

1 Oil palm expansion increases the vectorial capacity of dengue vectors in

2 Malaysian Borneo

3

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22 ABSTRACT

23 Changes in land-use and the associated shifts in environmental conditions can have large effects
24 on the transmission and emergence of disease. Mosquito-borne disease are particularly sensitive
25 to these changes because mosquito growth, reproduction, survival and susceptibility to infection
26 are all thermally sensitive traits, and land use change dramatically alters local microclimate.
27 Predicting disease transmission under environmental change is increasingly critical for targeting
28 mosquito-borne disease control and for identifying hotspots of disease emergence. Mechanistic
29 models offer a powerful tool for improving these predications. However, these approaches are
30 limited by the quality and scale of temperature data and the thermal response curves that
31 underlie predictions. Here, we used fine-scale temperature monitoring and a combination of
32 empirical, laboratory and temperature-dependent estimates to estimate the vectorial capacity of
33 *Aedes albopictus* mosquitoes across a tropical forest – oil palm plantation conversion gradient
34 in Malaysian Borneo. We found that fine-scale differences in temperature between logged forest
35 and oil palm plantation sites were not sufficient to produce differences in temperature-
36 dependent trait estimates using published thermal performance curves. However, when
37 measured under field conditions a key parameter, adult abundance, differed significantly
38 between land-use types, resulting in estimates of vectorial capacity that were 1.5 times higher in
39 plantations than in forests. The prediction that oil palm plantations would support mosquito
40 populations with higher vectorial capacity was robust to uncertainties in our adult survival
41 estimates. These results provide a mechanistic basis for understanding the effects of forest
42 conversion on mosquito-borne disease risk, and a framework for interpreting emergent
43 relationships between land-use and disease transmission. As rising demand for palm oil
44 products drives continued expansion of plantations, these findings have important implications
45 for conservation, land management and public health policy at the global scale.

46 AUTHOR SUMMARY

47 The large scale modification of landscapes by humans has contributed to the rise of emerging
48 and re-emerging mosquito-borne diseases. While the association between anthropogenic land-
49 use change and these shifts in disease risk are frequently observed, our understanding of exactly
50 how land-use change mechanistically alters disease risk remains unclear. Changes in local
51 environmental conditions (e.g. temperature) may play an important role, due to the effects on
52 mosquito life-history, but are rarely measured at scales relevant these small-bodied ectotherms.
53 Here we measure the impact of tropical forest conversion to oil palm plantation on each of the
54 components that determine the potential for mosquitoes to transmit pathogens (vectorial
55 capacity). By combining fine-scale temperature data from the field, published temperature
56 responses of mosquitoes and field data on adult mosquito populations, we show that land-use
57 change from forest to plantation can be expected to increase vectorial capacity by 150%. Our
58 results highlight the need to advance field research into fundamental mosquito ecology, and to
59 more critically evaluate the increased risk of *Aedes*-borne disease in dynamic working
60 landscapes against the benefits of economic development.

61

62 1. BACKGROUND

63 More than 80% of the global population is at risk of being infected with a mosquito-borne
64 disease (WHO 2017). Dengue virus, the most prevalent of the mosquito-borne diseases, is
65 estimated to infect 390 million people annually (Bhatt *et al.* 2013), and two previously obscure
66 arboviruses, Zika and chikungunya virus, infected over 1 million people between 2016 and 2017
67 (WHO 2017). Climate and environmental change (e.g. land-use) have been implicated as drivers
68 of mosquito-borne disease emergence (1, 2) due to the temperature sensitivity of parasite and
69 mosquito traits underlying transmission. However, the mechanisms by which environment
70 influences transmission dynamics remain poorly characterised.

71 Efforts to identify environmental drivers of disease have historically relied on statistical
72 approaches that link environmental data to disease prevalence, or on occurrence mapping of the
73 mosquito vectors (3, 4). Whilst useful for identifying broad, correlative patterns of disease
74 incidence, these models don't explicitly incorporate biological mechanisms, and are thus limited
75 in their capacity to address non-linear feedback pathways, spatiotemporal heterogeneities and
76 complex transmission dynamics (5). Mechanistic models that incorporate mosquito and parasite
77 life-history into a mathematical framework for transmission have shown promise. For example,
78 the vectorial capacity model, which incorporates both mosquito and pathogen traits to estimate
79 the total number of potentially infectious bites that would eventually arise from all the mosquitoes
80 biting a human on a single day explicitly (Garrett-Jones, 1964). A key limitation of these
81 mechanistic approaches has been a lack of data on the key entomological parameters (7, 8).

82

83 Mosquitoes are small-bodied ectotherms and their physiology is closely linked to ambient
84 environmental conditions (9). Temperature affects all components of vectorial capacity: mosquito
85 density, by determining rates of mosquito demographic traits, such as growth, survival and
86 reproduction (10-12), biting rate (13, 14), vector competence (15, 16), and the pathogen extrinsic
87 incubation period (17, 18). Naturally the vast majority of studies have focused on this source of
88 variation (19). Temperature has most recently been incorporated into mechanistic models using
89 thermal performance curves (TPCs) (20-22).

