

# Competition in depleting resource environments shapes the thermal response of population fitness in a disease vector

Paul Huxley (✉ [p.huxley@imperial.ac.uk](mailto:p.huxley@imperial.ac.uk))

Imperial College London <https://orcid.org/0000-0001-9211-9479>

Kris Murray

Imperial College London

Samraat Pawar

Imperial College London

Lauren Cator

Imperial College London <https://orcid.org/0000-0002-6627-1490>

---

## Article

**Keywords:** climatic warming, population models, ecology

**Posted Date:** June 25th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-624494/v1>

**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 at Communications Biology on January 19th, 2022. See the published version at <https://doi.org/10.1038/s42003-022-03030-7>.

1 **Title: Competition in depleting resource environments shapes the thermal response of population**  
2 **fitness in a disease vector**

3  
4 Paul J. Huxley<sup>1</sup>, Kris A. Murray<sup>1,2</sup>, Samraat Pawar<sup>3</sup>, Lauren J. Cator<sup>3</sup>

5  
6 <sup>1</sup>MRC Centre for Global Infectious Disease Analysis, School of Public Health, Imperial College  
7 London, London, UK. <sup>2</sup>MRC Unit The Gambia at London School of Hygiene & Tropical Medicine,  
8 Banjul, The Gambia. <sup>3</sup>Department of Life Sciences, Imperial College London, Ascot, UK.  
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 **ABSTRACT**

57  
58  
59  
60  
61  
62  
63  
64  
65  
66  
67  
68  
69  
70  
71  
72  
73  
74  
75  
76  
77  
78  
79  
80  
81  
82  
83  
84  
85  
86  
87  
88  
89  
90  
91  
92  
93  
94  
95  
96  
97  
98  
99  
100  
101  
102  
103  
104  
105  
106  
107  
108  
109  
110

Mathematical models that incorporate the temperature dependence of lab-measured life history traits are increasingly used to predict how climatic warming will affect ectotherms, including disease vectors and other arthropods. These temperature-trait relationships are typically measured under laboratory conditions that ignore how conspecific competition in depleting resource environments—a commonly occurring scenario in nature—regulates natural populations. Here, we used laboratory experiments on the mosquito *Aedes aegypti*, combined with a stage-structured population model, to show that intensified larval competition in ecologically-realistic depleting resource environments can significantly diminish the vector’s maximal population-level fitness across the entire temperature range, cause a 6°C decrease in the optimal temperature for fitness, and contract its thermal niche width by 10°C. Our results provide evidence for future studies to consider competition dynamics under depleting resources when predicting how eukaryotic ectotherms will respond to climatic warming.

## 111 INTRODUCTION

112

113 Global environmental change is predicted to affect the spatiotemporal distributions of arthropods,  
114 including disease vectors and the diseases they transmit (Mordecai *et al.* 2020; WHO 2020). For  
115 example, a recent study suggests that climatic warming may increase the thermal suitability for Zika  
116 virus transmission, leading to 1.3 billion more people being at risk of exposure by 2050 (Ryan *et al.*  
117 2021). Other studies have predicted that warming will increase the global invasion potential of *Aedes*  
118 *aegypti*, a principal vector of dengue, yellow fever and chikungunya (Iwamura *et al.* 2020). Such  
119 predictions typically arise from mathematical models that incorporate thermal performance curves  
120 (TPCs) for vector life history traits, such as juvenile development and mortality, which together define  
121 the TPC of maximal population growth rate ( $r_m$ , a measure of population fitness; Savage *et al.* 2004).

122

123 Typically, such trait-level TPC data come from larval populations reared under optimal food conditions  
124 in the laboratory (e.g., Shocket *et al.* 2020). However, recent studies suggest that many predictions of  
125 how vector populations will respond to climatic warming are likely to be biased. For example, when  
126 food is supplied at a constant rate, low resource availability in the larval stage can have a significant  
127 negative effect on temperature-trait relationships (Couret *et al.* 2014; Barreaux *et al.* 2018; Huxley *et*  
128 *al.* 2021). In particular, our recent work (Huxley *et al.* 2021) has shown that low-resource supply,  
129 through its adverse impact on juvenile traits, can significantly depress population fitness and decrease  
130 its predicted peak temperature. Despite such advances, resources in natural habitats are not constant  
131 and, in many, or arguably even most cases, deplete over time (Ostfeld & Keesing 2000; Yang *et al.*  
132 2008; Beltran *et al.* 2021). For example, *Ae. aegypti* is expected to be strongly regulated by conspecific  
133 competition between larvae (Southwood *et al.* 1972; Dye 1984), because this stage of the species'  
134 lifecycle is confined to small isolated water bodies that are susceptible to infrequent resource inputs  
135 and, therefore, resource depletion (Subra & Mouchet 1984; Arrivillaga & Barrera 2004; Barrera *et al.*  
136 2006; Yee & Juliano 2012).

137

138 As per-capita energy requirements intensify with increasing temperature, resource depletion rates and  
139 the strength of competition should also increase. These combined effects are bound to compromise the  
140 growth, development, and survival of individuals. These trait-level effects are then expected to  
141 propagate through the stage-structured population dynamics to affect the shape of the  $r_m$  TPC  
142 (Amarasekare & Savage 2012; Huey & Kingsolver 2019). This is because  $r_m$  is essentially proportional  
143 to the difference between biomass gained through consumption and that lost to respiration and mortality  
144 (Savage *et al.* 2004). Resource limitation and intensified competition would be expected to decrease  $r_m$   
145 across temperatures, as they would both undermine biomass intake and elevate biomass loss.

146

147 Furthermore, if the rate of biomass loss increases faster than any increase in biomass gain with  
148 temperature, the thermal optimum of  $r_m$  ( $T_{opt}$ ) may also shift downwards (García-Carreras *et al.* 2018).  
149 For the same reason, the range of temperatures over which  $r_m$  is positive (the thermal niche width) may  
150 become narrower. As a result, the combined effects of climatic warming and decreased resource  
151 availability could contribute to the contraction of species range boundaries. This effect could  
152 simultaneously decrease the burden of vector-borne diseases and agricultural pests but increase the  
153 extinction risk of vulnerable species (Amarasekare 2019; Lehmann *et al.* 2020). Conversely, concurrent  
154 increases in temperature and resource availability with climatic warming could have the opposite effect  
155 by optimising  $r_m$ , and thus, promoting the invasion and establishment of tropical taxa into temperate  
156 habitats (Amarasekare & Simon 2020). This effect could further increase the huge socioeconomic cost  
157 of invasions by disease vectors, such as *Aedes* mosquitoes (Diagne *et al.* 2021).

158

159 Studies across a broad range of taxa are needed to make generalisable predictions on the ecological  
160 impacts of environmental change on ectotherm populations, including disease vectors (Cross *et al.*  
161 2015; Mordecai *et al.* 2019). So far, however, the effects of competition in depleting resource  
162 environments on the temperature dependence of ectotherm fitness have mainly focused on single-celled  
163 prokaryotes (Thomas *et al.* 2017; Bestion *et al.* 2018; Siegel *et al.* 2020). To address this important  
164 deficit, we investigated the effects of competition on the  $r_m$  TPC by exposing *Ae. aegypti* larvae to an  
165 ecologically-realistic range of temperatures and depleting resource levels. We show that competition in

166 resource depletion scenarios will significantly change the shape of the thermal response of mosquito  
167 population fitness—key for predicting how disease vectors and other arthropods will respond to  
168 environmental change. Our findings allow us to infer that there are thresholds of resource availability,  
169 below which intensifying competition causes a sudden change in this temperature dependence of fitness.

170

## 171 RESULTS

172

173 All trait responses varied significantly with temperature and resource level, with a significant interaction  
174 between the two environmental variables (figure 1, tables 1, 2).

175

176 Larval competition at our lowest resource level (0.183 mg ml<sup>-1</sup>) increased the negative effect of  
177 increased temperature on juvenile mortality rate (figure 1a, table 2). As temperatures increased from 22  
178 to 34°C, non-overlapping 95% credible intervals indicate that juvenile mortality rate was significantly  
179 higher at low-resource levels than at intermediate-resource levels (0.367 mg ml<sup>-1</sup>). At 0.183 mg ml<sup>-1</sup>, it  
180 increased by ~300% from 0.05 at 22°C to 0.14 individual<sup>-1</sup> day<sup>-1</sup> at 34°C. In contrast, at 0.367 mg ml<sup>-1</sup>,  
181 the juvenile mortality rate increased by 20% (from 0.04 to 0.05 individual<sup>-1</sup> day<sup>-1</sup>) across this  
182 temperature range.

183

184 The interaction between temperature and resource level caused significant variation in development  
185 time across treatments (ANOVA;  $F_{9, 2.24} = 13.44, p < 0.001$ , table 1). Development time decreased with  
186 temperature at all resource levels, but the decrease with temperature was greater at the low resource  
187 level than at higher resource levels due to resource depletion (figure 1b). At 0.183 mg ml<sup>-1</sup>, development  
188 time decreased from 18.30 days at 22°C to 8.26 days at 34°C. Development time at the higher resource  
189 levels decreased from approximately 13.50 days at 22°C to ~7.50 days at 34°C (table 2).

190

191 Competition at low resource levels (0.183 mg ml<sup>-1</sup>) resulted in significant variation in size at maturity  
192 (mass, mg) between resource levels (ANOVA;  $F_{9, 0.92} = 24.26, p < 0.001$ , table 1). Adult size decreased  
193 both at warmer temperatures and at low-resource levels, though the decrease with temperature was  
194 greater at higher resource levels than at the low resource level. At low-resource levels, size decreased  
195 by 0.13 mg as temperatures increased from 22 to 34°C, while at the highest resource level (0.733 mg  
196 ml<sup>-1</sup>), size decreased by 0.26 mg (figure 1c, table 2).

