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Exploring the impact of temperature on the efficacy of replacing a wild Aedes aegypti population by a Wolbachia-carrying one

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ABSTRACT

A non-autonomous time-delayed differential system, with time-varying delay, is proposed to reproduce the competitive dynamics of *Wolbachia*-infected and non-infected mosquito populations in several scenarios that differ by daily environmental temperature, the bacterial strain carried by the mosquito, and the guidelines for release of infected mosquitoes. Both mosquito entomological parameters and infection traits depend on temperature, which *per se* depends on time. Therefore, inspired by the literature on insect populations, functional forms are proposed to describe the rates of birth, development, and survival (or mortality) of *Ae. aegypti* as a function of temperature, as well as the rate of *Wolbachia*-infection loss. Numerical results showed that: (i) multiple releases were more efficient than a single one, (ii) when the mosquito population is high is the best time to implement the release of infected mosquitoes, (iii) strains that produce both high levels of cytoplasmic incompatibility and maternal inheritance boost the efficacy of the technique, and (iv) high temperature can jeopardize the efficacy of the technique.

1. Introduction

The importance of abiotic and biotic factors to the spatio-temporal dynamics of insect populations has been explored globally in the contexts of epidemiology and agriculture. In epidemiology, due to the roles of such factors in vector-borne diseases [1]; and in agriculture, because of the economic impact of insect-pest damage to crops [2]. Among all factors, daily temperature and landscape features seem to be the main drivers of insect dynamics [3]. Therefore, mathematical, statistical, and computational models developed to reproduce insect dynamics must take into account these factors to be able to predict and explain the spatio-temporal patterns obtained from field and laboratory data [4].

Recently, a new symbiont that is attracting attention is *Wolbachia* bacteria in the *Aedes aegypti* (Linnaeus, 1762) mosquito. A *Wolbachia* infection is caused artificially by microinjection of the endosymbiont from another insect species into developing embryos of *Ae. aegypti*. The fitness cost of carrying an infection that increases the mosquito mortality rate and decreases the oviposition rate [5–7] is balanced by levels of maternal inheritance and cytoplasmic incompatibility that may give an advantage to the infected mosquito, depending on the density of bacteria in the mosquito germinal cells [8]. Therefore, once

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this transinfection is established, the release of *Wolbachia*-carrying mosquitoes, into an environment where a *Wolbachia*-free mosquito population is already established can suppress or replace the resident population, depending on the strain of the bacterium that causes the infection, and on the ratio of female to male infected-mosquitoes released [9,10]. This comprises an environment-friendly technique that can be used to diminish or to halt *Aedes*-borne arbovirus infections, especially Dengue, Chikungunya, and Zika [11,12].

Complete suppression of the wild population is not necessary to block transmission, since it depends on the ratio of vectors to humans [13], focusing on mosquito competence as a vector, which is not the case for *Wolbachia*-infected mosquitoes [14]. Overall, after a release of *Wolbachia*-infected mosquitoes, reduction of *Aedes*-borne arbovirus infections is observed, as a result of *Wolbachia* frequency effects (such as disease blockage) and of decreases in the vector population size (negative fitness effects of *Wolbachia*-carrying and ongoing cytoplasmic incompatibility). The first field release of *Wolbachia*-carrying mosquitoes was done in 2011, in Cairns, Australia [15]. Since then, several other countries have joined the project (see World Mosquito Program, National Environment Agency, Institute For Medical Research, etc.).

As temperature may impact mosquito fitness and bacteria loss, addressing its effect on the prevalence of the bacteria under scenarios where infected and non-infected mosquitoes compete is crucial to guarantee the success of the technique of disease suppression through the release of *Wolbachia*-carrying mosquitoes [16–18]. Few mathematical models have discussed it [19–21], and none of them has explicitly incorporated the effect of temperature on mosquito dynamics and on infection traits. Here, we propose a non-autonomous time-delayed differential system, with time-varying delay, to simulate the competitive dynamics between *Wolbachia*-infected and non-infected mosquito populations in several scenarios differing by temperature, bacterial strain, and release guidelines. For this, different functional forms are used to characterize the rates of birth, development, and survival (or mortality) of *Ae. aegypti* as a function of temperature, as well as the rate of *Wolbachia*-infection loss. These functions together with the daily temperature are plugged into the proposed system, providing a framework to explore mosquito temporal dynamics under controlled scenarios.

2. Methods

A non-autonomous time-delayed differential system, with time-varying delay, is proposed to analyze the temporal dynamics of two *Ae. aegypti* populations, one *Wolbachia*-carrying and the other *Wolbachia*-free. It is a sex-structured population where X_i means female ($X = F$) or male ($X = M$) adult mosquito populations, not carrying ($i = u$) or carrying ($i = w$) the bacterium [19,20].