90 The temperature dependence of mosquito traits is typically assessed under laboratory
91 conditions, where the response of a relevant trait is measured across a range of constant
92 temperatures and yields a curve where performance increases slowly with temperature to a
93 maximum level then rapidly declines (11, 23, 24). However, mosquitoes are subject to daily
94 temperature fluctuations in the field, and a growing body of work demonstrates that these

95 variations can produce trait responses that differ to those derived under constant conditions (25,
96 26)

97 Similarly, the environmental data used to drive transmission models is often coarse in
98 scale, such as average monthly temperatures or broad categories of land-use. These data are
99 unlikely to represent the realised environments of mosquitoes or their pathogens, and the
100 mismatch between the underlying biological processes driving transmission and covariates can
101 have profound effects on predictions for transmission (7, 21, 27, 28).

102 Fine-scale heterogeneity in landscape structure can significantly increase the disparity
103 between available environmental data and actual environmental conditions (Jucker *et al.* 2011;
104 Cator *et al.* 2013). For example, the temperature data underpinning many disease transmission
105 models is obtained from the WorldClim2 database, which uses data interpolated from weather
106 stations located in open areas, and has a resolution of approximately 1km. In contrast, vegetation
107 structure mediates microclimates such that temperatures under dense canopy can be $\sim 2\text{-}3^\circ\text{C}$
108 cooler than in open areas (29, 30) and are highly heterogeneous over small spatial scales. These
109 differences are even greater when compared to satellite estimates of local temperatures, with one
110 study finding that within-forest temperatures differ from satellite estimates by $5\text{-}10^\circ\text{C}$ (31).
111 Similarly, land cover data from satellite-based remote sensing (e.g. Landsat) are typically
112 available at a resolution of 15-60 m, and suffers from high cloud cover in the tropics (32).

113 Characterising the dynamics of tropical environments is particularly important because
114 they both experience some of the highest rates of anthropogenic land-use change (33) and bear
115 significant and increasing morbidity and mortality due to mosquito-borne diseases (34). For
116 example, an increase in demand for African oil palm (*Elaeis guineensis*) products has resulted in
117 the dramatic expansion of industrial plantations in the last 20 years (35). More than 80% of global
118 palm oil is produced in Malaysia and Indonesia (36). Conversion has been at the expense of either
119 selectively logged or old growth forest (37). The effects of land-use change on arbovirus

120 transmission in this region remain largely unexplored, despite observations that the abundance
121 of *Aedes albopictus*, an important arbovirus vector, increases following forest conversion (38, 39).
122 This aggressive, day-biting mosquito is native to the forests of Southeast Asia and considered an
123 important vector of the dengue virus and a potential bridge vector for emerging pathogens (40-
124 42). There has been a dramatic increase in the intensity and magnitude of dengue outbreaks in
125 Malaysia over the last few decades (43, 44). The majority of recent cases were reported from
126 Selangor state, the most populous state in peninsular Malaysia, however, an increasing number
127 of sub-urban and rural cases have been reported (40). Notably, in 2007 a fifth dengue virus
128 serotype was isolated from an outbreak in the Bornean state of Sarawak. The serotype was
129 identified as a member of a sylvatic lineage of DENV-2, representing the first identification of a
130 sylvatic DENV circulating in Asia since 1975 (Normile 2013).

131 We used a mechanistic approach to investigate how tropical forest conversion will affect
132 the vectorial capacity of *Ae. albopictus* mosquitoes. We directly measured *Ae. albopictus* survival,
133 and abundance in forest and oil palm sites. We then measured the effect of thermal environment
134 on adult gonotrophic cycle length by subjecting females to field thermal conditions in a controlled
135 experiment. These measures were then combined to parameterise a dengue-specific vectorial
136 capacity model to investigate differences in transmission potential between land-use types. We
137 also estimated adult survival and abundance from published TPCs to determine if these
138 predictions differed to our field data. Based on our data, vectorial capacity was estimated to be
139 greater in oil palm plantation than in forest, largely driven by greater mosquito abundance in oil
140 palm. This key difference between land-use types was not predicted by commonly used TPCs. Our
141 results suggest that oil palm conversion may be an important driver of *Aedes*-borne disease
142 emergence.

143

144

145 2. Methods

146 2.1 Study site

147 Fieldwork was conducted at sites within the Stability of Altered Forest Ecosystems (SAFE)
148 Project, a large-scale deforestation and forest fragmentation experiment located within lowland
149 dipterocarp forest regions of East Sabah in Malaysian Borneo (4°33'N, 117°16'E; Ewers et al 2011).
150 Climate in the region is typically aseasonal (Walsh & Newbery 1999), with occasional droughts
151 that are often, but not always, associated with the positive phase of ENSO events (46). The logged
152 forest sites have undergone two rounds of selective logging since 1978, and have a mean
153 aboveground biomass (ABG) of 122.4 t/ha (47). Logging intensity in this area varies considerably,
154 however most stands are heavily degraded and are characterised by a paucity of commercial
155 timber species, few emergent trees and the dominance of pioneer and invasive vegetation (Pfeifer
156 *et al.* 2016) . Oil palm plantations were established in 2006 (Ewers *et al.* 2011) and are
157 characterised by monocrop stands of closed or nearly-closed canopy oil palm. The plantation sites
158 have considerably lower plant biomass than the forest sites (ABG = 38.1 t/ha; Pfeifer *et al.* 2016).
159 Mean altitude across the sampling points is 450m (median = 460m, interquartile range = 72m).
160 Further details of the sites are available in the electronic Supplementary materials (S1).

161

162 2.2 Fine-Scale Temperature Data

163 Hourly temperature data were collected during the same period from nine field sites in each of
164 logged forest and oil palm plantations (N = 18; Gregory *et al.* 2019). These data were collected
165 using Data Loggers ERL-USB-2 (LASCAR electronics, Salisbury) secured to small wooden posts
166 at a height of 5 cm, and shaded from rain and direct sunlight with plastic plates suspended
167 approximately 30 cm above each post.

