Parasitism of Aedes albopictus by Ascogregarina taiwanensis lowers its competitive ability against Aedes triseriatus.

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Research

Keywords: mosquito population dynamics, competition, Aedes albopictus, Aedes triseriatus, parasitism, Ascogregarina taiwanensis, Ascogregarina barretti

Posted Date: January 19th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-51719/v3

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Version of Record: A version of this preprint was published on January 25th, 2021. See the published version at https://doi.org/10.1186/s13071-021-04581-0.
Parasitism of Aedes albopictus by Ascogregarina taiwanensis lowers its competitive ability against Aedes triseriatus

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Abstract

Background: Mosquitoes are vectors for diseases that significantly impact the human population such as dengue, malaria and La Crosse virus. When multiple mosquito species are present, the competition between species may alter population dynamics as well as disease spread. Two mosquito species, *Aedes albopictus* and *Aedes triseriatus*, both inhabit areas where La Crosse virus is found. Infection of *Aedes albopictus* by the parasite *Ascogregarina taiwanensis* and *Aedes triseriatus* by the parasite *Ascogregarina barretti* can decrease a mosquito’s fitness, respectively. In particular, the decrease in fitness of *Aedes albopictus* occurs through the impact of *Ascogregarina taiwanensis* on female fecundity, larval development rate, and larval mortality and may impact its initial competitive advantage over *Aedes triseriatus* during invasion.

Methods: We examine the effects of parasitism of gregarine parasites on *Aedes albopictus* and *triseriatus* population dynamics and competition with a focus on when *Aedes albopictus* is new to an area. We build a compartmental model including competition between *Aedes albopictus* and *triseriatus* while under parasitism of the gregarine parasites. Using parameters based on literature, we simulate the dynamics and analyze the equilibrium population proportion of the two species. We consider the presence of both parasites and potential dilution effects.

Results: We show that increased levels of parasitism in *Aedes albopictus* will decrease the initial competitive advantage of the species over *Aedes triseriatus* and increase the survivorship of *Aedes triseriatus*. We find *Aedes albopictus* is better able to invade when there is more extreme parasitism of *Aedes triseriatus*. Furthermore, although the transient dynamics differ, dilution of the parasite density through uptake by both species does not alter the equilibrium population sizes of either species.

Conclusions: Mosquito population dynamics are affected by many factors, such as abiotic factors (e.g. temperature and humidity) and competition between mosquito species. This is especially true when multiple mosquito species are vying to live in the same area. Knowledge of how population dynamics are affected by gregarine parasites among competing species can inform future mosquito control efforts and help prevent the spread of vector-borne disease.

Keywords: mosquito population dynamics; competition; *Aedes albopictus*; *Aedes triseriatus*; parasitism; *Ascogregarina taiwanensis*; *Ascogregarina barretti*
Discussion of triseriatus and its parasite

Parasitism relating to albopictus parameters throughout

Story "if albopictus invading" but over time likely to gain parasites

Make sure categories are numbers throughout.

Background

La Crosse encephalitis virus (LACV) can cause brain swelling and lead to severe neuroinvasive disease in children under 15 [1], which can cause lifelong health effects [2] While it only leads to a few reported cases each year, it is likely under reported.

We focus on two species known to transmit LACV, Aedes albopictus and Aedes triseriatus, and competition between them [3, 4]. Female mosquitoes of these species may become disease vectors when they feed on infected individuals and transmit the virus to other animals or humans via a second blood meal [5].

Aedes (Ae.) albopictus, also known as the Asian tiger mosquito, is native to subtropical regions of southeast Asia, and is a common vector of arboviruses such as Dengue fever virus, West Nile virus, and La Crosse encephalitis virus [6]. The first appearance of Ae. albopictus in the United States was in Houston, Texas in 1985 [7, 8]. Since its introduction, Ae. albopictus has spread throughout the continental United States, and now occupies much of the southern and eastern US, stretching from Texas to New Jersey [9]. Ae. albopictus is known for its ability to adapt to a range of climates and to be a strong competitor to other species that share larval habitats [10]. In 2001, La Crosse virus was isolated in Ae. albopictus [11]. Fourteen years later, it was estimated that 3.01 of every 1000 Ae. albopictus were infected with the La Crosse virus [12].

Ae. triseriatus, known as the eastern tree hole mosquito, is native to the eastern United States. Ae triseriatus is the primary vector for the La Crosse virus [3, 4], a pathogen endemic to southwest Virginia [3, 2]. Ae. albopictus will bite both small mammals and humans, making it more likely to infect human’s than Ae triseriatus whose preference is for small mammals [4].

Several laboratory studies have shown that Ae. albopictus is the superior competitor compared to Ae. triseriatus [13, 14, 15, 16, 17, 18, 19]. In Bevins [14], they showed a ten percent drop in survival for Ae. triseriatus when a quarter of the
mosquitoes present were *Ae. albopictus* and a twenty percent drop in *Ae. triseriatus* survival when half of the mosquitoes were *Ae. albopictus*. In Ho et al. [13], the authors showed that while the development time of *Ae. albopictus* was not significantly altered by competition, the development time of *Ae. triseriatus* was increased when in a shared habitat with other *Aedes* species. Moreover, *Ae. albopictus* larvae inhibit egg hatching of other species such as *Ae. triseriatus*, while there is no significant inhibition on their own species [15]. However, in a more recent meta-analysis, competitive equivalence of *Ae. albopictus* and *Ae. triseriatus* was suggested [20]. In a study with two different environments, they found that *Ae. albopictus* did much better in tires, but did worse than *Ae. triseriatus* in treeholes [16].

*Ae. albopictus* and *Ae. triseriatus* are parasitized by *Ascogregarina (As.) taiwanensis* and *Ascogregarina (As.) barretti*, respectively. *Ascogregarina* are intestinal protozoan parasites that inhabit the gut of the mosquito throughout its life cycle [7, 21]. The effects and prevalence of these parasites are heterogeneous. In the wild, typically 67 to 95% of a given population of *Ae. albopictus* are infected with *As. taiwanensis* [22]. Infection of *Ae. albopictus* by *As. taiwanensis* lengthens larval development time for both males and females mosquitoes, reduces adult female fecundity, increases larval mortality, and reduces egg laying and hatching rates [7, 23]. However, Aliabadi and Juliano saw that mortality of *Ae. albopictus* was not significantly affected by *As. taiwanensis* [7]. For *Ae. triseriatus*, one study found 80% of their collected sites harbored *As. barretti*. Treeholes showed more infected sites than tires [24]. In contrast another study found that only 5% and 23.6% of *Ae. triseriatus* are infected [25]. Development time and mortality have been seen to increase in *Ae. triseriatus* when infected by *As. barretti* [21, 25]. However, Beier and Harris [24] showed no significant effect of *As. barretti* on *Ae. triseriatus* mortality. While *As. barretti* impacts the fitness of *Ae. triseriatus*, its effects are mostly dependent on resource availability [21]. In low resources they find that *Ae. triseriatus* development time is increased significantly, but with sufficient resources there is not a significant difference. Another study showed a significant difference in survival of *Ae. triseriatus* infected with *As. barretti* as compared to those uninfected [25].

