

Short Communication

Aedes albopictus (Diptera: Culicidae) Has Not Become the Dominant Species in Artificial Container Habitats in a Temperate Forest More Than a Decade After Establishment

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Abstract

Aedes albopictus (Skuse) (Diptera: Culicidae) is one of the most invasive species globally, and has led to rapid declines and local extirpations of resident mosquitoes where it becomes established. A potential mechanism behind these displacements is the superior competitive ability of *Ae. albopictus* in larval habitats. Research on the context-dependent nature of competitive displacement predicts that *Ae. albopictus* will not replace native *Aedes triseriatus* (Say) (Diptera: Culicidae) in treeholes but could do so in artificial container habitats. *Aedes albopictus* remains rare in temperate treeholes but less is known about how *Ae. albopictus* fares in artificial containers in forests. Tyson Research Center (TRC) is a field station composed of mostly oak-hickory forest located outside Saint Louis, MO. The container community has been studied regularly at TRC since 2007 with permanently established artificial containers on the property since 2013. *Aedes albopictus* was detected each year when these communities were sampled; however, its abundance remains low and it fails to numerically dominate other species in these communities. We present data that show *Ae. albopictus* numbers have not increased in the last decade. We compare egg counts from 2007 to 2016 and combine larval sample data from 2012 to 2017. We present average larval densities and prevalence of *Ae. albopictus* and two competitors, *Ae. triseriatus* and *Aedes japonicus* (Theobald) (Diptera: Culicidae), as well as monthly averages by year. These data highlight a circumstance in which *Ae. albopictus* fails to dominate the *Aedes* community despite it doing so in more human-impacted habitats. We present hypotheses for these patterns based upon abiotic and biotic environmental conditions.

Key words: *Aedes albopictus*, *Aedes triseriatus*, *Aedes japonicus*, invasive species, context-dependence

Aedes albopictus (Skuse) (Diptera: Culicidae) has been designated one of the 100 most invasive species globally (Lowe et al. 2000). Its invasion success story is due, in part, to its negative impacts on resident species; it is often a superior competitor in the larval habitat and is capable of mating interference and satyrization of *Aedes aegypti* (L.) (Bargielowski and Lounibos 2016, Fader 2016). Following its introduction and rapid spread across the continental United States, local extirpations of resident species occurred, often within only a few years (e.g., O'Meara et al. 1993, 1995). These extirpations were not complete across the landscape however, and areas of coexistence with resident species, and later invaders (e.g., *Aedes japonicus* Theobald (Diptera: Culicidae)), persist. This spurred decades of theoretical and empirical research to determine the ecological factors that facilitate coexistence or lead to exclusion (Juliano 2009, Kaufman and Fonseca 2014, Fader 2016). One pattern that emerges from this body of work, especially for

interactions with *Ae. aegypti*, is the context-dependent nature of larval competition. Microclimates (Lounibos et al. 2010), detritus resources (Murrell and Juliano 2008), parasitism (Aliabadi and Juliano 2002), and predation (Juliano et al. 2010) all have the potential to change the outcomes of competitive interactions, and likely explain the observed patterns of coexistence and exclusion in the United States. The relationship between *Ae. albopictus* and *Aedes triseriatus* (Say) (Diptera: Culicidae) is less clearly understood, however. While individual studies (Livdahl and Willey 1991, Novak et al. 1993, Teng and Apperson 2000, Aliabadi and Juliano 2002, Bevins 2007, Yee et al. 2007) and reviews (see Juliano 2009) suggest that *Ae. albopictus* is the superior competitor, a meta-analysis, including a subset of these studies, found the two species to be competitively equivalent (Juliano 2010).

One of the earliest papers investigating the role of larval competition in the potential extirpation of *Ae. triseriatus* pitted the species

against each other in tire and treehole habitats. Combining models and experiments, the authors concluded that *Ae. albopictus* could exclude *Ae. triseriatus* in tires but that the two species could coexist in treeholes (Livdahl and Willey 1991). To some degree, their predictions have held in the 30 yr since their experiments were conducted. Although *Ae. triseriatus* can still be found in artificial containers, *Ae. albopictus* is much more abundant in such containers and remains rare in treeholes where *Ae. triseriatus* dominates (Fukuda et al. 1997, Kesavaraju et al. 2008, Bartlett-Healy et al. 2012, Yee et al. 2012). Much less is known, however, about how *Ae. albopictus* fares in artificial containers in sylvan habitats; these containers may be rare or rarely studied. One exception to this is Tyson Research Center (TRC). Located 38 km from Saint Louis, MO, TRC is a 2,000 acre, mostly oak-hickory forested field station where mosquitoes have been studied in artificial containers since 2007.

