Original Research Article

Mathematical modelling of the mosquito *Aedes polynesiensis* in a heterogeneous environment

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ARTICLE INFO

ABSTRACT

Background: The mosquito *Aedes polynesiensis* inhabits Pacific islands and territories and transmits arboviruses and parasites. In the context of rapid environmental change, understanding the effects of environmental heterogeneity on mosquitoes is crucial.
Methods: First, empirical field data and remote sensing data were combined to model spatial heterogeneity in the environmental suitability for *Ae. polynesiensis*. Second, a model of mosquito population dynamics was applied to predict mosquito distributions over a heterogeneous landscape assuming different dispersal behaviours. *Motu* Tautau, French Polynesia, was used as a case study of the utility of this methodological approach. *Ae. polynesiensis* use land crab *Cardisoma carnifex* burrows for oviposition in French Polynesia; environmental suitability was therefore quantified using *C. carnifex* burrow density.
Results: Micro-regions with large *Ae. polynesiensis* populations facilitated by high *C. carnifex* burrow density were accurately captured by our methodology. Preferential dispersal towards oviposition sites promoted larger population sizes than non-preferential dispersal but did not offer greater resilience to environmental change. Reduced environmental suitability for *Ae. polynesiensis* resulted in spatially non-linear effects upon the mosquito distribution.
Conclusions: Environmental change has complex spatial effects upon mosquito populations. Mosquito control strategies must carefully balance spatial effects with net effects.

1. Introduction

Mosquito-borne disease contributes substantially to the global infectious disease burden [1]. Spatial heterogeneity in mosquito populations and mosquito-borne infections arises due to variation in habitat quality, habitat quantity, host density, temperature or rainfall among others [2–7]. Mosquito persistence is linked to human land-use changes such as agriculture, urbanisation and deforestation [8–12]. In particular, the quantity and availability of oviposition sites influences adult mosquito population sizes by increasing the environmental carrying capacity [7,13,14]. Environmental heterogeneity, including availability of larval habitats, also influences mosquito dispersal [14–17].

Models of mosquito behaviour in response to environmental heterogeneity are vital to inform control strategies as rapid land-use change occurs globally [18]. Lutambi et al. (2013) modelled mosquito dispersal in hypothetical heterogeneous environments and found the spatial distribution of resources to be highly influential upon adult mosquito dynamics [19]. A small number of other mosquito modelling studies have incorporated migration or dispersal effects [20–24], most

using a meta-population approach. However, few existing models have incorporated environmental heterogeneity, mosquito dispersal, host dispersal or environmental heterogeneity [25–28]. Fewer still have used field data to do so.

We addressed the absence of environmental factors in existing models by integrating field sampling, remote sensing and mathematical modelling to consider the effects of environmental heterogeneity and mosquito dispersal on spatial mosquito distributions.

A *motu* is a reef islet surrounding an atoll. We used *motu* Tautau, French Polynesia, as a study site. In the South Pacific, the mosquito *Aedes polynesiensis* is the major vector of *Wuchereria bancrofti* (the causative agent of lymphatic filariasis) and a vector of dengue and other arboviruses [29]. *Ae. polynesiensis* primarily exploit land crab, *Cardisoma carnifex*, burrows for oviposition in certain French Polynesian atolls [30–32]. *C. carnifex* dig burrows to the water table where mosquito larvae are protected in a freshwater chamber. Burrows remain active for around 25 days, which is sufficient for larval emergence [33].

Exploitation of *C. carnifex* burrows as a primary larval habitat renders *Ae. polynesiensis* an excellent study species to consider the

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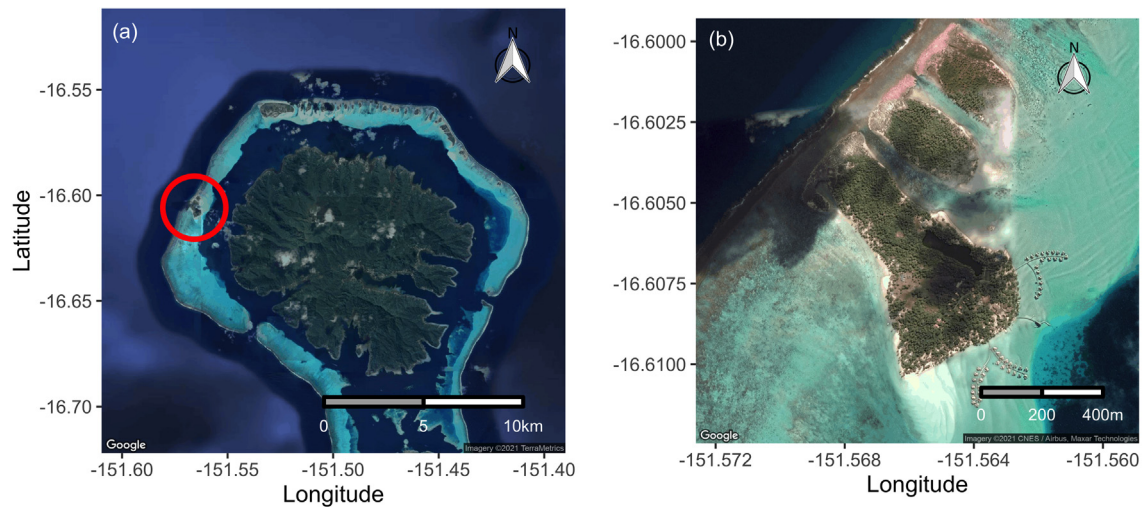*E-mail address:* katie.heath@burnet.edu.au (K. Heath).

Fig. 1. Maps displaying (a) the location of *motu* Tautau (circled) on Taha'a's outer coral reef and (b) *motu* Tautau, where luxury hotel development is visible on the south end of the *motu*. In the south and southwest of the *motu* there are staff living facilities and a small number of independent residents. The north section of the *motu* is mostly forested and free from human development. Figures (a) and (b) were obtained using the ggmap package [40] for R version 3.6.0 [41] accessed 1st November 2021. Image (a) © TerraMetrics and (b) © 2021 CNES/Airbus, Maxar Technologies.

importance of oviposition site availability because burrow presence and abundance are easy to measure empirically. In addition, 141 species of mosquitoes are dependent on crab burrows for oviposition globally, making our findings widely applicable [34–36]. Our methodological approach had two major objectives:

1. Estimate spatial heterogeneity in *C. carnifex* burrow density

Field sampling was conducted to characterise the distribution of *C. carnifex* burrows on *motu* Tautau. Field data were used to train and validate machine-learning algorithms. Machine-learning algorithms were applied to remote sensing data to estimate the spatial distribution of *C. carnifex* burrows used by *Ae. polynesiensis* for oviposition.

2. Model the effects of environmental heterogeneity on *Ae. polynesiensis* dynamics

Lutambi et al.'s (2013) model of mosquito dispersal was adapted for *Ae. polynesiensis*. The model was applied to the estimated spatial distribution of *C. carnifex* burrows to consider the effects of spatial heterogeneity upon mosquito density. Two dispersal behaviours were compared: preferential dispersal towards *C. carnifex* burrows and non-preferential dispersal. The effects of different patterns of environmental change upon mosquito populations were considered. The model was validated by comparison to trap data.

2. Methods

2.1. Study site

Motu Tautau, Taha'a, French Polynesia (Fig. 1), was used as a case study. In the absence of competitors or predators on *motu* Tautau, *C. carnifex* are exceptionally abundant and support large *Ae. polynesiensis* populations [37,38]. Modelling mosquito populations on *motu* Tautau is of particular interest as it is the target of a *Wolbachia* mosquito control programme conducted by Institut Louis Malardé (https://www.ilm.pf) [39]. Control methods were not yet implemented at the time of field sampling. Taha'a has a warm tropical climate of approximately 22–31 °C with heavy rainfall between November and March.