In this work, we build a mathematical model of *Aedes* population dynamics accounting for parasitism of *Ae. albopictus* by *As. taiwanensis* and *Ae. triseriatus* by *As. barretti*. Our model formulation encodes competition between the two species of
Aedes using the Lokta-Volterra model, a basis for many inter-specific competition models [26, 27, 28, 29, 30, 31] including mosquito populations [16, 32, 33, 34]. In Kuno [35], a two species Lokta-Volterra competition model is introduced, which includes reproductive interference. Other competition models also show the importance of reproductive interference between Ae. aegypti and Ae. albopictus [34, 36]. However, in contrast to the reports on reproductive interference seen with Ae. albopictus and Ae. aegypti, there appears to be a lack of studies evaluating reproductive interference between Ae. albopictus and Ae. triseriatus. Livdahl and Willey [16] compared Ae. albopictus and Ae. triseriatus using a Lokta-Volterra model to explain possible competition affects either in tree holes or in tires. This model was then extended to include La Crosse spread [32] and showed a lack of importance of Ae. albopictus in recent resurgence of LACV.

The life cycle of gregarine parasites mimics that of their host: each stage of its development is analogous to a stage within mosquito development. See the inset into Fig 1. Transmission of gregarine parasites is horizontal between individuals of Aedes mosquitoes, and does not occur from parent to offspring [22]. Initial infection occurs when the mosquito larvae ingest oocysts. After ingestion, the gregarine parasite travels through the midgut, epithelial tissues, and excretory system of the mosquito, transitioning into different life stages as the mosquito matures to adulthood. From there, the parasite reproduces and offspring are excreted by the adult mosquitoes into breeding containers [37, 38].

Since new Ae. albopictus habitats are unlikely to be contaminated with As. taiwanensis, then new populations of Ae. albopictus can initially escape parasitism. This lack of parasite infection in newly established populations gives the mosquito a potential competitive advantage over Ae. triseriatus [7, 22]. Knowledge of how parasite infection affects the survivorship of Ae. albopictus will provide insight into the competition between the two mosquito species, and subsequently, help to deepen understanding of the spread of mosquito-borne infectious disease. In this study, we examine whether the parasitism of Ae. albopictus by As. taiwanensis decreases the mosquito’s competitive ability enough to alter the dynamics between the two Aedes mosquitoes. We build a compartmental model of the interactions of the two mosquito species and the effect of the parasites As. taiwanensis and As. barretti. We
parameterize the model from published literature, simulate dynamics, investigate a wide parameter space, and examine the effects of parasitism.

**Methods**

We constructed a four compartment model of mosquito population dynamics including larval and adult stages of both *Ae. albopictus* and *Ae. triseriatus* (Eq. 1). We simplify the life cycle of the *Aedes* mosquito to just two stages because most, if not all, of the effects of competition and parasitism are felt at the larval and adult stages. Furthermore, including all mosquito life stages would unnecessarily complicate the model. We based our model of competition on the Lotka-Volterra model of species interaction [39, 40, 41, 42]. We use the Lotka-Volterra model to incorporate inter-specific competition between the two species and include effects of parasitism. We assume a fixed level of parasitism in *Ae. triseriatus*, impacting development time and mortality. We consider two conditions: either a high or low effect of *As. barretti*. To model the effect of different *As. taiwanensis* parasite levels as *Ae. triseriatus* becomes established, we vary the level parasitism. We incorporate the effect of parasitism on *Ae. albopictus* in three ways: (i) decreased fecundity, (ii) increased development time, and (iii) increased larval mortality. This provides a potential decrease in the competitive advantage of *Ae. albopictus* over the population of *Ae. triseriatus* as *Ae. albopictus* becomes established in a new area.

The model includes four compartments: larval *Ae. albopictus* (*L_a*), adult *Ae. albopictus* (*A_a*), larval *Ae. triseriatus* (*L_t*), and adult *Ae. triseriatus* (*A_t*). Larval mosquitoes *L_i* are born at rate $\beta_i$, die at rate $\mu_{L_i}$, and develop at rate $\delta_i$ where $i \in \{a, t\}$. Adults emerge from larva at rate $\delta_i$ and die at rate $\mu_{A_i}$ where $i \in \{a, t\}$ for *Ae. albopictus* and *Ae. triseriatus*, respectively. Similar formulations for *Ae. albopictus* population dynamics are found in [43]. The parameters $\rho_{a}$ and $\rho_{t}$ represent the proportion of adults that are female. $K$ is the carrying capacity of the larval population for the two species. The Lotka-Volterra competition coefficients, $\alpha_a$ and $\alpha_t$, quantify the intrinsic effect of one species on the other. Parasitism for *Ae. albopictus* is included through the parameters representing effects on female fecundity ($\gamma_{b_a}$), larval development rate ($\gamma_{d_a}$), and larval mortality ($\gamma_{m_a}$). The parasite parameters for *Ae. triseriatus* are larval development rate ($\gamma_{d_t}$), and larval mortality ($\gamma_{m_t}$). This forms our system of ordinary differential equations:
\[
\frac{dL_a}{dt} = \frac{\beta_a}{\gamma_a} L_a \rho_a A_a \left( 1 - \alpha_L L_t + \frac{\alpha_a L_a + \alpha_L L_t}{K} \right) - \frac{1}{\gamma_{da} \delta_a} L_a - \gamma_{m_a}\mu L_a L_a,
\]
\[
\frac{dA_a}{dt} = \frac{1}{\gamma_a \delta_a} L_a - \mu A_a A_a,
\]
\[
\frac{dL_t}{dt} = \rho_t \beta_t A_t \left( 1 - \frac{\alpha_a L_a + \alpha_L L_t}{K} \right) - \frac{1}{\gamma_{d_L} \delta_t} L_t - \gamma_{m_L} \mu L_t L_t,
\]
\[
\frac{dA_t}{dt} = \frac{1}{\gamma_{d_L} \delta_t} L_t - \mu A_t A_t.
\]

(1)

From a literature search, we determined biologically relevant ranges for parameter values. A description of the parameters is provided in Table 1. As it was often difficult to directly find relevant values in the literature, we transformed values found to meet our parameter descriptions. The birthrate was calculated from data for gross reproductive rate (GRR) and length of gonotrophic cycle (GC) by taking the minimum GRR and dividing by the maximum length of the GC. The maximum value was found by dividing the maximum GRR by the minimum GC length [44]. With this, we calculated a range of 2.5 to 56 eggs laid per adult female per day. A similar calculation was performed to find a birthrate for *Ae. triseriatus*, where we calculated a range of 3 to 26 eggs laid per adult female per day [45, 46]. Development time can vary based on a variety of factors and has been found to be as short as 9 days and as long as 40 days for *Ae. albopictus* [13, 47, 48]. *Ae. triseriatus* has been shown to develop slower than *Ae. albopictus* [13, 18]. In the model, these values are incorporated directly as development time of larvae, \((\delta_a)\) and \((\delta_t)\). Larval \((\mu_{L_a})\) and adult \((\mu_{A_a})\) mortality for *Ae. albopictus* were calculated to be 0.067 and 0.05, respectively, from survival rates and development rates [13, 44, 47, 48], such that \(\mu = 1 - (\text{survival rate})^{(1/\delta)}\). For *Ae. triseriatus*, larval \((\mu_{L_t})\) and adult \((\mu_{A_t})\) mortality were found to be 0.009 and 0.1, respectively [49, 50]. The carrying capacity for the larval population of both species \((K)\) was set at 60 as was used for a study performed in 200ml of water [7]. It is important to note that this number is relative and could be scaled to fit different size larval containers. In this study we focus on the proportion of each species such that raw population sizes are not influential. There is evidence of potential sex imbalance among mosquitoes especially under low food resources. Thus, for *Ae. triseriatus*, we set the proportion of females, \(\rho_t\), to be
between 0.2 and 0.6 [17]. In the same study, *Ae. albopictus* showed less variation, 0.4 – 0.55, in the proportion females, so we set \( \rho_a \) accordingly.