Here, we present data from multiple years of sampling *Aedes* eggs and larval communities (2007, and 2012–2017) in a temperate forest that demonstrate that despite the permanent establishment of artificial containers on the study site, *Ae. albopictus* has not excluded *Ae. triseriatus* or other species. Rather, our data show that *Ae. albopictus* larval and egg abundances are lower than those for *Ae. japonicus* for the most of the active season, and are lower than those for *Ae. triseriatus* for the entire season. Additionally, fewer *Ae. albopictus* eggs were collected in 2016 compared with 2007.

Methods

Egg Sampling: 2007 and 2016

Eggs were collected using identical protocols during 2007 and 2016 to compare the average number of *Ae. albopictus* eggs laid at TRC when these communities were first studied (2007) and a decade later (2016). Fifty 500-ml black plastic cups lined with seed germination paper (thus forth ‘egg papers’) were attached to trees 1–2 m from the ground and filled with 270-ml tap water and 30 ml of a 10%, by weight, hay infusion incubated for 7 d. Cups were placed along five transects, in approximately the same locations for both years. Per transect, five traps were placed along the forest edge on service roads (2-m wide, full canopy) 50 m apart, and five were placed 50 m into the forest. Egg papers were collected on three dates, at weekly intervals, within each of three collection periods; early June, mid-July, and late August after each paper had been in the field for 4 d (450 samples/year). Egg papers were incubated in an environmental chamber for 4–7 d before being placed in 0.35 g/liter nutrient broth solution (Difco) to stimulate egg hatching. Larvae were identified to species as third or fourth instars. No attempt was made to count total eggs laid or to identify unhatched eggs. Larvae identified as *Ae. albopictus* are reported as the number of *Ae. albopictus* eggs laid per day. We used a Generalized Linear Mixed Model (GLMM) with a zero inflated Poisson error distribution using eggs laid per day as the response variable, year and month as independent variables, and transect as a random effect (PROC GLIMMIX). The three samples within each month and the forest versus edge samples were collapsed into ‘month’. We also analyzed proportion of egg papers with *Ae. albopictus* present using a GLMM (PROC GLIMMIX) with a binary distribution (present vs absent) testing for effects of years, months, and interaction, with transect as a random variable. Both analyses were performed in SAS 9.4.

Larval Sampling: 2007 and 2012–2017

To compare the larval densities and frequency of collection of common species at TRC, we summarized the data collected from

larval samples from 2012 to 2017. These data were collected from black plastic containers which always received an initial input of rainwater and oak leaf detritus. Each year of data originates from a different field experiment, with different manipulations, designed to answer research questions not directly related to this study and is repurposed here (Westby and Juliano 2017, Juliano et al. 2019, Westby et al. 2019). Details about the experimental manipulations and sampling schedule can be found in the supplemental file. Depending on the year, larval communities were either subsampled destructively or the entire community was identified and returned to its container. To standardize the data, accounting for differences in methods, we present the prevalence of each *Aedes* species in samples from containers by month with the years 2012–2017 combined, in addition to prevalence for the dominant predator *Toxorhynchites rutilus* (Coquillett). We also present mean densities (larvae/liter) from containers where the focal species was present. We present the average monthly *Ae. albopictus* larval density for every liter of water sampled (e.g., not excluding samples where they absent) and prevalence by month for all the years including larval samples collected in 2007 (not included in the prevalence and density data above). Larval samples were collected in 2007 but volumes were not recorded.

We limited our statistical treatment to the egg sampling data collected in the 2 yr in which we replicated field methods exactly (2007 vs 2016). For other years, the data were collected differently or there were not enough data points in each month for each manipulation in all years to include in a statistical model. We also present no data on *Culex* as they were rare in larval samples later in the season when we began to detect *Ae. albopictus*.