2.2. Field sampling

Adult mosquito trapping data from BG-Sentinel (BGS) traps using BG-Lures (Biogents AG, Regensburg, Germany) [39,42,43] were available weekly between 20th August 2018 and 15th October 2018 at 12

locations on *motu* Tautau, collected by Institut Louis Malardé, Tahiti, French Polynesia. Within their protocol, traps were hung from tree branches between 20–50 cm from the ground. Engine grease was applied to the rope to prevent ant predation. Traps were run for the same 24-hour cycle weekly. Collected mosquitoes were frozen, identified and counted by sex and species using taxonomic keys [44,45].

Exploitation of *C. carnifex* burrows by *Ae. polynesiensis* for oviposition was confirmed by burrow extraction. The distribution of copepods was estimated from extracted samples. Copepods predate heavily on mosquito larvae and have been suggested as a control strategy [46–50]. Sampling methodology and results are shown in Supplementary Material S.1.

Motu Tautau covers around 0.25 km². A grid of sampling points at distances of 100 m (116 total sampling points) was defined encompassing the whole island. At each point, the number of burrows within a 10 m radius was recorded and converted to burrow density (burrows per 100 m²). The diameters of 20 burrows selected at random within a 10 m radius of the sampling point were recorded. Land cover at each point was classified as forest, exposed rock, beach, residential/hotel, freshwater lake or industrial/construction.

2.3. Remote sensing

Eleven-band remote sensing data from 16th July 2018 (date closest to field sampling (November 2018) with < 20% cloud cover) were downloaded from NASA's Landsat 8. Data were pre-processed using QGIS version 2.18 and the SCP plugin [51]. Dark Object Subtraction (DOS1) atmospheric correction was applied to obtain surface reflectance [52]. Pre-processed data were cropped to the study area, which was −151.574 to −151.556 longitude and −16.614 to −16.597 latitude.

For land cover classification, three land type classes – easily identifiable from maps – were added to those from cartographical data to account for ocean water types: deep ocean, lagoon and exposed coral reef. A spectral signature using the 11-band Landsat 8 raster stack was estimated for each land cover class from collected field data using the SCP plugin. Euclidean Minimum Distance land classification was used to estimate the land cover class for the entire clipped map [53,54]. The sensitivity and specificity of the classification algorithm were calculated for each land cover class.

2.4. Spatial distribution of oviposition sites

Random forest machine learning algorithms were used to predict *C. carnifex* burrow density on *motu* Tautau from 11-band Landsat 8 data using the randomForest package for R version 3.5.2 [41,55,56]. Individual regression trees within a single random forest model use m bootstrapped samples with replacement of the training data, D, and each split uses a subset of the predictor variables [56]. As such, random forests internally cross-validate and reduce individual variable dominance and over-fitting. Random forests were particularly appropriate for the given study because they do not require prior information about the association between Landsat 8 data and *C. carnifex* burrow presence or density. Model hyper-parameters and further details of the random forest methodology are given in Supplementary Material S.2.

Random forest models were applied in a two-stage approach as detailed below. Both models used the 11-band Landsat 8 data at each grid cell as the predictor variables.

Step 1: Random forest classification with binary *C. carnifex* presence/absence as the response variable. Random forest classification yielded two data subsets: Φ_0 and Φ_1 where *C. carnifex* are absent and present, respectively, and $\Phi_0 \subset D$, $\Phi_1 \subset D$ and $\Phi_0 \setminus \Phi_1 = \Phi_0$. Cohen's κ was used to determine the ability of random forest classification to improve upon an expected level of classification accuracy under random chance for *C. carnifex* presence/absence [57]. The importance of each Landsat 8 band for random forest classification was considered using the mean decrease in Gini index.

Step 2: Random forest regression with *C. carnifex* burrow density (burrows/100 m^2) as the response variable. Burrow density in grid cells where *C. carnifex* were estimated to be absent from random forest classification (Φ_0) was set to zero following random forest regression. Predicted burrow densities were converted to the number of burrows in each cell, rounded to the nearest whole number. Pseudo-R^2 values were used to evaluate random forest regression. Feature importance was assessed for random forest regression using the decrease in model accuracy (measured by the mean squared error) when the focal trait is randomised.

2.5. Ae. polynesiensis dynamics without dispersal

A model of *Ae. polynesiensis* population dynamics was applied to random forest regression estimates of burrow density. The model was comprised of a grid with each cell, (i, j), corresponding to a 15×15 m Landsat 8 cell. Male and female mosquitoes were modelled separately due to different dispersal behaviours and mortality rates [58]; low recapture rates of male *Ae. polynesiensis* and *Aedes aegypti* compared to females suggest a severely shorter male lifespan [16,59–62]. The model was as follows:

$$\frac{dJ_{i,j}}{dt} = (1-c)\, b\sigma_{i,j} F_{i,j} - \mu_{J_{i,j}} J_{i,j} - p J_{i,j} \tag{1}$$

$$\frac{dF_{i,j}}{dt} = g p J_{i,j} - \mu_F F_{i,j} \tag{2}$$

$$\frac{dM_{i,j}}{dt} = g p J_{i,j} - \mu_M M_{i,j} \tag{3}$$

where J is the number of juvenile mosquitoes (encompassing egg, larval and pupal stages), F is the number of female adult mosquitoes and M is the number of male adult mosquitoes. c is the proportion of burrows colonised by copepods; b is the fecundity (eggs laid per unit time); μ_J is the juvenile death rate; g is the male:female gender emergence ratio; p is the pupation rate; μ_F is the adult female death rate; μ_M is the adult male death rate. Subscript i, j indicates the value of a parameter in cell (i, j). All model parameters, their values and sources are shown in Table 1.

$$\sigma_{i,j} = \begin{cases} 1 \ if \ \alpha_{i,j} > 0 \\ 0 \ if \ \alpha_{i,j} = 0 \end{cases} \tag{4}$$

where $\alpha_{i,j}$ is the number of crab burrows in cell (i, j). Larval mortality was described as follows:

$$\mu_{J_{i,j}} = \frac{\kappa J_{i,j}}{\alpha_{i,j}(1-c)} \tag{5}$$

where κ is a numeric constant. Further discussion of density-dependent mortality in our model is given in Supplementary Material S.3.

Our model retained males for two reasons. First, the gender ratio in trap data was unequal (see Results) and, as such, our model framework incorporated gender-specific dispersal behaviours and mortality rates to examine whether gender-biased mosquito populations in the field could arise from these mechanisms. Second, males contributed to the total number of mosquitoes in traps and these data were used for model validation. The model implicitly assumed that eggs were distributed equally among burrows and that 100% of eggs laid in copepod-infested burrows died through predation [46–49].

Derivation of equilibrium values and demonstration of model stability are shown in Supplementary Material S.4. All analysis was performed in R version 3.5.2 using a Runge–Kutta 4 algorithm [41].

2.6. Ae. polynesiensis dynamics with dispersal

We adapted the discrete-space dispersal model developed by Lutambi et al. (2013), where a comprehensive description of the methodology is available [19]. Dispersal was a Markov process because the mosquito distribution at time *t+1* was determined only by the state of the system at time *t*. Males and females have been observed to disperse different distances in *Ae. polynesiensis* and *Ae. aegypti* with females dispersing further [58,60,61,73]. Gender-dependent dispersal parameters, D_M and D_F were defined for male and females respectively:

$$D_M = \frac{D_M^*}{A} \ and \ D_F = \frac{D_F^*}{A} \tag{6}$$

where A is the area of each Landsat 8 grid cell (225 m^2) and D_M^* and D_F^* are the distances travelled per unit time (m^2 day^{-1}) by male and female mosquitoes, respectively.