In Livdahl and Willey [16], the competition parameters from the Lokta-Volterra model were fit using nutrient fluids. The competition parameter of *Ae. albopictus* on *Ae. triseriatus* (\( \alpha_a \)) and the competition parameter of *Ae. triseriatus* on *Ae. albopictus* (\( \alpha_t \)) were found to be 0.42 and 0.73 in treehole fluid and 0.83 and 0.25 in tire fluid, respectively. There are many factors that dictate which species will be the better competitor; however, as we consider that *Ae. albopictus* is generally the greater competitor, we choose a range of [0, 0.75] for the effect on *Ae. albopictus* from *Ae. triseriatus* and a range of [0.4, 1] for the effect on *Ae. triseriatus* from *Ae. albopictus*.

The effects of parasitism for *Ae. albopictus* on female fecundity (\( \gamma_{b_a} \)), larval development rate (\( \gamma_{d_a} \)), and larval mortality (\( \gamma_{m_a} \)) were shown to vary with resource availability and environmental context [23, 7, 25, 51]. In Comiskey et al. [23], they found that in low resources the mortality of infected *Ae. albopictus* larvae was seven times greater than uninfected. They also found that fecundity and fertility was reduced by over 20% as well as development time was increased by 44%. In Aliabadi and Juliano [7], they showed that development time of infected *Ae. albopictus* increases with greater interspecific competition with *Ae. triseriatus*. Whereas without *Ae. triseriatus*, the median development time of infected *Ae. albopictus* was not significantly different. They also found that survival rates were significantly different for *Ae. triseriatus* at lower densities with *Ae. albopictus*. They did not observe a significant change in survival for *Ae. albopictus* from parasitism, but a greater effect from intra- and inter-specific competition. *Ae. triseriatus* was found in one study to have as high as 2.8 to 3.5 greater death rates when infected [25]. In a relatively recent study by Soghigian and Livdahl [51], they show that in the absence of parasite infection, survival of *Ae. albopictus* is about 98%, but with the greatest amount of infection observed, the survival decreases to approximately 71%. This constitutes a 15 times greater mortality rate. In another study by Walker et al. [21], they found an increase in development time for *Ae. triseriatus* in the laboratory with low resources, but not in the field experiment.

We initially set all *Ae. albopictus* parasite parameter values to one, which represents the case with no parasitism. We then consider ranges from 1 to 2 for parasite’s
effect on fecundity and development time and 1 to 16 for mortality. These values were chosen to cover the ranges of changes found in [23, 51]. We will extend the ranges of the parasite parameters for development time and fecundity in further analyses. We are assuming that *Ae. triseriatus* is already infected, so we initially fix these parameter values as $\gamma_{dt} = 1.2$ and $\gamma_{mt} = 1.5$ to be a relatively small effect. We also consider a higher effect to parasitism with $\gamma_{dt} = 2$ and $\gamma_{mt} = 4$ as a comparison. If $\gamma_{dt} = 5$, this would mean that the development time was 5 times greater when *Ae. albopictus* is infected with its parasite. If any of the parasite parameters are set to one this indicates no effect of parasitism.

We simulated the mosquito population dynamics from our ODE model in Matlab. Fixed parameter values, shown in Table 1, were used in these simulations. The initial conditions used for all simulations were $L_a = 30$, $A_a = 0$, $L_t = 30$, and $A_t = 0$. We use these initial condition for consistency with Aliabadi and Juliano [7], but as we run the simulation until equilibrium other initial values will give the same results. Simulations were run for 2000 days, long enough such that the population of *Ae. albopictus* and *Ae. triseriatus* larvae and adults reached equilibrium. To begin we considered two competition scenarios. The first is the environment within a tire ($\alpha_a = 0.83, \alpha_t = 0.25$), which indicates that *Ae. albopictus* has more effect on *Ae. triseriatus*. In the second scenario, the environment in a treehole ($\alpha_a = 0.42, \alpha_t = 0.73$), such that *Ae. triseriatus* has a greater effect on *Ae. albopictus*. These parameters were from fitted data in Livdahl and Willey [16].

We performed a parameter sweep by sampling ranges of the parameters using Latin Hypercube Sampling (LHS) in Matlab [52]. We conducted this with a sample size of 100,000, and sampled 12 of the parameters: $\beta_a$, $\beta_t$, $\delta_a$, $\delta_t$, $\mu_{L_t}$, $\mu_{A_t}$, $\mu_{L_a}$, $\mu_{A_a}$, $\alpha_t$, $\alpha_a$, $\rho_t$, and $\rho_a$. Values for parasitism on *Ae. albopictus* ($\gamma_{ba}$, $\gamma_{da}$, $\gamma_{ma}$) were fixed at 1, and $K$ was fixed at 60. The LHS was completed twice: first with the parasite parameters for *Ae. triseriatus* set at $\gamma_{dt} = 1.2$ and $\gamma_{mt} = 1.5$ and then again with them set at $\gamma_{dt} = 2$ and $\gamma_{mt} = 4$. With the results generated by the LHS, we generated a histogram reflecting the type of outcomes of each of the samples. We categorized the results into seven categories, described in Table 2. These categories were based on the proportion of the population occupied by *Ae. albopictus* as follows: In category (1), a proportion of less than 0.01; in category (2), a proportion of 0.01 to 0.2; in category (3), a proportion between 0.2 and 0.4;
in category (4), a proportion between 0.4 and 0.6; in category (5), a proportion between 0.6 and 0.8; in category (6), a proportion between 0.8 and 0.99; and in category (7) a proportion greater than 0.99. We then did a sensitivity analysis on the parameters to account for uncertainty and variation in parameters by partial rank correlation coefficient [53].

After sampling the space of the twelve parameters in the model in the absence of parasitism in *Ae. albopictus*, we focused on investigating the effects of the parasite. We repeated the LHS including the parasite parameters for *Ae. albopictus*. We also performed sensitivity analysis on the 100,000 samples that includes varied parasite effects. The mortality and fecundity parasite parameter were varied from 1 to 4 and the development time parasite parameter varied from 1 to 16, where a value of 1 means the parasite has no effect and a value of 3 means a 3 fold increase of the associated parameter value. This means that mortality or development time is increased or fecundity is decreased compared to the value without parasitism.

To examine the varying effects of parasitism, all parameters were fixed as listed in Table 1 except we varied the three *Ae. albopictus* parasite parameters with *Ae. triseriatus* fixed at either a high or low parasite effect. We compared effects on female fecundity, larval development rate, and larval mortality to see how these different combinations led to different outcomes in terms of the proportion *Ae. albopictus* in the final population. We extended the range of the parasite parameters so that all were varied from 1 to 10.

