

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

Emma Stump

Virginia Polytechnic Institute and State University

Lauren M Childs

Virginia Polytechnic Institute and State University

Melody Walker (✉ melody@vt.edu)

Virginia Polytechnic Institute and State University <https://orcid.org/0000-0002-6421-3772>

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>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

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>.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

RESEARCH

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

Emma Stump¹, Lauren M. Childs² and Melody Walker^{2*†}

Correspondence: melody@vt.edu

Department of Mathematics,
Virginia Tech, 460 McBryde Hall,
25 Stanger Street, 24061
Blacksburg, USA

Full list of author information is
available at the end of the article

Equal contributor

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*

1

2

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65



- 3 • Discussion of triseriatus and its parasite
- 4 • Parasitism relating to albopictus parameters throughout
- 5 • Story "if albopictus invading" but over time likely to gain parasites
- 6 • Make sure categories are numbers throughout.

7 Background

8 La Crosse encephalitis virus (LACV) can cause brain swelling and lead to severe
9 neuroinvasive disease in children under 15 [1], which can cause lifelong health effects
10 [2] While it only leads to a few reported cases each year, it is likely under reported.
11 We focus on two species known to transmit LACV, *Aedes albopictus* and *Aedes*
12 *triseriatus*, and competition between them [3, 4]. Female mosquitoes of these species
13 may become disease vectors when they feed on infected individuals and transmit
14 the virus to other animals or humans via a second blood meal [5].

15 *Aedes (Ae.) albopictus*, also known as the Asian tiger mosquito, is native to sub-
16 tropical regions of southeast Asia, and is a common vector of arboviruses such as
17 Dengue fever virus, West Nile virus, and La Crosse encephalitis virus [6]. The first
18 appearance of *Ae. albopictus* in the United States was in Houston, Texas in 1985
19 [7, 8]. Since its introduction, *Ae. albopictus* has spread throughout the continental
20 United States, and now occupies much of the southern and eastern US, stretching
21 from Texas to New Jersey [9]. *Ae. albopictus* is known for its ability to adapt to a
22 range of climates and to be a strong competitor to other species that share larval
23 habitats [10]. In 2001, La Crosse virus was isolated in *Ae. albopictus* [11]. Fourteen
24 years later, it was estimated that 3.01 of every 1000 *Ae. albopictus* were infected
25 with the La Crosse virus [12].

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

31 Several laboratory studies have shown that *Ae. albopictus* is the superior com-
32 petitor compared to *Ae. triseriatus* [13, 14, 15, 16, 17, 18, 19]. In Bevins [14],
33 they showed a ten percent drop in survival for *Ae. triseriatus* when a quarter of the

1
2
3
4
5
6 34 mosquitoes present were *Ae. albopictus* and a twenty percent drop in *Ae. triseriatus*
7
8 35 survival when half of the mosquitoes were *Ae. albopictus*. In Ho et al. [13], the au-
9
10 36 thors showed that while the development time of *Ae. albopictus* was not significantly
11
12 37 altered by competition, the development time of *Ae. triseriatus* was increased when
13
14 38 in a shared habitat with other *Aedes* species. Moreover, *Ae. albopictus* larvae inhibit
15
16 39 egg hatching of other species such as *Ae. triseriatus*, while there is no significant
17
18 40 inhibition on their own species [15]. However, in a more recent meta-analysis, com-
19
20 41 petitive equivalence of *Ae. albopictus* and *Ae. triseriatus* was suggested [20]. In a
21
22 42 study with two different environments, they found that *Ae. albopictus* did much
23
24 43 better in tires, but did worse than *Ae. triseriatus* in treeholes [16].

25
26 44 *Ae. albopictus* and *Ae. triseriatus* are parasitized by *Ascogregarina (As.) taiwa-*
27
28 45 *nensis* and *Ascogregarina (As.) barretti*, respectively. *Ascogregarina* are intestinal
29
30 46 protozoan parasites that inhabit the gut of the mosquito throughout its life cycle
31
32 47 [7, 21]. The effects and prevalence of these parasites are heterogeneous. In the wild,
33
34 48 typically 67 to 95% of a given population of *Ae. albopictus* are infected with *As.*
35
36 49 *taiwanensis* [22]. Infection of *Ae. albopictus* by *As. taiwanensis* lengthens larval
37
38 50 development time for both males and females mosquitoes, reduces adult female fe-
39
40 51 cundity, increases larval mortality, and reduces egg laying and hatching rates [7, 23].
41
42 52 However, Aliabadi and Juliano saw that mortality of *Ae. albopictus* was not signif-
43
44 53 icantly affected by *As. taiwanensis* [7]. For *Ae. triseriatus*, one study found 80%
45
46 54 of their collected sites harbored *As. barretti*. Treeholes showed more infected sites
47
48 55 than tires [24]. In contrast another study found that only 5% and 23.6% of *Ae.*
49
50 56 *triseriatus* are infected [25]. Development time and mortality have been seen to in-
51
52 57 crease in *Ae. triseriatus* when infected by *As. barretti* [21, 25]. However, Beier and
53
54 58 Harris [24] showed no significant effect of *As. barretti* on *Ae. triseriatus* mortality.
55
56 59 While *As. barretti* impacts the fitness of *Ae. triseriatus*, its effects are mostly de-
57
58 60 pendent on resource availability [21]. In low resources they find that *Ae. triseriatus*
59
60 61 development time is increased significantly, but with sufficient resources there is not
61
62 62 a significant difference. Another study showed a significant difference in survival of
63
64 63 *Ae. triseriatus* infected with *As. barretti* as compared to those uninfected [25].
65

64 64 In this work, we build a mathematical model of *Aedes* population dynamics ac-
65
66 65 counting for parasitism of *Ae. albopictus* by *As. taiwanensis* and *Ae. triseriatus* by
67
68 66 *As. barretti*. Our model formulation encodes competition between the two species of

1
2
3
4
5
6 67 *Aedes* using the Lotka-Volterra model, a basis for many inter-specific competition
7
8 68 models [26, 27, 28, 29, 30, 31] including mosquito populations [16, 32, 33, 34]. In
9
10 69 Kuno [35], a two species Lotka-Volterra competition model is introduced, which 70
11 includes reproductive interference. Other competition models also show the impor-71
12 tance of reproductive interference between *Ae. aegypti* and *Ae. albopictus* [34, 36]. 72
13
14 However, in contrast to the reports on reproductive interference seen with *Ae. al-73*
15 *bopictus* and *Ae. aegypti*, there appears to be a lack of studies evaluating repro-74
16 ductive interference between *Ae. albopictus* and *Ae. triseriatus*. Livdahl and Willey 75 [16]
17 compared *Ae. albopictus* and *Ae. triseriatus* using a Lotka-Volterra model to 76 explain
18 possible competition affects either in tree holes or in tires. This model was 77 then
19 extended to include La Crosse spread [32] and showed a lack of importance of 78 *Ae.*
20 *albopictus* in recent resurgence of LACV.
21
22
23
24
25
26

27
28 79 The life cycle of gregarine parasites mimics that of their host: each stage of its
29
30 80 development is analogous to a stage within mosquito development. See the inset into
31 Fig 1. Transmission of gregarine parasites is horizontal between individuals of *Aedes*
32
33 82 mosquitoes, and does not occur from parent to offspring [22]. Initial infection occurs
34
35 83 when the mosquito larvae ingest oocysts. After ingestion, the gregarine parasite
36
37 84 travels through the midgut, epithelial tissues, and excretory system of the mosquito,
38
39 85 transitioning into different life stages as the mosquito matures to adulthood. From
40
41 86 there, the parasite reproduces and offspring are excreted by the adult mosquitoes
42
43 87 into breeding containers [37, 38].
44

44
45 88 Since new *Ae. albopictus* habitats are unlikely to be contaminated with *As. tai-*
46
47 89 *wanensis*, then new populations of *Ae. albopictus* can initially escape parasitism.
48
49 90 This lack of parasite infection in newly established populations gives the mosquito a
50
51 91 potential competitive advantage over *Ae. triseriatus* [7, 22]. Knowledge of how par-
52
53 92 asite infection affects the survivorship of *Ae. albopictus* will provide insight into the
54
55 93 competition between the two mosquito species, and subsequently, help to deepen
56
57 94 understanding of the spread of mosquito-borne infectious disease. In this study,
58
59 95 we examine whether the parasitism of *Ae. albopictus* by *As. taiwanensis* decreases
60
61 96 the mosquito's competitive ability enough to alter the dynamics between the two
62
63 97 *Aedes* mosquitoes. We build a compartmental model of the interactions of the two
64
65 98 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 β_i , die at rate μ_{L_i} , and develop at rate δ_i where $i \in \{a, t\}$. Adults emerge from larva at rate δ_i and die at rate μ_{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 ρ_a and ρ_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, α_a and α_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 (γ_{b_a}), larval development rate (γ_{d_a}), and larval mortality (γ_{m_a}). The parasite parameters for *Ae. triseriatus* are larval development rate (γ_{d_t}), and larval mortality (γ_{m_t}). This forms our system of ordinary differential equations:

$$\begin{aligned}
\frac{dL_a}{dt} &= \frac{\beta_a}{\gamma_{b_a}} \rho_a A_a \left(1 - \frac{L_a + \alpha_t L_t}{K} \right) - \frac{1}{\gamma_{d_a} \delta_a} L_a - \gamma_{m_a} \mu_{L_a} L_a, \\
\frac{dA_a}{dt} &= \frac{1}{\gamma_{d_a} \delta_a} L_a - \mu_{A_a} A_a, \\
\frac{dL_t}{dt} &= \rho_t \beta_t A_t \left(1 - \frac{\alpha_a L_a + L_t}{K} \right) - \frac{1}{\gamma_{d_t} \delta_t} L_t - \gamma_{m_t} \mu_{L_t} L_t, \\
\frac{dA_t}{dt} &= \frac{1}{\gamma_{d_t} \delta_t} L_t - \mu_{A_t} A_t.
\end{aligned} \tag{1}$$