Let Π be the set of all cells and (i, j) be a cell within Π. Eight cells surround each cell to form a neighbourhood, $n_{i,j}$

$$n_{i,j} = \left\{ \begin{array}{c} (i-1, j-1), (i-1, j), (i-1, j+1), (i, j-1), (i, j+1), \\ (i+1, j-1), (i+1, j), (i+1, j+1), (i, j) \end{array} \right\} \tag{7}$$

Dispersal from a cell, (i, j), was dependent only on the state of cells within $n_{i,j}$ because it is not thought that mosquitoes can visually perceive targets beyond their immediate proximity (e.g. > 20 m) [74,75]. Recall that $n_{i,j}$ is cell (i, j) and its eight neighbours. $n_{i',j'}$ is cell (i', j') and its eight neighbours, one of which is (i, j). χ is a cell within Π and χ' is a cell neighbouring χ. The notation of χ, χ', (i, j) and (i', j') is sufficient to describe every possible relationship between cells. The following notation was used to describe dispersal:

α_χ = number of burrows in cell χ
$\alpha_{n_{i,j}}$ = number of burrows in $n_{i,j}$
$\alpha_{\chi'}$ = number of burrows in cell χ'
$\alpha_{n_{i',j'}}$ = number of burrows in $n_{i',j'}$
$\overline{\alpha}_{\chi \in n_{i,j}}$ = proportion of burrows in $n_{i,j}$ which are in $\chi \in n_{i,j}$
$\overline{\alpha}_{\chi' \in n_{i,j}}$ = proportion of burrows in $n_{i,j}$ which are in $\chi' \in n_{i,j}$
$\overline{\alpha}_{\chi \in n_{i',j'}}$ = proportion of burrows in $n_{i',j'}$ which are in $\chi \in n_{i',j'}$
$\overline{\alpha}_{\chi' \in n_{i',j'}}$ = proportion of burrows in $n_{i',j'}$ which are in $\chi' \in n_{i',j'}$
The total number of burrows in a neighbourhood was calculated by

$$\alpha_{n_{i,j}} = \sum_{\chi \in n_{i,j}} \alpha_\chi \ and \ \alpha_{n_{i',j'}} = \sum_{\chi \in n_{i',j'}} \alpha_\chi \tag{8}$$

The proportion of burrows in a group of cells, $n_{i,j}$, which are in $\chi \in n_{i,j}$ was calculated by

$$\overline{\alpha}_{\chi \in n_{i,j}} = \frac{\alpha_\chi}{\alpha_{n_{i,j}}} \tag{9}$$

Table 1
Descriptions, values and sources of key model parameters.

Parameter	Description	Value	Units	Source and Notes
α	Number of *C. carnifex* burrows	N/A	burrows	Estimated from random forest models using field data (see Methods Section 2.4).
c	Proportion of burrows inhabited by copepods	0.475	N/A	Field data (see Supplementary Material S.1)
σ	Binary parameter controlling oviposition	0 if $\alpha_{i,j} = 0$ 1 if $\alpha_{i,j} > 0$	N/A	N/A
b	Adult fecundity	1.62	eggs mosquito^{-1} day^{-1}	No published data for *Ae. polynesiensis*; *Ae. aegypti* data used. Joy et al. (2014) observed approximately 55 eggs/mosquito over four lifetime reproductive cycles in the laboratory [63]. Eggs per mosquito per day were calculated by $1/\vartheta$ where ϑ is *Ae. aegypti* lifespan in the laboratory. Literature review of lab-reared *Ae. aegypti* yielded $\vartheta = 33.95$ [64–69].
μ_J	Juvenile mortality	See Eq. (5)	day^{-1}	N/A
κ	Density-dependent mortality constant	8.5×10^{-4}	N/A	Estimate. See Supplementary Material S.3. for more information.
g	Male:female gender emergence ratio	0.5	N/A	An equal emergence ratio of male:female adult mosquitoes was assumed
p	Egg to adult emergence rate	0.12	day^{-1}	No published data for *Ae. polynesiensis*. Estimated for a mean temperature of 27 °C in *Ae. aegypti* [70].
μ_F	Female adult mortality	0.11	day^{-1}	$\frac{1}{\tau_F}$ where τ_F is the estimated average female lifespan (see below).
μ_M	Male adult mortality	0.32	day^{-1}	$\frac{1}{\tau_M}$ where τ_M is the estimated average male lifespan (see below).
τ_F	Mean adult female stage duration	9.14	days	No published data for *Ae. polynesiensis* in wild populations; *Ae. aegypti* data used. Lab data not used due to artificially extended lifespans [60]. Mean estimated lifespan from mark–release–recapture (MRR) experiments used [60,61,71]. In cases where studies reported daily survival rates, S, mean longevity calculated by $1/S$.
τ_M	Mean adult male stage duration	3.09	days	No published data for *Ae. polynesiensis* in wild populations; *Ae. aegypti* data used. Lab data not used due to artificially extended lifespans [60]. Mean estimated lifespan from MRR experiments used [60,61,71]. In cases where studies reported daily survival rates, S, mean longevity calculated by $1/S$.
τ_J	Mean juvenile stage duration	9.86	days	The mean of female and male emergence times taken from Mercer (1999); male and female times were comparable [72].
D_F^*	Female diffusion coefficient	153.39	m^{2}day^{-1}	Hapairai et al. (2013) observed mean of 123.87 m dispersal for female *Ae. polynesiensis* over five days [58], or a diffusion length of 24.77 m per day. The diffusion coefficient was estimated by rearranging Fick's law where the diffusion length $= 2\sqrt{D_F^* t}$, where t is the time elapsed (days), and solving for D_F^*.
D_M^*	Male diffusion coefficient	116.21	m^{2}day^{-1}	Hapairai et al. (2013) observed mean of 107.68 m dispersal for male *Ae. polynesiensis* over five days [58], or a diffusion length of 21.56 m per day. The diffusion coefficient was estimated by rearranging Fick's law where the diffusion length $= 2\sqrt{D_M^* t}$, where t is the time elapsed (days), and solving for D_M^*.
A	Area of study cell	225	m^2	Each LandSat 8 grid cell was 15×15 m.
λ	Constant dimensionless decay parameter	1	N/A	Estimate. See Lutambi et al. (2013) for further specification [19].

where

$$\sum_{\chi \in n_{i,j}} \overline{\alpha}_{\chi \in n_{i,j}} = 1 \tag{10}$$

Similarly

$$\overline{\alpha}_{\chi' \in n_{i,j}} = \frac{\alpha_{\chi'}}{\alpha_{n_{i,j}}} \tag{11}$$

$$\overline{\alpha}_{\chi \in n_{i',j'}} = \frac{\alpha_{\chi}}{\alpha_{n_{i',j'}}} \tag{12}$$

$$\overline{\alpha}_{\chi' \in n_{i',j'}} = \frac{\alpha_{\chi'}}{\alpha_{n_{i',j'}}} \tag{13}$$

To counteract edging effects, female mosquitoes did not preferentially migrate into neighbouring cells over oceans or lakes (i.e. where there were no *C. carnifex* burrows). The rate of movement out of a cell, (i,j), into a neighbouring cell, $\chi' \in n_{i,j}$, was defined by

$$\beta_{[(i,j) \to \chi']} = \begin{cases} De^{-\lambda\left(\overline{\alpha}_{\chi \in n_{i,j}} - \overline{\alpha}_{\chi' \in n_{i,j}}\right)} & if\ \alpha_{\chi'} > 0 \\ 0\ if\ \alpha_{\chi'} = 0 \end{cases} \tag{14}$$

and the rate of movement into a cell was

$$\beta_{[\chi' \to (i,j)]} = \begin{cases} De^{-\lambda\left(\overline{\alpha}_{\chi' \in n_{i',j'}} - \overline{\alpha}_{\chi \in n_{i',j'}}\right)} & if\ \alpha_{\chi} > 0 \\ 0\ if\ \alpha_{\chi} = 0 \end{cases} \tag{15}$$

where $D \in \{D_M, D_F\}$ and λ is a dimensionless, constant parameter for the decay function. If $\left(\overline{\alpha}_{\chi \in n_{i,j}} - \overline{\alpha}_{\chi' \in n_{i,j}}\right) = 0$ then adult mosquitoes disperse non-preferentially between all neighbouring cells. In this case, Eqs. (15) and (16) become

$$\beta_{[(i,j) \to \chi']} = \begin{cases} D\ if\ \alpha_{\chi'} > 0 \\ 0\ if\ \alpha_{\chi'} = 0 \end{cases} \tag{16}$$

$$\beta_{[\chi' \to (i,j)]} = \begin{cases} D \ if \ \alpha_\chi > 0 \\ 0 \ if \ \alpha_\chi = 0 \end{cases} \qquad (17)$$

Some cells on land were predicted to have a *C. carnifex* burrow density of zero using random forests. As defined above, our model prevented preferential mosquito dispersal to cells with no burrows. Therefore, negligible error term sampled from a Poisson distribution (mean = 2) was added to the predicted burrow density in each cell on land, to ensure that all cells on land had $\alpha > 0$. This prevented mosquitoes becoming trapped in small areas due to their inability to migrate over surrounding land.