197

198 The interaction between temperature and resource level caused significant variation in adult lifespan  
199 across treatments (ANOVA;  $F_{9, 699.60} = 7.96, p < 0.001$ , table 1). Lifespan was greatest at 0.733 mg ml<sup>-1</sup>,  
200 where it was 11.24 days at 22°C, 11.65 days at 26°C, and 4.68 days at 34°C. In contrast, at low resource  
201 levels, lifespan decreased from 8.00 days at 22°C to 3.76 days at 34°C mg (figure 1d, table 2).

202

203 At all resource levels, predicted daily fecundity rate increased with temperature (table 2), though the  
204 increase was greater at the lowest resource level than at higher resource levels. At the lowest resource  
205 level, fecundity increased with temperature from 1.77 eggs individual<sup>-1</sup> day<sup>-1</sup> at 22°C to 6.87 eggs  
206 individual<sup>-1</sup> day<sup>-1</sup> at 34°C. At the higher resource levels, fecundity increased from ~2 eggs at 22°C to  
207 ~5 eggs individual<sup>-1</sup> day<sup>-1</sup> at 34°C.

208

209

210

211

212

213

214

215

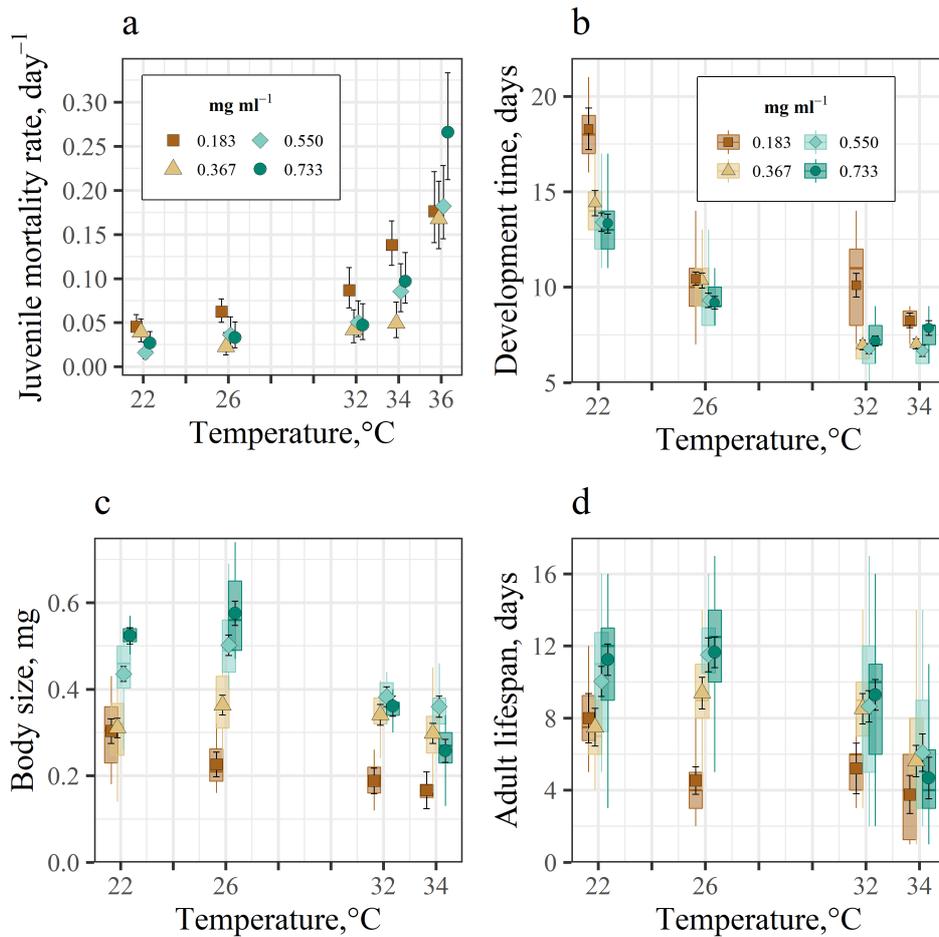
216

217

218

219

220



222

223

224

225

226

227

228

229

230

231

232

233

234

235

236

237

238

239

240

241

242

243

244

245

246

247

248

**Figure 1. The effect of larval competition on fitness traits in *Ae. aegypti* with 95% credible intervals (CIs).** **a**, Competition at low resource levels (0.183 mg ml<sup>-1</sup>) increased the negative effect of increased temperature on juvenile mortality. **b**, Development time decreased with temperature at all resource levels but, at most temperatures, it was significantly extended by competition at 0.183 mg ml<sup>-1</sup>. **c**, As temperatures increased from 22°C, competition at 0.183 mg ml<sup>-1</sup> significantly reduced size at emergence. **d**, As temperatures increased from 22 to 32°C, competition at 0.183 mg ml<sup>-1</sup> significantly reduced adult lifespan. Symbols denote the regression estimated means with 95% CIs calculated from the standard errors (replicate dropped, table 2) for the resource levels at each temperature. The resulting ANOVAs of the regressions for each trait are presented in table 1. Boxplot horizontal lines represent medians. Lower and upper hinges are the 25th and 75th percentiles. Upper whiskers extend from the hinge to the largest value no further than 1.5 × inter-quartile range (IQR) from the hinge. The lower whisker extends from the hinge to the smallest value at most 1.5 × IQR of the hinge.

Trait	Predictor	$\chi^2$	df	F value	p value
Development time (GLM) $R^2 = 0.83$	<b>Temperature</b>	<b>50.28</b>	<b>3</b>	<b>903.40</b>	<b>&lt;0.001 ***</b>
	<b>RL</b>	<b>3.97</b>	<b>3</b>	<b>71.28</b>	<b>&lt;0.001 ***</b>
	<b>Temperature × RL</b>	<b>2.24</b>	<b>9</b>	<b>13.44</b>	<b>&lt;0.001 ***</b>
	Replicate	0.07	2	1.77	0.17
	Residuals	12.63	681		
Adult lifespan (LM) $R^2 = 0.41$	<b>Temperature</b>	<b>1594.80</b>	<b>3</b>	<b>54.44</b>	<b>&lt;0.001 ***</b>
	<b>RC</b>	<b>1908.60</b>	<b>3</b>	<b>65.15</b>	<b>&lt;0.001 ***</b>
	<b>Temperature × RL</b>	<b>699.60</b>	<b>9</b>	<b>7.96</b>	<b>&lt;0.001 ***</b>
	Replicate	15.70	2	<b>0.81</b>	0.45
	Residuals	6533.10	669		
Body size (LM) $R^2 = 0.73$	<b>Temperature</b>	<b>1.32</b>	<b>3</b>	<b>104.92</b>	<b>&lt;0.001 ***</b>
	<b>RC</b>	<b>2.58</b>	<b>3</b>	<b>204.38</b>	<b>&lt;0.001 ***</b>
	<b>Temperature × RL</b>	<b>0.92</b>	<b>9</b>	<b>24.26</b>	<b>&lt;0.001 ***</b>
	Replicate	0.02	2	2.31	0.10
	Residuals	1.81	431		

250

251

252

253

254

255

256

257

258

259

260

261

262

263

264

265

266

267

268

269

270

271

272

273

274

275

**Table 1. Type II Analysis of Variance results from mixed effect regression models fitted to the responses of life history traits to temperature and resource level (RL).** Significant effects are shown in boldface type. \*  $\Rightarrow$   $p$  value < 0.05; \*\*  $\Rightarrow$   $p$  value < 0.01 \*\*\*  $\Rightarrow$   $p$  value < 0.001.

Trait	Temperature (°C)	Resource level (mg ml <sup>-1</sup> )			
		Mean ± s.e.m.			
		0.183	0.367	0.550	0.733
Development time (days)	22	18.30 ± 0.56	14.41 ± 0.34	13.41 ± 0.25	13.33 ± 0.25
	26	10.45 ± 0.18	10.35 ± 0.20	9.32 ± 0.19	9.19 ± 0.17
	32	10.11 ± 0.32	6.98 ± 0.13	6.78 ± 0.13	7.19 ± 0.13
	34	8.26 ± 0.19	7.04 ± 0.14	6.67 ± 0.15	7.87 ± 0.20
Juvenile mortality rate (individual <sup>-1</sup> day <sup>-1</sup> )	22	0.05 ± 0.01	0.04 ± 0.01	0.02 ± 0.00	0.03 ± 0.01
	26	0.06 ± 0.01	0.02 ± 0.01	0.04 ± 0.01	0.03 ± 0.01
	32	0.09 ± 0.01	0.04 ± 0.01	0.05 ± 0.01	0.05 ± 0.01
	34	0.14 ± 0.01	0.05 ± 0.01	0.09 ± 0.01	0.10 ± 0.01
Adult lifespan (days)	22	8.00 ± 0.70	7.50 ± 0.54	10.04 ± 0.43	11.24 ± 0.45
	26	4.54 ± 0.39	9.39 ± 0.45	11.51 ± 0.48	11.65 ± 0.43
	32	5.21 ± 0.72	8.53 ± 0.43	8.66 ± 0.44	9.29 ± 0.43
	34	3.76 ± 0.54	5.62 ± 0.44	6.09 ± 0.53	4.68 ± 0.59
Body size (dry mass (mg))	22	0.30 ± 0.01	0.31 ± 0.01	0.44 ± 0.01	0.52 ± 0.01
	26	0.23 ± 0.01	0.36 ± 0.01	0.50 ± 0.01	0.58 ± 0.01
	32	0.19 ± 0.01	0.34 ± 0.01	0.38 ± 0.01	0.36 ± 0.01
	34	0.17 ± 0.02	0.30 ± 0.01	0.36 ± 0.01	0.26 ± 0.01
Daily fecundity rate (eggs individual <sup>-1</sup> day <sup>-1</sup> )	22	1.77 ± 0.06	1.95 ± 0.05	1.99 ± 0.06	2.59 ± 0.54
	26	1.52 ± 0.07	1.96 ± 0.08	2.54 ± 0.37	3.00 ± 0.30
	32	3.79 ± 0.26	3.04 ± 0.33	3.55 ± 0.51	2.64 ± 0.22
	34	6.87 ± 1.87	5.07 ± 0.82	4.91 ± 0.52	5.76 ± 0.89
Population-level fitness ( $r_m$ )	22	-0.05 ± 0.03	0.06 ± 0.02	0.10 ± 0.01	0.08 ± 0.02
	26	0.05 ± 0.02	0.12 ± 0.02	0.14 ± 0.02	0.16 ± 0.02
	32	-0.04 ± 0.04	0.24 ± 0.03	0.23 ± 0.03	0.20 ± 0.03
	34	-0.21 ± 0.05	0.22 ± 0.03	0.15 ± 0.04	0.02 ± 0.05
	36	-2.10 ± 0.15	-2.11 ± 0.21	-2.19 ± 0.22	-2.68 ± 0.20