131

132 From a literature search, we determined biologically relevant ranges for parameter
133 values. A description of the parameters is provided in Table 1. As it was often
134 difficult to directly find relevant values in the literature, we transformed values
135 found to meet our parameter descriptions. The birthrate was calculated from data
136 for gross reproductive rate (GRR) and length of gonotrophic cycle (GC) by taking
137 the minimum GRR and dividing by the maximum length of the GC. The maximum
138 value was found by dividing the maximum GRR by the minimum GC length [44].
139 With this, we calculated a range of 2.5 to 56 eggs laid per adult female per day. A
140 similar calculation was performed to find a birthrate for *Ae. triseriatus*, where we
141 calculated a range of 3 to 26 eggs laid per adult female per day [45, 46]. Development
142 time can vary based on a variety of factors and has been found to be as short as
143 9 days and as long as 40 days for *Ae. albopictus* [13, 47, 48]. *Ae. triseriatus* has
144 been shown to develop slower than *Ae. albopictus* [13, 18]. In the model, these
145 values are incorporated directly as development time of larvae, (δ_a) and (δ_t). Larval
146 (μ_{L_a}) and adult (μ_{A_a}) mortality for *Ae. albopictus* were calculated to be 0.067 and
147 0.05, respectively, from survival rates and development rates [13, 44, 47, 48], such
148 that $\mu = 1 - (\text{survival rate})^{(1/\delta)}$. For *Ae. triseriatus*, larval (μ_{L_t}) and adult (μ_{A_t})
149 mortality were found to be 0.009 and 0.1, respectively [49, 50]. The carrying capacity
150 for the larval population of both species (K) was set at 60 as was used for a study
151 performed in 200ml of water [7]. It is important to note that this number is relative
152 and could be scaled to fit different size larval containers. In this study we focus on
153 the proportion of each species such that raw population sizes are not influential.
154 There is evidence of potential sex imbalance among mosquitoes especially under low
155 food resources. Thus, for *Ae. triseriatus*, we set the proportion of females, ρ_t , to be

1
2
3
4
5
6 between 0.2 and 0.6 [17]. In the same study, *Ae. albopictus* showed less variation,
7 0.4 – 0.55, in the proportion females, so we set ρ_a accordingly.
8

9 In Livdahl and Willey [16], the competition parameters from the Lokta-Volterra
10 model were fit using nutrient fluids. The competition parameter of *Ae. albopictus*
11 on *Ae. triseriatus* (α_a) and the competition parameter of *Ae. triseriatus* on *Ae.* ¹⁶¹
12 *albopictus* (α_t) were found to be 0.42 and 0.73 in treehole fluid and 0.83 and 0.25 ¹⁶² in tire
13 fluid, respectively. There are many factors that dictate which species will be ¹⁶³ the better
14 competitor; however, as we consider that *Ae. albopictus* is generally the ¹⁶⁴ greater
15 competitor, we choose a range of [0, 0.75] for the effect on *Ae. albopictus* ¹⁶⁵ from *Ae.*
16 *triseriatus* and a range of [0.4, 1] for the effect on *Ae. triseriatus* from *Ae.* ¹⁶⁶ *albopictus*.
17
18
19
20
21
22
23
24

25 The effects of parasitism for *Ae. albopictus* on female fecundity (γ_{b_a}), larval de-
26 velopment rate (γ_{d_a}), and larval mortality (γ_{m_a}) were shown to vary with resource
27 availability and environmental context [23, 7, 25, 51]. In Comiskey et al. [23], they
28 found that in low resources the mortality of infected *Ae. albopictus* larvae was seven
29 times greater than uninfected. They also found that fecundity and fertility was re-
30 duced by over 20% as well as development time was increased by 44%. In Aliabadi
31 and Juliano [7], they showed that development time of infected *Ae. albopictus* in-
32 creases with greater interspecific competition with *Ae. triseriatus*. Whereas without
33 *Ae. triseriatus*, the median development time of infected *Ae. albopictus* was not sig-
34 nificantly different. They also found that survival rates were significantly different
35 for *Ae. triseriatus* at lower densities with *Ae. albopictus*. They did not observe a
36 significant change in survival for *Ae. albopictus* from parasitism, but a greater ef-
37 fect from intra- and inter-specific competition. *Ae. triseriatus* was found in one
38 study to have as high as 2.8 to 3.5 greater death rates when infected [25]. In a rel-
39 atively recent study by Soghigian and Livdahl [51], they show that in the absence
40 of parasite infection, survival of *Ae. albopictus* is about 98%, but with the greatest
41 amount of infection observed, the survival decreases to approximately 71%. This
42 constitutes a 15 times greater mortality rate. In another study by Walker et al. [21],
43 they found an increase in development time for *Ae. triseriatus* in the laboratory
44 with low resources, but not in the field experiment.
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59

60 We initially set all *Ae. albopictus* parasite parameter values to one, which repre-
61 sents the case with no parasitism. We then consider ranges from 1 to 2 for parasite's
62
63
64
65

1
2
3
4
5
6 189 effect on fecundity and development time and 1 to 16 for mortality. These values
7
8 190 were chosen to cover the ranges of changes found in [23, 51]. We will extend the
9
10 191 ranges of the parasite parameters for development time and fecundity in further
11
12 192 analyses. We are assuming that *Ae. triseriatus* is already infected, so we initially
13
14 193 fix these parameter values as $\gamma_{d_t} = 1.2$ and $\gamma_{m_t} = 1.5$ to be a relatively small effect.
15
16 194 We also consider a higher effect to parasitism with $\gamma_{d_t} = 2$ and $\gamma_{m_t} = 4$ as a com-
17
18 195 parison. If $\gamma_{d_a} = 5$, this would mean that the development time was 5 times greater
19
20 196 when *Ae. albopictus* is infected with its parasite. If any of the parasite parameters
21
22 197 are set to one this indicates no effect of parasitism.

23
24 198 We simulated the mosquito population dynamics from our ODE model in Matlab.
25
26 199 Fixed parameter values, shown in Table 1, were used in these simulations. The initial
27
28 200 conditions used for all simulations were $L_a = 30$, $A_a = 0$, $L_t = 30$, and $A_t = 0$. We
29
30 201 use these initial condition for consistency with Aliabadi and Juliano [7], but as we
31
32 202 run the simulation until equilibrium other initial values will give the same results.
33
34 203 Simulations were run for 2000 days, long enough such that the population of *Ae.*
35
36 204 *albopictus* and *Ae. triseriatus* larvae and adults reached equilibrium. To begin we
37
38 205 considered two competition scenarios. The first is the environment within a tire
39
40 206 ($\alpha_a = 0.83$, $\alpha_t = 0.25$), which indicates that *Ae. albopictus* has more effect on
41
42 207 *Ae. triseriatus*. In the second scenario, the environment in a treehole ($\alpha_a = 0.42$,
43
44 208 $\alpha_t = 0.73$), such that *Ae. triseriatus* has a greater effect on *Ae. albopictus*. These
45
46 209 parameters were from fitted data in Livdahl and Willey [16].

47
48 210 We performed a parameter sweep by sampling ranges of the parameters using
49
50 211 Latin Hypercube Sampling (LHS) in Matlab [52]. We conducted this with a sample
51
52 212 size of 100,000, and sampled 12 of the parameters: β_a , β_t , δ_a , δ_t , μ_{L_t} , μ_{A_t} , μ_{L_a} ,
53
54 213 μ_{A_a} , α_t , α_a , ρ_t , and ρ_a . Values for parasitism on *Ae. albopictus* (γ_{b_a} , γ_{d_a} , γ_{m_a})
55
56 214 were fixed at 1, and K was fixed at 60. The LHS was completed twice: first with
57
58 215 the parasite parameters for *Ae. triseriatus* set at $\gamma_{d_t} = 1.2$ and $\gamma_{m_t} = 1.5$ and
59
60 216 then again with them set at $\gamma_{d_t} = 2$ and $\gamma_{m_t} = 4$. With the results generated
61
62 217 by the LHS, we generated a histogram reflecting the type of outcomes of each of
63
64 218 the samples. We categorized the results into seven categories, described in Table 2.
65
66 219 These categories were based on the proportion of the population occupied by *Ae.*
67
68 220 *albopictus* as follows: In category (1), a proportion of less than 0.01; in category
69
70 221 (2), a proportion of 0.01 to 0.2; in category (3), a proportion between 0.2 and 0.4;

1
2
3
4
5
6 222 in category (4), a proportion between 0.4 and 0.6; in category (5), a proportion
7 223 between 0.6 and 0.8; In category (6), a proportion between 0.8 and 0.99; and in
8
9 224 category (7) a proportion greater than 0.99. We then did a sensitivity analysis on
10
11 225 the parameters to account for uncertainty and variation in parameters by partial
12
13 226 rank correlation coefficient [53].

