry and rainy seasons of Medellín. Medellín has two distinct periods of high and low precipitation annually (see Fig. 5). We combined data for the dry seasons (first: January and February; second: June, July and August) and rainy seasons (first: March, April and May; second: September, October, and November). At a local scale, we found a similar pattern of patch and gap distribution for both males and females during the first and second dry season (Figure S3A, B, E, F). However, the distribution of patches and gaps for both sexes differed between the first and second wet season. Interestingly, the pattern observed in the second wet season resembled that observed in the first dry season for both sexes (Figure S3C, D, G, H). Due to the within-year variation observed for the rainy and dry seasons, it is difficult to describe general differences in *Ae. albopictus* distribution for both sexes. Differences in male and female distribution in the dry and wet seasons may indicate that each sex aggregates differently in space during the year and that this distribution may be influenced by weather variables. We also observed significant associations in certain areas of the park of both sexes, mainly at sites 4 and 5 (Figure S3I, J, K, L) where high vegetation was found.

Vegetation coverage influences *Aedes albopictus* captures

We next examined if vegetation coverage influenced *Ae. albopictus* captures, classifying each collection site by its percentage vegetation cover, which ranged from very low to very high (Table S1). Vegetation coverage had a significant effect on adult captures (LMM: $F = 2.8583$; $DF = 4$; $p < 0.001$; Fig. 4A). The majority of *Ae. albopictus* were captured at areas classified as high or very high vegetation coverage (Fig. 4A). Males and females were uniquely distributed across the differing vegetation coverages (LMM: $F = 16.7731$; $DF = 4$; $p < 0.001$; Fig. 4B)—significantly more males were found at areas with very high or high vegetation coverage sites compared to females, who were similarly distributed between sites with low to high vegetation coverage (Fig. 4B).

***Aedes albopictus* have a bimodal distribution in relation to weather variables**

We examined how weather variables correlated with our monthly *Ae. albopictus* collections. *Aedes albopictus* captures had a bimodal distribution with distinct peaks during April-May and October-November in both 2018 and 2019, coinciding with months with the highest cumulative precipitation (Fig. 5A); we found a significant positive correlation with male and female captures during these months (LMM: $p < 0.05$; Table S4). Relative humidity also had a significant positive correlation with male and female captures (LMM: $p < 0.05$; Fig. 5B; Table S4). Temperature and wind speed showed a significant

inverse correlation with adult captures (LMM: $p < 0.05$; Fig. 6B; Table S4). We also observed a significant correlation between precipitation and total larvae collected (LMM: $F = 10.19$; $p = 0.0042$; Table S5)—the highest number of larvae collected occurred during months with the highest precipitation in both 2018 and 2019 (Figure S4), although we also collected larvae in high numbers in January of 2019, a month with low rain levels. We found no significant correlation with the total larvae collected for other evaluated environmental variables (Table S5).

Environmental factors influence *Aedes albopictus* body size

Because mosquito body size is related to female longevity and reproductive output [37, 38], we examined how *Ae. albopictus* size changed during the study period and asked if collection site or environmental variables influenced this trait. Using wing length as a proxy for body size [29], we found significant differences in size between species and sex of the adults collected (LMM: $DF = 1$, $F = 4.71$, $p = 0.030$; Figure S5A). Female *Ae. albopictus* had an average wing length of $2638.16 \pm 0.55 \mu\text{m}$ and males $2197.18 \pm 0.31 \mu\text{m}$. Female *Ae. aegypti* had an average wing length of $2914.54 \pm 11.26 \mu\text{m}$ and males $2335.65 \pm 7.73 \mu\text{m}$ (Figure S5A).

We next analyzed how size changed during the study period by testing the significance of month, collection site, environmental variables and size as predictor variables of *Ae. albopictus* captures. We found that male size significantly changed with the month during the study (LMM: $DF = 5$, $F = 2.64$, $p = 0.022$; Figure S5B) but female size did not (LMM: $DF = 5$; $F = 1.309$; $p = 0.258$). Similarly, we found an effect of collection site (LMM: $DF = 18$; $F = 1.855$; $p = 0.01$; Figure S5C) and vegetation coverage on male size (LMM: $DF = 4$; $F = 3.97$; $p = 0.003$; Figure S5D)—larger males were found in sites with medium vegetation coverage. In contrast, female size was not affected by collection site (LMM: $DF = 18$; $F = 1.894$; $p = 0.265$; Figure S5C) or vegetation coverage (LMM: $DF = 4$; $F = 1.491$; $p = 0.20$; Figure S5D). We also observed a significant association of *Ae. albopictus* size with precipitation, temperature and wind speed for both sexes (Table S6). Precipitation was directly proportional (Figure S5E), while temperature and wind speed were both inversely proportional to adult wing size (Figure S5F, G).