277

278

279

280

281

282

283

284

**Table 2. Comparison of the effect of larval competition on the temperature-dependence of  $r_m$  and its component traits.** The means with standard errors for juvenile mortality rate were estimated by fitting an exponential function to each treatment. The means with standard errors for development time, lifespan and size were estimated by using the statistical models in table 1 (replicate dropped). For fecundity, the standard errors were estimated using the `Rmisc` package in R. For  $r_m$ , 95% CIs were approximated using the delta method (Skalski *et al.* 2007). For  $r_m$  TPC fitting, non-positive matrix projection  $r_m$  values at 36°C were adjusted to -0.30. For plotting (figure 2a), non-positive  $r_m$  values were cut off at -0.10.

285 **Population fitness**

286

287 At all resource levels,  $r_m$  responded unimodally to temperature. However, intensified larval competition  
288 at low resource levels ( $0.183 \text{ mg ml}^{-1}$ ) significantly depressed  $r_m$  across the entire temperature range  
289 (figure 2a) and caused it to peak at a significantly lower temperature than at intermediate resource levels  
290 ( $0.367 \text{ mg ml}^{-1}$ ; figure 2b, table 3). Competition at  $0.183 \text{ mg ml}^{-1}$  also significantly narrowed the thermal  
291 niche width for  $r_m$  compared to higher resource levels (figure 2a, table 3).

292

293 At  $0.183 \text{ mg ml}^{-1}$ ,  $r_m$  was negative until temperatures increased to  $23.3^\circ\text{C}$  (figure 2, table 3). At this  
294 resource level,  $r_m$  reached a peak of 0.05 at its  $T_{\text{opt}}$  ( $26.6^\circ\text{C}$ ); it then declined to negative growth at  
295  $30.1^\circ\text{C}$ . The breadth of  $r_m$ 's thermal niche width at the lowest resource level was  $6.8^\circ\text{C}$ . In contrast, at  
296 the intermediate food level ( $0.367 \text{ mg ml}^{-1}$ ),  $r_m$  became positive as temperatures increased to  $18.8^\circ\text{C}$ ; it  
297 was maximal at  $33.0^\circ\text{C}$  (0.24, figure 2, table 3). At  $0.367 \text{ mg ml}^{-1}$ ,  $r_m$  declined to negative growth at  
298  $35.4^\circ\text{C}$ . The thermal niche width for  $r_m$  at this resource level was  $16.6^\circ\text{C}$ . Overlapping CIs indicate that  
299 the predicted differences between the intermediate resource level and the higher resource levels ( $0.550$   
300 and  $0.733 \text{ mg ml}^{-1}$ ) in  $r_m$  at  $T_{\text{opt}}$ ,  $T_{\text{opt}}$ , and the thermal niche width were non-significant (figure 2, table  
301 3).

302

303

304

305

306

307

308

309

310

311

312

313

314

315

316

317

318

319

320

321

322

323

324

325

326

327

328

329

330

331

332

333

334

335

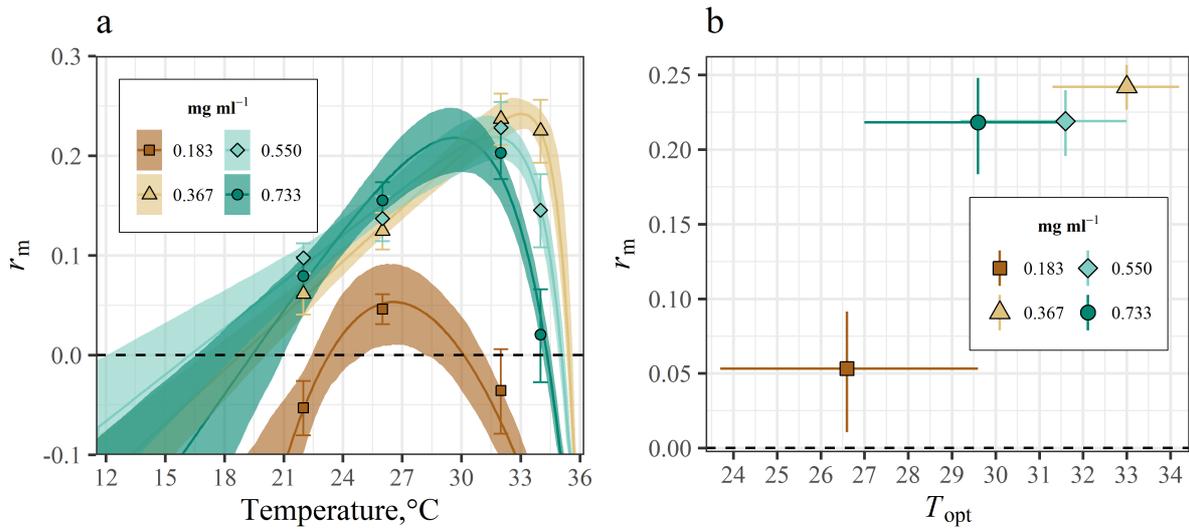
336

337

338

339

340



341  
 342  
 343  
 344  
 345  
 346  
 347  
 348  
 349  
 350  
 351  
 352  
 353  
 354  
 355  
 356  
 357  
 358  
 359  
 360  
 361  
 362  
 363  
 364  
 365  
 366  
 367  
 368  
 369  
 370  
 371  
 372  
 373  
 374  
 375  
 376  
 377  
 378  
 379

**Figure 2. The effect of larval competition on the thermal response of population-level *Ae. aegypti* fitness ( $r_m$ ) with bootstrapped 95% prediction bounds. a,** Competition at 0.183 mg ml<sup>-1</sup> significantly depressed  $r_m$  across the entire temperature range and narrowed its thermal niche width compared to the higher resource levels (non-overlapping 95% prediction bounds, table 3). Symbols denote matrix projection estimates with 95% confidence intervals (table 2). **b,** Competition at 0.183 mg ml<sup>-1</sup> significantly (non-overlapping 95% confidence intervals) lowered maximal  $r_m$  and caused it to peak at a significantly lower temperature than at the intermediate resource level (0.367 mg ml<sup>-1</sup>). Predicted  $r_m T_{opt}$  at 0.183 mg ml<sup>-1</sup> indicates that competition could decrease  $r_m T_{opt}$  by 6.4°C, when compared to the intermediate resource level (0.367 mg ml<sup>-1</sup>, table 3).

Resource level (mg ml <sup>-1</sup> )	$r_m$ at $T_{opt}$ ( $\pm$ 95% CI)	$T_{opt}$ (°C) (95% CI)	$T_{min}$ (°C) (95% CI)	$T_{max}$ (°C) (95% CI)	Thermal niche width (°C) (95% CI)
0.183	0.05 $\pm$ 0.04	26.6 (23.7 - 29.6)	23.3 (22.4 - 24.9)	30.1 (28.6 - 31.2)	6.8 (3.7 - 8.8)
0.367	0.24 $\pm$ 0.02	33.0 (31.3 - 34.2)	18.8 (17.1 - 20.2)	35.4 (35.4 - 35.7)	16.6 (15.2 - 18.6)
0.550	0.22 $\pm$ 0.02	31.6 (29.2 - 33)	16.2 (12.4 - 18.6)	35.1 (35.0 - 35.3)	18.8 (16.4 - 22.9)
0.733	0.22 $\pm$ 0.03	29.6 (27.0 - 31.5)	19.4 (16.6 - 21.0)	34.3 (34.2 - 34.6)	14.9 (13.2 - 18)

381

382

383

384

385

386

387

388

389

390

391

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

412

413

414

415

416

417

418

419

420

421

422

423

**Table 3. Parameter estimates of the Thermal Performance Curves of  $r_m$  by resource level.** Non-overlapping 95% Confidence Intervals (CIs) indicate that larval competition at the lowest resource level (0.183 mg ml<sup>-1</sup>) significantly depressed maximal growth ( $r_m$  at  $T_{opt}$ ) compared to the higher resource levels. Competition at 0.183 mg ml<sup>-1</sup> caused a significant decrease in  $r_m$   $T_{opt}$  compared to  $r_m$   $T_{opt}$  at 0.367 mg ml<sup>-1</sup>; it also caused a significantly narrower thermal niche width compared to the higher resource levels.

424 **Sensitivity analyses**

425

426 *Elasticities*

427

428 Juvenile traits (development time and survival) contributed more substantially to  $r_m$  than adult traits  
429 (figure 3). For example, at the lowest resource level ( $0.183 \text{ mg ml}^{-1}$ ) at  $26^\circ\text{C}$ , a 0.5 proportional increase  
430 in juvenile traits would increase rate of increase from 0.046 to 0.063 (figure 3d). By contrast, for the  
431 same treatment, increases of equal proportions in adult survival and fecundity would increase  $r_m$  from  
432 0.046 to 0.050 (figure 3e) and from 0.046 to 0.048 (figure 3f), respectively This highlights how the  
433 temperature-dependence of  $r_m$  stems mainly from how competition impacts juvenile survival and  
434 development. Juvenile survival determines the number of reproducing individuals, whereas,  
435 development rate governs the timing of reproduction. The carry over effect of reduced size at maturity  
436 on  $r_m$  is relatively weak, because fecundity and adult survival have comparatively small effects on  $r_m$ .