14
15 227 After sampling the space of the twelve parameters in the model in the absence of
16
17 228 parasitism in *Ae. albopictus*, we focused on investigating the effects of the parasite.
18
19 229 We repeated the LHS including the parasite parameters for *Ae. albopictus*. We also
20
21 230 performed sensitivity analysis on the 100,000 samples that includes varied parasite
22
23 231 effects. The mortality and fecundity parasite parameter were varied from 1 to 4
24
25 232 and the development time parasite parameter varied from 1 to 16, where a value
26
27 233 of 1 means the parasite has no effect and a value of 3 means a 3 fold increase of
28
29 234 the associated parameter value. This means that mortality or development time is
30
31 235 increased or fecundity is decreased compared to the value without parasitism.

32
33 236 To examine the varying effects of parasitism, all parameters were fixed as listed
34
35 237 in Table 1 except we varied the three *Ae. albopictus* parasite parameters with *Ae.*
36
37 238 *triseriatus* fixed at either a high or low parasite effect. We compared effects on female
38
39 239 fecundity, larval development rate, and larval mortality to see how these different
40
41 240 combinations led to different outcomes in terms of the proportion *Ae. albopictus* in
42
43 241 the final population. We extended the range of the parasite parameters so that all
44
45 242 were varied from 1 to 10.

46 47 243 Dilution effects

48
49 244 A recent study by Westby et al. [54] showed that with *Ae. japonicus* and *Ae.*
50
51 245 *triseriatus* there was a dilution effect on the amount of parasitism. *Ae. japonicus*
52
53 246 decreased the number of *As. barretti* by consuming the parasite and not propagating
54
55 247 it [54]. We consider this idea with the two species model, by allowing the parasitism
56
57 248 parameters to have decreased effect in the presence of greater proportions of the
58
59 249 competing species, a so-called ‘dilution’ effect. We modify the model by making all
60
61 250 parasite parameters a function of the proportion of the total population. Specifically
62
63 251 each parasite parameter will linearly decrease from the maximum value $\gamma_{i_{max}}$ to one.
64
65

252 This is captured by:

$$\gamma_i(p) = (\gamma_{i_{max}} - 1)p + 1 \quad (2)$$

253 where p is the proportion of a species. We choose a linear function for simplicity.
 254 Notice that if $p = 1$, $\gamma_i = \gamma_{i_{max}}$ which indicates that if a particular species is 100%
 255 of the population, then their parasite parameters will be at its maximum. If $p = 0$,
 256 $\gamma_i = 1$, this means that as the species goes to 0% of the population, the parasite
 257 effect of the parameter will linearly decrease to no parasite effect. In Westby et al.
 258 [54], they see a large decrease in the amount of parasitism ($\approx 82\%$ reduction), so
 259 we allow parasitism parameters to approach 1, as the proportion of larvae goes to
 260 zero. Recall that, when the parasite parameters equal one, this represents no effect
 261 of parasitism. Thus, our revised system of equations becomes:

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

262 where $P_a = \frac{L_a}{L_a + L_t}$ and $P_t = \frac{L_t}{L_a + L_t}$.

263 We then consider four cases by choosing different maximum parameters for para-
 264 sitism, $\gamma_{i_{max}}$. These combination are: *Ae. albopictus* and *Ae. triseriatus* both have
 265 minor effects of parasitism, both have more severe effects, and only one has severe
 266 effect and the other minor effect. See Table 3 for specific choices for maximum
 267 parasite parameters.

268 Results

269 To begin, we model the population dynamics of *Ae. albopictus* and *Ae. triseriatus*
 270 without parasitism. We consider two separate environments: tire and treehole. The
 271 difference between the two scenarios is the Lotka-Volterra competition parameters
 272 (α_t and α_a) that were fit for each environment from Livdahl and Willey [16]. In
 273 both cases, the populations settle to an equilibrium. In the tire environment, the

1
2
3
4
5
6 274 population ends in category 6, in which *Ae. albopictus* dominates, but *Ae. trise-*
7
8 275 *riatus* remain at low levels (Fig. 2, right). After 150 days, we find 126 adult *Ae.*
9
10 276 *albopictus* compared to about 5 adult *Ae. triseriatus*. For the treehole environment,
11
12 277 the population ends in category 5 (Fig. 2, left), where *Ae. albopictus* is still the
13
14 278 dominant species, but *Ae. triseriatus* has a sizeable population. After 150 days,
15
16 279 there are approximately 54 *Ae. albopictus* and 19 *Ae. triseriatus*. Parameter values
17
18 280 are estimated averages from literature and are found in Table 1.

19
20 281 To account for known variability in parameters, we examined dynamics across
21
22 282 broad parameter space using a LHS with the ranges indicated in Table 1. Assum-
23
24 283 ing no effects of parasitism in *Ae. albopictus* and low effect in *Ae. triseriatus*, we
25
26 284 find that the majority, 56%, of simulations fall into category 6 (Fig. 2, a), where
27
28 285 *Ae. albopictus* strongly dominates. This is the same result as in the tire scenario.
29
30 286 In addition, approximately 25% of the simulations fall into the same category as
31
32 287 the treehole scenario (category 5). Only 3.5% of the total 100,000 samples led to
33
34 288 categories in which *Ae. triseriatus* is greater in population than *Ae. albopictus*
35
36 289 (categories 1, 2 and 3). A further 10.5% of the simulation fell into coexistence with
37
38 290 approximately equal amounts of both species (category 4). For a small number of
39
40 291 simulations (5%) *Ae. albopictus* completely eliminated *Ae. triseriatus* without par-
41
42 292 asitism (category 7), but the most common scenario was for *Ae. albopictus* to be
43
44 293 the dominant species and strongly limit the population of *Ae. triseriatus*.

45
46 294 If we increase the effect of parasitism in *Ae. triseriatus*, we find that their is
47
48 295 a strong shift in scenarios to where *Ae. albopictus* is the dominant species (Fig.
49
50 296 2c). In this case, approximately 66% of parameter selected fall into category 6
51
52 297 (few *Ae. triseriatus*) and 9.9% of situations lead to elimination of *Ae. triseriatus*
53
54 298 (category 7). *Ae. triseriatus* is only ends in greater proportion that *Ae. albopictus*
55
56 299 in approximately 1% of the parameters sampled.

57 58 300 Including parasitism in *Ae. albopictus*

59
60 301 When we include the effects of parasitism for *Ae. albopictus* in the dynamics, we
61
62 302 greatly increase the parameter space where *Ae. triseriatus* is the dominant species.
63
64 303 We use LHS but include the parameters for parasitism: γ_{da} , γ_{ma} , and γ_{ba} . We find
65
66 304 that results falling in categories 1-4 have greatly increased while those in categories
67
68 305 6 and 7 have significantly decreased (Fig. 2 b, d). In fact, *Ae. triseriatus* complete

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

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 (α_t and α_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 (γ_{m_a}) and larval development time (γ_{d_a}) were varied with three constant levels of the effect on female fecundity ($\gamma_{b_a} = 1, 3, 5$) (Fig. 3). Then, parasite effects on female fecundity (γ_{b_a}) and larval development time (γ_{d_a}) were varied with three constant levels of the effect on mortality ($\gamma_{m_a} = 1, 3, 5$). Finally, parasite effects on larval mortality (γ_{m_a}) and female fecundity (γ_{b_a}) were varied with three constant levels of the effect on larval development time ($\gamma_{m_a} = 1, 3, 5$). 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 (γ_{b_a}) is fixed at one,

1
2
3
4
5
6 339 the transition to a greater level coexistence between the mosquito species is only
7
8 340 seen at higher levels of effects on larval development rate (γ_{d_a}), with values around
9
10 341 $\gamma_{d_a} > 4$ (Fig. 3b quadrant I and IV). For female fecundity (γ_{b_a}) fixed at three and
11
12 342 five (Figure 3d,f quadrant I and IV), development time effects as low as $\gamma_{d_a} \approx 2$
13
14 343 result in a shift to a low proportion of *Ae. albopictus* (category 5 green). In order
15
16 344 for *Ae. triseriatus* to be the dominant species there must be very high effects of all
17
18 345 three parasitism parameters effecting *Ae. albopictus*, regardless of *Ae. triseriatus*'
19
20 346 level of parasitism.