Dilution effects

A recent study by Westby et al. [54] showed that with *Ae. japonicus* and *Ae. triseriatus* there was a dilution effect on the amount of parasitism. *Ae. japonicus* decreased the number of *As. barretti* by consuming the parasite and not propagating it [54]. We consider this idea with the two species model, by allowing the parasitism parameters to have decreased effect in the presence of greater proportions of the competing species, a so-called ‘dilution’ effect. We modify the model by making all parasite parameters a function of the proportion of the total population. Specifically each parasite parameter will linearly decrease from the maximum value $\gamma_{i,\text{max}}$ to one.
This is captured by:

\[ \gamma_i(p) = (\gamma_{i_{\text{max}}} - 1)p + 1 \]  

(2)

where \( p \) is the proportion of a species. We choose a linear function for simplicity.

Notice that if \( p = 1 \), \( \gamma_i = \gamma_{i_{\text{max}}} \) which indicates that if a particular species is 100% of the population, then their parasite parameters will be at its maximum. If \( p = 0 \), \( \gamma_i = 1 \), this means that as the species goes to 0% of the population, the parasite effect of the parameter will linearly decrease to no parasite effect. In Westby et al. [54], they see a large decrease in the amount of parasitism (≈ 82% reduction), so we allow parasitism parameters to approach 1, as the proportion of larvae goes to zero. Recall that, when the parasite parameters equal one, this represents no effect of parasitism. Thus, our revised system of equations becomes:

\[
\begin{align*}
\frac{dL_a}{dt} &= \frac{\beta_a \rho_a A_a}{\gamma_{d_a}(P_a)} \left( 1 - \frac{L_a + \alpha_t L_t}{K} \right) - \frac{1}{\gamma_{d_a}(P_a) \delta_a} L_a - \gamma_{m_a}(P_a) \mu_{L_a} L_a, \\
\frac{dA_a}{dt} &= \frac{1}{\gamma_{d_a}(P_a) \delta_a} L_a - \mu_{A_a} A_a, \\
\frac{dL_t}{dt} &= \rho_t \beta_t A_t \left( 1 - \frac{\alpha_t L_a + L_t}{K} \right) - \frac{1}{\gamma_{d_t}(P_t) \delta_t} L_t - \gamma_{m_t}(P_t) \mu_{L_t} L_t, \\
\frac{dA_t}{dt} &= \frac{1}{\gamma_{d_t}(P_t) \delta_t} L_t - \mu_{A_t} A_t.
\end{align*}
\]

where \( P_a = \frac{L_a}{L_a + L_t} \) and \( P_t = \frac{L_t}{L_a + L_t} \).

We then consider four cases by choosing different maximum parameters for parasitism, \( \gamma_{i_{\text{max}}} \). These combinations are: \textit{Ae. albopictus} and \textit{Ae. triseriatus} both have minor effects of parasitism, both have more severe effects, and only one has severe effect and the other minor effect. See Table 3 for specific choices for maximum parasite parameters.

\textbf{Results}

To begin, we model the population dynamics of \textit{Ae. albopictus} and \textit{Ae. triseriatus} without parasitism. We consider two separate environments: tire and treehole. The difference between the two scenarios is the Lokta-Volterra competition parameters \((\alpha_t \text{ and } \alpha_a)\) that were fit for each environment from Livdahl and Willey [16]. In both cases, the populations settle to an equilibrium. In the tire environment, the
population ends in category 6, in which *Ae. albopictus* dominates, but *Ae. triseriatus* remain at low levels (Fig. 2, right). After 150 days, we find 126 adult *Ae. albopictus* compared to about 5 adult *Ae. triseriatus*. For the treehole environment, the population ends in category 5 (Fig. 2, left), where *Ae. albopictus* is still the dominant species, but *Ae. triseriatus* has a sizeable population. After 150 days, there are approximately 54 *Ae. albopictus* and 19 *Ae. triseriatus*. Parameter values are estimated averages from literature and are found in Table 1.

To account for known variability in parameters, we examined dynamics across broad parameter space using a LHS with the ranges indicated in Table 1. Assuming no effects of parasitism in *Ae. albopictus* and low effect in *Ae. triseriatus*, we find that the majority, 56%, of simulations fall into category 6 (Fig. 2, a), where *Ae. albopictus* strongly dominates. This is the same result as in the tire scenario. In addition, approximately 25% of the simulations fall into the same category as the treehole scenario (category 5). Only 3.5% of the total 100,000 samples led to categories in which *Ae. triseriatus* is greater in population than *Ae. albopictus* (categories 1, 2 and 3). A further 10.5% of the simulation fell into coexistence with approximately equal amounts of both species (category 4). For a small number of simulations (5%) *Ae. albopictus* completely eliminated *Ae. triseriatus* without parasitism (category 7), but the most common scenario was for *Ae. albopictus* to be the dominant species and strongly limit the population of *Ae. triseriatus*.

If we increase the effect of parasitism in *Ae. triseriatus*, we find that their is a strong shift in scenarios to where *Ae. albopictus* is the dominant species (Fig. 2c). In this case, approximately 66% of parameter selected fall into category 6 (few *Ae. triseriatus*) and 9.9% of situations lead to elimination of *Ae. triseriatus* (category 7). *Ae. triseriatus* is only ends in greater proportion that *Ae. albopictus* in approximately 1% of the parameters sampled.

**Including parasitism in *Ae. albopictus***

When we include the effects of parasitism for *Ae. albopictus* in the dynamics, we greatly increase the parameter space where *Ae. triseriatus* is the dominant species. We use LHS but include the parameters for parasitism: $\gamma_d$, $\gamma_m$, and $\gamma_b$. We find that results falling in categories 1-4 have greatly increased while those in categories 6 and 7 have significantly decreased (Fig. 2 b, d). In fact, *Ae. triseriatus* complete
eliminates (category 1) *Ae. albopictus* in approximately 15.0% and 15.3% of the simulations for low and high *Ae. triseriatus* parasitism, respectively. Rather, in 30.7% and 24.4% of the simulations *Ae. triseriatus* is the dominant species (category 1,2,3) and the sum of all categories where *Ae. albopictus* will be the dominant species is reduced to 54.7% and 64.8% (sum of category 5,6,7) with low and high parasitism for *Ae. triseriatus*, respectively. The total simulations with outcomes in categories 5,6,7 is similar to the amount in only in category 6 without *Ae. albopictus* parasitism. With parasitism of *Ae. albopictus* category 6 still has the most outcomes, but the outcomes have spread out. Overall, we see that without parasitism *Ae. albopictus* will be the dominant vector; however, once parasitism takes place *Ae. triseriatus* can become dominant.

To further examine the effects of parasitism, we vary the level of each of the three parasitism parameters. We perform these variations pairwise under four environmental scenarios: tire (Fig. 3 Quadrants I and IV) and tree hole (Fig. 3 Quadrants II and III) with both low and high parasite effect on *Ae. triseriatus*. Recall, the difference between the two scenarios is the competition parameters ($\alpha_t$ and $\alpha_a$). In the tire scenario, the competition effect of *Ae. albopictus* on *Ae. triseriatus* is greater ($\alpha_a = 0.83 > 0.25 = \alpha_t$) and for the treehole scenario, the competition effect of *Ae. triseriatus* on *Ae. albopictus* is greater ($\alpha_a = 0.42 < 0.73 = \alpha_t$). All other parameters are fixed (Table 1). The colors in these images correspond to the colors the seven categories from Table 2, although only six colors appear as category 7 never occurs in these simulations. Parasitism effects were varied pairwise. First, parasite effects on larval mortality ($\gamma_{ma}$) and larval development time ($\gamma_{da}$) were varied with three constant levels of the effect on female fecundity ($\gamma_{ba} = 1,3,5$) (Fig. 3). Then, parasite effects on female fecundity ($\gamma_{ba}$) and larval development time ($\gamma_{da}$) were varied with three constant levels of the effect on mortality ($\gamma_{ma} = 1,3,5$). Finally, parasite effects on larval mortality ($\gamma_{ma}$) and female fecundity ($\gamma_{ba}$) were varied with three constant levels of the effect on larval development time ($\gamma_{ma} = 1,3,5$). We present these results in the supplemental material as they are very similar to those found from fecundity versus development time.