Both the mosquito entomological parameters and the infection traits depend on temperature (T), which *per se* depends on time (t). Therefore, we must take their temporal dynamics into account. The parameters are the survival of the immature phase S_i; the survival of the infection during the immature phase σ; the development time τ; the sex ratio r_i; the oviposition rate b_i; the mosquito mortality rates d_i and d_{ij} for the adult and immature phases, respectively; the cytoplasmic incompatibility strength q; the maternal inheritance ξ; the rate of *Wolbachia*-infection loss θ and θ_j for adults and immatures, respectively; the carrying capacity η; and the mating competitive advantage ϵ. All model parameters are positive. Besides, while S_i, σ, and τ are driven by a differential system, the others are given directly as functions of time.

At each time t, the wild female population $F_u(t)$ increases through oviposition of infected females $F_w(t-\tau(t))$ and non-infected females $F_u(t-\tau(t))$ that lay eggs at $t-\tau(t)$ at *per-capita* rates of $b_w(T(t-\tau(t))$ and $b_u(T(t-\tau(t))$, respectively. In both cases, the function $\phi(T(t-\tau(t)))$ takes into account the competition between the two populations that modulates these rates. The sex ratio is taken into account by counting the contribution of each proportion of eggs (coming through infected, r_w, and non-infected r_u, females) to the $F_u(t)$ compartment. Because of cytoplasmic incompatibility (q), the term $1-q\nu(t-\tau(t))$ takes into account all viable eggs produced by mating of wild (non-infected) females and infected males, where $\nu(t-\tau(t))$ is the probability of mating with an infected mosquito. As an infected female can produce viable eggs after mating with both populations of males (infected and non-infected one), the term $1-q\nu(t-\tau(t))$ does not multiply $F_w(t-\tau(t))$. On the other hand, a contribution from the infected female to the uninfected female compartment can only happen if one of two situations occurs: (i) vertical transmission of the infection does not occur $(1-\xi)$ or (ii) vertical transmission occurs but the infection is lost during the immature phase $\xi(1-\sigma(t))$. Combining these two possibilities, the contribution of the infected female population $F_w(t-\tau(t))$ to the non-infected female compartment is multiplied by $(1-\xi\sigma(t))$.

Finally, $S_u(t)$ and $S_w(t)$ take into account the survival of uninfected and infected individuals during their immature phase. Infected adult mosquitoes can lose their infection due to temperature, thus the term $\theta(T(t))F_w(t)$ measures the number of individuals that move from the infected female compartment to the non-infected female one. Finally, natural mortality decreases the wild population by a factor of $d_u(T(t))F_u(t)$. Therefore, the derivative of $F_u(t)$ is given by $r_u(1-q\nu(t-\tau(t)))b_u(T(t-\tau(t)))F_u(t-\tau(t))S_u(t)\phi(T(t-\tau(t))) + (1-\xi\sigma(t))r_w b_w(T(t-\tau(t)))F_w(t-\tau(t))S_w(t)\phi(T(t-\tau(t))) + \theta(T(t))F_w(t) - d_u(T(t))F_u(t)$. Following these assumptions, the equations of the other populations can be easily obtained:

$$\begin{aligned}\frac{dF_u(t)}{dt} &= r_u(1-q\nu(t-\tau(t)))b_u(T(t-\tau(t)))F_u(t-\tau(t))S_u(t)\phi(T(t-\tau(t)))\\ &\quad + (1-\xi\sigma(t))r_w b_w(T(t-\tau(t)))F_w(t-\tau(t))S_w(t)\phi(T(t-\tau(t)))\\ &\quad - d_u(T(t))F_u(t) + \theta(T(t))F_w(t),\end{aligned}$$

Table 1
Parameters of the mathematical model, their meaning, and units. The indices u, w, and J are related to uninfected, infected with *Wolbachia*, and immature (juvenile) phase, respectively.

Notation	Meaning	Units
ξ	maternal inheritance	-
τ	development time	days
q	cytoplasmic incompatibility	-
η	carrying capacity	individual^{-1}
r_u, r_w	sex ratios	-
b_u, b_w	birth rates	days^{-1}
θ, θ_J	rates of *Wolbachia* infection loss	days^{-1}
d_u, d_w, d_{uJ}, d_{wJ}	rates of mortality	days^{-1}
ϵ	mating competitive advantage	-