Discussion

Aedes albopictus is a major vector of arboviruses in several countries [39], as the physiological and ecological plasticity of this vector has allowed it to rapidly spread. However, we know little about how climate variables or site characteristics affect the biology and behavior of this species. Further, there is little information regarding how population interactions between *Ae. aegypti* and *Ae. albopictus* influence mosquito behavior. We sampled local mosquito populations for 2 years in the Medellín Botanical Garden (Medellín, Colombia), a high vegetation area surrounded by a dense urban environment.

The Medellín Botanical Garden consists of human intervened environments that are suitable for the establishment of mosquito populations. *Aedes albopictus* remained the predominant species throughout our study, even considering that the WMP released *Wolbachia*-infected *Ae. aegypti* in nearby Loading [MathJax]/jax/output/CommonHTML/jax.js and *Ae. albopictus* often shared breeding sites but that *Ae.*

albopictus was always found in higher numbers. The Medellín Botanical Garden is well maintained with little peri-domestic containers present in common areas. However, bromeliads, bamboos, palms, and other plants and trees with the ability to act as breeding sites are commonly found around the park. We collected larva from natural containers—tree holes and bamboo posts—as they were sites that consistently collect water and sustain larvae. Egg-laying preferences may have played a role in *Ae. albopictus* remaining dominant in the study area, as females prefer to oviposit in natural containers [41] and are attracted to sites with existing larvae [42]. The types of vegetation present in the Botanical Garden may also influence species predominance, as detritus present in rearing pools can influence larval competition outcomes, often favoring *Ae. albopictus* over *Ae. aegypti* [43]. *Aedes albopictus* is frequently associated with peri-urban areas with a high density of vegetation coverage, although invasion into urban areas increases larval development rates and adult longevity [44], suggesting that urbanization of *Ae. albopictus* populations may increase their vectorial capacity. Factors that favor *Ae. albopictus* establishment may be important in disease transmission by this species, particularly in a dense tropical city such as Medellín.

During our study, more adult males were collected despite using human landing catch and sweep nets to capture adults, the opposite to what has been described using this method [45]. This prompted us to examine the spatial distributions of each sex. While *Aedes* population density is correlated with increased vegetation [46], we detected unique spatial distributions of males and females that correlated with vegetation coverage. Males were primarily captured in areas with high coverage while females were more evenly distributed. Male and female conspecifics can have similar spatial distributions based on the homogeneous allocation of resources and/or risks that occur at local scales [47]. However, sub-population structures based on local resource competition such as breeding sites, mating partners or food sources may occur [48]. For instance, in polygynous species, males have to disperse more widely to find receptive females, while females have smaller dispersion ranges [48, 49]. In monogamous species, however, there may be no benefit for differential dispersion patterns of males and females. *Aedes* mosquitoes have polygamous males and monogamous females [37, 50, 51], but we still observed different distribution patterns of males and females, suggesting unique factors may influence dispersion of *Ae. albopictus* males and female at a local scale. For instance, male and female feeding preferences—males feed on nectar while females can feed on nectar and/or blood-feed—may also have contributed to their unique spatial distributions. At sites with high vegetation coverage, we observed significant male-female coexistence and also captured more males than females. These sites had flowering plants, suggesting that nectar sources may influence male-female distributions at local scale, potentially an important consideration for control programs that release only male mosquitoes [23, 28].

Climatic variables strongly influence population dynamics of *Ae. aegypti* and *Ae. albopictus* [52]. We found that precipitation was the main environmental factor influencing mosquito captures. Rainfall was directly proportional to mosquito density—more breeding sites develop to increase the population—and is associated with *Ae. albopictus* incidence [39]. However, we observed that adult captures were inversely proportional to temperature. Higher temperatures are associated with the *Aedes* incidence due to optimal temperatures [39]. However, adult longevity is increased at lower

temperatures [53], which may reflect adult activity levels. It is possible that adults are less active with higher temperature, so this negative association might be attributed to our collection methods or the time of day when our collections were conducted.