437

438 *Fecundity estimates*

439

440 Figure 4 shows that the  $r_m$  TPCs were insensitive to uncertainty in our fecundity estimates. Comparison  
441 with the central estimates shows that, for all resource levels, using the upper and lower 95% exponents  
442 (Supplementary file 1—Equation S1 and figure S1b) for the scaling between lifetime fecundity and size  
443 does not qualitatively change the predicted  $r_m$  TPCs, or the matrix projection  $r_m$  estimates that were  
444 used to fit the  $r_m$  TPCs. Predicted  $r_m T_{\text{opt}}$  was also insensitive to uncertainty in our fecundity estimates.  
445 Also, using the upper and lower 95% exponents (Supplementary file 1—Equation S1 and figure S1b)  
446 for the scaling between lifetime fecundity and size does not qualitatively change predicted maximal  $r_m$   
447 or  $r_m T_{\text{opt}}$ .

448

449

450

451

452

453

454

455

456

457

458

459

460

461

462

463

464

465

466

467

468

469

470

471

472

473

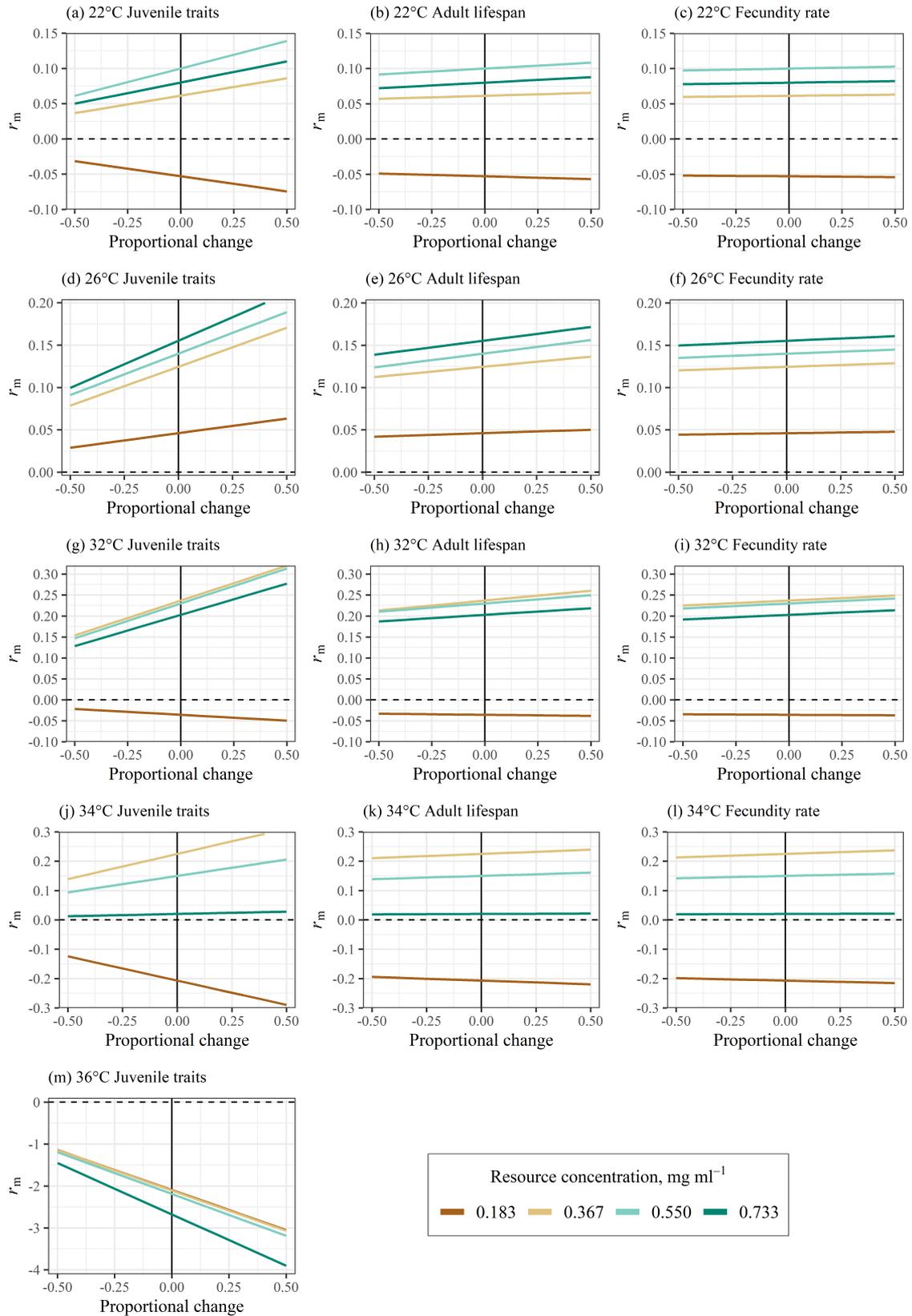
474

475

476

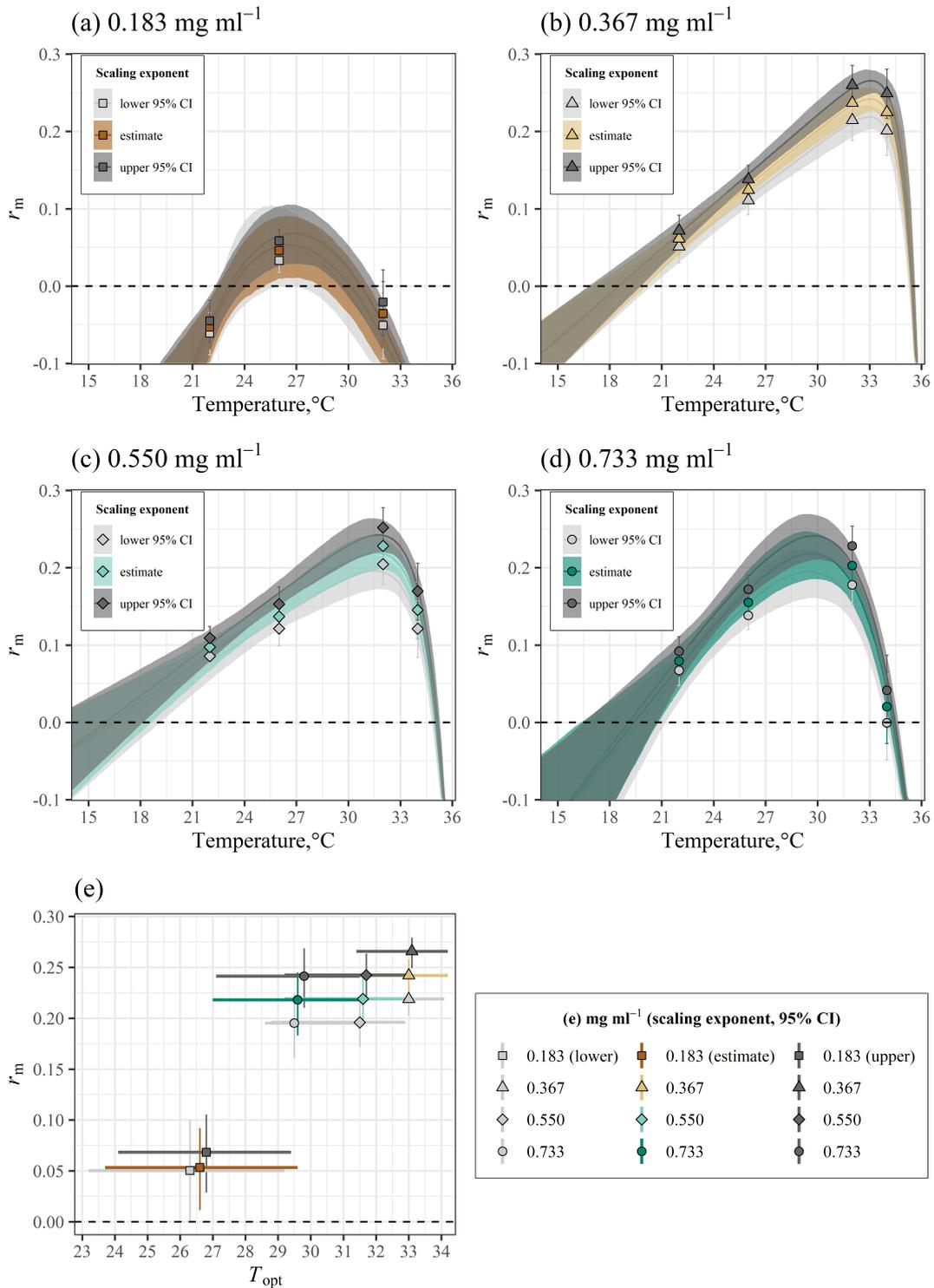
477

478



480  
481  
482  
483  
484  
485

**Figure 3. Sensitivity of  $r_m$  to proportional changes in juvenile and adult traits by temperature across resource levels.** Juvenile survival and development contributed more substantially to  $r_m$ , as relatively small changes in the summed matrix elements for these traits would result in relatively large changes in  $r_m$ . Sensitivity of  $r_m$  to adult traits was much weaker compared to sensitivity to juvenile traits.