$$
\begin{aligned}
\frac{dM_u(t)}{dt} &= (1-r_u)(1-q\nu(t-\tau(t)))b_u(T(t-\tau(t)))F_u(t-\tau(t))S_u(t)\phi(T(t-\tau(t))) \\
&\quad + (1-r_w)(1-\xi\sigma(t))b_w(T(t-\tau(t)))F_w(t-\tau(t))S_w(t)\phi(T(t-\tau(t))) \\
&\quad - d_u(T(t))M_u(t) + \theta(T(t))M_w(t), \\
\frac{dF_w(t)}{dt} &= r_w\xi\sigma(t)b_w(T(t-\tau))F_w(t-\tau(t))S_w(t)\phi(T(t-\tau(t))) \\
&\quad - (\theta(T(t)) + d_w(T(t)))F_w(t), \\
\frac{dM_w(t)}{dt} &= (1-r_w)\xi\sigma(t)b_w(T(t-\tau(t)))F_w(t-\tau(t))S_w(t)\phi(T(t-\tau(t))) \\
&\quad - (\theta(T(t)) + d_w(T(t)))M_w(t),
\end{aligned} \tag{1}
$$

where

$$\phi(T(t-\tau(t))) = e^{-\eta(T(t-\tau(t)))(F_u(t-\tau(t))+F_w(t-\tau(t)))},$$

and

$$\nu(t-\tau(t)) = \frac{M_w(t-\tau(t))}{\epsilon M_u(t-\tau(t)) + M_w(t-\tau(t))},$$

represent the competition among female mosquitoes for oviposition sites [22], and the probability of mating an infected male, respectively.

We followed the approach described in [23,24] to model the dependence of S_u, S_w, σ, and τ on temperature T. First, the ratio $m(T(t))/m(T(t-\tau(t))$ determines how temperature affects individual growth. The function $m(\cdot)$ is chosen based on the mosquito growth (from egg to adult) as a function of temperature, which is measured in laboratory experiments. Therefore, the mosquito development time $\tau(t)$ can be obtained by solving the ordinary differential equation given by $d\tau(t)/dt = 1 - m(T(t))/m(T(t-\tau(t)))$. Besides, the derivative of the survival functions, for example $S_u(t)$, is given by $S_u(t)\left[\frac{m(T(t))d_{uJ}(T(t-\tau(t)))}{m(T(t-\tau(t)))} - d_{uJ}(T(t))\right]$ (see [24] for the detailed derivation of these equations). Observe that, if temperature does not affect growth, $d\tau(t)/dt = 0$, i.e., τ is constant; which also implies that $S_u = e^{-\tau d_{uj}}$, $S_w = e^{-\tau d_{wj}}$, and $\sigma = e^{-\tau\theta_j}$ are constant. Therefore, the general case is given by

$$
\begin{aligned}
\frac{dS_u(t)}{dt} &= S_u(t)\left[\frac{m(T(t))d_{uJ}(T(t-\tau(t)))}{m(T(t-\tau(t)))} - d_{uJ}(T(t))\right], \\
\frac{dS_w(t)}{dt} &= S_w(t)\left[\frac{m(T(t))d_{wJ}(T(t-\tau(t)))}{m(T(t-\tau(t)))} - d_{wJ}(T(t))\right], \\
\frac{d\sigma(t)}{dt} &= \sigma(t)\left[\frac{m(T(t))\theta_J(T(t-\tau(t)))}{m(T(t-\tau(t)))} - \theta_J(T(t))\right], \\
\frac{d\tau(t)}{dt} &= 1 - \frac{m(T(t))}{m(T(t-\tau(t)))}.
\end{aligned} \tag{2}
$$

Observe that (1) is the non-autonomous time-delayed differential system, with time-varying delay, that models the mosquito populations; and (2) is the system that drives temperature-dependent parameters.

Table 1 lists the model parameters, their meaning, and units. In particular, the parameters $q,\ \xi \in [0,1]$ can increase the fitness of the *Wolbachia*-carrying mosquito; if $q = 1$, only mating between *Wolbachia*-free mosquitoes result in viable non-infected offspring; while for $q = 0$ the infection does not confer any reproductive advantage to the infected population. Furthermore, for $\xi = 1$, all offspring from an infected mosquito are also infected, while for $\xi = 0$, the infection is not transmitted from the *Wolbachia*-infected mosquito to its offspring.