In the tire scenario ($\alpha_a = 0.83 > 0.25 = \alpha_t$), we find that in large portions of parameter space *Ae. albopictus* strongly dominates, i.e. category 6 (Fig. 3 quadrants I and IV, dark yellow). When the effect on female fecundity ($\gamma_{ba}$) is fixed at one,
the transition to a greater level coexistence between the mosquito species is only
seen at higher levels of effects on larval development rate ($\gamma_{da}$), with values around
$\gamma_{da} > 4$ (Fig. 3b quadrant I and IV). For female fecundity ($\gamma_{ba}$) fixed at three and
five (Figure 3d,f quadrant I and IV), development time effects as low as $\gamma_{da} \approx 2$
result in a shift to a low proportion of *Ae. albopictus* (category 5 green). In order
for *Ae. triseriatus* to be the dominant species there must be very high effects of all
three parasitism parameters effecting *Ae. albopictus*, regardless of *Ae. triseriatus’
level of parasitism.

Parasite effects on development time have more significant effects than on mortal-
ity or fecundity. In the tire scenario, this is most apparent when there is no change
in development time (Fig. 3a), then *Ae. albopictus* always strongly dominates. Ad-
ditionally, there is no change in category, regardless of the strength of the effect on
mortality and fecundity or parasitism on *Ae. triseriatus*. In the tire scenario, if the
effect on development time is increased by three times (Figure 3c), both effects on
fecundity and mortality must be relatively high to get higher levels of *Ae. trise-
riatus*. Furthermore, *Ae. triseriatus* will only dominate if both parasite effects on
fecundity and mortality are greater than ten. When development time in tires is five
times greater, only a small effect by the other two parameters is needed to decrease
the proportion of *Ae. albopictus* to category 5. Similarly, with fixed fecundity, when
the parasite increases the development time seven fold, we see that regardless of the
other two parameters, the proportion of *Ae. albopictus* decreases to at minimum
category 5 (Fig. 3f, green and blue).

In the treehole scenario, *Ae. triseriatus* has more of a competitive effect on *Ae.
albopictus*. As seen with the absence of parasitism for *Ae. albopictus* with low effect
of parasitism on *Ae. triseriatus*, the default is category 5 (Fig. 3 a,b Quadrant III,
green in bottom left corner), in which *Ae. albopictus* is still the dominant species,
but there are a larger number of *Ae. triseriatus*. In this situation, the effect on
development time must only increase two-fold for the proportion of *Ae. albopictus
to decrease to category 4 (Fig. 3b Quadrant III, teal), in which there are relatively
similar amounts of both species. When the effect on fecundity is set to 3 (Fig.
3d Quadrants II, III) and the effect of development time is greater than four, *Ae.
triseriatus* will be the dominant species (all three shades of blue). When the effect of
fecundity is set to 5 (Fig. 3f Quadrants II, III) and the development time is above
three, *Ae. triseriatus* will dominate. A similar result is seen when development
time is five times greater (Fig. 3e Quadrants II, III). For all values of the other
two parameters, *Ae. triseriatus* is the dominant species. In fact, almost half of the
parameter space considered falls into category 1 where *Ae. albopictus* is eliminated
darkest blue). Without any parasite effects on development time (Fig. 3a Quadrants
II, III) there is only a chance for the two species to be relatively equal if both other
parameters are greater than 7 and low effect of parasitism on *Ae. triseriatus*.

Overall, in tires, only with very high effects on all three parameters do we find
that *Ae. albopictus* is dominated by *Ae. triseriatus*. While in treeholes, we find that
less parasitism is needed to eliminate *Ae. albopictus*, i.e. only high effects on two of
the *Ae. albopictus* parasite parameters. In both scenarios, as we increase the effects
of the parasite parameters we see that the proportion of *Ae. albopictus* decreases.
The change is most notable as the parasite effect on *Ae. albopictus* development
time is increased, regardless of the scenario.

**Importance of parameters**

From the parameters selected using LHS with low effect of parasitism on *Ae. triseriatus*, we looked at the partial rank correlation coefficient (PRCC) for each parameter with respect to the final proportion of *Ae. albopictus* at 2000 days. In the case without parasitism, we find that all parameters have a significant impact on the model (Fig. 4, top row). When parasitism is included (Fig. 4, bottom row), the parameters which are not significant are all related to *Ae. triseriatus*: death of larvae, $\mu_L$; and proportion of females, $\rho_f$.

In the case without parasitism, the parameter with the most influence (largest
PRCC value in magnitude) is the competition parameter $\alpha_a$, which is the inter-
specific competition effects on *Ae. triseriatus* from *Ae. albopictus*. With a PRCC
value of 0.8469, the more $\alpha_a$ increases the greater proportion of *Ae. albopictus*. There
are several parameters which have fairly large correlation. The following parameters
all have a PRCC value greater than 0.5 in magnitude (in the order of greatest
magnitude to lowest): death rate of adult *Ae. albopictus*, $\mu_{A_a}$; *Ae. albopictus* larval
development time, $\delta_a$; *Ae. triseriatus* larval development time, $\delta_t$, the competition
parameter $\alpha_t$ on *Ae. albopictus*; and death rate of adult *Ae. triseriatus*, $\mu_{A_t}$. We see
that the most important parameters are the death rates of adults, transition rate
to adults, and the Lokta-Volterra competition parameters.

When we introduce parasitism parameters into the LHS, we see that the parasite’s
effect on development time $\gamma_{ma}$ has the 6th greatest impact, but the largest of all
the parasitism parameters. With a PRCC of $-0.1359$, we expect the increase of
$\gamma_{ma}$ to decrease the proportion of $\textit{Ae. albopictus}$. The death of adult $\textit{Ae. albopictus}$,
$\textit{Ae. albopictus}$ larval development time $\delta_{a}$, $\textit{Ae. albopictus}$ birth rate $\beta_{a}$, the Lokta-
Volterra competition parameter $\alpha_{t}$, and the death of $\textit{Ae. albopictus}$ larvae all have
greater PRCC values in magnitude than $\gamma_{da}$ (-0.2525, -0.2081, 0.1754, -0.1517, and
-0.1581, respectively). While less important than $\gamma_{ma}$, the other two parasite pa-
rameters are statistically significant ($p < 0.00001$) as well. The PRCC value for the
parasite’s effect on development time is $-0.1039$ and the for the parasite’s effect on
fecundity is $-0.05$.

When we consider the LHS with high effect of parasitism on $\textit{Ae. triseriatus}$, all
parameters have much lower effect, as indicated by the lower magnitude of PRCC
value. The parameter with the greatest magnitude PRCC (0.1666) is the Lokta-
Volterra competition parameter $\alpha_{a}$; this is the same parameter as found to have
the most impact when considering a low effect of parasitism on $\textit{Ae. triseriatus}$
and no parasite effect on $\textit{Ae. albopictus}$. In general, the trends of PRCC values for
the parameters are similar to with low effect of parasitism on $\textit{Ae. triseriatus}$. See
supplemental figure 5.