Results

Egg Sampling: 2007 and 2016

We detected significantly more *Ae. albopictus* eggs per day in 2007 (2,054 total eggs collected) compared with 2016 (117 eggs collected; $F_{1,4} = 59.06$ $P = 0.0015$) in addition to significant differences among months ($F_{2,8} = 6.93$ $P = 0.018$), but the interaction of year and month was not significant ($F_{2,8} = 1.71$ $P = 0.2406$) (Fig. 1A). The same pattern held for the proportion of ovicup samples in which *Ae. albopictus* was present. *Aedes albopictus* was significantly more likely to be present in a sample in 2007 (present in $26.1 \pm 5.7\%$ of samples, mean \pm SE) compared with 2016 (present in $3.1 \pm 1.2\%$ if samples) ($F_{1,881} = 65.90$, $P < 0.0001$). *Aedes albopictus* presence was significantly influenced by month ($F_{2,881} = 7.94$, $P = 0.0004$), but the interaction with year was not significant ($F_{2,881} = 1.71$, $P = 0.1812$). There was significant spatial variation among transects ($c^2 = 28.60$, $P = 0.0001$). Least squares means for percent *Ae. albopictus* present are shown in Fig. 1B.

Larval Sampling: 2007 and 2012–2017

When the data from 2012 to 2017 were combined, *Ae. albopictus* was observed in less than 5% of all larval samples collected from May to July and reached its greatest prevalence in September when it was present in 25% of samples. The three *Aedes* species were relatively equal in prevalence in larval samples collected during August and September. The predatory species *Tx. rutilus* was not detected in more than 10% of larval samples from any month (Fig. 2A). When calculated only from samples where they were present, average *Ae. albopictus* larval densities did not exceed 4 larvae/liter, which was lower than that of *Ae. triseriatus* (~12 larvae/liter) and closer to that of *Ae. japonicus* (~6 larvae/liter) though these average numbers changed slightly during the summer (Fig. 2B). When the samples in

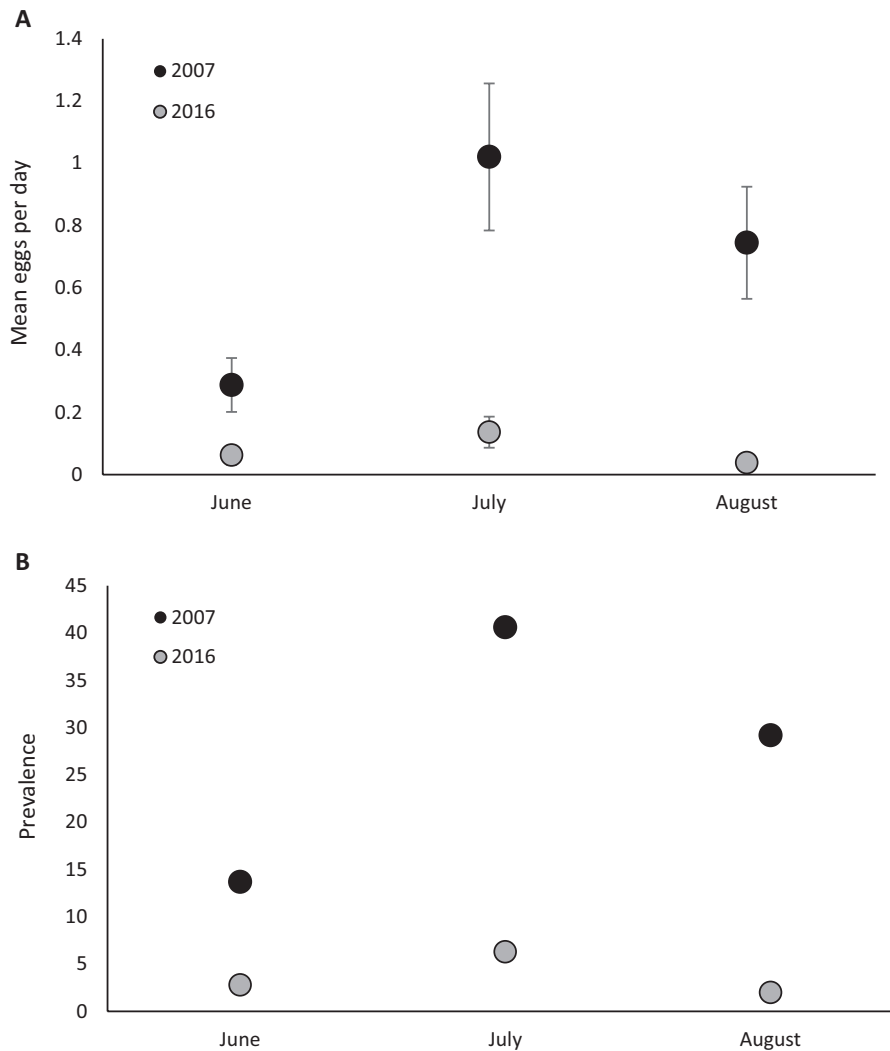


Fig. 1. (A) Least squares means number of *Aedes albopictus* eggs laid per day in 500-ml black oviposition cups. The same sampling protocol, in approximately the same locations, was conducted in 2007 and 2016. (B) Least squares means prevalence (% occupancy) of *Ae. albopictus* in the same egg samples.