The total of the non-infected (not carrying the bacterium) and *Wolbachia*-infected (carrying the bacterium) populations is given by

$$N_u(t) = F_u(t) + M_u(t) \quad \text{and} \quad N_w(t) = F_w(t) + M_w(t),$$

and, if r_u and r_w are constant, we can rewrite System (1) as

$$\begin{aligned}
\frac{dN_u(t)}{dt} &= r_u(1 - q\nu(t-\tau(t)))b_u(T(t-\tau(t)))N_u(t-\tau(t))S_u(t)\phi(T(t-\tau(t))) \\
&\quad + (1-\xi\sigma(t))r_w b_w(T(t-\tau(t)))N_w(t-\tau(t))S_w(t)\phi(T(t-\tau(t))) \\
&\quad - d_u(T(t))N_u(t) + \theta(T(t))N_w(t), \\
\frac{dN_w(t)}{dt} &= r_w\xi\sigma(t)b_w(T(t-\tau(t)))N_w(t-\tau(t))S_w(t)\phi(T(t-\tau(t))) \\
&\quad - (\theta(T(t)) + d_w(T(t)))N_w(t),
\end{aligned} \tag{3}$$

with

$$\phi(T(t-\tau(t))) = e^{-\eta(T(t-\tau(t)))(r_u N_u(t-\tau(t)) + r_w N_w(t-\tau(t)))},$$

and

$$\nu(t-\tau(t)) = \frac{(1-r_w)N_w(t-\tau(t))}{\epsilon(1-r_u)N_u(t-\tau(t)) + (1-r_w)N_w(t-\tau(t))}.$$

If we assume that (i) $T := T(t) = T(t-\tau(t))$, i.e., the temperature is constant; (ii) $\nu := \nu(t-\tau(t))$, i.e., the probability of mating an infected mosquito is constant; and (iii) $r := r_u = r_w$, i.e., the infection does not alter the sex ratio of the infected-population, we recover the scenario already studied in [19,20].

3. Results

3.1. Mosquito entomological parameters, infection traits, and temperature

The use of analytical models to describe the temperature-dependent response of life-history traits of insect species may help to elucidate their behavior in thermally variable environments. Following this approach, different functional forms are used to describe the rates of birth, development, and mortality (or survival) of *Ae. aegypti* mosquito populations as a function of temperature. These functions, plus the daily temperature, are plugged into Systems (2) and (3) to understand the temporal evolution of both, uninfected and infected, mosquito populations.

The per capita birth rates $b_u(T)$ and $b_w(T)$ are assumed to follow symmetric and unimodal responses to the temperature which are well described by a Gaussian function [23,25–27],

$$H(T) = \overline{H}e^{-\frac{(T-T_P)^2}{2\sigma_P^2}} \tag{4}$$

where $H(T) \in \{b_u(T), b_w(T)\}$ is the trait's value at temperature T (in K); $\overline{H} \in \{\bar{b}_u, \bar{b}_w\}$ is the maximum value attained by $H(T)$ at an optimal temperature of T_P; and σ_P is the variability of the trait's value about its optimum.

The mortality rates of the juvenile and adult stages F ($F \in \{d_{uJ}, d_{wJ}, d_u, d_w\}$) increase for low and high temperatures, following polynomial curves of degree two

$$F(T) = a_F T^2 + b_F T + c_F \tag{5}$$

where a_F, b_F and c_F are model parameters. In the simulations, we assume that $d_J := d_{uJ} = d_{wJ}$. Similarly, for the egg stage, the survival function is given by

$$S(T) = -a_E T^2 + b_E T + c_E \tag{6}$$

where a_E, b_E, and c_E are model parameters.

It will be assumed that the rates of bacteria-infection loss θ_J and θ exhibit a monotonic temperature response that is well described by the BoltzmannArrhenius function [28],

$$G(T) = \overline{G}e^{A_D\left(\frac{1}{T_l} - \frac{1}{T}\right)} \tag{7}$$

where $G(T) \in \{\theta_J(T), \theta(T)\}$ is the trait's value at temperature T (in K), $\overline{G} \in \{\bar{\theta}_J, \bar{\theta}\}$ is the trait value at a reference temperature of T_l (in K), and A_D is the Arrhenius constant. In fact, the effect of temperature on *Wolbachia* features such as cytoplasmic incompatibility, maternal inheritance, and pathogen blocking depends on the strain, and is not clear. Some studies have shown a recovery of *Wolbachia* density inside mosquito cells after the heat stress has ceased [29]. Additionally, the instability of the infection at high temperatures is mosquito stage dependent [30].

Table 2
Parameters appearing in the mathematical Equations (4)-(8). The indices u, w, J, and E are related to uninfected, infected with *Wolbachia*, juvenile, and egg phase, respectively.