Body size of adult *Ae. albopictus* was also influenced by vegetation and climatic variables. However, the influence of vegetation on adult size differed by sex. Similar to our adult captures, precipitation was positively correlated with body size and possibly fitness, as larger body size is associated with increased fertility in *Aedes* males and females [37, 54, 55]. However, adult size decreased as temperature increased. *Aedes albopictus* females reared at lower temperatures develop into larger adults, with their ovaries displaying higher levels of protein, lipids and carbohydrates than females reared at higher temperatures, which is suggested to contribute to their increased longevity [56]. Interestingly, vegetation coverage influenced male size, but had no effect on female size. Body size estimations of natural populations, and how environmental factors influence mosquito size, are important parameters to understand interspecific competition and can give baseline information for mosquito control programs that are based on insect release.

Conclusions

Our study reveals that *Ae. albopictus* populations in high vegetation areas such as the Medellín Botanical Garden can remain dominant even if a competitor species is artificially introduced into surrounding areas. Control methods that release adult mosquitoes into the environment need to consider *Ae. albopictus* presence and density as a potential complicating factor in their successful establishment. Male and female *Ae. albopictus* also had unique local distributions, suggesting that local factors influence how the sexes disperse across the environment. Whether other mosquito species behave similarly, and if similar distributions occur in urban areas with little vegetation, is an area for further exploration. The identification of local factors that favor *Aedes* establishment, and how these factors influence male-female distributions, will highlight characteristics that influence conspecific population dynamics and ultimately contribute to the success of contemporary mosquito control programs.

Abbreviations

SE
Standard error
LMM
Linear mixed model
GLMM
Generalized linear mixed model
SADIE
Spatial analysis by distance indices
SIATA

Sistema de Alerta Temprana de Medellín y el Valle de Aburrá (i.e., Early alert system of Medellín and the Aburrá Valley).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The datasets generated during and/or analyzed during the current study are available from the corresponding authors upon reasonable request.

Competing interests

The authors declare no competing interests.

Funding

This work was supported by the COLCIENCIAS, Universidad de Antioquia and Max Planck Society cooperation grant 566-1-2014 to FWA.

Author contributions

FWA, CAP, and CC conceived and designed the experiments, CC, CAP, SDZ, LFRS, JA, LMB, SVA, and FWA performed the field work and processed specimens in the lab. CC, CAP, and DFR analyzed the data. CC prepared the figures. FWA, CAP, and CC wrote the manuscript. All authors reviewed the manuscript.

Acknowledgements

We are thankful to the Jardín Botánico de Medellín for allowing us to collect mosquitoes for this study, Miguel Toro and Carolina Bedoya for help with mosquito collection, and RutaN for laboratory support.

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Tables

Due to technical limitations, table 1 is only available as a download in the Supplemental Files section.