Dilution effects
When we consider including dilution effects into parasitism, we find that the equi-
librium values appear to be identical to the case without dilution. To ensure com-
parison of equivalent cases, we find the equilibrium proportion $\hat{P}_{a}$ of $\textit{Ae. albopictus}$
larvae under dilution. We use this in our dilution formula $\gamma_{i} = (\gamma_{max} - 1)\hat{P}_{a} + 1$
to find comparable parasitism parameters for the absence of dilution. Thus, at our
starting condition the parasite parameters in the two cases differ, due to the differ-
ent population proportions, but approach the same values at equilibrium (Fig. 5).
In Fig. 5, we plotted four different situations at which we have either high or low
parasite effect for the initial maximum parasite value (Table 3). While the equilibria
are identical, there is a difference in the dynamics before reaching the equilibrium.
This is particularly apparent in the case where *Ae. albopictus* starts with high parasite effect. In this case, *Ae. triseriatus* initially has a greater population, before *Ae. albopictus* becomes the dominant species.

**Analytical formulation of proportion of *Ae. albopictus***

We analyzed our model to determine the long term behavior for the proportion of *Ae. albopictus*. From the system of equations there are four possible equilibrium: extinction of mosquitoes, competitive exclusion with each species type present, and coexistence. Before we discuss our formula for the population proportion, we introduce the ratio which represents the reproduction number of each species, $R_t$ and $R_a$, for *Ae. triseriatus* and *Ae. albopictus*, respectively. These are given by:

$$
R_a = \frac{\beta_a \rho_a}{\gamma_{d_a}} \frac{1}{\mu A_a} \frac{1}{\frac{1}{\gamma_{d_a} \delta_a} + \gamma_{m_a} \mu L_a + 1},
$$

$$
R_t = \frac{\beta_t \rho_t}{\mu A_t} \frac{1}{\frac{1}{\gamma_{d_t} \delta_t} + \gamma_{m_t} \mu L_t + 1}.
$$

In each reproduction number, the first term is the the birth rate, $\frac{\beta_a \rho_a}{\gamma_{d_a}}$ for *Ae. albopictus* and $\frac{\beta_t \rho_t}{\mu A_t}$ for *Ae. triseriatus*. This is multiplied by the inverse of adult death rate, i.e. the expected life span of an adult mosquito. Together, these terms are the total expected number of eggs a female will lay in her life time. The final term has the development rate, (i.e. $\frac{1}{\gamma_{d_a} \delta_a}$ and $\frac{1}{\gamma_{d_t} \delta_t}$), divided by the sum of the development rate and death rate of larvae. This proportion is the probability of an egg surviving to adulthood. Overall, the reproductive number gives the total surviving children that a single female will lay. If $R_t > 1$, the population of *Ae. triseriatus* can establish. Similarly, if $R_a > 1$, *Ae. albopictus* can establish.

We determine the equilibrium for coexistence in terms of $R_t$ and $R_a$ (see supplemental material). From these we calculate the equilibrium proportion of adult *Ae. albopictus* by:

$$
\frac{A_a}{A_a + A_t} = \frac{w_d(1 - \alpha_t + \frac{\alpha_t}{\mu A_t} - \frac{1}{\frac{\gamma_{d_t} \delta_t} + \gamma_{m_t} \mu L_t})}{w_d(1 - \alpha_t + \frac{\alpha_t}{\mu A_t} - \frac{1}{\frac{\gamma_{d_t} \delta_t} + \gamma_{m_t} \mu L_t}) + q_d(1 - \alpha_a + \frac{\alpha_a}{\mu A_a} - \frac{1}{\frac{\gamma_{d_a} \delta_a} + \gamma_{m_a} \mu L_a})}
$$

where

$$
w_d = \frac{1}{\gamma_{d_a} \delta_a \mu A_a}.
$$
\[ q_d = \frac{1}{\gamma_d \delta t A_t}. \]

Notice that the parameters \( w_d \) and \( q_d \) are the inverse of the quantity of development time multiplied by the adult death for \( Ae. \text{albopictus} \) and \( Ae. \text{triseriatus} \), respectively. This represents the expected life span. From our analytical description of the proportion of \( Ae. \text{albopictus} \), we can determine the importance of different parameters.

**Discussion**

While some studies suggest that \( Ae. \text{albopictus} \) is the stronger competitor, consistently eggs of both species are found together in the wild even in the presence of high levels of parasitism \([3, 7, 23, 55]\). Indeed, our results show that high levels of infection of \( Ae. \text{albopictus} \) with \( As. \text{taiwanensis} \) have a significant effect on the population levels and level the playing field between the two mosquito species. We find a wide range of situations in which \( Ae. \text{triseriatus} \) is the dominant species, but primarily in the presence of unrealistically high effects of parasitism in \( Ae. \text{albopictus} \) (Fig. 3). Thus, it is unlikely that \( Ae. \text{triseriatus} \) would dominate \( Ae. \text{albopictus} \) without significant drastic effects of parasitism on the mosquito species.

Furthermore, the combined effects of the parasite would likely not result in complete elimination of \( Ae. \text{albopictus} \) in the wild.

There are additional factors other than the effects of gregarine parasites, that contribute to coexistence. One of these is that the competitive effects are lessened when resources are sufficient \([17]\). Although \( Ae. \text{triseriatus} \) develops slower and has a smaller survival rate, it can survive at a lower temperature than \( Ae. \text{albopictus} \) [18]. We also make the assumption that the reproductive cycles and seasons of the two \textit{Aedes} mosquitoes overlap completely. However, the populations of the two mosquitoes peak at different times: \( Ae. \text{triseriatus} \) peaks in late June and early July, while \( Ae. \text{albopictus} \) peaks in late July through late August \([3]\), which could give \( Ae. \text{triseriatus} \) a slight edge that is not incorporated into this model. Although this is most likely due to other factors, we also saw these dynamics when we considered dilution of parameters and \( Ae. \text{albopictus} \) has a high parasite effect. These temporal changes where \( Ae. \text{triseriatus} \) initially has a greater population, but then returns to the same coexistence equilibrium, show that the initial seasonal population of \( Ae. \)
triseriatus might return to the same equilibrium with the return of Ae. albopictus.

It would be possible to study these alterations by changing the initial conditions of the simulations. For example, changing the initial conditions so that Ae. triseriatus starts with both adults and larvae and Ae. albopictus starts only with larvae. Additionally, we could simulate a later introduction of Ae. albopictus to compensate for this difference.

Ae. triseriatus is native to the areas in which it competes with Ae. albopictus, and is subsequently unable to escape its parasite in the same way as Ae. albopictus. Consequently, a fixed level parasitism is assumed to occur when the population is at equilibrium. We only consider two levels of infection of Ae. triseriatus by its parasite As. barretti, which affects development time and mortality of Ae. triseriatus. Thus, we do not consider all possible combinations of parasitism, but it does indicate that the increase of parasitism on Ae. triseriatus increased the proportion of Ae. albopictus, but did not drastically effect the overall dynamics. Additional evidence suggests that Ae. triseriatus that are infected with As. barretti were killed less often by a predator, Toxorhynchites rutilus, than compared to uninfected Ae. triseriatus [56]. This shows that while the effect of the parasite does have an effect on the competition between the two species, there are other species which might exacerbate or mitigate the effects of As. taiwanensis on Ae. albopictus.