487  
 488  
 489  
 490  
 491  
 492  
 493  
 494  
 495  
 496  
 497

**Figure 4. a-d, The insensitivity of the  $r_m$  TPCs to uncertainty in our fecundity estimates by resource level.** Comparison with the central estimates (coloured lines and 95% confidence bounds compared with greyscale lines and CBs) shows that, for all resource levels, using the upper and lower 95% exponents (Supplementary file 1—Equation S1, figure S1b) for the scaling between lifetime fecundity and size does not qualitatively change the predicted  $r_m$  TPCs, or the matrix projection  $r_m$  estimates (represented by symbols) that were used to fit the  $r_m$  TPCs. **e, The insensitivity of predicted  $r_m$   $T_{opt}$  to uncertainty in our fecundity estimates by resource level.** Using the upper and lower 95% exponents (Supplementary file 1—Equation S1, figure S1b) for the scaling between lifetime fecundity and size does not qualitatively change predicted maximal  $r_m$  (symbols with 95% CIs (vertical, coloured lines)) or  $r_m$   $T_{opt}$  (symbols with 95% CIs (horizontal coloured lines)).

## 498 Discussion

499

500 Previous studies on the effects of resource depletion on the temperature dependence of population  
501 fitness in ectotherms have mainly focused on single-celled organisms (Thomas *et al.* 2017; Bestion *et*  
502 *al.* 2018; Siegel *et al.* 2020). We show that larval competition in depleting resource environments can  
503 significantly change the shape of the  $r_m$  thermal response in *Ae. aegypti*. We also show that there are  
504 resource availability thresholds, below which competition intensifies, causing a dramatic change in the  
505 temperature dependence of fitness. Together, our findings indicate that competition in depleting  
506 resource environments is an important regulatory mechanism that needs to be considered when  
507 predicting how organisms with complex life cycles will respond to anticipated shifts in environmental  
508 temperature with global change.

509

510 At the lowest resource level (0.183 mg ml<sup>-1</sup>), competition had a consistent negative effect on the thermal  
511 responses of underlying fitness traits (figure 1), which caused a marked divergence between the  $r_m$  TPCs  
512 (figure 2). Competition at the lowest resource level significantly depressed  $r_m$  across the entire  
513 temperature range, caused a significant decrease ( $\sim 6^\circ\text{C}$ ) in  $r_m T_{\text{opt}}$  compared to the intermediate resource  
514 level (0.367 mg ml<sup>-1</sup>), and led to a 300% contraction of the  $r_m$  thermal niche width compared to the  
515 higher resource levels (figure 2, table 3).

516

517 The elasticity analysis shows that the key mechanism underlying the divergent temperature dependence  
518 of  $r_m$  across resource levels is increased juvenile development time and mortality at low resource levels  
519 (figure 3). The negative effect of competition at low-resource levels on these traits delayed the onset of  
520 reproduction and population-level reproductive output, respectively. This finding—that juvenile traits  
521 contribute more to  $r_m$  than adult traits—is consistent with general studies of fitness in organisms with  
522 complex lifecycles (Caswell 1978; Kammenga *et al.* 1996; Huey & Berrigan 2001; Cator *et al.* 2020),  
523 including mosquitoes (Juliano 1998; Huxley *et al.* 2021).

524

525 Furthermore, individual fecundity rate and adult lifespan had negligible effects on  $r_m$  compared to  
526 juvenile traits, suggesting that the carry over effect of reduced size at maturity on  $r_m$  is relatively weak  
527 (figure 3). For example, at low-resource levels, lifetime fecundity was greater at 22°C than at 26°C  
528 because body size and adult lifespan were greater at 22°C. Despite this difference,  $r_m$  at 26°C was  
529 predicted to be  $\sim 200\%$  greater than at 22°C (figures 1 and 2, table 2). This result derives from how  
530 juvenile development time almost halved as temperatures increased from 22 to 26°C (table 2). Although  
531 juvenile mortality rates for these treatments were similar (0.05 at 22°C versus 0.06 at 26°C, table 2),  
532 faster development at 26°C meant that greater numbers of individuals could contribute to population  
533 growth through reproductive output. This finding is consistent with recent studies that have used  
534 constant resource supply rates (Huxley *et al.* 2021) in suggesting that most projections of how warming  
535 will affect disease transmission through its effects on vector abundance are likely to be biased because  
536 they are likely to underestimate the effect of temperature on juvenile traits and overestimate its effect  
537 on adult traits.

538

539 Studies on how constant high-resource supply rates affect the temperature dependence of  $r_m$  in *Ae.*  
540 *Aegypti* similarly report that the optimal temperature for growth in this species is  $\sim 32^\circ\text{C}$  (Farjana *et al.*  
541 2012; Huxley *et al.* 2021). However, it appears that competition in depleting resource environments can  
542 have a negative effect on  $r_m$ , even when initial resource levels are high. For example, Huxley *et al.*  
543 (2021) found that  $r_m$  at high-resource supply was 0.28 at 32°C, whereas, it was 0.24 at 32°C at the  
544 optimal resource level (0.367 mg ml<sup>-1</sup>) for  $r_m$  in this study.

545

546 The trait-level responses at our higher resource levels are congruent with studies that have used the trait  
547 responses of optimally-fed lab strains to predict how vector fitness and disease transmission will  
548 respond to climatic warming. In these studies, mosquitoes are expected to develop at  $\sim 0.07$  individual<sup>-1</sup>  
549 day<sup>-1</sup> at 22°C; increasing to  $\sim 0.14$  individual<sup>-1</sup> day<sup>-1</sup> at 32°C (Mordecai *et al.* 2019). In the present  
550 study, development rate (1/development time; figure 1b, table 2) increased by a similar margin when  
551 the strength of competition was lessened by high resource availability. In contrast, at low-resource  
552 levels, we found juvenile development rate increased from 0.05 day<sup>-1</sup> at 22°C to 0.12 day<sup>-1</sup> at 32°C

553 (figure 1b, table 2). Although these differences in juvenile development rate may appear small, we show  
554 that they can have dramatic effects on the temperature dependence of  $r_m$  when combined with the  
555 negative impact of intensified competition on juvenile survival (figure 1a, table 2).

556  
557 Juvenile mortality rate increased significantly with temperature and it was consistently higher at low  
558 resource levels (figure 1a) than at higher resource levels. This is probably because somatic maintenance  
559 costs increase with metabolic rate (Kooijman 2000), which cannot be met below a threshold resource  
560 level. Intensified competition at low resource levels is also likely to have contributed to preventing  
561 some individuals from meeting this increased energy demand. This explains why juvenile mortality  
562 rates were highest at 32 and 34°C at low-resource levels (except at 36°C where no individuals survived  
563 at all) where the energy supply-demand deficit was expected to be the largest.

564  
565 Since larval competition can mediate the temperature dependence of  $r_m$ , it is also important to determine  
566 the temperature dependence of resource availability itself (Huey & Kingsolver 2019). For example, the  
567 natural diet of mosquito larvae comprises of detritus and microbial decomposers (Merritt *et al.* 1992),  
568 which are both sensitive to temperature (Craine *et al.* 2010; Smith *et al.* 2019). Therefore, shifts in  
569 environmental temperature could alter the concentration of food in the environment, which could affect  
570 the growth of detritivore populations. While recent studies have provided useful insights into the  
571 relationships between microbes, detritus and mosquito vectors (Yee *et al.* 2007; Chouaia *et al.* 2012;  
572 Dickson *et al.* 2017; Souza *et al.* 2019; Hery *et al.* 2021), future work could focus on the temperature-  
573 dependencies of these relationships.

574  
575 Such a focus could provide important insights into how disease vectors and other arthropods will  
576 respond to environmental change. For example, if resource availability increases with climatic warming  
577 (e.g., due to increases in decomposition and microbial growth rates), its regulatory effect on population  
578 growth and abundance could be relaxed through increased juvenile development and adult recruitment  
579 rates. Indeed, increased resource availability with warming could contribute to the expansion of disease  
580 vectors and other invasive pest species into regions that were previously prohibitive by broadening  $r_m$ 's  
581 thermal niche width (Amarasekare & Simon 2020; Lehmann *et al.* 2020). On the other hand, evidence  
582 from our high resource level treatments (e.g., a lower  $T_{opt}$  at 0.733 than at 0.367 mg ml<sup>-1</sup>) may suggest  
583 that warming could have a negative impact on population growth by causing resources to be  
584 overabundant, which could lead to eutrophication and hypoxia in aquatic environments (Liikanen *et al.*  
585 2002).

586  
587 Alternatively, if climate change reduces resource availability (e.g., by disrupting temperature-dependent  
588 consumer-resource relationships), species' spatiotemporal ranges could contract (Lister & Garcia 2018;  
589 Huey & Kingsolver 2019). This is because, as we have shown here, intensified competition at low food  
590 levels can prevent  $r_m$  from being positive at lower temperatures, can lower  $r_m T_{opt}$ , and can force  $r_m$  to  
591 become negative at lower temperatures. In this way, the effects of rising temperatures on vulnerable  
592 arthropod populations could be especially pernicious, if resource availability is simultaneously reduced  
593 (Huey & Kingsolver 2019).

594  
595 We used size-scaling to estimate the effect of temperature and resource level on fecundity, because it is  
596 anticipated that most of the effect of intensified larval competition at low-resource levels affects adult  
597 mosquitoes indirectly by reducing size at emergence and lifespan (Steinwascher 1982; Briegel 1990).  
598 Despite these assumptions, we show that substantial error in our fecundity estimates would not alter our  
599 main conclusions. This is because predicted fitness was relatively insensitive to these traits (figures 3  
600 and 4).

601  
602 Rapid global change is expected to have far-reaching and disruptive ecological impacts (Trisos *et al.*  
603 2020). Climate-driven shifts in the spatiotemporal distributions and abundances of organisms are likely  
604 to cause widespread harm to ecosystems, biodiversity and society (Parmesan 2006; Diagne *et al.* 2021).  
605 This concern has prompted calls for a more complete understanding of how interactions between  
606 environmental factors can affect population-level responses (Cross *et al.* 2015; Huey & Kingsolver  
607 2019; Taheri *et al.* 2021). Attempts to understand the population-level effects of temperature × resource

608 interactions have focused on prokaryotes or have not considered competition in depleting resource  
609 environments. Our study provides rare evidence of how intensified competition below certain resource  
610 thresholds can affect the temperature dependence of fitness in a predictable and generalisable way.