Figures

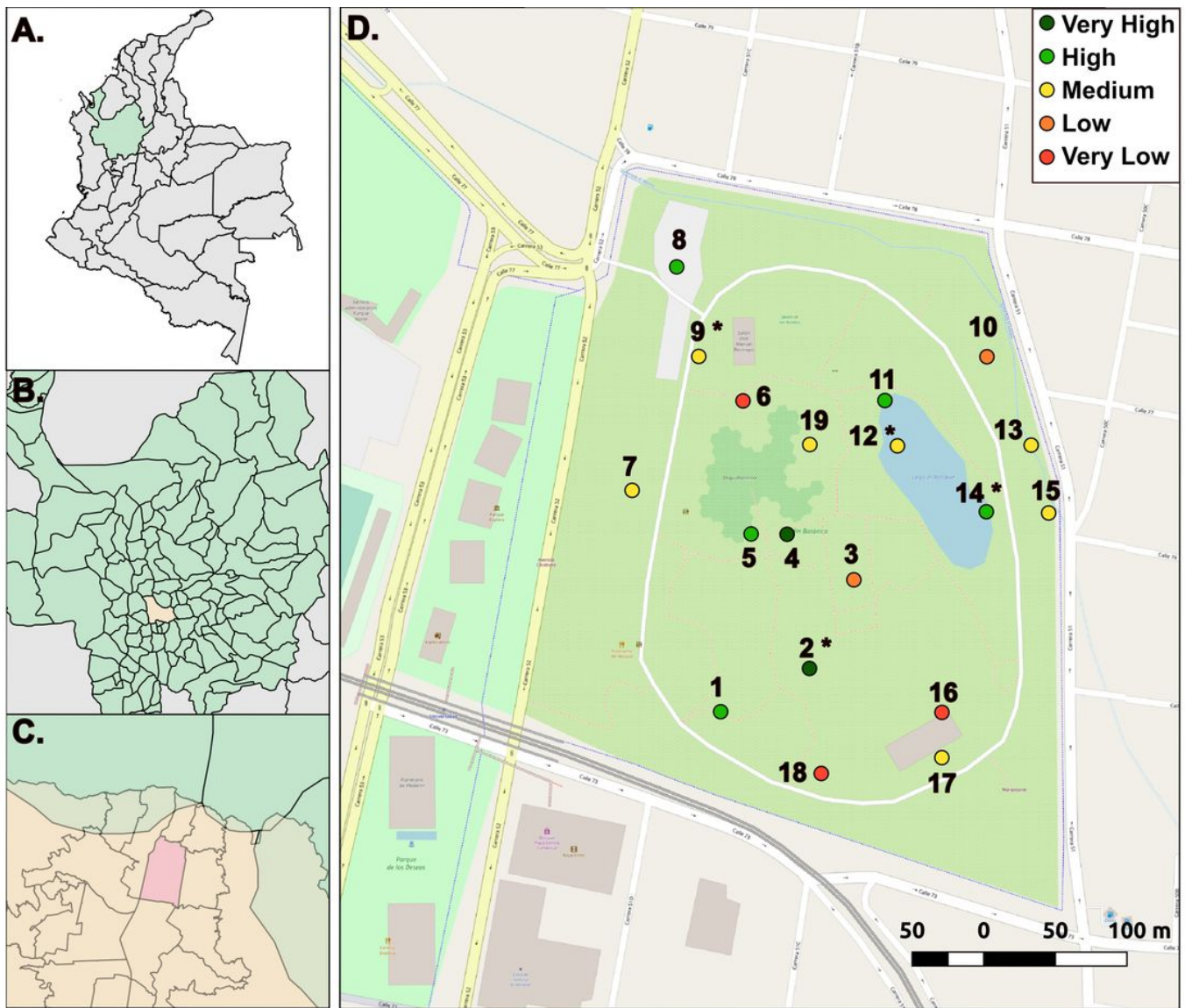


Figure 1

Location of the Medellín Botanical Garden. Map of Colombia with the department of Antioquia in green (A), Antioquia with the city Medellín in yellow (B), Medellín with the location of the botanical garden in pink (C). Larvae and adult collection sites are shown in (D). Adults were collected at all sites shown, and larvae at sites marked with an asterisk (*). Colors for each site represent the level of vegetation coverage (upper right corner). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