21
22 347 Parasite effects on development time have more significant effects than on mortal-
23
24 348 ity or fecundity. In the tire scenario, this is most apparent when there is no change
25
26 349 in development time (Fig. 3a), then *Ae. albopictus* always strongly dominates. Ad-
27
28 350 ditionally, there is no change in category, regardless of the strength of the effect on
29
30 351 mortality and fecundity or parasitism on *Ae. triseriatus*. In the tire scenario, if the
31
32 352 effect on development time is increased by three times (Figure 3c), both effects on
33
34 353 fecundity and mortality must be relatively high to get higher levels of *Ae. trise-*
35
36 354 *riatus*. Furthermore, *Ae. triseriatus* will only dominate if both parasite effects on
37
38 355 fecundity and mortality are greater than ten. When development time in tires is five
39
40 356 times greater, only a small effect by the other two parameters is needed to decrease
41
42 357 the proportion of *Ae. albopictus* to category 5. Similarly, with fixed fecundity, when
43
44 358 the parasite increases the development time seven fold, we see that regardless of the
45
46 359 other two parameters, the proportion of *Ae. albopictus* decreases to at minimum
47
48 360 category 5 (Fig. 3f, green and blue).

49
50 361 In the treehole scenario, *Ae. triseriatus* has more of a competitive effect on *Ae.*
51
52 362 *albopictus*. As seen with the absence of parasitism for *Ae. albopictus* with low effect
53
54 363 of parasitism on *Ae. triseriatus*, the default is category 5 (Fig. 3 a,b Quadrant III,
55
56 364 green in bottom left corner), in which *Ae. albopictus* is still the dominant species,
57
58 365 but there are a larger number of *Ae. triseriatus*. In this situation, the effect on
59
60 366 development time must only increase two-fold for the proportion of *Ae. albopictus*
61
62 367 to decrease to category 4 (Fig. 3b Quadrant III, teal), in which there are relatively
63
64 368 similar amounts of both species. When the effect on fecundity is set to 3 (Fig.
65
66 369 3d Quadrants II, III) and the effect of development time is greater than four, *Ae.*
67
68 370 *triseriatus* will be the dominant species (all three shades of blue). When the effect of
69
70 371 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, μ_{L_t} ; and proportion of females, ρ_t

In the case without parasitism, the parameter with the most influence (largest PRCC value in magnitude) is the competition parameter α_a , which is the inter-specific competition effects on *Ae. triseriatus* from *Ae. albopictus*. With a PRCC value of 0.8469, the more α_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*, μ_{A_a} ; *Ae. albopictus* larval development time, δ_a ; *Ae. triseriatus* larval development time, δ_t , the competition parameter α_t on *Ae. albopictus*; and death rate of adult *Ae. triseriatus*, μ_{A_t} . We see

1
2
3
4
5
6 403 that the most important parameters are the death rates of adults, transition rate
7
8 404 to adults, and the Lotka-Volterra competition parameters.

9
10 405 When we introduce parasitism parameters into the LHS, we see that the parasite's
11 406 effect on development time γ_{m_a} has the 6th greatest impact, but the largest of all
12
13 407 the parasitism parameters. With a PRCC of -0.1359 , we expect the increase of
14
15 408 γ_{m_a} to decrease the proportion of *Ae. albopictus*. The death of adult *Ae. albopictus*,
16
17 409 *Ae. albopictus* larval development time δ_a , *Ae. albopictus* birth rate β_a , the Lotka-
18
19 410 Volterra competition parameter α_t , and the death of *Ae. albopictus* larvae all have
20
21 411 greater PRCC values in magnitude than γ_{d_a} (-0.2525 , -0.2081 , 0.1754 , -0.1517 , and
22
23 412 -0.1581 , respectively). While less important than γ_{m_a} , the other two parasite pa-
24
25 413 rameters are statistically significant ($p < 0.00001$) as well. The PRCC value for the
26
27 414 parasite's effect on development time is -0.1039 and the for the parasite's effect on
28
29 415 fecundity is -0.05 .

30
31 416 When we consider the LHS with high effect of parasitism on *Ae. triseriatus*, all
32
33 417 parameters have much lower effect, as indicated by the lower magnitude of PRCC
34
35 418 value. The parameter with the greatest magnitude PRCC (0.1666) is the Lotka-
36
37 419 Volterra competition parameter α_a ; this is the same parameter as found to have
38
39 420 the most impact when considering a low effect of parasitism on *Ae. triseriatus*
40
41 421 and no parasite effect on *Ae. albopictus*. In general, the trends of PRCC values for
42
43 422 the parameters are similar to with low effect of parasitism on *Ae. triseriatus*. See
44
45 423 supplemental figure 5.

44 424 Dilution effects

46 425 When we consider including dilution effects into parasitism, we find that the equi-
47
48 426 librium values appear to be identical to the case without dilution. To ensure com-
49
50 427 parison of equivalent cases, we find the equilibrium proportion \hat{P}_a of *Ae. albopictus*
51
52 428 larvae under dilution. We use this in our dilution formula $\gamma_i = (\gamma_{max} - 1)\hat{P}_a + 1$
53
54 429 to find comparable parasitism parameters for the absence of dilution. Thus, at our
55
56 430 starting condition the parasite parameters in the two cases differ, due to the differ-
57
58 431 ent population proportions, but approach the same values at equilibrium (Fig. 5).
59
60 432 In Fig. 5, we plotted four different situations at which we have either high or low
61
62 433 parasite effect for the initial maximum parasite value (Table 3). While the equilibria
63
64 434 are identical, there is a difference in the dynamics before reaching the equilibrium.
65

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. The equilibrium equations can be found in the supplementary material. 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:

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

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

In each reproduction number, the first term is the the birth rate, $\frac{\beta_a \rho_a}{\gamma_b a}$ for *Ae. albopictus* and $\beta_t \rho_t$ 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. $\frac{1}{\gamma_{d_t} \delta_t}$ and $\frac{1}{\gamma_{d_a} \delta_a}$, respectively), 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:

$$\frac{A_a}{A_a + A_t} = \frac{w_d \left(1 - \alpha_t + \frac{\alpha_t}{R_t} - \frac{1}{R_a}\right)}{w_d \left(1 - \alpha_t + \frac{\alpha_t}{R_t} - \frac{1}{R_a}\right) + q_d \left(1 - \alpha_a + \frac{\alpha_a}{R_a} - \frac{1}{R_t}\right)}$$

where

$$w_d = \frac{1}{\gamma_{d_a} \delta_a \mu_{A_a}},$$

$$q_d = \frac{1}{\gamma_{d_t} \delta_t \mu_{A_t}}.$$

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. albopictus* and *Ae. triseriatus*, respectively. This represents the expected life span. From our analytical description of the proportion of *Ae. albopictus*, we can determine the importance of different parameters.

Discussion

While some studies suggest that *Ae. 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. albopictus* with *As. 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. triseriatus* is the dominant species, but primarily in the presence of unrealistically high effects of parasitism in *Ae. albopictus* (Fig. 3). Thus, it is unlikely that *Ae. triseriatus* would dominate *Ae. 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. 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. triseriatus* develops slower and has a smaller survival rate, it can survive at a lower temperature than *Ae. albopictus* [18]. We also make the assumption that the reproductive cycles and seasons of the two *Aedes* mosquitoes overlap completely. However, the populations of the two mosquitoes peak at different times: *Ae. triseriatus* peaks in late June and early July, while *Ae. albopictus* peaks in late July through late August [3], which could give *Ae. 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. albopictus* has a high parasite effect. These temporal changes where *Ae. triseriatus* initially has a greater population, but then returns to the same coexistence equilibrium, show that the initial seasonal population of *Ae.*

1
2
3
4
5
6 489 *triseriatus* might return to the same equilibrium with the return of *Ae. albopictus*.
7
8 490 It would be possible to study these alterations by changing the initial conditions of
9
10 491 the simulations. For example, changing the initial conditions so that *Ae. triseriatus*
11
12 492 starts with both adults and larvae and *Ae. albopictus* starts only with larvae. Ad-
13
14 493 ditionally, we could simulate a later introduction of *Ae. albopictus* to compensate
15
16 494 for this difference.

17 495 *Ae. triseriatus* is native to the areas in which it competes with *Ae. albopictus*,
18
19 496 and is subsequently unable to escape its parasite in the same way as *Ae. albopictus*.
20
21 497 Consequently, a fixed level parasitism is assumed to occur when the population is at
22
23 498 equilibrium. We only consider two levels of infection of *Ae. triseriatus* by its parasite
24
25 499 *As. barretti*, which affects development time and mortality of *Ae. triseriatus*. Thus,
26
27 500 we do not consider all possible combinations of parasitism, but it does indicate
28
29 501 that the increase of parasitism on *Ae. triseriatus* increased the proportion of *Ae.*
30
31 502 *albopictus*, but did not drastically effect the overall dynamics. Additional evidence
32
33 503 suggests that *Ae. triseriatus* that are infected with *As. barretti* were killed less often
34
35 504 by a predator, *Toxohrynychites rutilus*, than compared to uninfected *Ae. triseriatus*
36
37 505 [56]. This shows that while the effect of the parasite does have an effect on the
38
39 506 competition between the two species, there are other species which might exacerbate
40
41 507 or mitigate the effects of *As. taiwanensis* on *Ae. albopictus*.