Notation	Meaning	Values and Units	Equation
$\bar{b}_u$	maximum u birth rate	9.52 days^{-1}	(4)
$\bar{b}_w$	maximum w birth rate	9.00 days^{-1}	(4)
T_P	optimal temperature	301.15 K (28.55°C)	(4)
σ_P	variability	4.88 K	(4)
$a_{d_u}, b_{d_u}, c_{d_u}$	adult u mortality	2.67×10^{-4}, −0.16, 23.73	(5)
$a_{d_w}, b_{d_w}, c_{d_w}$	adult w mortality	2.67×10^{-4}, −0.16, 23.74	(5)
$a_{d_j}, b_{d_j}, c_{d_j}$	juvenile mortality	9.44×10^{-4}, −0.56, 83.36	(5)
a_E, b_E, c_E	eggs survive	-3.50×10^{-3}, 2.07, −306.27	(6)
$\bar{\theta}_J$	juvenile infection loss	0.007 days^{-1}	(7)
$\bar{\theta}$	adult infection loss	0.003 days^{-1}	(7)
T_I	reference temperature	298.15 K (25°C)	(7)
A_D	activation energy	10^4cal×mol^{-1}	(7)
$\overline{m}$	development rate	0.74 days^{-1}	(8)
A_M	activation energy	9.43×10^3cal×mol^{-1}	(8)
A_L	activation energy	1.07×10^4 cal × mol^{-1}	(8)
A_H	activation energy	15.93×10^4 cal × mol^{-1}	(8)
T_R	reference temperature	317.2 K (44.05°C)	(8)
$T_{H/2}$	enthalpy changes	309.8 K (36.65°C)	(8)
$T_{L/2}$	enthalpy changes	315.0 K (41.85°C)	(8)

Finally, the mean development rate exhibits a left-skewed temperature response that results from a reduction in reaction rates (single rate-controlling enzyme reaction) at temperature extremes due to enzyme inactivation, which is well described by [31],

$$m(T) = \frac{\left(\overline{m}\frac{T}{T_R}\right)e^{A_M\left(\frac{1}{T_R}-\frac{1}{T}\right)}}{1+e^{A_L\left(\frac{1}{T_{L/2}}-\frac{1}{T}\right)}+e^{A_H\left(\frac{1}{T_{H/2}}-\frac{1}{T}\right)}} \tag{8}$$

where $\overline{m}$ is the development rate at the reference temperature T_R, at which the enzyme is 100% active; A_M (enthalpy of activation divided by the universal gas constant $R = 1.987$ cal × K^{-1} × mol^{-1}) quantifies temperature sensitivity; $T_{L/2}$ and $T_{H/2}$ are, respectively, the low and high temperatures at which the enzyme is 50% active; and A_L and A_H are the enthalpy changes associated with low and high-temperature enzyme inactivation divided by R.

Table 2 lists the parameter values used in Equations (4)-(8), and Fig. 1 shows the behavior of each parameter as a function of temperature. The data displayed in Fig. 1 were extracted from [32–34] and used to parametrize the model. The fitting curves, seen in red, were obtained by using the function nls in the R package nlstools [35]. The blue curves were drawn assuming that the infection impacts the rates of oviposition ($b_w(T) < b_u(T)$) and adult mortality ($d_w(T) > d_u(T)$). In each case, the fitting curves were redrawn with the new parameters.

3.2. Silico

experiments To understand the impact of temperature on the dynamics of both mosquito populations (non-infected and infected), we ran several scenarios that differed by: (i) the number of times that the same number of *Wolbachia*-carrying mosquitoes is released, (ii) the period of the year when the mosquitoes are released, (iii) the mean temperature in the target area, and (iv) the strain of bacteria used during the release. The simulations were run using the function `ddesd` of the software `MATLAB`. Table 2 lists the baseline parameter values used in the simulations. The other parameters are $q = 0.95$, $\xi = 0.99$, $r_u = r_w = 0.5$, $\epsilon = 1$, and $\eta = 0.02$ individuals^{-1}.

Assuming a periodic variation of temperature over a year, the temperature as a function of time t is given by

$$T(t) = T_M - \sigma_T \cos\left(\frac{2\pi t}{365}\right), \tag{9}$$

where T_M and σ_T are the mean temperature and its standard deviation. The initial condition is $N_u(t) = 200 + 200\left|\cos\left(t+\frac{\pi}{2}\right)\right|$, and $N_w(t) = 0$, for $t \in [-\tau, 0]$, $S_u(0) = e^{-\tau(0)d_{uJ}(T(0))}$, $S_w(0) = e^{-\tau(0)d_{wJ}(T(0))}$, and $\sigma(0) = e^{-\tau(0)\bar{\theta}_J(T(0))}$ with $\tau(0) = m(T(0))^{-1}$ where $m(\cdot)$ is given by Equation (8).