2.7. Two models of mosquito dispersal behaviour

Field evidence suggests that male *Ae. polynesiensis* dispersal behaviours are less influenced by environmental heterogeneity than females [58]. Therefore, the rate of change of male mosquito populations was defined as:

$$\frac{d M_{i,j}}{dt} = gp J_{i,j} - \mu_M M_{i,j} - \left(\sum_{\chi' \in n_{i,j}} D_M \right) M_{i,j} + \left(\sum_{\chi' \in n_{i,j}} D_M M_{\chi'} \right) \qquad (18)$$

Two models of female mosquito dispersal were compared. The preferential dispersal model assumed that female mosquitoes disperse seeking oviposition sites and that $D = D_F$:

$$\frac{d F_{i,j}}{dt} = gp J_{i,j} - \mu_F F_{i,j} - \left(\sum_{\chi' \in n_{i,j}} \beta_{[(i,j) \to \chi']} \right) F_{i,j} + \left(\sum_{\chi' \in n_{i,j}} \beta_{[\chi' \to (i,j)]} F_{\chi'} \right) \quad (19)$$

The non-preferential dispersal model assumed the female adult mosquitoes disperse non-preferentially:

$$\frac{d F_{i,j}}{dt} = gp J_{i,j} - \mu_F F_{i,j} - \left(\sum_{\chi' \in n_{i,j}} D_F \right) F_{i,j} + \left(\sum_{\chi' \in n_{i,j}} D_F F_{\chi'} \right) \qquad (20)$$

Eqs. (1) and (18) remained constant in both models.

2.8. Comparison of model estimates with trap data

The estimated number of adult mosquitoes in the neighbourhood $n_{i,j}$ of a trap, located in (i, j) is contained by

$$\overline{A}_{i,j} = \sum_{\chi' \in n_{i,j}} A_{\chi'} \qquad (21)$$

where $A_{i,j} = F_{i,j} + M_{i,j}$. The median predicted population size across the neighbourhoods of all 12 traps is

$$\varpi = med \left\{ \overline{A}_{i_1,j_1}, \overline{A}_{i_2,j_2}, \ldots, \overline{A}_{i_{12},j_{12}} \right\} \qquad (22)$$

The median number of mosquitoes captured across all BGS traps is ω. The median was used to avoid skew effects caused by outliers. A scaling factor, $\Psi = \frac{\omega}{\varpi}$, was used to re-project model estimates to facilitate comparison with trap data by applying Ψ to the model estimates at each trap: $\left\{ \Psi \overline{A}_{i_1,j_1}, \Psi \overline{A}_{i_2,j_2}, \ldots, \Psi \overline{A}_{i_{12},j_{12}} \right\}$. The absolute difference between rescaled model estimates and BGS trap data was used as a comparative measure.

2.9. Change in environmental suitability

The effect of changes in environmental suitability was considered in the context of larval source management (LSM). LSM is a vector control strategy, which removes potential oviposition sites to disrupt the mosquito life cycle [76]. Decreased environmental suitability due to LSM was defined as

$$\alpha^\Lambda = \begin{cases} (1 - \varepsilon) \alpha^\Lambda \ if \ t \geq T \\ \alpha^\Lambda \ if \ t < T \end{cases} \qquad (23)$$

where ε is LSM efficacy (the proportion of *C. carnifex* burrows removed or rendered uninhabitable for larvae), Λ is LSM coverage (a set of cells with length, θ, where LSM is implemented) and T is the time of intervention, which was set to occur once the model without LSM had reached stable equilibrium. Equilibrium was assumed to be achieved when each discrete cell had an adult mosquito population that did not increase or decrease by greater than 1.0 for at least 200 continuous iterations (days). Although our model simulates LSM, the formulation in Eq. (23) is not limited to the effects of human intervention. Our model could indicate the effects other processes that decrease environmental suitability for *Ae. polynesiensis,* including changes in *C. carnifex* behaviour, land cover or local water depletion and/or quality, where ε and θ represent the intensity and scale of environmental change, respectively.

Two spatial patterns of LSM were considered. First, targeted LSM defined Λ as the θ cells with the largest *Ae. polynesiensis* population at dispersal model equilibrium. Second, untargeted LSM defined Λ as θ cells randomly sampled from the set of all cells. Parameter ε was varied between 0.05 and 0.95 and θ was varied between 50 and 300 on iterative model runs. Examples of the LSM coverage grids with different values of θ are shown in Supplementary Material S.5. The model was run to equilibrium for each combination of ε and θ for preferential and non-preferential dispersal models and the change in *Ae. polynesiensis* population size was recorded. For untargeted LSM, the model was run for 20 bootstraps for each combination of ε and θ taking a different random sample of θ cells to avoid sampling bias. The net reduction in *Ae. polynesiensis* population size at equilibrium across bootstrapped simulations was recorded.

3. Results

3.1. Ae. polynesiensis distribution is spatially heterogeneous

Ae. polynesiensis accounted for >99.5% of mosquitoes in BGS traps. *Ae. aegypti* accounted for 0.02% and *Culex quinquefasciatus* for 0.46%. Only 3.7% of all captures were male mosquitoes. Mean captures in each trap and trap locations on *motu* Tautau are shown in Fig. 2(a) and the data spread is demonstrated in Fig. 2(b). There were no notable trends with time. Trap two saw the highest *Ae. polynesiensis* numbers per 24-hour cycle: 1,334 mosquitoes on average and a maximum of 2,767 on 10th September 2018. These numbers indicate very large *Ae. polynesiensis* populations; only between 17 and 241 mosquitoes per 24-hour cycle have been observed using the same equipment in parts of French Polynesia and other South Pacific islands [77,78]. Large *Ae. polynesiensis* populations appear endemic in the vicinity of Taha'a. On nearby *motu* Taomaro, MRR experiments estimated *Ae. polynesiensis* population densities of 6,055 per hectare for the dry season and 18,860 per hectare for the wet season [16].

3.2. Oviposition site availability is spatially heterogeneous

Predicted and observed land cover classes on *motu* Tautau are shown in Fig. 3. The mean specificity and sensitivity of the classifier across land cover classes were 92% and 51%, respectively. The confusion matrix of predicted and observed land cover types is shown in Supplementary Material S.6.

The estimated and observed *C. carnifex* burrow distributions are shown in Fig. 4. For random forest classification of *C. carnifex* presence/absence Cohen's κ was 0.28, indicating that Landsat 8 reflectance offers an improvement in classification accuracy over random chance [57]. The confusion matrix used to calculate Cohen's κ is shown in Supplementary Material S.7.