42
43 508 Evidence suggesting that endemic infection of *Ae. albopictus* by *As. taiwanen-*
44
45 509 *sis* decreases fitness has implications in the spread of mosquito-borne diseases. In
46
47 510 southwest Virginia, both *Aedes* species can act as a vector for La Crosse encephalitis
48
49 511 virus (LACV). While *Ae. triseriatus* is the primary vector for the virus, evidence
50
51 512 suggests that as *Ae. albopictus* becomes more established, it can transmit LACV
52
53 513 just as effectively as *Ae. triseriatus* [11, 12]. Importantly, as *Ae. albopictus* often
54
55 514 occurs in urban or para-urban settings, it can act as a bridge vector for LACV to
56
57 515 the human population. While La Crosse encephalitis is not widespread across the
58
59 516 United States, it one of the most common mosquito-borne pediatric diseases in the
60
61 517 country [57]. LACV infections result in inflammation of the brain, which can lead to
62
63 518 seizures and paralysis [2]. In the future, this understanding of mosquito population
64
65 519 dynamics can be implemented in the study of mosquito-borne diseases such as La
66
67 520 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 in 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.

553 **Abbreviations**

554 **Ae.:** *Aedes*

555 **LACV:** La Crosse encephalitis virus

556 **PRCC:** partial regression correlation coefficients.

557 **As.:** *Ascogregarina*

558 **GRR:** Gross reproductive rate

559 **GC:** Gonotrophic cycle

560 **Ethical declarations**

561 Ethics approval and consent to participate

562 Not applicable.

563 Consent for publication

564 Not applicable.

565 Competing interests

566 The authors declare that they have no competing interests.

567 **Acknowledgements**

568 Not applicable.

569 **Funding**

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

572 **Author's Information**

573 Contribution

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

578 Corresponding Author

579 Correspondence to Melody Walker

580 **Author details**

581 ¹Systems Biology, Virginia Tech, Hahn Hall South Suite 2108, 24061 Blacksburg, USA. ²Department of
582 Mathematics, Virginia Tech, 460 McBryde Hall, 225 Stanger Street, 24061 Blacksburg, USA.

583 **References**

- 584 1. Haddow AD, et al. The incidence risk, clustering, and clinical presentation of La Crosse virus infections in the
585 eastern United States, 2003–2007. *PLoS One*. 2009;4(7):e6145.
- 586 2. McJunkin JE, de los Reyes EC, Irazuzta JE, Caceres MJ, Khan RR, Minnich LL, et al. La Crosse encephalitis in
587 children. *N Engl J Med*. 2001;344(11):801–807.
- 588 3. Barker CM, Paulson SL, Cantrell S, Davis BS. Habitat preferences and phenology of *Ochlerotatus triseriatus*
589 and *Aedes albopictus* (Diptera: *Culicidae*) in southwestern Virginia. *J Med Entomol*. 2003;40(4):403–410.
- 590 4. Leishnam PT, Juliano SA. Impacts of climate, land use, and biological invasion on the ecology of immature
591 *Aedes* mosquitoes: implications for La Crosse emergence. *Ecohealth*. 2012;9(2):217–228.

- 592 5. Westby KM, Fritzen C, Paulsen D, Poindexter S, Moncayo AC. La Crosse encephalitis virus infection in
593 field-collected *Aedes albopictus*, *Aedes japonicus*, and *Aedes triseriatus* in Tennessee. *J Am Mosq Control*
594 *Assoc.* 2015;31(3):233–241.
- 595 6. Benedict MQ, Levine RS, Hawley WA, Lounibos LP. Spread of the tiger: global risk of invasion by the mosquito
596 *Aedes albopictus*. *Vector Borne Zoonotic Dis.* 2007;7(1):76–85.
- 597 7. Aliabadi BW, Juliano SA. Escape from gregarine parasites affects the competitive interactions of an invasive
598 mosquito. *Biol Invasions.* 2002;4(3):283–297.
- 599 8. Moore CG, Mitchell CJ. *Aedes albopictus* in the United States: ten-year presence and public health
600 implications. *Emerg Infect Dis.* 1997;3(3):329.
- 601 9. Yee DA, Juliano S, Vamosi SM. Seasonal photoperiods alter developmental time and mass of an invasive
602 mosquito, *Aedes albopictus* (Diptera: Culicidae), across its north-south range in the United States. *J Med*
603 *Entomol.* 2012;49(4):825–832.
- 604 10. Rai KS. *Aedes albopictus* in the Americas. *Annu Rev Entomol.* 1991;36(1):459–484.
- 605 11. Gerhardt RR, Gottfried KL, Apperson CS, Davis BS, Erwin PC, Smith AB, et al. First isolation of La Crosse
606 virus from naturally infected *Aedes albopictus*. *Emerg Infect Dis.* 2001;7(5):807.
- 607 12. Westby K, Juliano S. Simulated seasonal photoperiods and fluctuating temperatures have limited effects on
608 blood feeding and life history in *Aedes triseriatus* (Diptera: Culicidae). *J Med Entomol.* 2015;52(5):896–906.
- 609 13. Ho BC, Ewert A, Chew LM. Interspecific competition among *Aedes aegypti*, *Ae. albopictus*, and *Ae. triseriatus*
610 (Diptera: Culicidae): larval development in mixed cultures. *J Med Entomol.* 1989;26(6):615–623.
- 611 14. Bevins SN. Invasive mosquitoes, larval competition, and indirect effects on the vector competence of native
612 mosquito species (Diptera: Culicidae). *Biol Invasions.* 2008;10(7):1109–1117.
- 613 15. Edgarly JS, Willey MS, Livdahl TP. The community ecology of *Aedes* egg hatching: implications for a
614 mosquito invasion. *Ecol Entomol.* 1993;18(2):123–128.
- 615 16. Livdahl TP, Willey MS. Prospects for an invasion: competition between *Aedes albopictus* and native *Aedes*
616 *triseriatus*. *Science.* 1991;253(5016):189–191.
- 617 17. Novak MG, Higley LG, Christianssen CA, Rowley WA. Evaluating larval competition between *Aedes albopictus*
618 and *Aedes triseriatus* (Diptera: Culicidae) through replacement series experiments. *Environ Entomol.*
619 1993;22(2):311–318.
- 620 18. Teng HJ, Apperson CS. Development and survival of immature *Aedes albopictus* and *Aedes triseriatus*
621 (Diptera: Culicidae) in the laboratory: effects of density, food, and competition on response to temperature. *J*
622 *Med Entomol.* 2000;37(1):40–52.
- 623 19. Yee DA, Kaufman MG, Juliano SA. The significance of ratios of detritus types and micro-organism productivity
624 to competitive interactions between aquatic insect detritivores. *J Anim Ecol.* 2007;76(6):1105–1115.
- 625 20. Juliano SA. Coexistence, exclusion, or neutrality? A meta-analysis of competition between *Aedes albopictus*
626 and resident mosquitoes. *Isr J Ecol Evol.* 2010;56(3-4):325–351.
- 627 21. Walker ED, Poirier SJ, Veldman WT. Effects of *Ascogregarina barretti* (Eugregarinida: Lecudinidae) infection
628 on emergence success, development time, and size of *Aedes triseriatus* (Diptera: Culicidae) in microcosms and
629 tires. *J Med Entomol.* 1987;24(3):303–309.
- 630 22. Munstermann LE, Wesson DM. First record of *Ascogregarina taiwanensis* (Apicomplexa: Lecudinidae) in North
631 American *Aedes albopictus*. *J Am Mosq Control Assoc.* 1990;6(2):235–243.
- 632 23. Comiskey NM, Lowrie Jr RC, Wesson DM. Role of habitat components on the dynamics of *Aedes albopictus*
633 (Diptera: Culicidae) from New Orleans. *J Med Entomol.* 1999;36(3):313–320.
- 634 24. Beier JC, Harris C. *Ascogregarina barretti* (Sporozoa: diplocystidae) infections in natural populations of *Aedes*
635 *triseriatus* (Diptera: Culicidae). *J Parasitol.* 1983;69(2):430.
- 636 25. Siegel JP, Novak RJ, Maddox JV. Effects of *Ascogregarina barretti* (Eugregarinida: Lecudinidae) infection on
637 *Aedes triseriatus* (Diptera: Culicidae) in Illinois. *J Med Entomol.* 1992;29(6):968–973.
- 638 26. de Assis RA, Casacci LP, Bonelli S, Barbero F, de Assis LME, Venturino E. Effects of Host Interspecific
639 Interaction in the Maculinea–Myrmica Parasite–Host System. *Bull Math Biol.* 2018;80(9):2378–2407.
- 640 27. Gilpin W, Feldman MW, Aoki K. An ecocultural model predicts Neanderthal extinction through competition
641 with modern humans. *PNAS.* 2016;113(8):2134–2139.
- 642 28. Liu R, Liu G. Asymptotic behavior of a stochastic Two-Species competition model under the effect of disease.