3.2.1. Mosquito release strategy

Fig. 2 shows how temperature varies over time and the dynamics of the non-infected mosquito population under the temperature variations. Both curves show periodic oscillations. For the temperature dynamics, the period of oscillation is 365 days. On the other hand, for the mosquito population, the period of oscillation depends on the interaction among

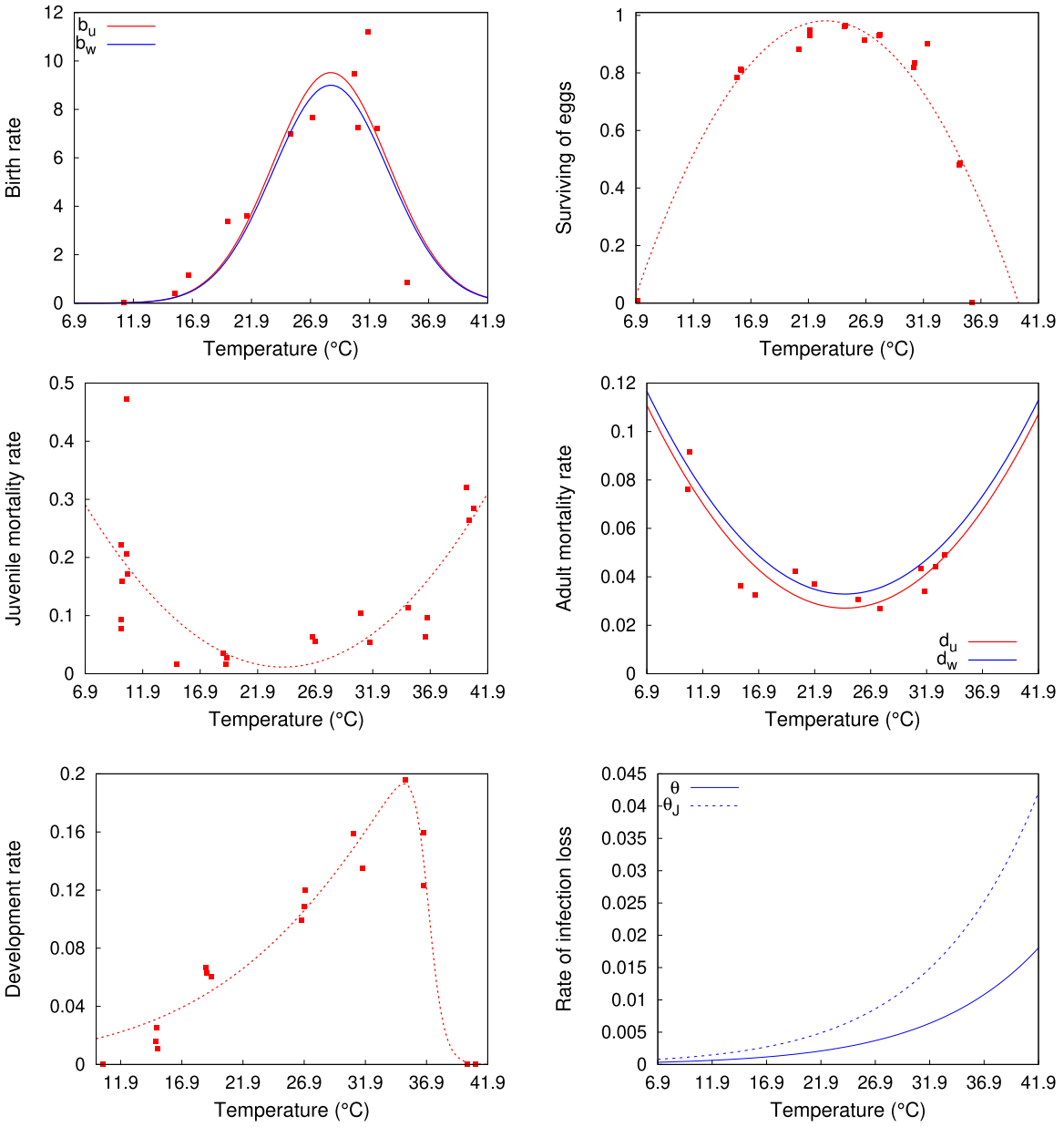


Fig. 1. Trait behavior of mosquito entomological parameters, and of *Wolbachia*-infection as a function of temperature. In red for the non-infected mosquito and in blue for the infected one. Dashed lines are for the immature phase, and continuous lines are for the adult phase. The data, showed as dotted in red, were extracted from [32–34] and the red curves fitted to it using Equations (4)-(8). The Figures are plotted in degrees Celsius for easy interpretation, but the fittings were done using the temperature in Kelvin. Table 2 shows the obtained parameters values.

several factors that affect its dynamics. From this figure, favorable and unfavorable periods for the mosquito population, at which it reach high or low levels, respectively, can be distinguished. This raises the following questions: what is the best period of the year to release *Wolbachia*-carrying mosquitoes in order to maximize *Wolbachia* prevalence? Besides, what is more effective, single or multiple *Wolbachia*-infected mosquito introductions?