168

169 2.3 Adult mosquito collection

170 We directly measured adult mosquito density from four human settlements. Two of these were
171 located within logged forest and two were located within oil palm sites. Host-seeking mosquitoes
172 were collected using the human landing catch (HLC) method, where a collector (NG) sat with their
173 limbs exposed and aspirated mosquitoes as they attempted to feed. Sampling was conducted at
174 each site between February and April in both 2017 and 2018. Collections were carried out for up
175 to three consecutive days, at least twice per site between 10:00 to 12:00. The collector was trained
176 in the HLC method prior to involvement in the project and their health monitored for three weeks
177 following collections.

178

179 2.3 Estimating mosquito survival

180 Adult survival was estimated using the proportion of host-seeking females that were found to have
181 laid one or more batches of eggs (48). Female mosquitoes collected during HLCs were
182 immobilised in a freezer and then had their ovaries removed for observation of the tracheole coils,
183 following Detinova (1962). Nulliparous mosquitoes have tightly coiled ovarioles that become
184 irreversibly distended during the passage of eggs, creating bead-like dilatations. The population
185 of adult females is thus split into two age groups representing young and old individuals. Adult
186 survival (s) can then be estimated using the equation:

187

188

$$s = M \frac{1}{i_0} \quad 1$$

189

190 where M is the parous rate of the sampled population and i_0 is the length of the first gonotrophic
191 cycle (Macdonald 1952c; Davidson 1954).

192 To determine gonotrophic cycle length (i_o) *Ae. albopictus* larvae were experimentally reared in
193 incubators (Panasonic MLR-350H). Eggs between 2-4 weeks old were hatched in dechlorinated
194 water over a period of 36 hours. First instar larvae were reared at a density of 50 larvae per cup
195 and provisioned with five pellets of fish food (*Tetra Cichlid Colour*TM) daily. Developing larvae
196 were exposed to temperature treatments simulating mean hourly diurnal temperatures
197 empirically recorded in either logged forest (mean = 24 °C, range = 6 °C) or oil palm plantation
198 (mean = 24 °C, range = 4 °C) sampling sites (Gregory *et al.* 2019) or a control treatment where
199 temperature was held constant (24 °C). Temperature data and rearing protocol are described in
200 further detail in the electronic supplementary materials (S2). Upon emergence, male and female
201 adults were housed together to allow for mating, and provisioned with 10 % sugar solution *ad*
202 *libitum*. Females were offered defibrinated horse blood via a Hemotek feeding system three days
203 after emergence. Mosquitoes that did not fully engorge were removed from the fecundity
204 experiments. Mosquitoes that failed to feed were offered a bloodmeal each day until a successful
205 feed was achieved or until four additional days had passed. Blood-fed females were transferred
206 into individual laying tubes (2.9cm x 11.7cm) containing damp filter paper as an egg laying
207 substrate. Papers were observed every day for the presence of eggs, and the length of the pre-
208 bloodmeal period as well as the first gonotrophic cycle were recorded. The first gonotrophic cycle
209 period was used as an estimate of average gonotrophic cycle length when calculating survival (49),
210 as only one bloodmeal was provided.

211

212 2.3 Estimating mosquito density based on published thermal performance data

213 We used our fine-scale data to approximate mosquito density using a method used in a number
214 of other VBD studies (7, 8, 20, 50). Here adult density is estimated using the equation:

215

$$m = \frac{EFD \cdot p_{EA} \cdot MDR}{\mu^2} \quad 2$$

216

217 where the parameters are the number of eggs laid per female per day (*EFD*), the egg to adult
218 survival probability (*p_{EA}*), the larval development rate (*MDR*), and adult daily probability of
219 mortality (μ) (51). Trait values were estimated using temperature-dependent trait response
220 curves from Mordecai *et al.* (2017), combined with the fine-scale temperature data collected from
221 the field. Rate summation was then used to incorporate the effects of diurnal temperature
222 fluctuation by estimating trait responses at each hour throughout the day and summing the
223 proportional hourly changes (52, 53).

224

225 2.5 Estimating vectorial capacity

226 Vectorial capacity was estimated using a dengue specific framework:

227

$$VC = \frac{m \cdot a^2 \cdot b \cdot c \cdot e^{\frac{-\mu}{REI}}}{-\mu} \quad 3$$

228

229 where *m* denotes vector to human ratio, *a* is the daily probability of a female mosquito taking a
230 bloodmeal, μ is the daily probability of adult mortality, *b* is the probability of transmission from
231 an infectious mosquito to a susceptible human, *c* is the probability of transmission from an
232 infectious human to susceptible mosquito, and *REI* is the rate of extrinsic incubation of the
233 pathogen.

234 We parameterized this model using a combination of our field-collected data on mosquito life
235 history and abundance (Table 1) and estimates derived from published TPCs. Mosquito density
236 and survival were measured in the field, and female biting rate was taken as the inverse of the
237 gonotrophic cycle length derived from our laboratory experiments (10, 20). Parameters that were
238 not measured in this study (REI , b , c) were estimated using field-collected temperature data and
239 rate summation as described above. As mosquito density (m) scales proportionally with vectorial
240 capacity, omitting abundance from the vectorial capacity equation allows us to compare the
241 relative contributions of an individual mosquito inhabiting logged forest and oil palm plantation
242 to transmission. We calculated this relative vectorial capacity (rVC , the vectorial capacity relative
243 to the vector : human population ratio) for each of the sites.