Evidence suggesting that endemic infection of Ae. albopictus by As. taiwanensis decreases fitness has implications in the spread of mosquito-borne diseases. In southwest Virginia, both Aedes species can act as a vector for La Crosse encephalitis virus (LACV). While Ae. triseriatus is the primary vector for the virus, evidence suggests that as Ae. albopictus becomes more established, it can transmit LACV just as effectively as Ae. triseriatus [11, 12]. Importantly, as Ae. albopictus often occurs in urban or para-urban settings, it can act as a bridge vector for LACV to the human population. While La Crosse encephalitis is not widespread across the United States, it one of the most common mosquito-borne pediatric diseases in the country [57]. LACV infections result in inflammation of the brain, which can lead to seizures and paralysis [2]. In the future, this understanding of mosquito population dynamics can be implemented in the study of mosquito-borne diseases such as La Crosse encephalitis.
Conclusion

We aimed to determine the extent that parasitism of *Ae. albopictus* by *As. taiwanensis* impacts its competition with *Ae. triseriatus*. Both *Aedes* mosquitoes are potentially competent vectors for a number of human arboviruses, and insight into the dynamics of these two species could help inform future disease mitigation efforts. Without parasitism due to *As. taiwanensis*, *Ae. albopictus* has a large and distinct competitive advantage over *Ae. triseriatus* in some environments. As *Ae. albopictus* is an often-invasive generalist species, its domination over native *Ae. triseriatus* in the absence of mitigating effects, such as parasitism, is likely. Our results suggest that the competitive advantage of *Ae. albopictus*, in the absence of parasitism, is so great that if the species has even the slightest edge over *Ae. triseriatus*, it will dominate given enough time. From our parameter sweep, 86% of the scenarios resulted in *Ae. albopictus* being the dominant species, with few scenarios leading to *Ae. triseriatus* as the dominant species, under low parasitism on *Ae. triseriatus*.

When we increase the effect of parasitism of *Ae. triseriatus* to a high level, *Ae. albopictus* is dominant 94% of the scenarios. Even in treeholes where the competition effect from *Ae. triseriatus* is greater, *Ae. albopictus* remains the dominant species. This is consistent with previous results [7, 16, 23]. When considering the impact of parasitism of *Ae. albopictus* by *As. taiwanensis*, we observe a decreased overall fitness of the species, and negative effects its competitive ability. Previous empirical results corroborate our findings [7]. To be clear, the reduction of individual traits is assumed, but our results indicate that the overall population levels are significantly affected by changes in these individual traits. This is seen when changing the effect of parasitism (Fig. 3). The three parasitism parameters all have significant effects on the balance between the two species, with the parasite effect on development time having the strongest effect on the proportion of *Ae. albopictus*. The greatest effect is observed when there is a combined effect on female fecundity, larval development time, and larval mortality. As we increase the effects of the parasite parameters we see that the proportion of *Ae. albopictus* decreases and leads to elimination of *Ae. albopictus* when parasitism is extremely high.

Availability of data and materials

The datasets generated during the current study are available in its additional files.
Abbreviations

Ae.: Aedes
LACV: La Crosse encephalitis virus
PRCC: partial regression correlation coefficients.
As.: Ascogregarina
GRR: Gross reproductive rate
GC: Gonotrophic cycle

Ethical declarations

Ethics approval and consent to participate
Not applicable.
Consent for publication
Not applicable.
Competing interests
The authors declare that they have no competing interests.

Acknowledgements

Not applicable.

Funding

LMC and MW were supported by National Science Foundation (NSF) Standard Grant 1853495. MW was partially supported by a grant from Virginia Tech.

Author’s Information

Emma Stump developed the model, determined the parameter values, ran initial simulations, developed initial code and drafted the manuscript. Melody Walker developed the model and code, analyzed the model, performed simulations, and revised the manuscript. Lauren Childs oversaw model development and analysis and edited the manuscript.

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Figure 1 Life cycle of the mosquito and parasite. Interaction between life cycles of Aedes mosquito, shown as the black lines, and Ascogregarina parasite, shown as the blue boxes. As the mosquito progresses from stage to stage in its life cycle, its gregarine parasite progresses through in a mirrored fashion. For details on the parasite life cycle see Chen [37].
**Figure 2 Competition Outcomes in Latin Hypercube Sampling.** The outcomes of competition with the 100,000 samples from the LHS. The categories shown in dark blue has *Ae. albopictus* (*Aa*) wiped out and the bright yellow is when *Ae. albopictus* completely dominates *Ae. triseriatus*. On the left *(a,c)* is without effects of parasitism on *Ae. albopictus* and the right *(b,d)* includes parasitism effects. The top row *(a,b)* has low parasite effect and the middle row *(c,d)* has high parasite effect on *Ae. triseriatus*. The black dashed lines in *(a,b,c,d)* are for reference to compare low versus high density, *(a)* to *(c)* and *(b)* to *(d)*. Categories are defined in Table 2. The dynamics plots *(e,f)* are expected temporal results without any parasitism in *Ae. albopictus* and low effect of parasitism in *Ae. triseriatus*. This represents when *Ae. albopictus* initially invades a new habitat. The left *(e)* is the tire scenario with competition parameters favoring *Ae. albopictus* *(α₂ = 0.25 < αₐ = 0.83)*. The right *(f)* is competition parameters that favor *Ae. triseriatus* *(α₂ = 0.73 > 0.42 = αₐ)*. All parameters are chosen to be the values in Table 1 with all *Ae. albopictus* parasite parameters set to 1.
**Figure 3 Effects of parasitism on Ae. albopictus proportion**  The proportion of *Ae. albopictus* when varying parasitism parameters. For all subplots, the right quadrants (I and IV) are the tire environment where there is greater competitive effect on *Ae. triseriatus* than on *Ae. albopictus*; the left quadrants (II and III) are the treehole environment where the reverse is true; the upper quadrants (I and II) have high parasite effects on *Ae. triseriatus*; and the lower quadrants (III and IV) have low parasite effect on *Ae. triseriatus*. All three *Ae. albopictus* parasitism parameters – $\gamma_b$, $\gamma_m$, $\gamma_d$ – are varied. All subplots vary mortality on the y-axis while left subplots (a,c,e) have fecundity on the x-axis and the right subplots (b,d,f) have development time on the x-axis. Each row fixes the third parasite parameter not varied: 1 (a,b), 3 (c,d), 5 (e,f). Lines distinguish between different outcome categories. For example, yellow is when the proportion of *Ae. albopictus* exceeds 0.8.
Figure 4 Partial rank correlation coefficients of the parameter values with the final proportion of *Ae. albopictus* at 2000 days. The stars indicate significance with a p-value less than 0.00001. The top plot shows the PRCC with the LHS with all parasitism parameters set to one ($\gamma_{d} = \gamma_{m} = \gamma_{b} = 1$), indicating no parasitism. The bottom plot is the PRCC with variation of parasitism included in the LHS for *Ae. albopictus*. Parasitism on *Ae. triseriatus* is low. Red bars (left side) are parameters associated with *Ae. albopictus* and blue bars (right side) with *Ae. triseriatus*. Parasitism parameters on *Ae. albopictus*, which only occur in the bottom plot, are shown by purple bars (middle). For each grouping, parameters are ordered from least to greatest effect when including parasitism. The PRCC for parameter values with high *Ae. triseriatus* parasitism is found in supplemental figure 5.
Figure 5 Dilution effects of parasitism. The proportion of *Ae. albopictus* when varying parasitism parameters. All subplots are in the tire scenarios ($\alpha_a = 0.83$ and $\alpha_t = 0.25$), where the effect of competition on *Ae. triseriatus* is greater than on *Ae. albopictus*. The solid lines indicate dilution of parasitism, which means that parasite parameters of a species decrease as their proportion decreases. The dashed line are in the absence of dilution and assume a constant parasite parameter. See the text for how the values are chosen. The left (a,c) have maximum parasite parameters larger for *Ae. albopictus* and the right (b,d) have smaller maximum parasite parameters. The top (a,b) have smaller maximum parasite parameters for *Ae. triseriatus* and the bottom (c,d) have larger values. All parameters are listed in Table 3.
### Table 1 Parameter Values and Latin Hypercube Sampling ranges.