each month were broken down by year, *Ae. albopictus* larvae per liter of water sampled (including samples in which they were absent) were an order of magnitude lower in all samples from 2012 to 2017 than in the sample from August 2007, when the average density was 23.65 larvae/liter (Table 1). Prevalence of *Ae. albopictus* across containers was also consistently high (>40% of containers) in 2007, but considerably lower ($\leq 25\%$ of containers) in all samples from 2012 to 2016 (Table 1). Only the final two samples of 2017 attained prevalence of >40% of containers (Table 1).

Discussion

Aedes albopictus larvae were collected each year that mosquitoes were sampled under the forest canopy at this site (TRC) except for 2012. Despite the absence of *Ae. albopictus* larvae in 2012, this species was present in egg samples from that year (data not shown). Published data show that *Ae. albopictus* also present at TRC in 2009 (Murrell et al. 2015), 2010 (Murrell and Juliano 2013), and 2011 (Murrell et al. 2014), indicating that either TRC has an established population or is recolonized from urban and suburban locations each summer. Data sets from the United States (Lounibos et al. 2001, Shragai and Harrington 2019), Brazil (Carvalho et al. 2014), and

Switzerland (Flacio et al. 2016) show that, within a shorter timespan than our data represent, *Ae. albopictus* prevalence increases after establishment. Using identical methods in 2016 as 2007, we detected a significant decline in egg abundance and prevalence for this species from 2007 to 2016. Acknowledging the limitations of inferring a trend from only two years of data, as interannual variation is well known to occur and is represented in the larval abundance data from TRC, our data suggest that there is no obvious long-term upward trend for *Ae. albopictus* populations at this site more than 10 yr after it established. Combining the data from 2012 to 2017, we see that *Ae. albopictus* abundance per liter remains below that of *Ae. triseriatus* and *Ae. japonicus* during the early summer and lower or equal in the later summer, and container prevalence remains low in most months and years (see Table 1). Our data on egg and larval abundances suggest that *Ae. albopictus* has not increased to dominate at this site and may have declined over the period we sampled. Further, if *Ae. albopictus* is overwintering at TRC, it takes several months from the time of first detection (May) until it reaches its highest container prevalence (August or September). This pattern is in stark contrast to the dominance that *Ae. albopictus* quickly achieves in urban and suburban Saint Louis (Westby and Medley, unpublished data, manuscript in preparation)