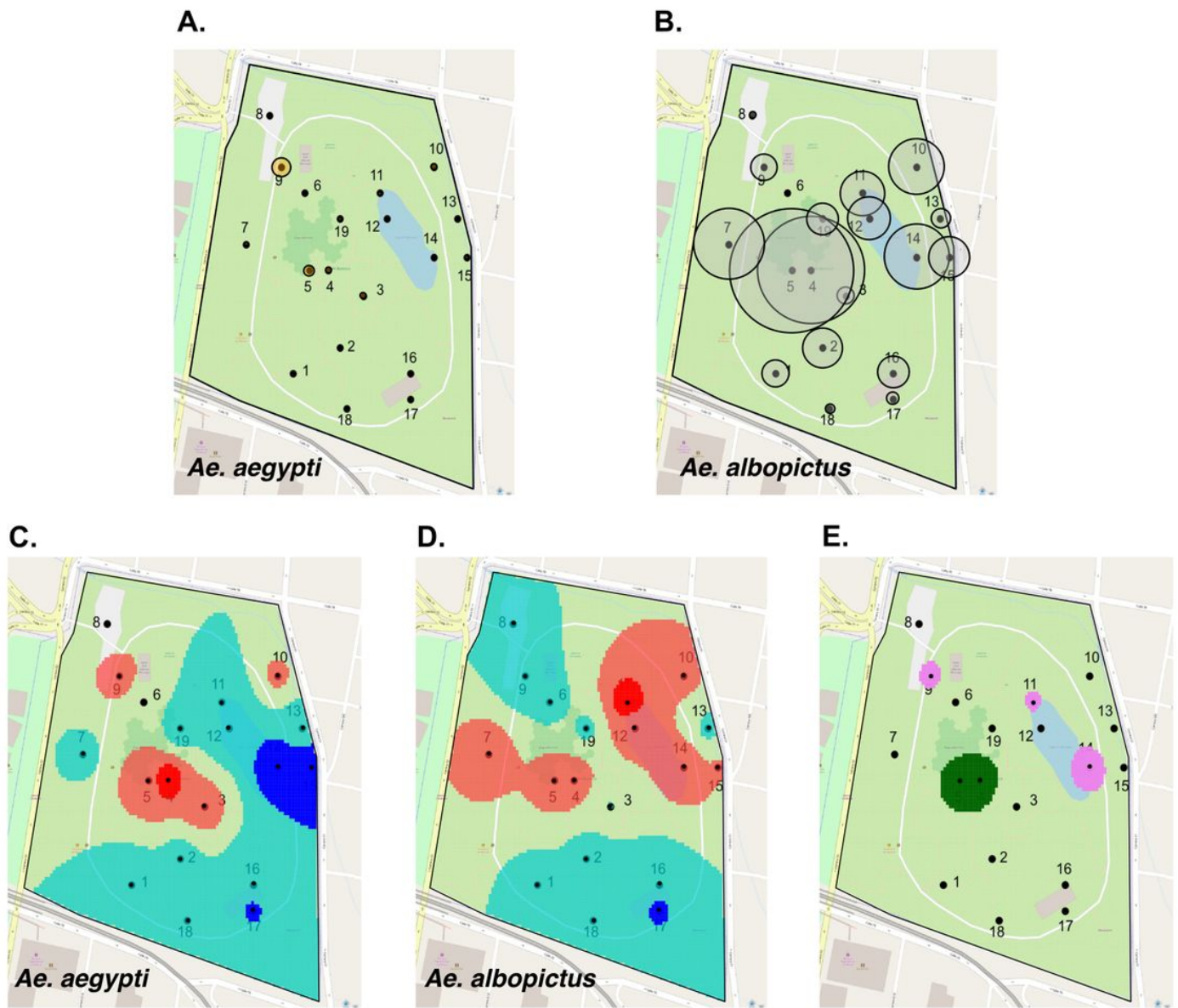


Figure 2

Spatial distribution of adult *Aedes aegypti* and *Aedes albopictus* in the Medellín Botanical Garden. Total captures per site for *Ae. aegypti* (A) and *Ae. albopictus* (B). Distribution pattern of *Ae. aegypti* (C) and *Ae. albopictus* within the park (D). Shaded areas represent local indices of clustering: orange above expectation ($V_i > 1$), red well above expectation ($V_i > 1.5$), green below expectation ($V_j < -1$) and blue well below expectation ($V_j < -1.5$). Map showing significant association (green) and disassociation (violet) of both species is shown in (E). The diameter of the bubbles in (A) and (B) is directly proportional to the counts in the respective centroid location. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning

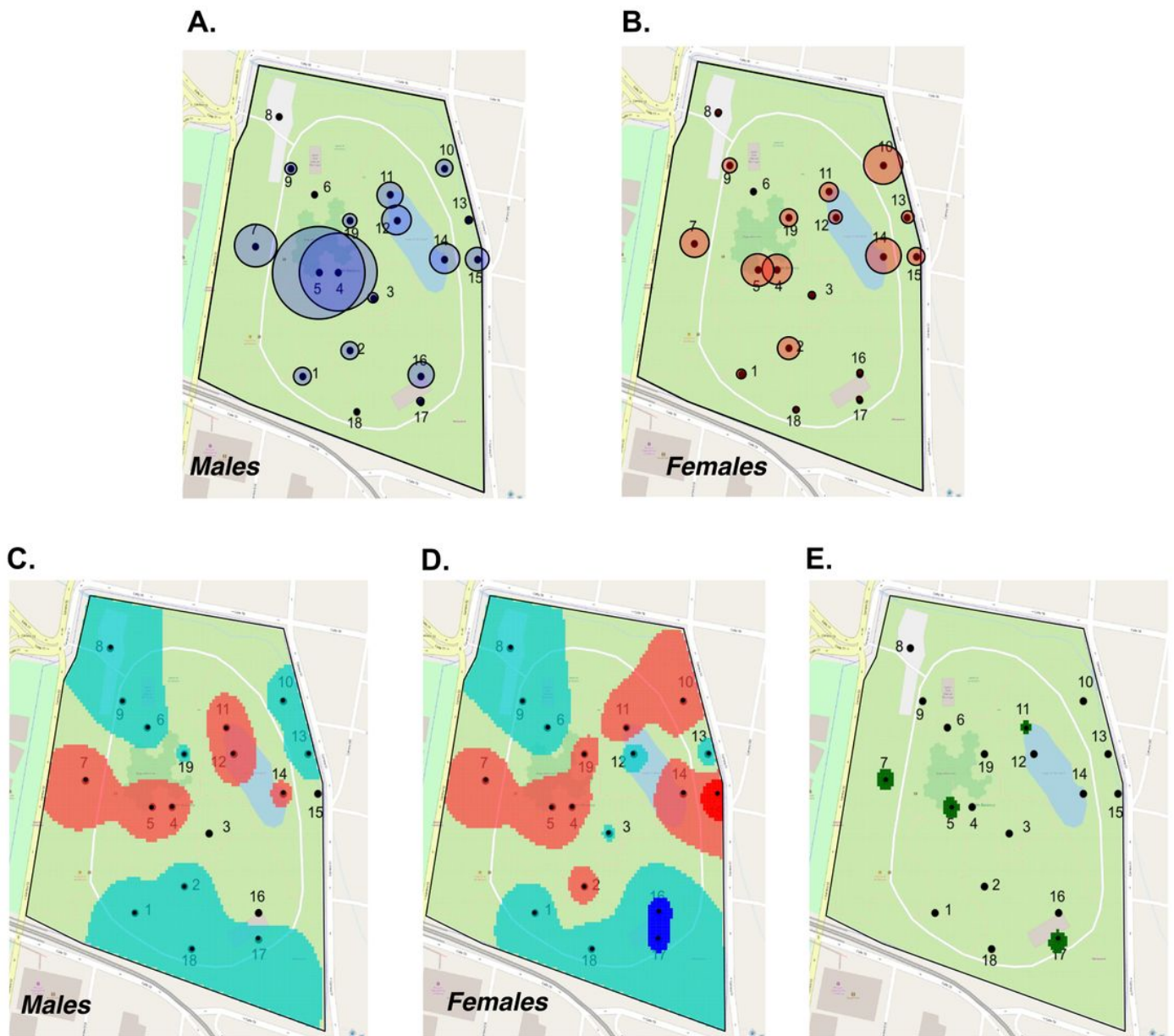


Figure 3

Spatial distribution of *Aedes albopictus* males and females in the Medellín Botanical Garden. Total male (A) and female (B) captures per site. Distribution pattern of *Ae. albopictus* males (C) and females (D) within the park. Shaded areas represent local indices of clustering: orange above expectation ($V_i > 1$), red well above expectation ($V_i > 1.5$), green below expectation ($V_j < -1$) and blue well below expectation ($V_j < -1.5$). Overall map showing sites with significant associations (green) of each sex is shown in (E). The diameter of the bubbles in (A) and (B) is directly proportional to the counts in the respective centroid location. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of