For regression trees of *C. carnifex* burrow density, the pseudo-R^2 was 0.19 which is relatively low, although it should be noted that random forests were able to capture the main features of the spatial distribution (Fig. 4) despite some error in the exact numbers of *C. carnifex* burrows estimated. The mean "Out-of-bag" (OOB) error in predicted burrow density was 12.56 burrows/100 m^2. Further information on
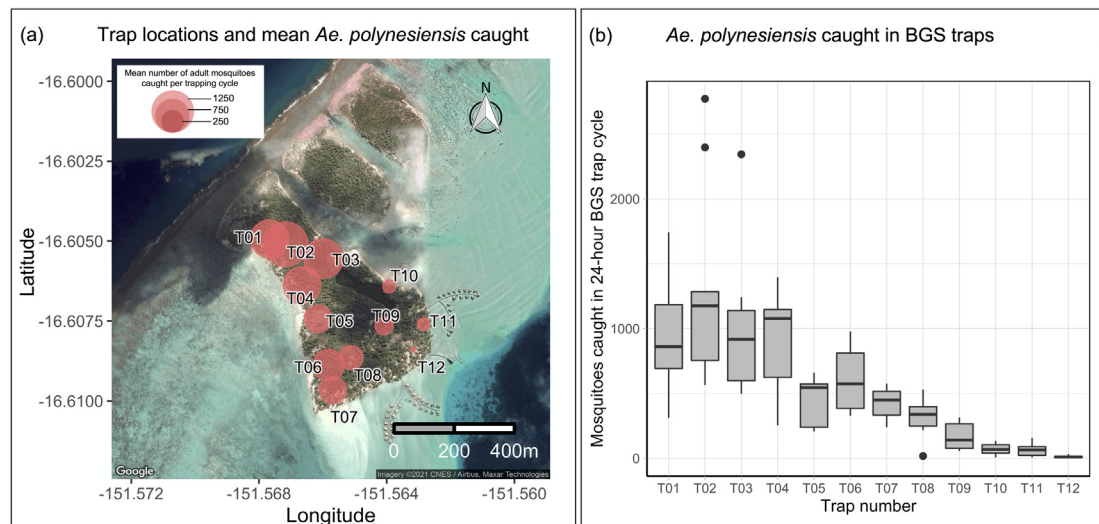
Fig. 2. *Ae. polynesiensis* mosquito numbers in BG-Sentinel (BGS) traps on *motu* Tautau between 20th August 2018 and 15th October 2018. The location of traps and their mean capture numbers are displayed in (a). Trap numbers of the 12 traps are denoted using T01-T12. The 0.25, 0.5 (median) and 0.75 percentiles are shown in (b) along with the data range. Trap data were collected by Institut Louis Malardé. Figure (a) was obtained using the ggmap package [40] for R version 3.6.0 [41], accessed 1st November 2021. Image (a) © 2021 CNES/Airbus, Maxar Technologies.
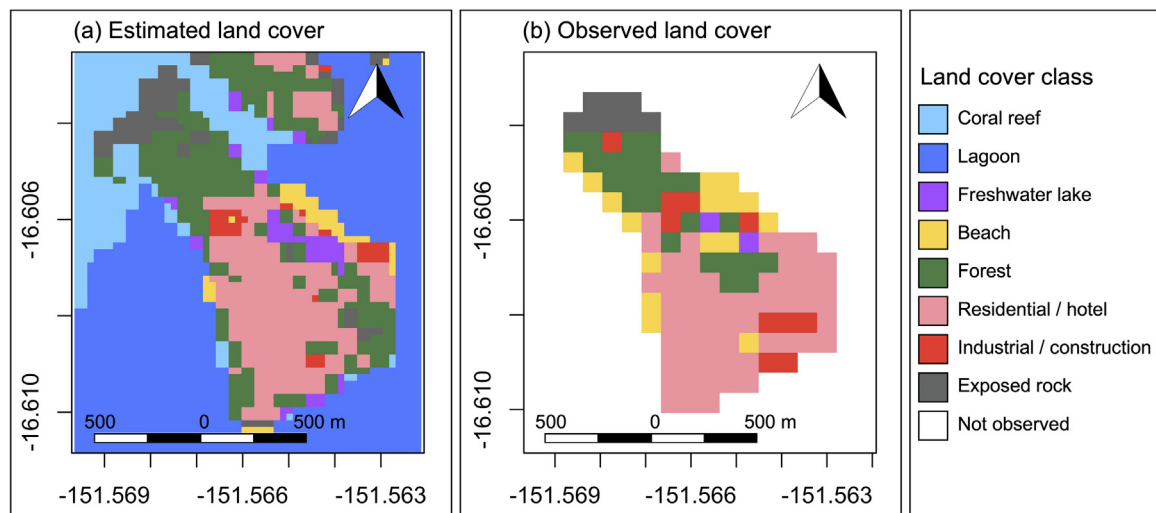
Fig. 3. Land cover class on *motu* Tautau and surrounding area (a) estimated from Euclidean Minimum Distance land clover classification and (b) observed from field sampling. Subfigure (a) is at a resolution of 15 m × 15 m and subfigure (b) is at a resolution of 100 m × 100 m.

random forest methodology and feature importance plots are shown in Supplementary Material S.2. and S.7. Random forest regression incurred mild smoothing, overestimating at low burrow densities and underestimating at high burrow densities as shown in Supplementary Material S.7.

3.3. Model estimates approximate trap data

The predicted spatial distribution of *Ae. polynesiensis* (male and female combined) for non-preferential and preferential dispersal models is shown in Fig. 5. Preferentially migrating *Ae. polynesiensis* population sizes (male and female combined) were 1.34-fold higher than non-preferentially migrating populations. Larval populations were 1.33-fold higher for preferentially compared to non-preferentially dispersing mosquitoes. The average male percentage of the *Ae. polynesiensis* population was 30.6% for preferential and 35.6% for non-preferential dispersal models.

A comparison of preferential and non-preferential dispersal model results with BGS trap data is shown in Fig. 6. The median non-preferential dispersal model predictions, $med\left(\Psi \overline{A}_{i,j}\right)$, in the neighbourhood, $n_{i,j}$, of each trap were marginally closer to the median observed mosquito numbers at each trap. The median difference between the number of trapped mosquitoes and model estimates was 199 for the preferential model and 162 for the non-preferential model. The trap with the largest absolute difference between model predictions and BGS trap data (trap T02 with an error of 597 and 599 burrows for non-preferential and preferential models, respectively) also had the largest error in the predicted *C. carnifex* burrow density out of all 12 traps (48.2 burrows/100 m^2).

3.4. Environmental change has spatially non-linear effects

The net effects of each LSM strategy upon preferentially and non-preferentially dispersing *Ae. polynesiensis* populations were comparable. While targeted LSM consistently suppressed a greater net proportion of
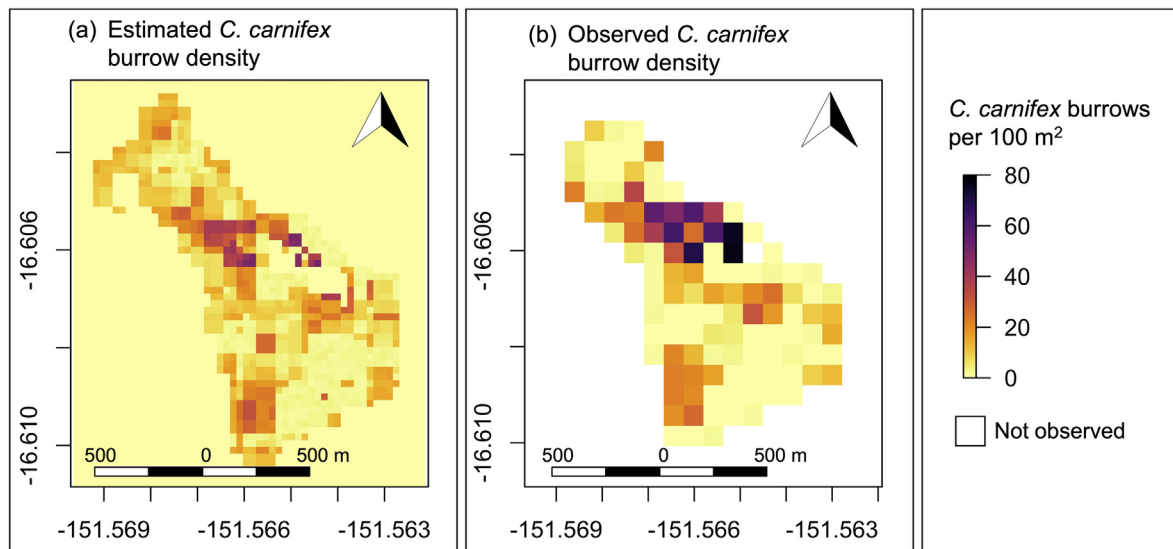
Fig. 4. Spatial distribution of *C. carnifex* burrows on *motu* Tautau (a) predicted using random forests and (b) observed from field sampling. Subfigure (a) is at a resolution of 15 × 15 m and subfigure (b) is at a resolution of 100 × 100 m.
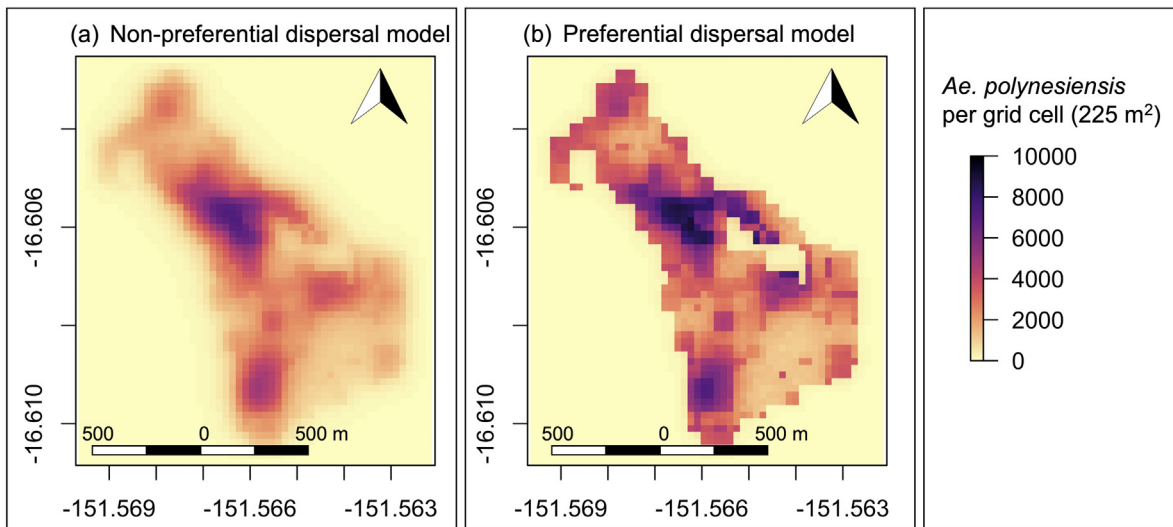