| Symbol | Description          | Value | LHS Range        | Units       | Reference |
|--------|----------------------|-------|------------------|-------------|-----------|
| $\beta_a$ | Birth Rate | 32.6  | 2.5 – 56         | Eggs/day    | [44]      |
| $\delta_a$ | Development Time | 10    | 9-45             | 1/days     | [47, 13, 48] |
| $\mu_{L_a}$ | Larval mortality | 0.067 | 0.005 – 0.4      | 1/day      | [13, 44] |
| $\mu_{A_a}$ | Adult mortality | 0.045 | 0.01 – 0.065     | 1/day      | [47, 44, 48] |
| $\alpha_a$ | Competition parameter | 0.83, 0.42 | 0.4 - 1 | unitless | [16] |
| $\rho_a$ | Adult female proportion | 0.5 | 0.2 - 0.6       | unitless   | [17] |

| Symbol | Description          | Value | LHS Range        | Units       | Reference |
|--------|----------------------|-------|------------------|-------------|-----------|
| $\beta_t$ | Birth rate | 11    | 3 – 26          | Eggs/day    | [46, 45, 50] |
| $\delta_t$ | Development time | 22    | 13 - 55        | 1/days      | [13, 18, 12] |
| $\mu_{L_t}$ | Larval mortality | 0.009 | 0.002 – 0.011  | 1/day       | [13, 48, 17] |
| $\mu_{A_t}$ | Adult mortality | 0.1   | 0.03 – 0.1      | 1/day       | [49]      |
| $\alpha_t$ | Competition Parameter | 0.25, .73 | 0 - 0.75 | unitless | [16] |
| $\rho_a$ | Adult female proportion | 0.5 | 0.4 - 0.55     | unitless   | [17] |

| Symbol | Description          | Value | LHS Range        | Units       | Reference |
|--------|----------------------|-------|------------------|-------------|-----------|
| $\gamma_{b_a}$ | Effect on fecundity | 1.0   | 1 - 2           | unitless    | varied    |
| $\gamma_{d_a}$ | Effect on development rate | 1.0  | 1 - 2        | unitless    | varied    |
| $\gamma_{m_a}$ | Effect on larval mortality | 1.0  | 1 - 16        | unitless    | varied    |
| $\gamma_{d_t}$ | Effect on development rate (Ae. Triseriatus) | 1.2, 2 | Fixed | unitless | varied |
| $\gamma_{m_t}$ | Effect on larval mortality (Ae. Triseriatus) | 1.5, 4 | Fixed | unitless | varied |
| $K$ | Carrying capacity | 60 | Fixed | Number of larvae | [16] |
**Table 2** Categorized outcomes. *Criteria is proportion of *Ae. albopictus* adults.*

| Category | Description | Criteria\(^\dagger\) \((A_a)\) |
|----------|-------------|------------------|
| 1        | *Ae. triseriatus* completely dominates, *Ae. albopictus* wiped out | \(A_a < 0.01\) |
| 2        | *Ae. triseriatus* dominates, few *Ae. albopictus* remain | \(0.01 < A_a < 0.15\) |
| 3        | *Ae. triseriatus* more present, *Ae. albopictus* still persists | \(0.20 < A_a < 0.40\) |
| 4        | Both species coexist in even proportions | \(0.40 < A_a < 0.60\) |
| 5        | *Ae. albopictus* more present, *Ae. triseriatus* persists | \(0.60 < A_a < 0.80\) |
| 6        | *Ae. albopictus* dominates, few *Ae. triseriatus* remain | \(0.80 < A_a < 0.99\) |
| 7        | *Ae. albopictus* completely dominates, *Ae. triseriatus* wiped out | \(A_a > 0.99\) |
Table 3 Dilution parasitism parameters. Each level variation for parasitism (high or low) for each species.

|                | max $\gamma_{m_{a}}$ | max $\gamma_{d_{a}}$ | max $\gamma_{b_{a}}$ | $Ae.~albopictus$ | max $\gamma_{m_{t}}$ | max $\gamma_{d_{t}}$ | $Ae.~triseriatus$ |
|----------------|-----------------------|-----------------------|-----------------------|--------------------|-----------------------|-----------------------|--------------------|
| low            | 1.5                   | 1.2                   | 1.2                   | low                | 1.5                   | 1.2                   | low                |
| high           | 16                    | 4                     | 4                     | high               | 8                     | 4                     | high               |
| low            | 1.5                   | 1.2                   | 1.2                   | high               | 8                     | 4                     | high               |
| high           | 16                    | 4                     | 4                     | high               | 8                     | 4                     | high               |
Additional Files

Additional file 1 — Equilibrium and Supplementary figure
This contains the equilibria values. The following supplementary figures are located in this file: File format is pdf.

Additional file 2 — Code
This is all the code used to run and analyze the model. File format is Matlab file (.m).

Additional file 3 — Generated data
This is all generated samples. The format is a Matlab file (.mat).
Figure 1

Life cycle of the mosquito and parasite. Interaction between life cycles of Aedes mosquito, shown as the black lines, and Ascogregarina parasite, shown as the blue boxes. As the mosquito progresses from stage to stage in its life cycle, its gregarine parasite progresses through in a mirrored fashion. For details on the parasite life cycle see Chen [37].
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Competition Outcomes in Latin Hypercube Sampling. The outcomes of competition with the 100,000 samples from the LHS. The categories shown in dark blue has Ae. albopictus (Aa) wiped out and the bright yellow is when Ae. albopictus completely dominates Ae. triseriatus. On the left (a,c) is without effects of parasitism on Ae. albopictus and the right (b,d) includes parasitism effects. The top row (a,b) has low parasite effect and the middle row (c,d) has high parasite effect on Ae. triseriatus. The black
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Partial rank correlation coefficients of the parameter values with the final proportion of Ae. albopictus at 2000 days. The stars indicate significance with a p-value less than 0.00001. The top plot shows the PRCC with the LHS with all parasitism parameters set to one ($\gamma_{da} = \gamma_{ma} = \gamma_{ba} = 1$), indicating no parasitism. The bottom plot is the PRCC with variation of parasitism included in the LHS for Ae. albopictus.
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Figure 5

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**Supplementary Files**

This is a list of supplementary files associated with this preprint. Click to download.

- Additionalfile1.pdf
- Additionalfile2.m
- Additionalfile3.mat
- graphicalabstract.png