611

## 612 **Materials and Methods**

613

614 We investigated the effects of temperature and resource depletion on mosquito life history using a 5×4  
615 factorial design comprised of five temperatures (22, 26, 32, 34, and 36°C) and four resource levels  
616 (0.183, 0.367, 0.550 and 0.733 mg ml<sup>-1</sup>). These experimental temperatures span the range of  
617 temperatures that this strain of *Ae. aegypti* (F16-19 originating from Fort Meyer, FL; (Bargielowski *et*  
618 *al.* 2013) is likely to experience in the wild between May (the onset of mosquito season) and November  
619 (Arguez *et al.* 2012). We extended our range to 36°C to determine the upper critical thermal limit for  
620 this strain. Our resource levels are within the range of studies that have investigated the effects of  
621 depleting larval resource environments on *Ae. aegypti* (Subra & Mouchet 1984). Our lowest resource  
622 level (0.183 mg ml<sup>-1</sup>) was chosen to simulate a level of resource limitation that is expected in natural  
623 juvenile habitats (Arrivillaga & Barrera 2004; Barrera *et al.* 2006). Further, our preliminary assays  
624 showed that resource levels below 0.183 mg ml<sup>-1</sup> resulted in complete juvenile mortality.

625

626 The experiment was carried out in two randomised blocks. Each block consisted of all five temperatures  
627 and two resource levels. On Day 0 of each block, batches of approximately 800 eggs were deposited  
628 into five (one per experimental temperature) plastic tubs containing 300 ml of dechlorinated tap water.  
629 We provided each tub with a pinch of powdered fish food (Cichlid Gold®, Hikari, Kyrin Food  
630 Industries Ltd., Japan) to prompt overnight hatching. Tubs were randomly assigned to a water bath  
631 (Grant Instruments: JAB Academy) set at one of the five experimental temperatures. Water baths were  
632 situated in a 20°C climate-controlled insectary with a 12L:12D photoperiod and 30 minutes of gradual  
633 transition of light levels to simulate sunrise and sunset. On the following day (Day 1), we created the  
634 treatments by separating first instar larvae into cohorts of 50, which were then transferred to clean  
635 tubs containing 300 ml of fresh water. Each treatment comprised of three replicate tubs (3×50  
636 individuals treatment<sup>-1</sup>). Resource levels were attained by adding 55, 110, 165 and 220 mg of powdered  
637 fish food to the tubs, respectively. To allow resource depletion, tubs received two pulses of equal  
638 quantity. Half of the assigned quantity was provided on Day 1; the remaining half was provided on Day  
639 4. After Day 4, resource levels were not adjusted but water volumes were topped up, if necessary.

640

## 641 **Fitness calculation**

642

643 We calculated  $r_m$  using a stage-structured matrix projection model (MPM), which describes change in  
644 a population over time (Equation 1; Caswell 1989):

645

$$\mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t, \quad (1)$$

646

647 where  $\mathbf{N}_t$  is a vector of abundances in the stage classes at time  $t$  and  $\mathbf{M}$  is the projection matrix. The first  
648 row of  $\mathbf{M}$  is populated with daily fecundity rate (the number of female offspring produced per female  
649 at age  $i$ ). The sub-diagonal of  $\mathbf{M}$  (Equation 1) is populated with the survival proportions from age  $i$  to  
650 age  $i+1$ . Multiplying  $\mathbf{N}_t$  and  $\mathbf{M}$  sequentially across time intervals gives the stage-structured population  
651 dynamics. When the stable stage distribution of  $\mathbf{N}_t$  is reached, the dominant eigenvalue of the system is  
652 the finite population rate of increase ( $\lambda$ ) (Caswell 1989). The intrinsic rate of population growth is then  
653  $r_m = \log(\lambda)$ ; a population's inherent capacity to reproduce, and therefore a measure of population-level  
654 fitness (Birch 1948; Cole 1954; Savage *et al.* 2004). Positive and negative  $r_m$  values indicate growth  
655 and decline, respectively. We used the `popbio` R package to build and analyse the MPMs (Stubben &  
656 Milligan 2007; R Core Team 2018).

657

658

659

660

661 **Model parameterisation**

662

663 *Immature development time and immature and adult survival proportions*

664

665 The survival proportions for the matrix survival elements (the sub-diagonal of  $\mathbf{M}$ ; Equation 1) were  
666 estimated using the `survival` R package (Therneau 2021). We defined the juvenile stage duration (i.e.,  
667 hatching-to-adult) as the mean duration of transitioning into and out of that stage, and a fixed age of  
668 adult emergence at the mean age of emergence.

669

670 Juvenile development times for each treatment's MPM were predicted using a regression model  
671 (detailed in the 'Statistical analyses' section) that was parametrised with individual-level hatching-to-  
672 adult times (days). Upon pupation, mosquitoes transferred to individual falcon tubes containing 5 ml of  
673 tap water, which allowed pupa-to-adult development times and the lifespans of individual starved adults  
674 to be recorded. In the absence of food, adult lifespan is positively associated with emergent size, so it  
675 is a useful indicator of the carry over effects of temperature and competition in the larval habitat (Briegel  
676 1990; Agnew *et al.* 2002).

677

678 *Daily fecundity rate*

679

680 Fecundity and body size are positively related in many insect taxa, including mosquitoes (Honěk 1993).  
681 For this reason, scaling relationships between fecundity and size are commonly used in predictions of  
682 population growth in *Aedes* (Livdahl & Sugihara 1984; Juliano & Lounibos 2005). We provide a  
683 detailed description of our method for estimating fecundity in Supplementary file 1. Briefly, we  
684 measured individual dry mass, and estimated lifetime fecundity using previously published datasets on  
685 the temperature-dependent scaling between mass and wing length (van den Heuvel 1963), and wing  
686 length and fecundity (Briegel 1990; Farjana & Tuno 2012). Temperature-specific individual daily  
687 fecundity rate is required for the MPMs (Equation 1), so we divided lifetime fecundity by lifespan and  
688 multiplied by 0.5 (assuming a 1:1 offspring sex ratio). Later, we show that this much variation in the  
689 scaling of fecundity does not qualitatively change our results.

690

691 **Parameter sensitivity**

692

693 We used the standard errors of the survival and fecundity element estimates to account for how  
694 uncertainty in these traits is propagated through to the  $r_m$  estimate (Caswell 1989; Skalski *et al.* 2007).  
695 For survival, we used the standard errors estimated by the Kaplan-Meier survival function in the  
696 `survival` R package. For fecundity, we calculated the standard errors of the mean daily fecundity rates  
697 (Supplementary file 1—table S2) for each treatment using the `Rmisc` R package (Hope 2013). As an  
698 additional sensitivity analysis, we recalculated fitness using the upper and lower 95% CIs of the  
699 exponents for the scaling of size and lifetime fecundity (figure 3).

700

701 **Elasticity analysis**

702

703 We used elasticities to quantify the relative contributions of individual life history traits to  $r_m$ . Elasticity,  
704  $e_{ij}$ , measures the proportional effect on  $\lambda$  of an infinitesimal change in an element of  $\mathbf{M}$  (Equation 1)  
705 with all other elements held constant (the partial derivative) (Caswell *et al.* 1984; de Kroon *et al.* 1986).  
706 This partial derivative of  $\lambda$ , with respect to each element of  $\mathbf{M}$ , is  $s_{ij} = \partial\lambda/\partial a_{ij} = v_i w_j$  with the dot product  
707  $\langle \mathbf{w}, \mathbf{v} \rangle = 1$ . Here,  $\mathbf{w}$  is the dominant right eigenvector (the stage distribution vector of  $\mathbf{M}$ ),  $\mathbf{v}$  is the  
708 dominant left eigenvector (the reproductive value vector of  $\mathbf{M}$ ), and  $a_{ij}$  is the  $i \times j^{\text{th}}$  element of  $\mathbf{M}$ .  
709 Elasticities can then be calculated using the relationship:  $e_{ij} = a_{ij}/\lambda \times s_{ij}$ . Multiplying an elasticity by  $\lambda$   
710 gives the absolute contribution of its corresponding  $a_{ij}$  to  $\lambda$  (Caswell *et al.* 1984; de Kroon *et al.* 1986).  
711 Absolute contributions for juvenile and adult elements were summed and changed proportionally to  
712 quantify the sensitivity of  $r_m$  to these traits.

713

714

715

716 **Statistical analyses**

717

718 In the first instance, we used mixed effects models in the `lme4` R package (Bates *et al.* 2015) to test for  
719 significant effects of our predictor variables on fitness traits. In the maximal models, temperature ×  
720 resource level and replicate were fixed effect predictors and block was a random effect. However, the  
721 lower AIC scores from versions of the maximal model suggested that variation among replicates within  
722 blocks had a non-significant effect on trait responses. Therefore, for normally distributed trait data  
723 (adult lifespan and size), we used a full factorial linear regression model (LM) with temperature ×  
724 resource level and replicate as fixed effects. Model diagnostics provided no evidence to suggest the  
725 development time data were normally distributed, so we used a generalised linear model (GLM) with  
726 family = gamma and link = identity.

727

728 We tested the effect of resource level on the temperature dependence of daily per capita juvenile  
729 mortality rate by fitting an exponential function to the survival data with R package `flexsurv` (Jackson  
730 2016). The final mortality model was obtained by dropping terms from the full model (consisting of  
731 temperature × resource level + replicate + block as fixed effect predictors). Terms were retained unless  
732 their removal worsened model fit ( $\Delta\text{AIC} > -2$ ) (Supplementary file 1—table 1). Maximum likelihood  
733 methods executed in `flexsurv` were used to estimate treatment-level juvenile mortality rates and their  
734 95% CIs. Significant effects were interpreted when CIs were nonoverlapping.