Fig. 5. Predicted distribution of *Ae. polynesiensis* adult mosquitoes (male and female) on *motu* Tautau for the (a) non-preferential and (b) preferential female dispersal models.

the *Ae. polynesiensis* population than untargeted LSM, the effect was small. In the preferential dispersal model, targeted LSM suppressed 3.2% (standard deviation (SD) = 1.7%) more of the *Ae. polynesiensis* population on average than non-targeted LSM for the parameter values of intervention coverage, $\theta = 50, \ldots, 300$, and efficacy, $\varepsilon = 0.05, \ldots, 0.95$. For non-preferential dispersal, targeted LSM suppressed 2.2% (SD = 1.1%) more of the population than non-targeted LSM. The net proportion of the *Ae. polynesiensis* population suppressed across the parameter space, $\theta = 50, \ldots, 300$ and $\varepsilon = 0.05, \ldots, 0.95$, for each dispersal behaviour and LSM strategy is shown in Supplementary Material S.8.

Fig. 7 shows the change in the *Ae. polynesiensis* population as a result of targeted and untargeted LSM for preferential and non-preferential dispersal models. Although the net effects of targeted and untargeted LSM strategies were comparable (Supplementary Material S.8.), each strategy had distinct, non-linear spatial effects upon the *Ae. polynesiensis* population. Targeted LSM had a negligible effect upon *Ae. polynesiensis* populations outside of the intervention zone (Fig. 7(a) and Fig. 7(c)). Whilst targeted LSM provided enhanced population suppression, its effects were restricted to an area localised around the target cells. In contrast, untargeted LSM provided a lower level of suppression across

a wider geographic area. Fig. 8 shows the absolute difference in the proportion of the *Ae. polynesiensis* population suppressed between LSM strategies for $\theta = 50, 300$ and $\varepsilon = 0.50$; the outcomes for other values of θ and ε are shown in Supplementary Material S.8. Whilst targeted LSM was more effective that untargeted LSM in its local intervention zone, untargeted LSM quickly became more effective as the distance from targeted LSM intervention zones increased.

4. Discussion

Complex and rapid land-use change is occurring globally [18,79]. Consideration of spatial heterogeneity is paramount in mosquito population models to predict the distributions of epidemiologically important species. We have integrated field sampling, remote sensing and mathematical modelling to examine the spatial distribution of *Ae. polynesiensis* on *motu* Tautau, French Polynesia. Our study provides an example of a methodological pipeline applicable on larger scales to (a) estimate many types of environmental heterogeneity and (b) consider the effects of environmental heterogeneity upon the behaviours of different mosquito species.
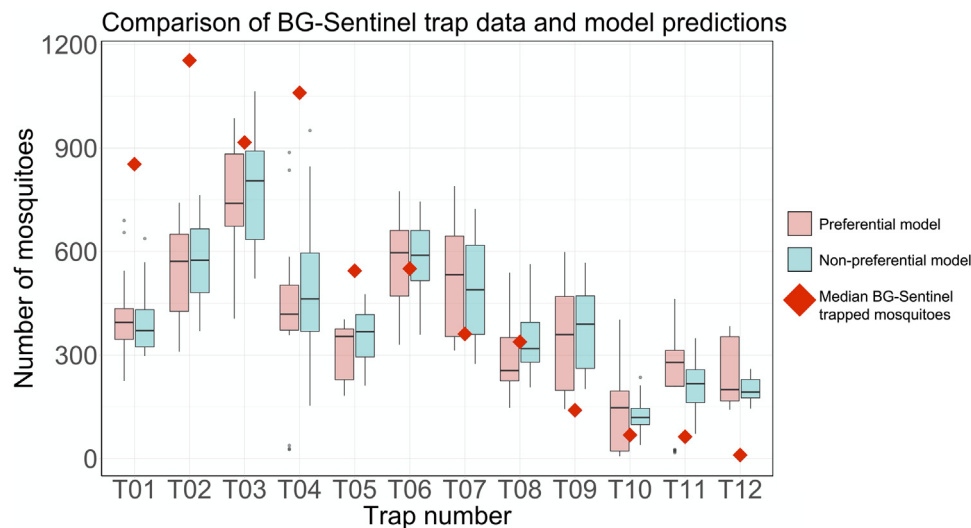
Fig. 6. Comparison of preferential and non-preferential female dispersal models with the median number of caught adult *Ae. polynesiensis* in BG-Sentinel (BGS) traps. The number of mosquitoes at each trap from estimated by the preferential and non-preferential dispersal models were subject to a scaling factor, Ψ, to facilitate comparison with trap data in this figure. Further details are given in the methods section.

We found that preferential dispersal of female *Ae. polynesiensis* towards oviposition sites resulted in 1.34-fold larger *Ae. polynesiensis* populations. This is intuitive because non-preferential dispersal results in a lower probability that a habitable area will be encountered and colonised [80]. The preferential dispersal model also yielded greater spatial heterogeneity in mosquito population sizes than non-preferential dispersal because spatial heterogeneity in crab burrow density had a greater effect on mosquito behaviour for preferential dispersal. Completeness and accuracy of environmental data may be more important if preferential dispersal is assumed. We found that the non-preferential model was more susceptible to changes in the diffusion coefficients D_F^* and D_M^* (see Supplementary Material S.9). Shorter dispersal distances yielded larger population sizes in areas with high densities of crab burrows than larger dispersal distances because adult mosquitoes were not dispersing as far from highly productive micro-environments.

The net proportion of the *Ae. polynesiensis* population suppressed by targeted and untargeted LSM strategies were comparable for preferentially and non-preferentially dispersing *Ae. polynesiensis* populations. This suggests that, although preferential dispersal was an advantageous ecological mechanism leading to larger *A. polynesiensis* population sizes, it did not offer substantial protection against environmental disruption. Targeted LSM offered a very marginal increase in the net proportion of the *Ae. polynesiensis* population suppressed compared to untargeted LSM. This result is consistent with previous models of mosquito control strategies. North et al. (2019) considered the effects of genetic mosquito control in West Africa and observed that a stratified release grid offered only a marginal increase in suppression than randomly selected release sites (95.9% compared to 93.6% suppression) [81].