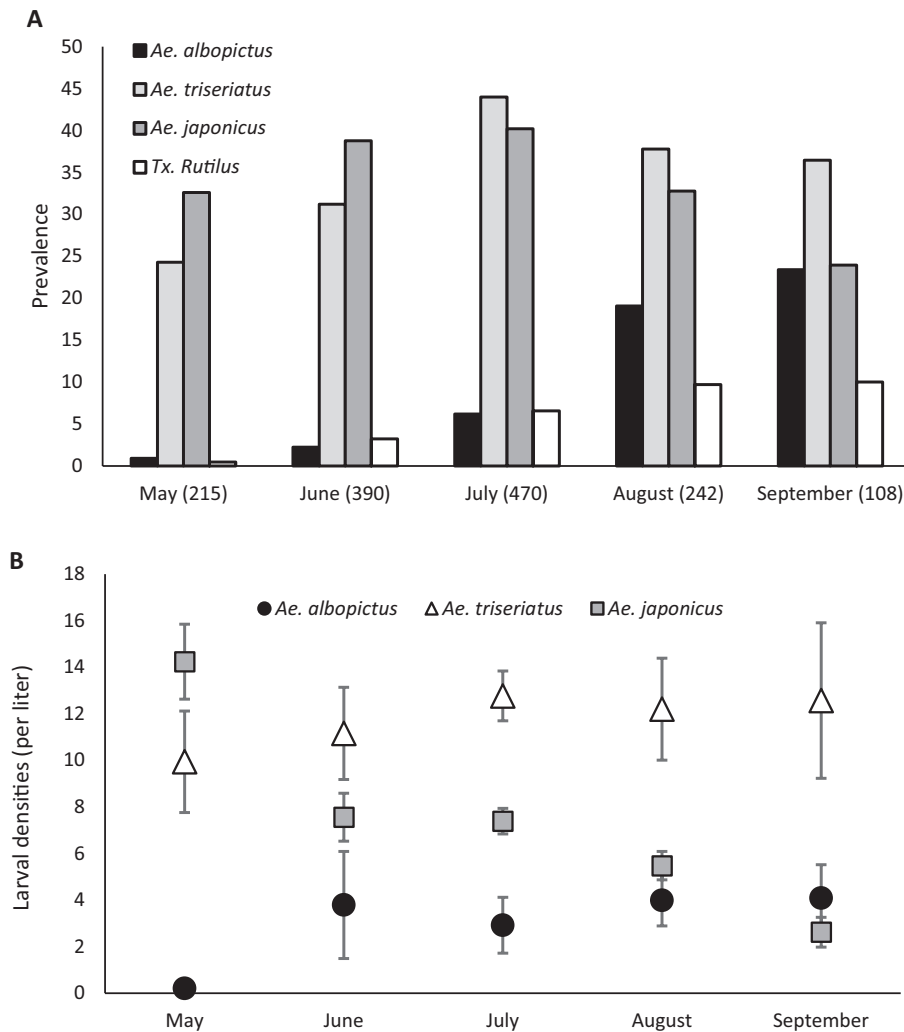


Fig. 2. (A) The prevalence (% occupancy) of *Aedes albopictus*, *Aedes triseriatus*, *Aedes japonicus*, and *Toxorhynchites rutilus* in larval samples taken in each month, combining the data from 2012 to 2017. Numbers in parentheses are the total number of samples collected. (B) Natural larval densities, in larvae per liter, of these species in artificial habitats at TRC, excluding samples where the focal species was absent.

It is not entirely clear why *Ae. albopictus* does not dominate the mosquito community in artificial containers in this temperate forest. *Aedes albopictus* has been described as a forest edge species in its native range (Hawley 1988) and has been repeatedly documented utilizing forested areas of Florida (Kesavaraju et al. 2008) and Brazil (Lourenço-de-Oliveira et al. 2004, Ferreira-de-Lima et al. 2020). The most common larval mosquito habitat in temperate oak-hickory forests are likely treeholes (Westby et al., personal observations), though it is plausible that forested areas are used as dump sites elsewhere. *Aedes albopictus* is rarely found in treehole surveys in northern latitudes potentially limiting the potential for populations to grow large in these habitats (Livdahl and Willey 1991, Edgerly et al. 1999, Bartlett-Healy et al. 2012, Freed and Leisnham 2014). The reason that *Ae. albopictus* is rare or absent from treeholes may be intense competition with, or intraguild predation by (Edgerly et al. 1999), the native *Ae. triseriatus* (the eastern treehole mosquito), differences in resource availability (Livdahl and Willey 1991, Yee et al. 2012), high tannin concentrations (Sota 1993), or predation by *Toxorhynchites* (Griswold and Lounibos 2005, Murrell and Juliano 2013, Freed and Leisnham 2014). *Toxorhynchites rutilus*, which is an effective predator on *Ae. albopictus*, was detected in $\leq 10\%$ of container samples throughout the course of this study

(Fig 2B), a pattern observed in a field experiment manipulating size and drying in plastic containers at TRC (Westby and Juliano 2017). These previous studies suggest that natural densities of this predator in artificial containers at TRC are unlikely to account for the habitat-wide paucity of *Ae. albopictus* at TRC, despite evidence from manipulative experiments that *Tx. rutilus* can impact community composition within experimental containers (Juliano et al. 2019). No *Ae. albopictus* have been found in treehole surveys at TRC (Westby, unpublished data; Juliano, unpublished data), though most of the data collected at this site have been from artificial containers. Importantly, dozens of artificial containers of multiple sizes have been permanently established on the TRC property since 2013, which would presumably allow for successful overwintering of populations and re-emergence in the spring.