- 643 Complexity. 2018;2018.
- 644 29. Sebastián-González E, Moleón M, Gibert JP, Botella F, Mateo-Tomás P, Olea PP, et al. Nested species-rich
645 networks of scavenging vertebrates support high levels of interspecific competition. *Ecology*. 2016;97(1):95–105.
- 646 30. Tan X, Gu H, Ruan Y, Zhong J, Parajuli K, Hu J. Effects of nitrogen on interspecific competition between two
647 cell-size cyanobacteria: *Microcystis aeruginosa* and *Synechococcus* sp. *Harmful Algae*. 2019;89:101661.
- 648 31. Zhou P, Zhao XQ. Global dynamics of a two species competition model in open stream environments. *J Dyn*
649 *Differ Equ*. 2018;30(2):613–636.
- 650 32. Bewick S, Agosto F, Calabrese JM, Muturi EJ, Fagan WF. Epidemiology of La Crosse virus emergence,
651 Appalachia Region, United States. *Emerg Infect Dis*. 2016;22(11):1921.
- 652 33. Marini G, Guzzetta G, Baldacchino F, Arnoldi D, Montarsi F, Capelli G, et al. The effect of interspecific
653 competition on the temporal dynamics of *Aedes albopictus* and *Culex pipiens*. *Parasit Vectors*. 2017;10(1):102.
- 654 34. Paton RS, Bonsall MB. The ecological and epidemiological consequences of reproductive interference between
655 the vectors *Aedes aegypti* and *Aedes albopictus*. *J R Soc Interface*. 2019;16(156):20190270.
- 656 35. Kuno E. Competitive exclusion through reproductive interference. *Popul Ecol*. 1992;34(2):275–284.
- 657 36. Kishi S, Nakazawa T. Analysis of species coexistence co-mediated by resource competition and reproductive
658 interference. *Popul Ecol*. 2013;55(2):305–313.
- 659 37. Chen W. The life cycle of *Ascogregarina taiwanensis* (Apicomplexa: Lecudinidae). *Parasitol Today*.
660 1999;15(4):153–156.
- 661 38. Prophiro JS, Pereira TN, Oliveira JGd, Dandolini GW, Silva MAND, Silva OSd. *Ascogregarina taiwanensis*
662 infection in *Aedes aegypti* and *Aedes albopictus* in Santa Catarina, South Brazil. *Rev Soc Bras Med Trop*.
663 2017;50(2):235–238.
- 664 39. Lotka AJ. Analytical note on certain rhythmic relations in organic systems. *PNAS*. 1920;6(7):410–415.
- 665 40. Lotka AJ. Contribution to the theory of periodic reactions. *J Phys*. 2002;14(3):271–274.
- 666 41. Smith TM, Smith RL. *Elements of ecology*. 574.5 S662e9. Pearson,; 2015.
- 667 42. Volterra V. Variations and fluctuations of the number of individuals in animal species living together. *ICES J*
668 *Mar Sci*. 1928;3(1):3–51.
- 669 43. Erickson RA, Presley SM, Allen LJ, Long KR, Cox SB. A stage-structured, *Aedes albopictus* population model.
670 *Ecol Model*. 2010;221(9):1273–1282.
- 671 44. Delatte H, Gimonneau G, Triboire A, Fontenille D. Influence of temperature on immature development,
672 survival, longevity, fecundity, and gonotrophic cycles of *Aedes albopictus*, vector of Chikungunya and dengue in
673 the Indian Ocean. *J Med Entomol*. 2009;46(1):33–41.
- 674 45. Jalil M. Observations on the fecundity of *Aedes triseriatus* (Diptera: *Culicidae*). *Entomol Exp Appl*.
675 1974;17(2):223–233.
- 676 46. Mather TN, DeFoliart GR. Effect of host blood source on the gonotrophic cycle of *Aedes triseriatus*. *Am J*
677 *Trop Med Hyg*. 1983;32(1):189–193.
- 678 47. Briegel H, Timmermann SE. *Aedes albopictus* (Diptera: *Culicidae*): physiological aspects of development and
679 reproduction. *J Med Entomol*. 2001;38(4):566–571.
- 680 48. Maimusa HA, Ahmad AH, Kassim NFA, Rahim J. Age-stage, two-sex life table characteristics of *Aedes*
681 *albopictus* and *Aedes Aegypti* in Penang Island, Malaysia. *J Am Mosq Control Assoc*. 2016;32(1):1–11.
- 682 49. Haramis LD, Foster WA. Survival and population density of *Aedes triseriatus* (Diptera: *Culicidae*) in a woodland
683 in central Ohio, USA. *J Med Entomol*. 1983;20(4):391–398.
- 684 50. Patrican L, DeFoliart G. Lack of adverse effect of transovarially acquired La Crosse virus infection on the
685 reproductive capacity of *Aedes triseriatus* (Diptera: *Culicidae*). *J Med Entomol*. 1985;22(6):604–611.
- 686 51. Soghigian J, Livdahl T. Differential response to mosquito host sex and parasite dosage suggest mixed dispersal
687 strategies in the parasite *Ascogregarina taiwanensis*. *PloS One*. 2017;12(9):e0184573.
- 688 52. Helton JC, Davis FJ. Latin hypercube sampling and the propagation of uncertainty in analyses of complex
689 systems. *Reliab Eng*. 2003;81(1):23–69.
- 690 53. Marino S, Hogue IB, Ray CJ, Kirschner DE. A methodology for performing global uncertainty and sensitivity
691 analysis in systems biology. *J Theor Biol*. 2008;254(1):178–196.
- 692 54. Westby KM, Sweetman BM, Van Horn TR, Biro EG, Medley KA. Invasive species reduces parasite prevalence
693 and neutralizes negative environmental effects on parasitism in a native mosquito. *J Anim Ecol*.

- 1
2
3
4
5
6 694 2019;88(8):1215–1225.
- 7 695 55. Dixson A, Jackson R, Rowe R, Nease R, Fryxell RT. *Aedes albopictus* oviposits with other *Aedes* species in
8 696 artificial oviposition cups: a case study in Knox County, Tennessee, USA. *J Vector Ecol.* 2020;45(1):2–15.
- 9 697 56. Soghigian J, Valsdottir LR, Livdahl TP. A parasite's modification of host behavior reduces predation on its
10 698 host. *Ecol Evol.* 2017;7(5):1453–1461.
- 11 699 57. Rust RS, Thompson WH, Matthews CG, Beaty BJ, Chun RW. Topical review: La Crosse and other forms of
12 700 California encephalitis. *J Child Neurol.* 1999;14(1):1–14.
- 13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

701 **Figures**

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].

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

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* (A_a) 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* ($\alpha_t = 0.25 < \alpha_a = 0.83$). The right (f) is competition parameters that favor *Ae. triseriatus* ($\alpha_t = 0.73 > 0.42 = \alpha_a$). 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 – γ_{b_a} , γ_{m_a} , γ_{d_a} – 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 ($\gamma_{d_a} = \gamma_{m_a} = \gamma_{b_a} = 1$), 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.

702 Tables

Table 1 Parameter Values and Latin Hypercube Sampling ranges.

<i>Aedes albopictus</i>					
Symbol	Description	Value	LHS Range	Units	Reference
β_a	Birth Rate	32.6	2.5 – 56	Eggs/day	[44]
δ_a	Development Time	10	9-45	1/days	[47, 13, 48]
μ_{L_a}	Larval mortality	0.067	0.005 – 0.4	1/day	[13, 44]
μ_{A_a}	Adult mortality	0.045	0.01 – 0.065	1/day	[47, 44, 48]
α_a	Competition parameter	0.83, 0.42	0.4 - 1	unitless	[16]
ρ_a	Adult female proportion	0.5	0.2 - 0.6	unitless	[17]
<i>Aedes triseriatus</i>					
Symbol	Description	Value	LHS Range	Units	Reference
β_t	Birth rate	11	3 – 26	Eggs/day	[46, 45, 50]
δ_t	Development time	22	13 - 55	1/days	[13, 18, 12],
μ_{L_t}	Larval mortality	0.009	0.002 – 0.011	1/day	[13, 48, 17]
μ_{A_t}	Adult mortality	0.1	0.03 – 0.1	1/day	[49]
α_t	Competition Parameter	0.25, .73	0 - 0.75	unitless	[16]
ρ_a	Adult female proportion	0.5	0.4 - 0.55	unitless	[17]
Other Parameters					
Symbol	Description	Value	LHS Range	Units	Reference
γ_{b_a}	Effect on fecundity	1.0	1 - 2	unitless	varied
γ_{d_a}	Effect on development rate	1.0	1 - 2	unitless	varied
γ_{m_a}	Effect on larval mortality	1.0	1 - 16	unitless	varied
γ_{d_t}	Effect on development rate (<i>Ae. Triseriatus</i>)	1.2, 2	Fixed	unitless	varied
γ_{m_t}	Effect on larval mortality (<i>Ae. Triseriatus</i>)	1.5, 4	Fixed	unitless	varied
K	Carrying capacity	60	Fixed	Number of larvae	[16]

703 Tables

Table 2 Categorized outcomes. #Criteria is proportion of *Ae. albopictus* adults.

Category	Description	Criteria# (A_a)
1	<i>Ae. triseriatus</i> completely dominates, <i>Ae. albopictus</i> wiped out	$A_a < 0.01$
2	<i>Ae. triseriatus</i> dominates, few <i>Ae. albopictus</i> remain	$0.01 < A_a < 0.15$
3	<i>Ae. triseriatus</i> more present, <i>Ae. albopictus</i> still persists	$0.20 < A_a < 0.40$
4	Both species coexist in even proportions	$0.40 < A_a < 0.60$
5	<i>Ae. albopictus</i> more present, <i>Ae. triseriatus</i> persists	$0.60 < A_a < 0.80$
6	<i>Ae. albopictus</i> dominates, few <i>Ae. triseriatus</i> remain	$0.80 < A_a < 0.99$
7	<i>Ae. albopictus</i> completely dominates, <i>Ae. triseriatus</i> wiped out	$A_a > 0.99$

704 Tables

Table 3 Dilution parasitism parameters. Each level variation for parasitism (high or low) for each species.