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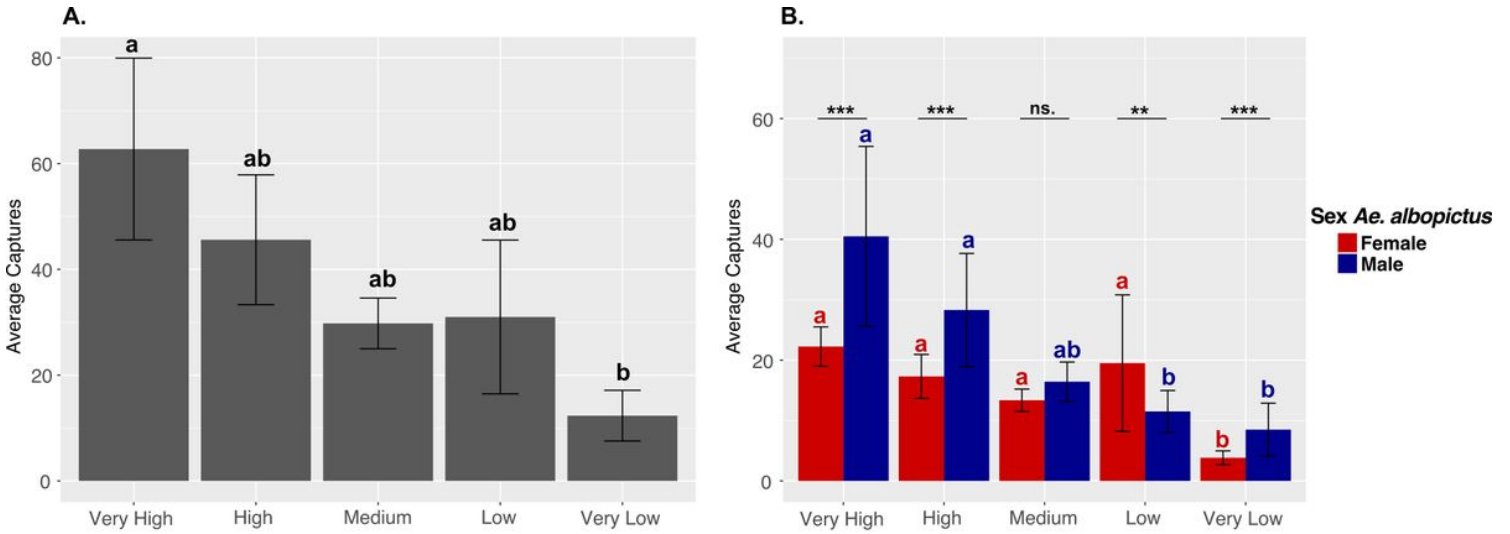


Figure 4

Total adults captured at sites with the corresponding vegetation coverage. Adult *Ae. albopictus* collected (average \pm SE) during the 2 year study period (A), and total males and females collected (B). Different letters show significant differences between classified vegetation coverage using a Tukey test ($***p < 0.0001$, $**p < 0.001$, $*p < 0.01$).

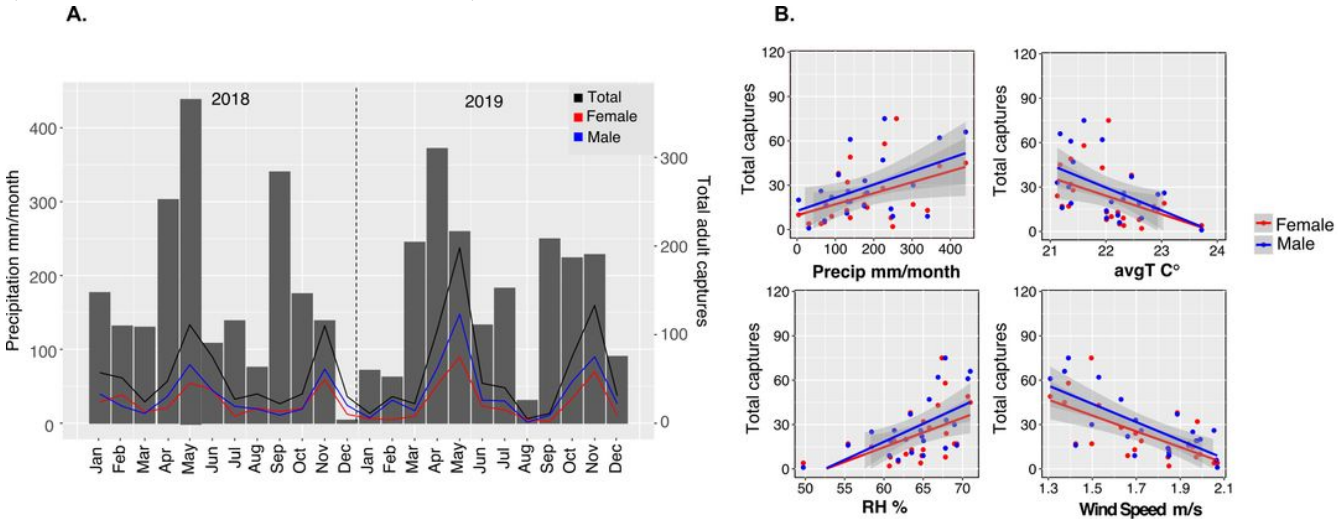


Figure 5

Correlation of *Aedes albopictus* adult captures with weather variables. Temporal distribution of male and female *Ae. albopictus* adult captures (A) in relation to precipitation during 2018 and 2019. Linear model fit between weather variables and male and female adult captures is shown in (B).

Supplementary Files

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