735

736 **Quantifying the  $r_m$  thermal performance curve**

737

738 To determine how resource depletion affected the shape of the  $r_m$  TPC, we fitted several mathematical  
739 models that allow for negative values at both cold and hot extremes, including polynomial models using  
740 linear regression, as well as non-linear models with non-linear least squares (NLLS) using the `rTPC` R  
741 package (Padfield *et al.* 2021). Overall, the `Lactin2` (Lactin *et al.* 1995) and Kamykowski (Kamykowski  
742 & McCollum 1986) models were equally best-fitting according to the AIC (Supplementary file 1—  
743 table 2). From these, we picked the Kamykowski model because it was better at describing the estimated  
744  $r_m$  at our lowest resource level. This model is defined as

745

$$r_m(T) = a(1 - e^{-b(T - T_{\min})})(1 - e^{-c(T_{\max} - T)}),$$

746

747 where  $T$  (°C), and  $T_{\max}$  and  $T_{\min}$  are the high and low temperatures at which  $r_m$  becomes negative,  
748 respectively, and  $a$ ,  $b$ , and  $c$ , are shape parameters without any biological meaning. Bootstrapping was  
749 used to calculate 95% prediction bounds for each  $r_m$  TPC (Padfield *et al.* 2021) and confidence intervals  
750 (CIs) around its  $T_{\text{opt}}$ , as well as the thermal niche width ( $T_{\max} - T_{\min}$ ).

751

752

753

754 **Data accessibility**

755

756 All data for analyses will be available at publication from the Imperial College London Research Data  
757 Repository: <https://doi.org/10.14469/hpc/8267>

758

759 Prior to publication, data are available from the corresponding author on reasonable request.

760

761 A previous preprint version of this manuscript is available at:

762 <https://doi.org/10.1101/2021.02.12.430918>

763

764

765

766

767

768

769 **Acknowledgements**

770

771 All authors contributed to the conception of the study and designed the experiments, L.J.C. provided  
772 the mosquitoes; P.J.H. and S.P. performed the modelling; P.J.H. collected the data and analysed it.  
773 P.J.H. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

774

775 **Competing interests**

776

777 We declare we have no competing interests.

778

779 **Funding**

780

781 This study was supported by Natural Environment Research Council (NE/L002515/1). We also  
782 acknowledge joint Centre funding from the UK Medical Research Council and Department for Inter-  
783 national Development (MR/R0156600/1).

784

785 **References**

786

787 Agnew, P., Hide, M., Sidobre, C. & Michalakis, Y. (2002). A minimalist approach to the effects of  
788 density-dependent competition on insect life-history traits. *Ecological Entomology*, 27, 396–402.

789 Amarasekare, P. (2019). Effects of Climate Warming on Consumer-Resource Interactions: A  
790 Latitudinal Perspective. *Frontiers in Ecology and Evolution*, 7.

791 Amarasekare, P. & Savage, V. (2012). A Framework for Elucidating the Temperature Dependence of  
792 Fitness. *The American Naturalist*, 179, 178–191.

793 Amarasekare, P. & Simon, M.W. (2020). Latitudinal directionality in ectotherm invasion success.  
794 *Proceedings of the Royal Society B: Biological Sciences*, 287, 20191411.

795 Arguez, A., Durre, I., Applequist, S., Vose, R.S., Squires, M.F., Yin, X., *et al.* (2012). NOAA's 1981–  
796 2010 U.S. Climate Normals: An Overview. *Bulletin of the American Meteorological Society*, 93,  
797 1687–1697.

798 Arrivillaga, J. & Barrera, R. (2004). Food as a limiting factor for *Aedes aegypti* in water-storage  
799 containers. *Journal of vector ecology*, 29, 11–20.

800 Bargielowski, I.E., Lounibos, L.P. & Carrasquilla, M.C. (2013). Evolution of resistance to satyri-  
801 zation through reproductive character displacement in populations of invasive dengue vectors.  
802 *Proceedings of the National Academy of Sciences of the United States of America*, 110, 2888–  
803 2892.

804 Barreaux, A.M.G., Stone, C.M., Barreaux, P. & Koella, J.C. (2018). The relationship between size  
805 and longevity of the malaria vector *Anopheles gambiae* (s.s.) depends on the larval environment.  
806 *Parasites & Vectors*, 11, 485.

807 Barrera, R., Amador, M. & Clark, G.G. (2006). Ecological Factors Influencing *Aedes aegypti*  
808 (Diptera: Culicidae) Productivity in Artificial Containers in Salinas, Puerto Rico. *Journal of*  
809 *Medical Entomology*, 43, 484–492.

810 Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using  
811 lme4. *Journal of Statistical Software*, 67.

812 Beltran, R.S., Kilpatrick, A.M., Breed, G.A., Adachi, T., Takahashi, A., Naito, Y., *et al.* (2021).  
813 Seasonal resource pulses and the foraging depth of a Southern Ocean top predator. *Proceedings*  
814 *of the Royal Society B: Biological Sciences*, 288, rspb.2020.2817.

- 815 Bestion, E., García-Carreras, B., Schaum, C.-E., Pawar, S. & Yvon-Durocher, G. (2018). Metabolic  
816 traits predict the effects of warming on phytoplankton competition. *Ecology Letters*, 21, 655–  
817 664.
- 818 Birch, L.C. (1948). The Intrinsic Rate of Natural Increase of an Insect Population. *The Journal of*  
819 *Animal Ecology*, 17, 15.
- 820 Briegel, H. (1990). Metabolic relationship between female body size, reserves, and fecundity of  
821 *Aedes aegypti*. *Journal of Insect Physiology*, 36, 165–172.
- 822 Caswell, H. (1978). A general formula for the sensitivity of population growth rate to changes in life  
823 history parameters. *Theoretical Population Biology*, 14, 215–230.
- 824 Caswell, H. (1989). *Matrix population models construction, analysis, and interpretation*. *Natural*  
825 *Resource Modeling*. Sinauer Associates, Sunderland, Massachusetts.
- 826 Caswell, H., Naiman, R.J. & Morin, R. (1984). Evaluating the consequences of reproduction in  
827 complex salmonid life cycles. *Aquaculture*, 43, 123–134.
- 828 Cator, L.J., Johnson, L.R., Mordecai, E.A., El Moustaid, F., Smallwood, T.R.C., LaDeau, S.L., *et al.*  
829 (2020). The Role of Vector Trait Variation in Vector-Borne Disease Dynamics. *Frontiers in*  
830 *Ecology and Evolution*, 8, 1–25.
- 831 Chouaia, B., Rossi, P., Epis, S., Mosca, M., Ricci, I., Damiani, C., *et al.* (2012). Delayed larval  
832 development in *Anopheles* mosquitoes deprived of *Asaia* bacterial symbionts. *BMC*  
833 *Microbiology*, 12, S2.
- 834 Cole, L.C. (1954). The population consequences of life history phenomena. *The Quarterly review of*  
835 *biology*, 29, 103–137.
- 836 Couret, J., Dotson, E. & Benedict, M.Q. (2014). Temperature, larval diet, and density effects on  
837 development rate and survival of *Aedes aegypti* (Diptera: Culicidae). *PLoS ONE*, 9, 1–9.
- 838 Craine, J.M., Fierer, N. & McLaughlan, K.K. (2010). Widespread coupling between the rate and  
839 temperature sensitivity of organic matter decay. *Nature Geoscience*, 3, 854–857.
- 840 Cross, W.F., Hood, J.M., Benstead, J.P., Hury, A.D. & Nelson, D. (2015). Interactions between  
841 temperature and nutrients across levels of ecological organization. *Global Change Biology*, 21,  
842 1025–1040.
- 843 Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R.E., Roiz, D., Jarić, I., *et al.* (2021). High and rising  
844 economic costs of biological invasions worldwide. *Nature*, In Press.
- 845 Dickson, L.B., Jiolle, D., Minard, G., Moltini-Conclois, I., Volant, S., Ghazlane, A., *et al.* (2017).  
846 Carryover effects of larval exposure to different environmental bacteria drive adult trait variation  
847 in a mosquito vector. *Science Advances*, 3, e1700585.
- 848 Dye, C. (1984). Models for the Population Dynamics of the Yellow Fever Mosquito, *Aedes aegypti*.  
849 *The Journal of Animal Ecology*, 53, 247.
- 850 Farjana, T. & Tuno, N. (2012). Effect of body size on multiple blood feeding and egg retention of  
851 *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) (Diptera: Culicidae). *Medical Entomology and*  
852 *Zoology*, 63, 123–131.
- 853 Farjana, T., Tuno, N. & Higa, Y. (2012). Effects of temperature and diet on development and  
854 interspecies competition in *Aedes aegypti* and *Aedes albopictus*. *Medical and Veterinary*  
855 *Entomology*, 26, 210–217.
- 856 García-Carreras, B., Sal, S., Padfield, D., Kontopoulos, D.-G., Bestion, E., Schaum, C.-E., *et al.*  
857 (2018). Role of carbon allocation efficiency in the temperature dependence of autotroph growth  
858 rates. *Proceedings of the National Academy of Sciences*, 115, E7361–E7368.