244

245 2.6 Sensitivity of vectorial capacity estimates to mortality and biting rate

246 Vectorial capacity is especially sensitive to variation in adult mosquito survival and biting rate. To
247 explore the impact of uncertainty in survival estimates derived from our field data, we recalculated
248 vectorial capacity for every combination of daily probability of survival and of biting rate in the
249 two land-use types at increments of 0.01, while holding all other parameters constant. We used a
250 contour plot to visualize how differences in relative survival affected transmission potential.

251

252

253

254 **Table 1. Traits and data sources for vectorial capacity parameters**

Trait	Symbol	Source
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Vector density	m	Measured directly in field collections
Daily probability of a female mosquito taking a bloodmeal	a	Calculated from laboratory experiments
Probability of transmission from an infectious mosquito to a susceptible human	b	Mordecai <i>et al.</i> (2017) temperature-dependent estimates combined with field-collected temperature data
Probability of transmission from an infectious human to a susceptible mosquito	c	Mordecai <i>et al.</i> (2017) temperature-dependent estimates combined with field-collected temperature data
Extrinsic incubation rate of the pathogen	REI	Mordecai <i>et al.</i> (2017) temperature-dependent estimates combined with field-collected temperature data
Daily probability of adult mortality	μ	Estimated from field parity assessments and gonotrophic cycle length determined in laboratory experiments

255

256

257

258 2.7 Statistical analysis

259 All analyses were carried out in R Version 3.5 (R Core Team 2014). A generalised linear negative
260 binomial model (link = log; R package MASS; Venables 2002), with land-use type set as a
261 predictor was used to compare the number of host-seeking mosquitoes collect in HLCs between
262 oil palm plantations and logged forest sites. Sampling site and year were initially nested as
263 random effects, but neither was significant in the model so were excluded from the final model.
264 To calculate survival, parous rates were compared between land-use type and sampling years
265 using a generalised linear model (family = Gamma, link = “log”). Laboratory data on gonotrophic

266 cycle length were compared using the same model structure with the length of the first
267 gonotrophic cycle in days set as the response variable and experimental treatment (forest or
268 plantation microclimatic conditions) set as the predictor. Adult survival was then calculated from
269 mean parous rate and gonotrophic cycle using Equation 4 . Mean trait estimates for each land-
270 use type were then used to calculate vectorial capacity at each location for which there was
271 temperature data (N = 18). If the point estimates for each trait did not differ significantly between
272 land-use types, we took the conservative approach of using the average trait value across both
273 land-use types. The *b*, *c*, and *REI* values estimated from Mordecai *et al.* (2017) were compared
274 between land-use types using Mann-Whitney U tests. The effect of land-use on vectorial capacity
275 estimates was then explored using linear models, with land-use and sampling year as predictors.
276 Relative vectorial capacity estimates were compared using a Mann-Whitney U test.

277

278 2.8 Ethical Statement

279 The use of HLCs was approved by the ethical committee of the Ministry of Health in Malaysia
280 (Approval Number: NMRR-17-3242-39250, Issued: 13 March 2018), and the Imperial College
281 London Research Ethics Committee (ICREC Reference: 17IC3799, Issued: 22/02/17).

282

283 3. Results

284 3.1 Human landing catches

285 A total of 276 *Ae. albopictus* mosquitoes were collected from 46 HLC surveys in 2017 and 22
286 surveys in 2018. Male mosquitoes typically arrived first, and made up 19–58 % of the collections
287 at each site (Table 2). However, this is likely an underestimate of the number of males swarming
288 as only those that landed on the collectors were counted. The number of female mosquitoes
289 collected per day ranged from 1–6 in logged forest and 1–15 in plantations, and were not

290 significantly different between sampling years (GLM, $RR = 0.01$, $df = 64$, 95% CI: $-0.29, 0.31$, p
291 $= 0.9$). Overall, human landing catches conducted in plantations yielded an average 1.5 times
292 more mosquitoes per session than those at logged forest sites (GLM, $RR = 0.42$, $df = 64$, 95% CI:
293 $1.17, 2.0$, $p = 0.002$). The mean number of mosquitoes collected per session was 3.59 ± 0.27 (SE)
294 in logged forest, and 5.48 ± 0.65 (SE) in plantation sites. The proportion of parous mosquitoes
295 was not significantly different between land-use types (GLM, $F_{1,6} = 0.2$, $p = 0.69$) or sampling
296 years (GLM, $F_{1,5} = 0.98$, $p = 0.37$). Parity rates were highly variable within sites, with both the
297 highest value in 2017, and the lowest value in 2018, observed at the same site (0.90 and 0.70 ,
298 respectively).

299

300 3.2 Adult survival and temperature-dependent transmission

301 Gonotrophic cycle length did not differ between logged forest and oil palm plantation
302 treatments (Mann-Whitney U, $Z = -0.99$, $n = 83$, $p = 0.33$), averaging 8.24 ± 3.2 (\pm SD) days. As
303 neither gonotrophic cycle length nor parity rate differed significantly between land-use types,
304 the median value across all sites was used to estimate adult survival (S) in both land-use types.
305 Daily probability of adult mortality (μ) was then taken as $1 - S$, and estimated to be $0.03 \pm$
306 0.006 (SE) for all sites, corresponding to an estimated adult lifespan of 33.3 ± 57 (SE) days.
307 Biting rate was taken as the inverse of the median gonotrophic cycle length, and set as 0.12 for
308 all sites.