<i>Ae. albopictus</i>	$\max \gamma_{m_a}$	$\max \gamma_{d_a}$	$\max \gamma_{b_a}$	<i>Ae. triseriatus</i>	$\max \gamma_{m_t}$	$\max \gamma_{d_t}$
low	1.5	1.2	1.2	low	1.5	1.2
high	16	4	4	low	1.5	1.2
low	1.5	1.2	1.2	high	8	4
high	16	4	4	high	8	4

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

705 **Additional Files**

706 Additional file 1 — Equilibrium and Supplementary figure

707 This contains the equilibria values. The following supplementary figures are located in this file: File format is pdf.

708 Additional file 2 — Code

709 This is all the code used to run and analyze the model. File format is Matlab file (.m).

710 Additional file 3— Generated data

711 This is the all generated samples. The format is a Matlab file (.mat).

Figures

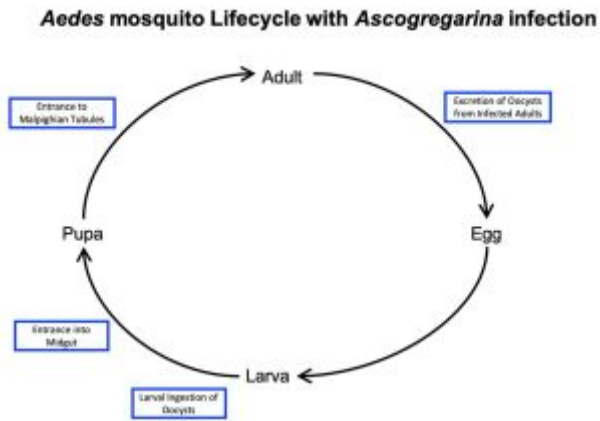


Figure 1

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].

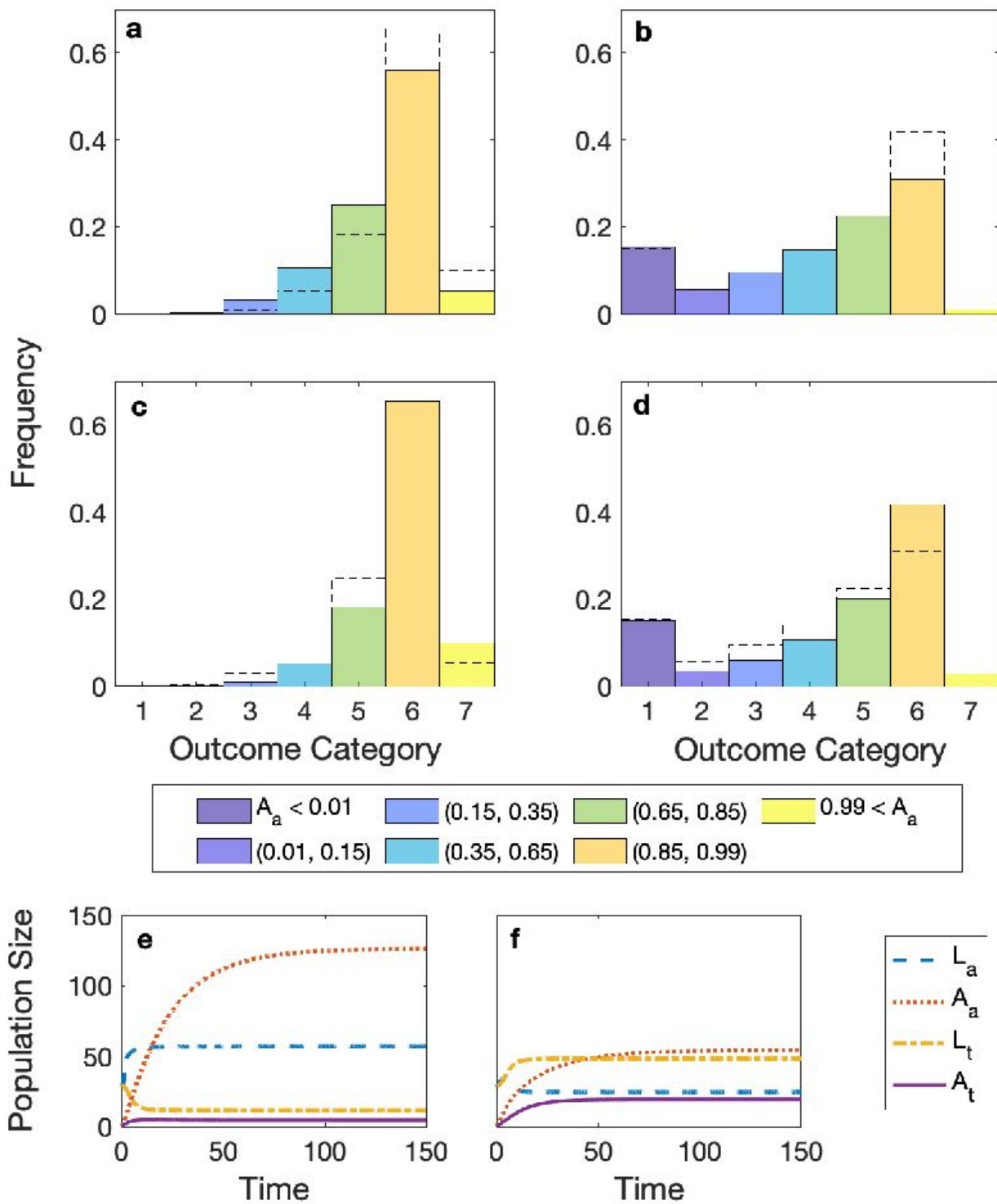


Figure 2

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* (A_a) 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* ($\alpha_t = 0.25 < \alpha_a = 0.83$). The right (f) is competition parameters that favor *Ae. triseriatus* ($\alpha_t = 0.73 > 0.42 = \alpha_a$). All parameters are chosen to be the values in Table 1 with all *Ae. albopictus* parasite parameters set to 1.

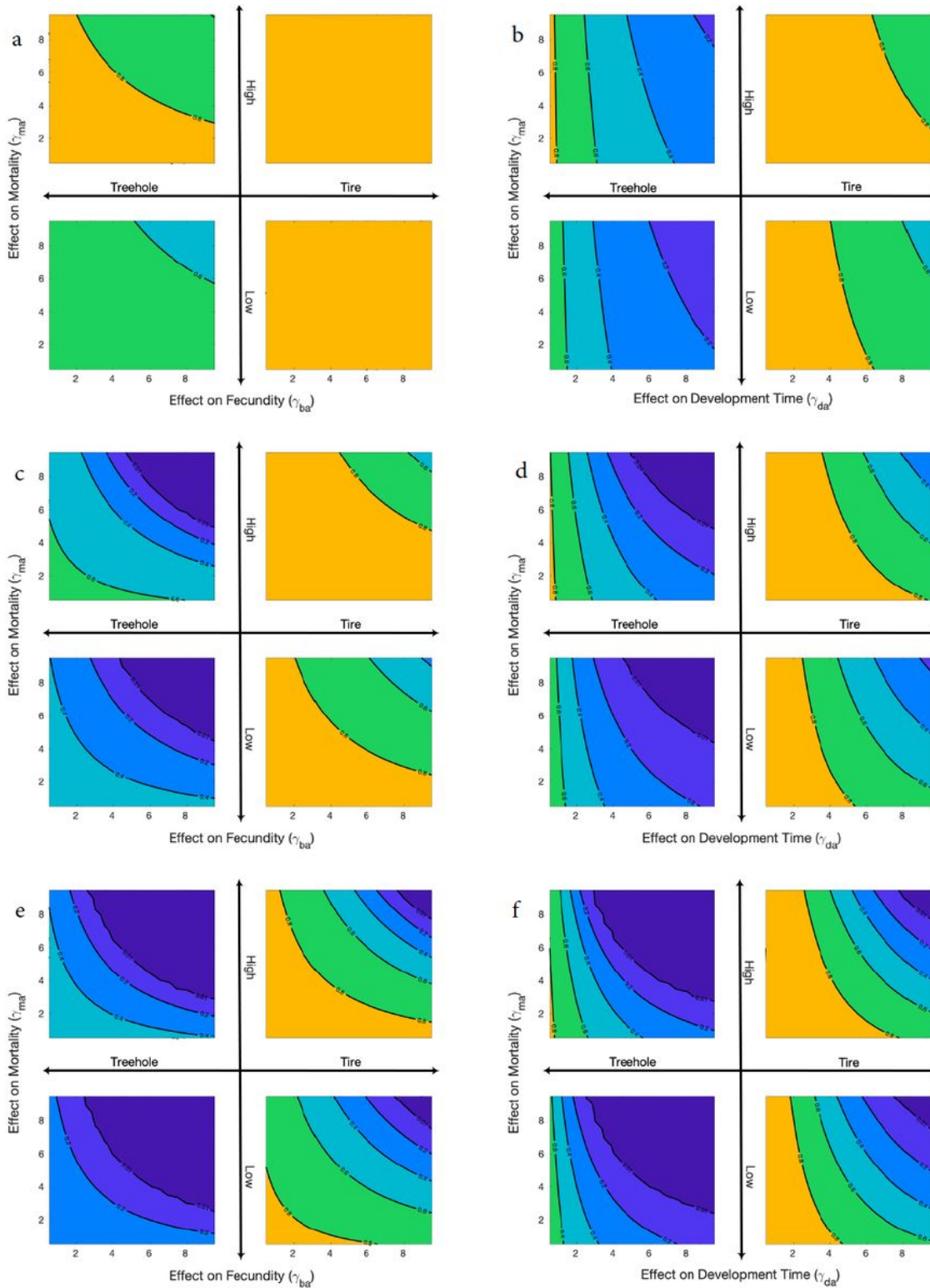


Figure 3

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 – γ_{ba} , γ_{ma} , γ_{da} – 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.