Fig. 3 shows the temporal evolution of both non-infected and infected mosquito populations when a fixed number of 3×10^3 *Wolbachia*-carrying mosquitoes are released. Four scenarios can be seen: (i) one release during the period when the wild mosquito population is low, (ii) one release during the period when the wild mosquito population is high, (iii) four releases during the period when the wild mosquito population is low, and (iv) four releases during the period when the wild mosquito population is high. In all scenarios, the non-infected population behaved in a stable oscillatory pattern prior to the introduction of the infected mosquitoes, and their release led to a decrease in the wild population. When four

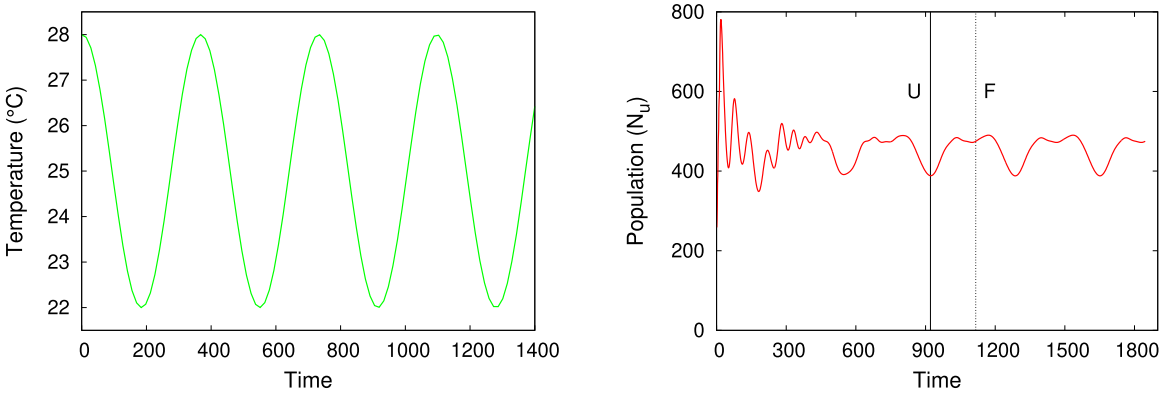


Fig. 2. On the left panel, the temporal behavior of the temperature (Equation (9), $T(t) = 25 - 3\cos(2\pi(t + 184)/365)$); on the right panel, the dynamics of the wild mosquito population over the influence of temperature. The two vertical dashed lines highlight the favorable (F) and unfavorable (U) periods for mosquito proliferation. The time is measured in days.