309

310 **Table 2. Human landing catch data.** Sampling sites are listed along with the number of
311 sampling days per site (n). For the proportion of parous females, n indicates the total number of
312 females for which parity status could be determined.

Year	Land-use type	Sampling site (n)	Total number of females/males	Mean number of females per day (95% CI)	Proportion parous (n)
------	---------------	-------------------	-------------------------------	---	-----------------------

2017	Oil palm	OPK1 (11)	76/22	6.91 (4.1, 9.7)	0.90 (44)
		OPSB (8)	32/25	4.57 (2.5, 5.5)	0.75 (18)
	Logged forest	SAFE (18)	58/14	3.22 (2.1, 7.0)	0.80 (41)
		SWML (5)	28/13	4.00 (2.7, 5.3)	0.82 (11)
2018	Oil palm	OPK1 (6)	28/38	4.67 (2.3, 7.0)	0.70 (20)
		OPSB (5)	23/9	5.75 (0.03, 12)	0.72 (18)
	Logged forest	SAFE (6)	38/7	4.75 (3.5, 7.0)	0.76 (37)
		SWML (5)	9/10	2.25 (0.7, 3.8)	0.89 (9)

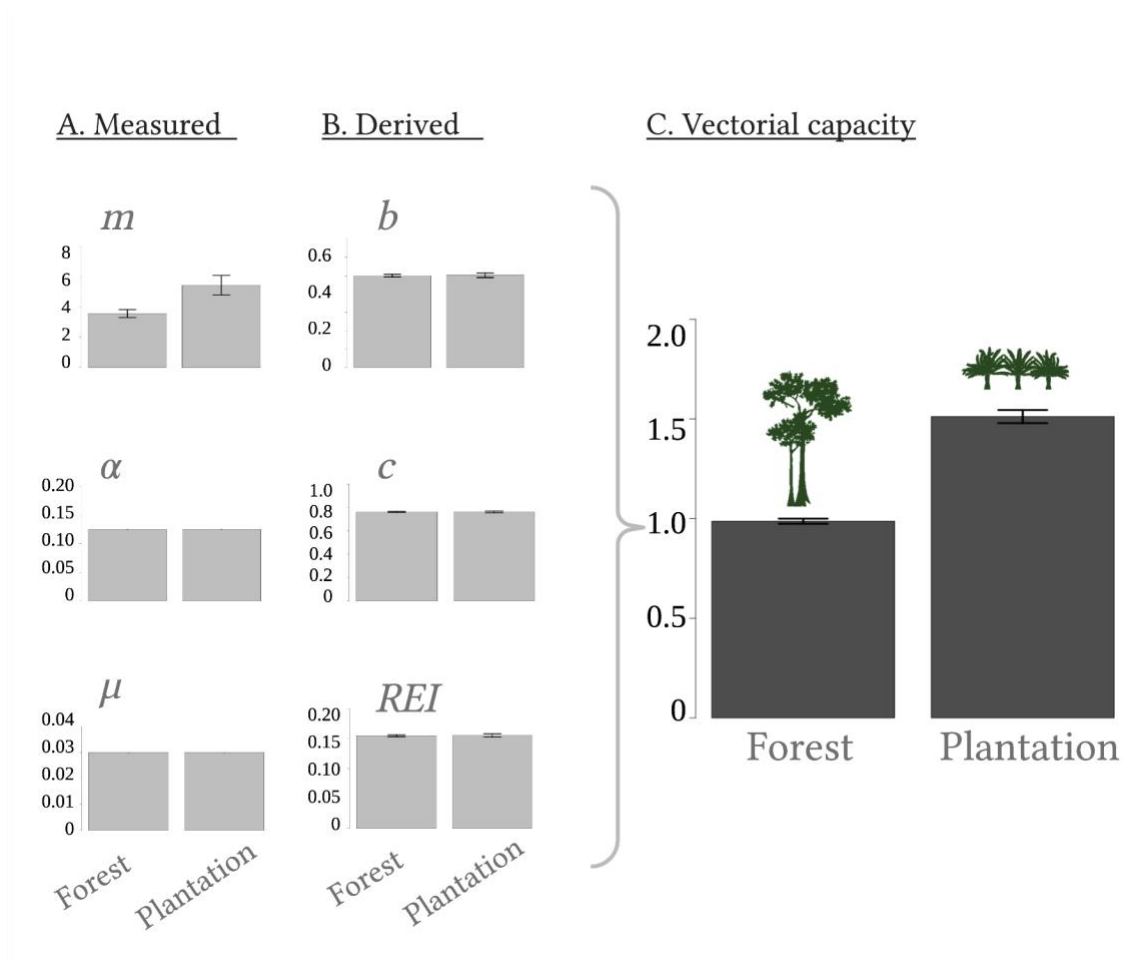
313

314

315 Temperature data indicated that although mean daily temperatures did not differ significantly
 316 between land-use types during the sampling period, daily temperature fluctuations were greater
 317 in oil palm plantations than in logged forest (Gregory *et al.* 2019). Despite warmer temperatures
 318 in plantation sites, none of the parameters estimated using the temperature-dependent
 319 responses from Mordecai *et al.* (2017) differed significantly between the land-use types for
 320 either sampling year (Wilcox, $Z=0.43$, $p = 0.663$; Fig 1). The probability of dengue transmission
 321 from an infectious mosquito to a susceptible human (b) was estimated to be 0.501 ± 0.01 in
 322 logged forest and 0.503 ± 0.012 (mean \pm SE) in oil palm. Human to mosquito transmission
 323 probability (c) was estimated to be 0.762 in both logged forest and oil palm, with marginally
 324 greater variation in the latter (logged forest SE = 0.005, oil palm SE = 0.008). The rate of
 325 extrinsic incubation (REI) was also the same in logged forest and oil palm, and estimated to be
 326 0.155 ± 0.01 .