Although the net effects of LSM were comparable between strategies, targeted and untargeted LSM strategies had different, non-linear spatial effects upon mosquito population sizes. The largest per-grid-cell reductions in *Ae. polynesiensis* density were achieved by targeted LSM. However, these reductions occurred on a local scale and failed to impact regions far from the intervention zone. By contrast, untargeted LSM resulted in smaller per-grid-cell reductions in *Ae. polynesiensis* density but these were distributed more homogeneously through space. These results have considerable implications for mosquito control strategies, three of which are discussed below.

First, our results suggest that localised changes in habitat quality do not have downstream effects for mosquito populations beyond the vicinity of the localised change. For mosquito control strategies, this

means that using net suppression as a target outcome may be a poor metric because key areas may be unaffected by an intervention. For example, on *motu* Tautau, hotel infrastructure and residential housing are restricted to the South end of the island (Fig. 1). Targeting LSM to regions with the largest *Ae. polynesiensis* populations resulted in the greatest net and per grid cell suppression effects. However, most of these effects were limited to areas on the North end of the *motu* and the South end was largely unaffected (Fig. 8(a) and Fig. 8(c)). Therefore, mosquito–human contacts might be unaffected by poorly targeted LSM strategies. Local and net effects must be carefully balanced and must be considered against the associated costs of each strategy. For example, whilst targeted LSM may be more costly in some cases due to the need for prior investigation to identify hotspots, it may be more effective than untargeted LSM if mosquito populations are very localised. The costs and benefits of each strategy may depend on the specifics of the environment in question, in particular heterogeneity in mosquito density within that environment.

Second, our model did not detect increases in mosquito density anywhere in the study region following LSM. This is because the models were at equilibrium prior to LSM intervention; cells were saturated at their environmental carrying capacity. Eggs laid by mosquitoes dispersing away from LSM intervention sites did not have a notable effect upon the *Ae. polynesiensis* population size because additional eggs exceeded the environmental carrying capacity, resulting in density-dependent larval mortality. Whether these dynamics hold in field environments depends upon the extent to which aquatic habitat carrying capacity is saturated under field conditions. Extraneous micro-environmental and micro-climatic variation may compromise the equilibration of larval populations at carrying capacity. Therefore, there is the potential for unintended increases in mosquito density in surrounding untreated areas if the environment is sufficiently unstable that mosquito populations do not equilibrate at carrying capacity.

The non-preferential dispersal model predicted patterns in *Ae. polynesiensis* density marginally closer to trapping data that the preferential model. However, it is not possible to conclude that non-preferential dispersal is the prevailing behaviour. Preferential and non-preferential models predicted disparate mosquito population sizes. Mosquito population size cannot be estimated from trap data without labour-intensive MRR studies [82], which have not yet been conducted on *motu* Tautau. In addition, our model may not capture all environmental features of importance. For example, dispersal of *Cx. quinquefasciatus* has been observed to occur predominantly downwind [83]. Wind direction was not accounted for by our model.
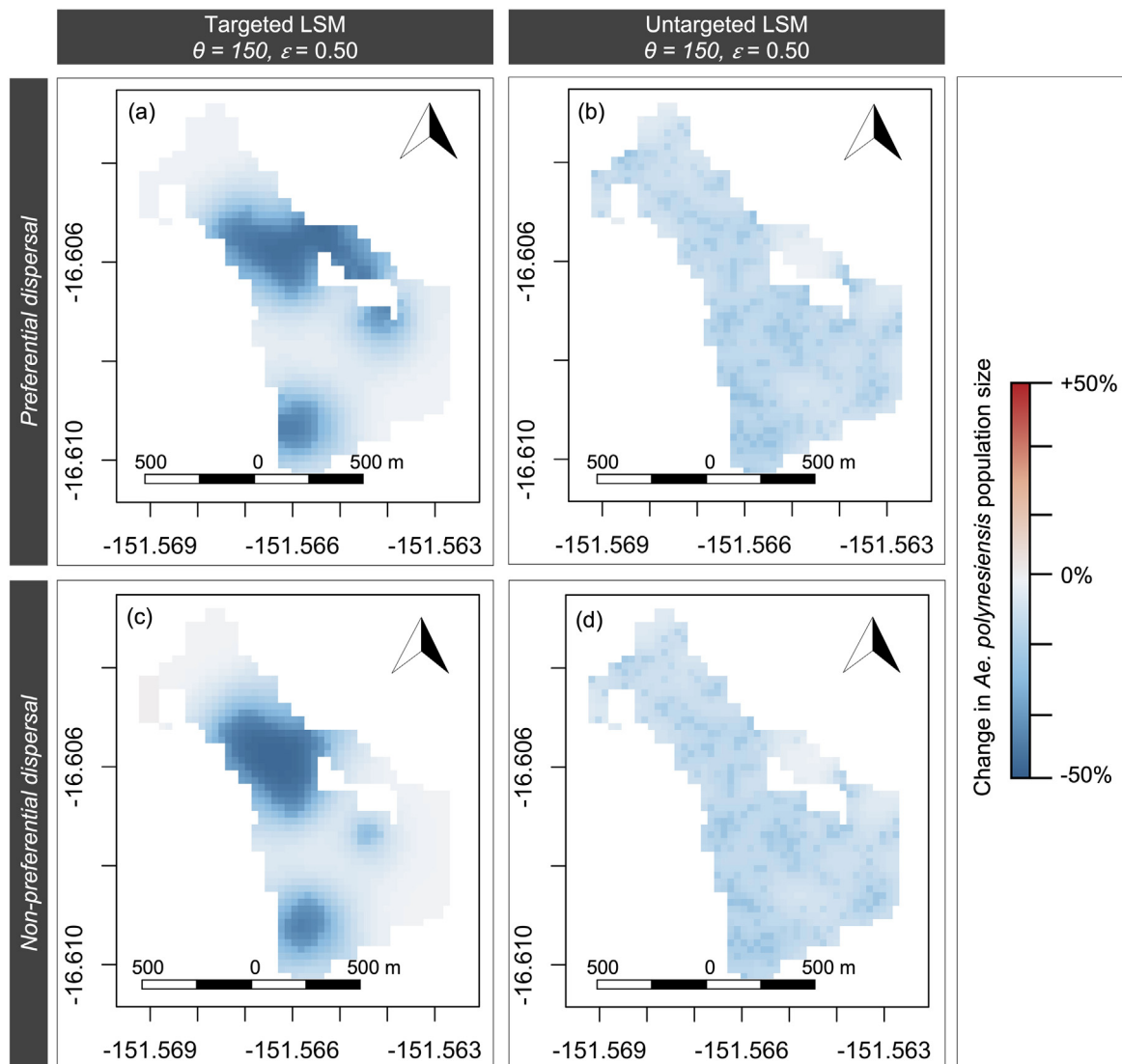
Fig. 7. The change in the *Ae. polynesiensis* population size in each grid cell following larval source management (LSM) intervention. Results are displayed for preferential dispersal (a)–(b) and non-preferential dispersal (c)–(d) using a targeted (a) & (c) and an untargeted (b) & (d) LSM intervention strategy. Results are displayed for a medium coverage, medium efficacy LSM intervention, where the LSM coverage in terms of the number of cells treated, θ, is 150 and the LSM efficacy in terms of the proportion of burrows removed at each treated cell, ε, is 0.5. Whilst targeted interventions ((a) & (c)) result in larger local reductions in the *Ae. polynesiensis* population size, untargeted interventions ((b) & (d)) result in more spatially homogeneous reductions. The effects for preferential and non-preferential dispersal models were comparable.

Despite challenges validating the mosquito population sizes predicted by our model, the importance of predicting spatial patterns – not sizes – of mosquito populations cannot be understated. It is visually evident by comparing Fig. 2(a) and Fig. 5 that our model accurately detects micro-regions with large *Ae. polynesiensis* populations. Spatial heterogeneity in animal populations arises from ensembles of complex mechanisms. Models with the capacity to incorporate spatial heterogeneity facilitate hypothesis testing that would be difficult to conduct empirically.