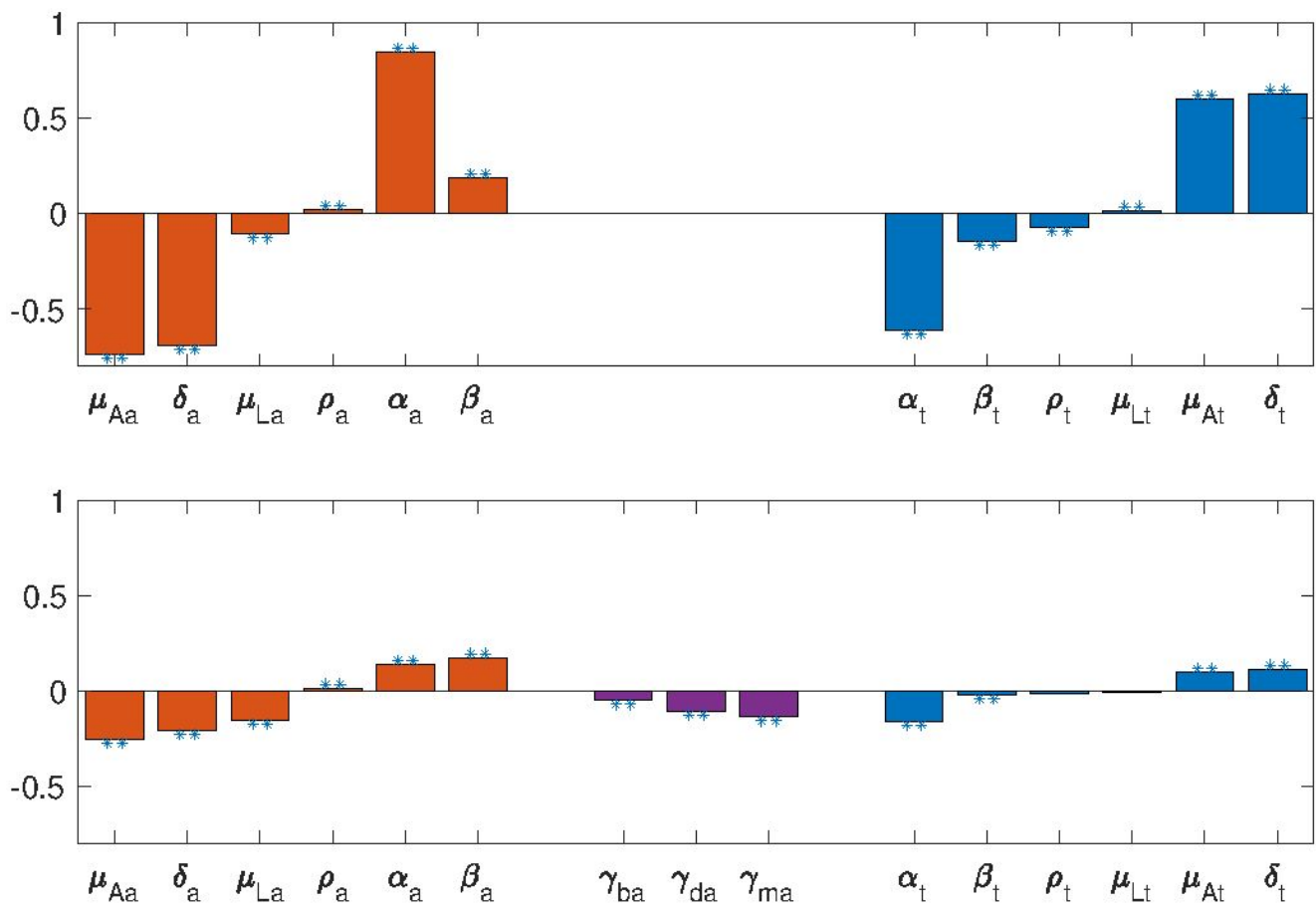


Figure 4

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 ($\gamma_{da} = \gamma_{ma} = \gamma_{ba} = 1$), indicating no parasitism. The bottom plot is the PRCC with variation of parasitism included in the LHS for *Ae. albopictus*.

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.

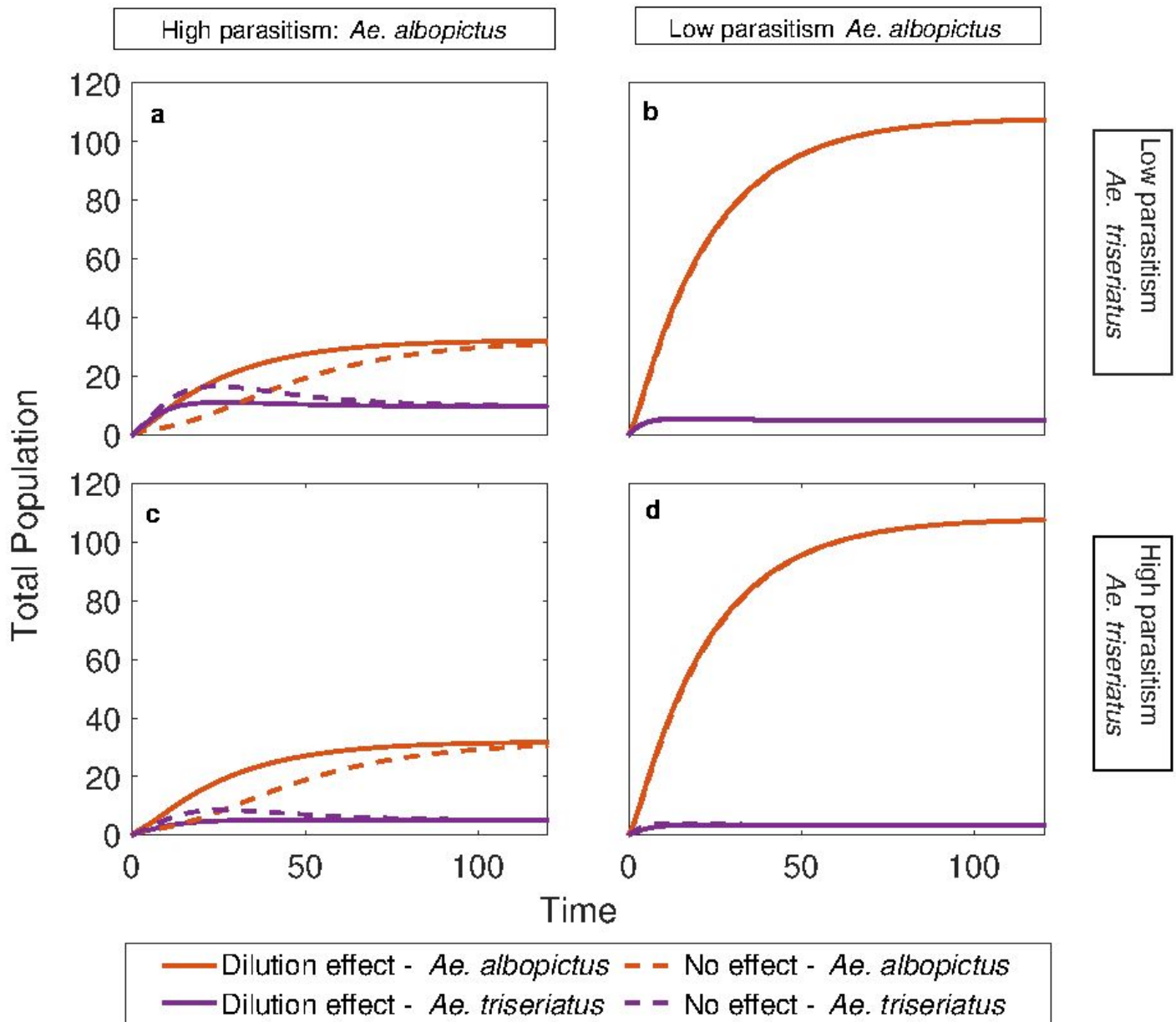


Figure 5

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.

Supplementary Files

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

- [Additionalfile1.pdf](#)
- [Additionalfile2.m](#)
- [Additionalfile3.mat](#)
- [graphicalabstract.png](#)