327 Vectorial capacity was found to be 1.5 times greater in oil palm plantations (1.51 ± 0.03 , mean \pm
 328 SE) than in logged forest (0.99 ± 0.01 , mean \pm SE; $F(1,4) = 61$, $\beta = 0.50$, $p < 0.001$) and did not
 329 differ significantly between sampling years ($\beta = -0.005$, $p = 0.93$). The higher vectorial capacity
 330 in oil palm plantations was driven by greater mosquito density (m) at plantation sites, as rVC

331 estimates did not differ significantly between land-use types (Wilcox, $W = 6.5$, $Z = 0.06$, $p =$
332 0.77).



333

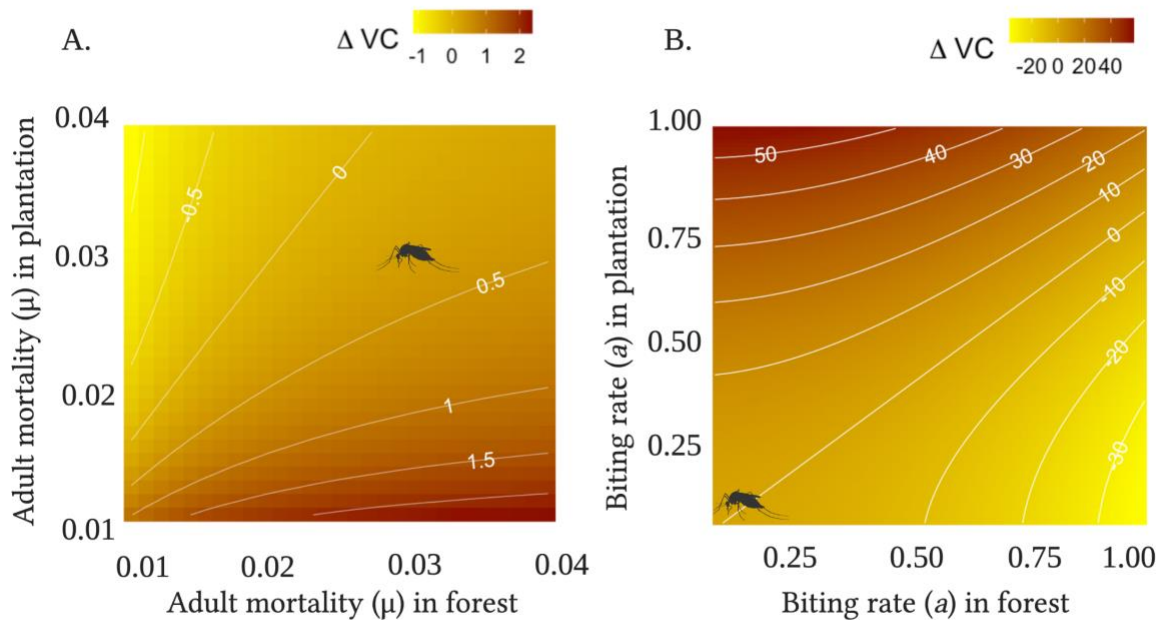
334

335 **Fig 1. Effects of land-use on vectorial capacity.** Estimates derived from temperature-dependent trait
336 responses and data measured in the field are shown for each parameter underlying vectorial capacity (VC)
337 for 2017. These are vector to human ratio (m), daily probability of a female mosquito taking a bloodmeal
338 (a), the daily probability of adult mortality (μ), the probability of transmission from an infectious mosquito
339 to a susceptible human (b), the probability of transmission from an infectious human to susceptible
340 mosquito (c), and the rate of extrinsic incubation of the pathogen (REI). Created with BioRender.com

341

342 3.3 Effects of adult mortality and biting rate on vectorial capacity

343 We found that holding all other parameters constant, if adult mortality was equal in logged forest
344 and oil palm plantations, vectorial capacity would always be higher in plantations (Fig 2A), with
345 the difference increasing exponentially with decreasing mortality rate. Given field estimates of
346 adult mortality in oil palm plantations ($\mu = 0.03$), vectorial capacity in logged forest could only
347 exceed that in plantations if mortality in forests was lower than 0.02. This would translate to an
348 adult lifespan of 50 days, compared to 33 days in oil palm. Calculating rVC with equal mortality
349 between the sites demonstrates that rVC will not differ significantly between the land-use types
350 within the range of most mosquito lifespans ($\mu < 0.007$, or a lifespan < 140 days; Wilcox, $W =$
351 42180 , $Z = -21.2$, $p = 0.72$). Similarly, we found that given equal biting rates in forest and
352 plantation, vectorial capacity will always be greater in the latter (Fig 2B). Given our biting rate
353 estimate of 0.125, or once every 8 days, vectorial capacity in forest will only exceed that in oil palm
354 at 0.23, or a frequency of every four days. When calculated from thermal performance curves,
355 biting rates were estimated to increase by 50% compared to estimates derived from laboratory
356 data on gonotrophic cycle length, and did not differ significantly between land-use types (Wilcox,
357 $Z = -1.55$, $p = 0.13$). Holding all other parameters constant, we found that this increase in biting
358 rate resulted in a four-fold increase in vectorial capacity for both logged forest and oil palm
359 plantation sites.