- 859 Hery, L., Guidez, A., Durand, A.-A., Delannay, C., Normandeau-Guimond, J., Reynaud, Y., *et al.*  
860 (2021). Natural Variation in Physicochemical Profiles and Bacterial Communities Associated  
861 with *Aedes aegypti* Breeding Sites and Larvae on Guadeloupe and French Guiana. *Microbial*  
862 *Ecology*, 81, 93–109.
- 863 van den Heuvel, M.J. (1963). The Effect of Rearing Temperature on the Wing Length, Thorax  
864 Length, Leg Length and Ovariolo Number of the Adult Mosquito, *Aedes Aegypti* (L.).  
865 *Transactions of the Royal Entomological Society of London*, 115, 197–216.
- 866 Honěk, A. (1993). Intraspecific Variation in Body Size and Fecundity in Insects: A General  
867 Relationship. *Oikos*, 66, 483.
- 868 Hope, R.M. (2013). Rmisc: Rmisc: Ryan Miscellaneous.
- 869 Huey, R.B. & Berrigan, D. (2001). Temperature, Demography, and Ectotherm Fitness. *The American*  
870 *Naturalist*, 158, 204–210.
- 871 Huey, R.B. & Kingsolver, J.G. (2019). Climate warming, resource availability, and the metabolic  
872 meltdown of ectotherms. *American Naturalist*, 194.
- 873 Huxley, P.J., Murray, K.A., Pawar, S. & Cator, L.J. (2021). The effect of resource limitation on the  
874 temperature dependence of mosquito population fitness. *Proceedings of the Royal Society B:*  
875 *Biological Sciences*, 288, rspb.2020.3217.
- 876 Iwamura, T., Guzman-Holst, A. & Murray, K.A. (2020). Accelerating invasion potential of disease  
877 vector *Aedes aegypti* under climate change. *Nature Communications*, 11, 2130.
- 878 Jackson, C. (2016). flexsurv: A Platform for Parametric Survival Modeling in R. *Journal of Statistical*  
879 *Software*, 70, 1–33.
- 880 Juliano, S.A. (1998). Species Introduction and Replacement among Mosquitoes: Interspecific  
881 Resource Competition or Apparent Competition? *Ecology*, 79, 255.
- 882 Juliano, S.A. & Lounibos, L.P. (2005). Ecology of invasive mosquitoes: effects on resident species  
883 and on human health. *Ecology Letters*, 8, 558–574.
- 884 Kammenga, J.E., Busschers, M., Straalen, N.M. Van, Jepson, P.C. & Bakker, J. (1996). Stress  
885 Induced Fitness Reduction is Not Determined by the Most Sensitive Life-Cycle Trait.  
886 *Functional Ecology*, 10, 106.
- 887 Kamykowski, D. & McCollum, S.A. (1986). The temperature acclimatized swimming speed of  
888 selected marine dinoflagellates. *Journal of Plankton Research*, 8, 275–287.
- 889 Kooijman, S.A.L.M. (2000). *Dynamic energy and mass budgets in biological systems*. Cambridge  
890 University Press, Cambridge.
- 891 de Kroon, H., Plaisier, A., van Groenendael, J. & Caswell, H. (1986). Elasticity: The Relative  
892 Contribution of Demographic Parameters to Population Growth Rate. *Ecology*, 67, 1427–1431.
- 893 Lactin, D.J., Holliday, N.J., Johnson, D.L. & Craigen, R. (1995). Improved Rate Model of  
894 Temperature-Dependent Development by Arthropods. *Environmental Entomology*, 24, 68–75.
- 895 Lehmann, P., Ammunét, T., Barton, M., Battisti, A., Eigenbrode, S.D., Jepsen, J.U., *et al.* (2020).  
896 Complex responses of global insect pests to climate warming. *Frontiers in Ecology and the*  
897 *Environment*, 18, 141–150.
- 898 Liikanen, A., Murtoniemi, T., Tanskanen, H., Väisänen, T. & Martikainen, P.J. (2002). Effects of  
899 temperature and oxygen availability on greenhouse gas and nutrient dynamics in sediment of a  
900 eutrophic mid-boreal lake. *Biogeochemistry*, 59, 269–286.

- 901 Lister, B.C. & Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a  
902 rainforest food web. *Proceedings of the National Academy of Sciences*, 115, E10397–E10406.
- 903 Livdahl, T.P. & Sugihara, G. (1984). Non-Linear Interactions of Populations and the Importance of  
904 Estimating Per Capita Rates of Change. *The Journal of Animal Ecology*, 53, 573.
- 905 Merritt, R.W., Dadd, R.H. & Walker, E.D. (1992). Feeding behaviour, natural food, and nutritional  
906 relationships and larval mosquitoes. *Annual Review of Entomology*, 349–76.
- 907 Mordecai, E.A., Caldwell, J.M., Grossman, M.K., Lippi, C.A., Johnson, L.R., Neira, M., *et al.* (2019).  
908 Thermal biology of mosquito-borne disease. *Ecology Letters*, 22, 1690–1708.
- 909 Mordecai, E.A., Ryan, S.J., Caldwell, J.M., Shah, M.M. & LaBeaud, A.D. (2020). Climate change  
910 could shift disease burden from malaria to arboviruses in Africa. *The Lancet Planetary Health*,  
911 4, e416-423.
- 912 Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in  
913 terrestrial ecosystems. *Trends in Ecology & Evolution*, 15, 232–237.
- 914 Padfield, D., O’Sullivan, H. & Pawar, S. (2021). rTPC and nls.multstart: A new pipeline to fit thermal  
915 performance curves in R. *Methods in Ecology and Evolution*, 12, 1138–1143.
- 916 Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review*  
917 *of Ecology, Evolution, and Systematics*, 37, 637–669.
- 918 R Core Team. (2018). R: A language and environment for statistical computing.
- 919 Ryan, S.J., Carlson, C.J., Tesla, B., Bonds, M.H., Ngonghala, C.N., Mordecai, E.A., *et al.* (2021).  
920 Warming temperatures could expose more than 1.3 billion new people to Zika virus risk by  
921 2050. *Global Change Biology*, 27, 84–93.
- 922 Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004). Effects of Body Size  
923 and Temperature on Population Growth. *The American Naturalist*, 163, 429–441.
- 924 Shocket, M.S., Verwillow, A.B., Numazu, M.G., Slamani, H., Cohen, J.M., El Moustaid, F., *et al.*  
925 (2020). Transmission of West Nile and five other temperate mosquito-borne viruses peaks at  
926 temperatures between 23°C and 26°C. *eLife*, 9, 1–67.
- 927 Siegel, P., Baker, K.G., Low-Décarie, E. & Geider, R.J. (2020). High predictability of direct  
928 competition between marine diatoms under different temperatures and nutrient states. *Ecology*  
929 *and Evolution*, 10, 7276–7290.
- 930 Skalski, J.R., Millsbaugh, J.J., Dillingham, P. & Buchanan, R.A. (2007). Calculating the variance of  
931 the finite rate of population change from a matrix model in Mathematica. *Environmental*  
932 *Modelling & Software*, 22, 359–364.
- 933 Smith, T.P., Thomas, T.J.H., García-Carreras, B., Sal, S., Yvon-Durocher, G., Bell, T., *et al.* (2019).  
934 Community-level respiration of prokaryotic microbes may rise with global warming. *Nature*  
935 *Communications*, 10, 5124.
- 936 Southwood, T.R., Murdie, G., Yasuno, M., Tonn, R.J. & Reader, P.M. (1972). Studies on the life  
937 budget of *Aedes aegypti* in Wat Samphaya, Bangkok, Thailand. *Bulletin of the World Health*  
938 *Organization*, 46, 211–226.
- 939 Souza, R.S., Virginio, F., Riback, T.I.S., Suesdek, L., Barufi, J.B. & Genta, F.A. (2019).  
940 Microorganism-Based Larval Diets Affect Mosquito Development, Size and Nutritional  
941 Reserves in the Yellow Fever Mosquito *Aedes aegypti* (Diptera: Culicidae). *Frontiers in*  
942 *Physiology*, 10, 1–24.
- 943 Steinwascher, K. (1982). Relationship Between Pupal Mass and Adult Survivorship and Fecundity for  
944 *Aedes aegypti*. *Environmental Entomology*, 11, 150–153.

- 945 Stubben, C. & Milligan, B. (2007). Estimating and Analyzing Demographic Models Using the popbio  
946 Package in R. *Journal of Statistical Software*, 22, 1–23.
- 947 Subra, R. & Mouchet, J. (1984). The regulation of preimaginal populations of *Aedes aegypti* (L.)  
948 (Diptera: Culicidae) on the Kenya coast. *Annals of Tropical Medicine & Parasitology*, 78, 63–  
949 70.
- 950 Taheri, S., Naimi, B., Rahbek, C. & Araújo, M.B. (2021). Improvements in reports of species  
951 redistribution under climate change are required. *Science Advances*, 7, eabe1110.
- 952 Therneau, T. (2021). A Package for Survival Analysis in R.
- 953 Thomas, M.K., Aranguren-Gassis, M., Kremer, C.T., Gould, M.R., Anderson, K., Klausmeier, C.A.,  
954 *et al.* (2017). Temperature-nutrient interactions exacerbate sensitivity to warming in  
955 phytoplankton. *Global Change Biology*, 23, 3269–3280.
- 956 Trisos, C.H., Merow, C. & Pigot, A.L. (2020). The projected timing of abrupt ecological disruption  
957 from climate change. *Nature*, 580, 496–501.
- 958 WHO. (2020). *Multisectoral Approach to the Prevention and Control of Vector-Borne Diseases*.  
959 Geneva.
- 960 Yang, L.H., Bastow, J.L., Spence, K.O. & Wright, A.N. (2008). What Can We Learn From Resource  
961 Pulses? *Ecology*, 89, 621–634.
- 962 Yee, D.A. & Juliano, S.A. (2012). Concurrent effects of resource pulse amount, type, and frequency  
963 on community and population properties of consumers in detritus-based systems. *Oecologia*,  
964 169, 511–522.
- 965 Yee, D.A., Kaufman, M.G. & Juliano, S.A. (2007). The significance of ratios of detritus types and  
966 micro-organism productivity to competitive interactions between aquatic insect detritivores.  
967 *Journal of Animal Ecology*, 76, 1105–1115.

968  
969  
970  
971  
972  
973  
974  
975  
976  
977  
978  
979  
980  
981  
982  
983  
984  
985  
986  
987  
988  
989  
990  
991  
992

## Supplementary Files

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

- [CommsBSI.pdf](#)