Aedes albopictus is often shown to be the superior competitor compared with *Ae. triseriatus* and *Ae. japonicus* (Novak et al. 1993, Aliabadi and Juliano 2002, Bevins 2007, Armistead et al. 2008, Freed and Leisnham 2014) or competing simultaneously against both of these species (Murrell et al. 2015) in controlled experiments. A meta-analysis, however, yielded no evidence of competitive advantage of one species over the other and suggested competitive equivalence (Juliano 2010). Controlled laboratory and field competition experiments, however, are likely a poor representation of the conditions larvae

Table 1. Mean *Aedes albopictus* larvae collected per liter of water sampled in 2007 and from 2012 to 2017, the total number of samples taken in each month and year, and the number and percent of those samples that were occupied by *Ae. albopictus* na = larvae per liter is not available because water volume was not recorded. *Aedes albopictus* was collected in 2012 from egg samples; data not presented.

Year	Month	Mean larval density (per liter)	Standard error	Total samples taken	Number of containers occupied	Percent of containers occupied
2007	July	na	na	19	8	42.11
2007	Aug.	23.65	10	20	9	45
2007	Oct.	na	na	10	5	50
2012	June	0	0	36	0	0
2012	July	0	0	36	0	0
2012	Aug.	0	0	36	0	0
2013	May	0	0	123	0	0
2013	June	0.21	0.2	100	2	2
2013	July	2.6	2	132	19	14.39
2013	Aug.	5	3.9	98	13	13.27
2013	Sept.	2.7	2	78	9	11.54
2014	June	0	0	48	0	0
2014	July	0.07	0.05	96	3	3.13
2014	Aug.	0.33	0.11	48	10	20.83
2015	June	0	0	160	1	0.63
2015	July	0.01	0	160	3	1.88
2016	May	0.01	0.01	32	2	6.25
2016	June	0.62	0.58	16	4	25
2016	July	0.1	0.05	16	4	25
2017	May	0	0	60	0	0
2017	June	0.12	0.09	30	2	6.67
2017	July	0.12	0.09	30	2	6.67
2017	Aug.	1.56	0.32	60	33	55
2017	Sept.	2.32	0.62	30	24	80

encounter in these containers at TRC. First, the natural densities of *Ae. albopictus* recorded at TRC are well below the numbers typically used in these experiments by as much as an order of magnitude (see [Supp File \[online only\]](#)). Second, these experiments always begin with synchronously hatched, 24-h-old larvae. With installment hatching and phenological differences, *Aedes* larvae in natural communities would interact with all instars for much of the summer. Importantly, *Ae. triseriatus* and *Ae. japonicus* hatch earlier in the spring than *Ae. albopictus* (Murrell et al. 2014) potentially leading to priority effects that may partially explain why *Ae. albopictus* has failed to dominate artificial containers in this forest. Additionally, work in Japan has indicated that *Ae. albopictus* is not competitively dominant in forest habitats and may only be able to dominate in areas with large numbers of ephemeral, artificial containers where other species are rare or absent (e.g., urban centers; Sunahara et al. 2002; Mogi et al. 2017, 2020). Predation and larval competition are not the only plausible explanations for the patterns observed at TRC.

In fact, *Ae. albopictus* is often considered a human adapted, synanthropic species that is more abundant in urban and suburban areas compared with rural and sylvan areas (Barker et al. 2003, Obenauer et al. 2009, Li et al. 2014). Females have been documented migrating toward human habitats from forested areas of Brazil, implying a preference for human habitats which could explain the results presented here (Maciel-de-Freitas et al. 2006). Additionally, the abiotic environment in forests may be a factor. *Aedes albopictus* may be more adapted to higher temperatures than the species that dominate forested areas giving *Ae. albopictus* an advantage in cities which experience a heat island effect (Alam and Tuno 2020), although

lower survival has been documented in urban areas compared with suburban and rural areas of Georgia (Murdoch et al. 2017). It is also plausible that a preference for human and domestic animal hosts is limiting the abundance of this species in forests (Faraji et al. 2014).

Further research is needed to test the different proposed hypotheses about why it appears that *Ae. albopictus* does not dominate in these sylvan artificial containers (e.g., priority effects, temperature, host preferences). It would be informative to locate other large forest plots with an abundance of artificial containers to validate the findings of this study. Finally, it is important to continue to monitor these populations in the long term to assess changes in abundance and community composition under climate change.

Supplementary Data

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

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Data Availability

Data from this study are available from the Dryad Digital Repository: doi:10.5061/dryad.3r2280gdr (Westby, 2020).

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