360

361 **Fig 2. Effects of adult mortality (A) and biting rate (B) on vectorial capacity.** Contour plot of
362 differences in vectorial capacity estimates between oil palm plantations and logged forest, with positive
363 values of ΔVC denoting higher vectorial capacity in oil palm plantation and negative values denoting
364 higher vectorial capacity in logged forest. As you move along the x-axis, the respective traits increase in
365 logged forest, and the same applies for oil palm plantation along the y-axis. The mosquito icon indicates
366 the value of the trait observed from the empirical data.

367

368 4. Discussion

369 The advantages of using mechanistic models for understanding the impacts of environmental
370 change on mosquito-borne disease dynamics have been demonstrated in a number of studies (7,
371 8, 50). A key limitation to the development of these frameworks has been a lack of field data for
372 model parameterization. By integrating fine-scale field data and temperature-dependent

373 estimates from the literature into a mathematical framework for transmission potential, our study
374 furthers progress in this area in three key ways.

375 First, in contrast with studies that use coarse, aggregated temperature data or that simulate
376 diurnal temperature to investigate the impacts of environmental change on mosquito traits, we
377 measured fine-scale temperature at field sites where mosquito data were collected. Second, we
378 account for non-linear thermal trait responses and incorporate diurnal temperature fluctuations
379 in trait estimates. Finally, we parameterize our vectorial capacity model using field data on two
380 crucial and challenging to measure parameters: adult abundance and survival.

381 We estimated the vectorial capacity of *Ae. albopictus* mosquitoes in oil palm plantations to be 1.5
382 times that of those in logged forests; a result driven by a greater mosquito abundance in
383 plantations. The observation that *Ae. albopictus* abundance increases in disturbed habitats is
384 supported by previous empirical work conducted in the region (38, 39, 54), and reflects the well-
385 established ecological plasticity of the species (41). This increased abundance was not estimated
386 from TPCs, as diurnal temperatures did not differ sufficiently between habitat types to produce
387 divergent responses in the underlying demographic traits. However, our temperature data
388 contrast with a number of other studies, which have found mean temperatures in plantations to
389 be up to 4°C warmer than in logged forests (30, 55). Microclimates vary significantly through the
390 forest to plantation conversion timeline, and as plantations mature, leaf litter and canopy cover
391 increases, buffering microclimates (55). Our observations that mean temperatures did not differ
392 significantly between sites is thus likely due to selection of older plantations and significantly
393 degraded forest, and it's possible that using temperature data from a wider range of forest and
394 plantation sites to drive our model may have produced different estimates for abundance and
395 vectorial capacity.

396 An additional consideration is that, although the broad temperatures sampled in this study
397 represent the temperatures experienced by mosquitoes more accurately than those derived from

398 weather station and remotely sensed data, in reality an even wider range of microclimates are
399 available at fine spatial scales (56). Behavioural avoidance of unsuitable temperatures by
400 mosquitoes may further mediate the relationship between mosquito traits and ambient
401 temperature. Although typically constrained to small bodies of water, mosquito larvae may move
402 up and down between warmer and cooler layers of water, and adults may simply move away from
403 extreme temperatures (57). Experimental studies that characterize fine-scale behavioural
404 thermoregulation of mosquitoes remain limited, however a study of *Anopheles gambiae* found
405 that, given access to range of temperatures, almost half of the mosquitoes consistently selected
406 resting sites within 24-27°C, suggesting some capacity for behavioural thermoregulation (58).
407 Further experimental work would contribute significantly to our understanding of their realized
408 thermal niche. In the meantime, assessing the effects of temperature on mosquito traits may thus
409 benefit from a temperature envelope approach, whereby the distribution of temperatures are used
410 to evaluate trait responses rather than a single measure per unit time (59).

411 The characterisation of *Ae. albopictus* thermal responses has advanced mechanistic efforts to
412 understand temperature-pathogen transmission relationships, however an important caveat to
413 consider is that these relationships are produced under constant laboratory conditions, using a
414 variety of laboratory-adapted mosquito strains (20). Key features of thermal responses curves are
415 often adapted to local climatic conditions (60), and curves aggregated across a range of different
416 mosquito strains, as well as number of laboratory generations, may obscure fine-scale variation
417 in trait responses. In one study, *Ae. albopictus* adults collected across an urbanization gradient in
418 Malaysia exhibited considerable variation in survival, with urban strains surviving approximately
419 one week longer than rural strains, and two weeks longer than laboratory strains under
420 standardised conditions (61). In a previous study conducted at these same field sites, we found
421 that differences in daily temperature fluctuations resulted in faster larval development rates in oil
422 palm plantations (62), an effect not predicted by published TPCs. Accurately characterising
423 thermal response curves is particularly important given their asymmetric nature. A temperature

424 higher than the thermal optimum depresses fitness more than a temperature displaced an
425 equivalent amount below the thermal optimum (63), meaning that even small shifts in the shape
426 and distribution of key features (e.g. thermal optimum) can dramatically alter how temperature
427 fluctuations are predicted to impact trait performance. This explains the similarity of our
428 temperature-dependent trait estimates, as the daily temperature fluctuations at our sites are small
429 relative to those defining the operational range of *Ae. albopictus*. For example, the thermal
430 optimum for biting rate is approximately 33 °C (20), which is warmer than the maximum
431 temperatures in both oil palm and logged forest sites. Below the thermal optimum, temperature-
432 dependent trait performance approximates a linear response, thus, small differences in daily
433 temperature fluctuation are not sufficient to produce significant differences in estimated trait
434 performance.