We hypothesise three reasons for over- and under-estimation of *Ae. polynesiensis* population sizes at some BGS traps (Fig. 6). First, BG-Lures used by BGS traps could facilitate large trap counts in areas with few oviposition sites (i.e. traps T01 and T04) by attracting host-seeking mosquitoes from nearby high-density areas. Second, landscape features may offer additional oviposition sites heterogeneously distributed across *motu* Tautau. For example, coconut husks chewed by rats or split in half and bromeliad phytotelmata were widely present in certain areas of *motu* Tautau, both of which are known breeding sites for *Ae. polynesiensis* among other mosquito species [84–86].

Third, errors in the prediction of *C. carnifex* burrow density may have influenced model estimates. Random forests cannot exploit trends in the data to predict outside of their training set, as they do not fit relationships between variables. Many implementations of random forests smooth the estimated response surface by averaging across trees [87]. When field data recorded ≤5 burrows/100 m^2, all random forest errors were positive (overestimation). At >5 burrows/100 m^2, all errors were negative (underestimation). The errors were also larger at the tails of the distribution of field data. The distribution of prediction errors is shown in Supplementary Material S.7. Larger datasets may fare better at capturing tail ends of the distribution.

A discrepancy between the observed and predicted gender distribution should also be noted. 3.7% of trapped mosquitoes were male. Our model predicted between 30%–36% of mosquitoes to be male. This may have occurred because (i) differences in life history traits between females and males may be larger than suggested by the empirical literature, (ii) the gender emergence ratio of pupae may not be 1:1, or (iii) the trapping protocol may be biased towards trapping female mosquitoes. BGS traps have been observed to have a higher recapture
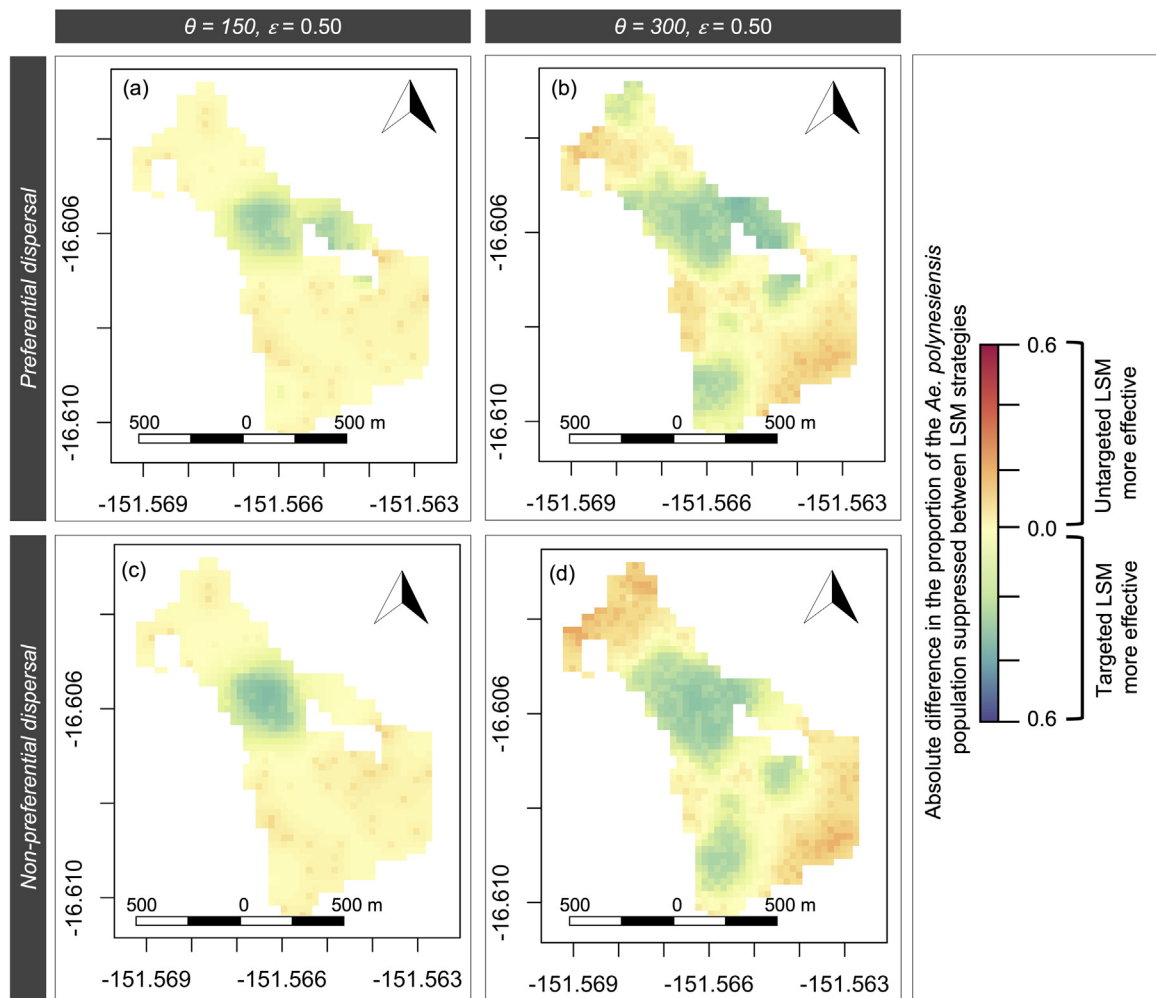
Fig. 8. The absolute difference between larval source management (LSM) strategies in the proportion of the *Ae. polynesiensis* population suppressed. Results are displayed for preferential dispersal (a)–(b) and non-preferential dispersal (c)–(d). Results are displayed for different values of LSM coverage in terms of the number of grid cells treated (θ) and LSM efficacy in terms of the proportion of *C. carnifex* burrows removed at treated grid cells (ε). Subfigures (a) and (c) display low coverage, medium efficacy LSM with $\theta = 50$ and $\varepsilon = 0.5$. Subfigures (b) and (d) display high coverage, medium efficacy LSM with $\theta = 300$ and $\varepsilon = 0.5$. Orange/red colours indicate that untargeted LSM is more effective. Green/blue colours indicate that targeted LSM is more effective. Yellow indicates no substantial difference in the proportion of the population suppressed between LSM strategies.

rate of female as opposed to male *Ae. aegypti*, *Aedes albopictus* and *Cx. quinquefasciatus* [88,89]. Further empirical work is needed to clarify these considerations.

We note three main areas for future work. First, other mosquito dispersal behaviours – notably, host-seeking – are well documented and their inclusion would be a valuable contribution to our model [90–92]. Additional data on host distribution would be required for this to be possible. Second, the diameter of burrows as a proxy for burrow volume was not used to control intra-burrow density-dependent mortality, despite the linear relationship observed between the two. This was because the prediction errors of random forest regression for burrow diameter were unsuitably large (data not shown). In addition, absence of rainfall time-series data means that the stability of the relationship between burrow diameter and volume cannot be certain. Third, our model does not incorporate *C. carnifex* dynamics. However, Micheli et al. (1991) observed that *C. carnifex* and *Sesarma meinerti* burrow density remain relatively constant across time [33].

We have presented an integrative methodology to model mosquito dispersal in a heterogeneous environment driven by oviposition site availability. Our model has demonstrated that changes in the environment inhabited by mosquitoes, such as LSM, have non-linear and spatially heterogeneous effects on *Ae. polynesiensis*. Therefore, mosquito control strategies must carefully balance spatial and net effects. Further adaptation of the integrative methodological pipeline we have

presented could facilitate model application at larger spatial scales and for additional sources of environmental heterogeneity.

CRediT authorship contribution statement

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Disclaimer

The findings and conclusion of this paper are those of the authors and do not necessarily represent the official position of Institut Louis Malardé or the University of Oxford.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.mbs.2022.108811.

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