435 By focusing solely on temperature-dependent responses, our vectorial capacity estimates ignore
436 some potentially important sources of ecological variation between land-use types. For example,
437 as forest conversion to oil palm plantation reduces invertebrate diversity and abundance (64, 65),
438 predation and competition may also be reduced. Additionally, the homogenisation of vegetation
439 associated with monoculture may reduce breeding habitats by removing trees, but may also
440 increase the availability of artificial breeding sites due to increases in human activity. Although
441 we can only speculate as to the relative impact of these factors, our empirical data suggest that at
442 least one key trait, survival, does not differ significantly between land-use types.

443 In our modest sample of host-seeking female mosquitoes, we did not observe differences in parity
444 rates among habitat types. Overall parity rates were high across the sites, which we cautiously
445 interpret as indicative of older host-seeking mosquito populations. However, when we used
446 gonotrophic cycle length to calculate lifespan, we estimated that mosquitoes only live for
447 approximately 33 days. We believe this may be an overestimate for two reasons: 1) although our
448 data did not indicate an effect of temperature fluctuations on gonotrophic cycle length, a number

449 of laboratory and field studies have found this trait to be temperature sensitive (10, 14, 25), and
450 2) we were only able to measure the first gonotrophic cycle length, which can be twice as long as
451 subsequent cycles (66). Shorter gonotrophic cycles would affect vectorial capacity estimates by
452 decreasing calculated survival and increasing biting rate. For example, halving the gonotrophic
453 cycle would result in a 95 % decrease in vectorial capacity due to effects on the probability of
454 surviving the extrinsic incubation period. However, in this scenario biting rate would increase by
455 50 %. Together these changes in survival and biting rate estimates would reduce vectorial capacity
456 by ~52%. Though ubiquitous, the use of gonotrophic cycle length to infer biting rates introduces
457 an additional source of uncertainty, as Aedine mosquitoes are frequently observed taking multiple
458 bloodmeals within a cycle (67-69). As biting rate is raised to the power of 2 in the vectorial capacity
459 equation, small changes in this parameter can result in relatively large changes in transmission
460 intensity. Sensitivity analyses suggests that our results are robust to uncertainties in survival and
461 biting rate estimates, however further sampling is needed to understand how these traits vary
462 over space and time.

463 Despite the dominant role of oil palm plantation expansion on deforestation in Malaysia's Borneo
464 states, few studies have explicitly investigated the impacts on mosquito vectors. To our
465 knowledge, this study represents the first attempt to mechanistically characterise the effects of
466 tropical forest conversion on the vectorial capacity of *Ae. albopictus*. Our finding that vectorial
467 capacity increases in plantations highlights the need to more critically evaluate the increased risk
468 of *Aedes*-borne disease against the benefits of economic development. Borneo is a region that
469 continues to experience rapid urbanisation, with many urban centers surrounded by forest, or
470 strongly connected to forest via logging and palm oil transport routes. The region is endemic for
471 all four dengue serotypes, and has experienced an increasing number of dengue cases in recent
472 years. In 2018, a total of 3,423 dengue cases were reported from Sabah, a substantial increase
473 from the 2,560 cases in the year previous (Murphy et al. 2019), and Chikungunya has also recently
474 re-emerged in the region (AbuBakar et al. 2007). *Ae. albopictus* is suspected to be the dominant

475 vector of both arboviruses in the region (Murphy *et al.* 2019). Increasing urbanisation in Borneo
476 may present an additional risk to human health, in that human exposure to circulating sylvatic
477 arboviruses likely increases at the forest interface. The evolutionary histories of dengue and
478 Chikungunya viruses represent a cautionary tale, highlighting the potentially devastating
479 consequences of disease spillover from sylvatic to human cycles (70). Given their propensity for
480 zoophily, their competence for a number of arboviruses, and their capacity to thrive in both
481 converted and forested areas, *Ae. albopictus* is an obvious candidate for facilitating contacts with
482 enzootic cycles and increasing the risk of spillover events. In Borneo, this has already occurred
483 with Anopheline vectors and the simian malaria, *Plasmodium knowlesi*, for which disease risk is
484 closely linked to proximity to forest (Grigg *et al.* 2014; Fornace *et al.* 2016), and to a lesser extent,
485 for some sylvatic dengue strains (71). The effects of land-use change on vector-borne disease risk
486 will be an emergent property of interactions between host and vector ecology, behaviour,
487 physiology and immunity and their idiosyncratic responses to change.

488
489 Current understanding of mosquito biology stems largely from studies evaluating specific control
490 interventions, which has left significant knowledge gaps in fundamental mosquito ecology (72).
491 Mechanistic models, which will play a crucial role in predicting disease transmission dynamics
492 under changing land-use and climate depend heavily on the accuracy of the underlying
493 parameters. As such, there is a need to invest in studies that characterise mosquito ecology, as
494 well as evaluate how they vary in space and time (5). This is particularly important for many
495 *Aedes*-borne pathogens, for which disease control is currently entirely dependent on management
496 of complex and dynamic vector populations.

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