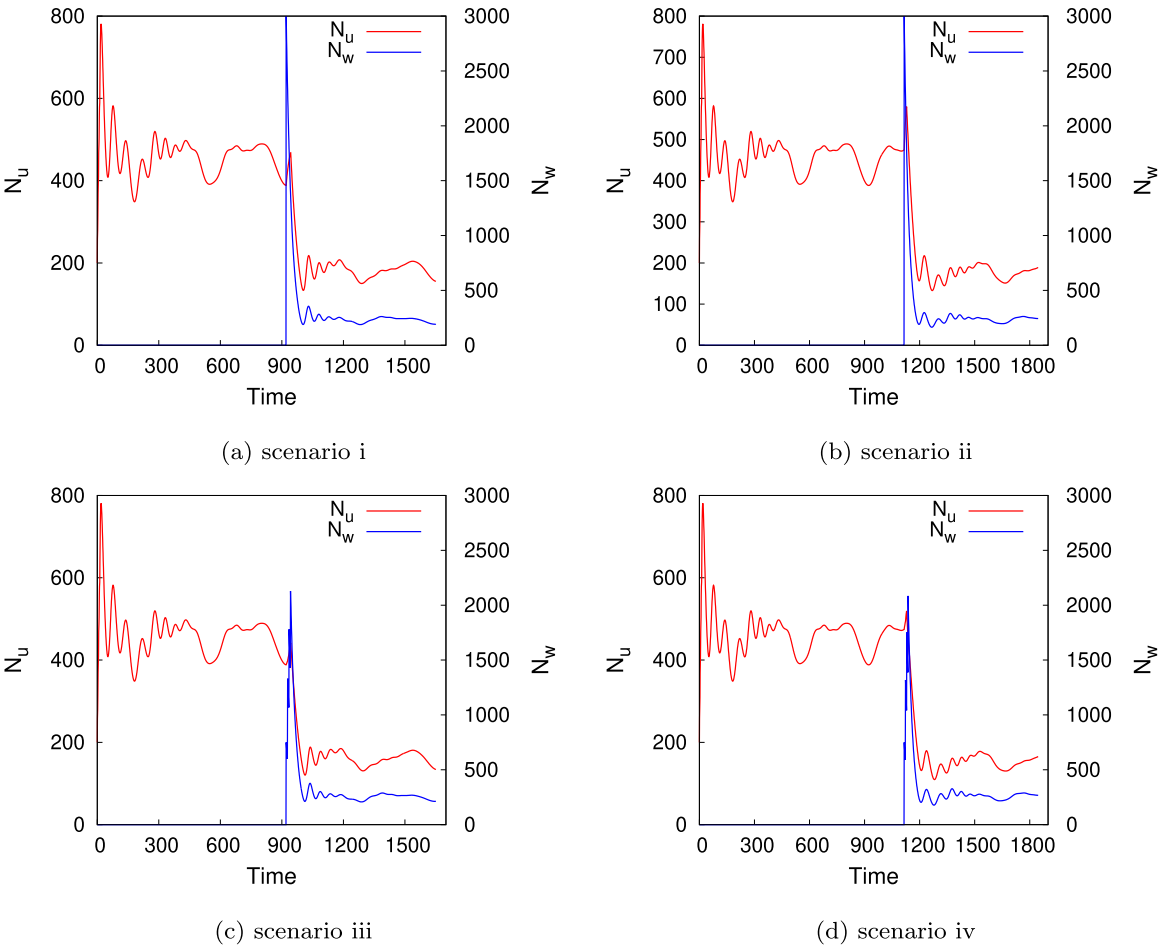


Fig. 3. Temporal evolution of non-infected (N_u) and *Wolbachia* infected (N_w) mosquito populations. Both populations are affected by the daily temperature behavior shown in Fig. 2. A total of 3×10^3 *Wolbachia*-carrying mosquitoes (blue lines) were released. The release was performed during two periods of the year, favorable (scenario ii and iv) and unfavorable (scenario i and iii) for mosquito population: one release of 3×10^3 (scenario i and ii) or four releases (scenario iii and iv) of 750 individuals every 7 days were performed.

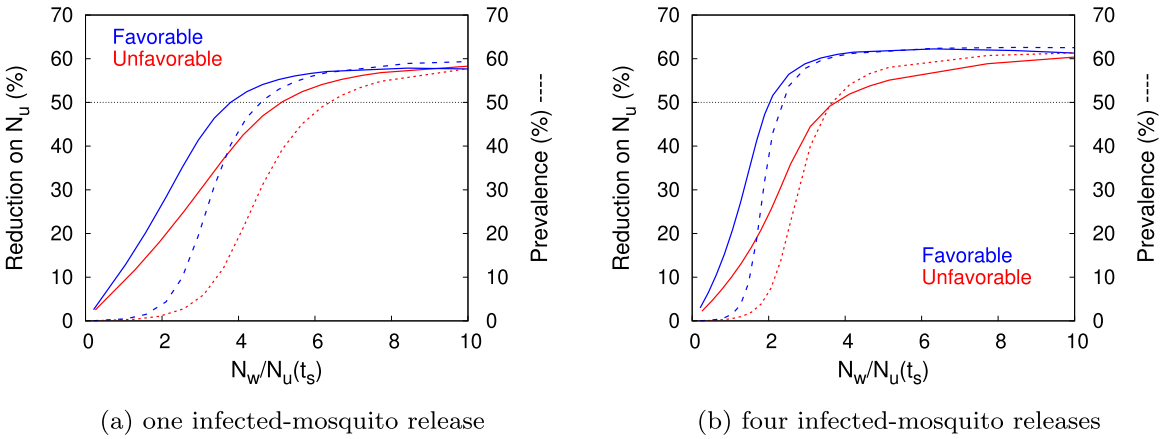


Fig. 4. On the left, we have one release, and on the right, four releases of infected mosquitoes. The temperature profile is the same as described in Fig. 2. The four curves, at each panel, were obtained by varying the ratio of infected to wild populations at the time of the first *Wolbachia*-infected mosquito release. One and four infected-mosquito releases were done during favorable and unfavorable periods. The continuous lines show the reduction on N_u, and the dashed lines the prevalence of the infection.

releases were made, the total number of individuals released every seven days was equal, i.e., 750. Remember that without *Wolbachia*-carrying mosquitoes released, the wild mosquito population follows the dynamics observed in Fig. 2.

In order to measure the efficacy of the technique of releasing *Wolbachia*-carrying mosquitoes to suppress or diminish the wild population, we define

$$E_k = 1 - \frac{I_c}{I_0} \quad \text{with} \quad I_j = \int_{t_i}^{t_f} N_u(t)\ dt,$$

where I_j with $j \in \{0, c\}$ measures the cumulative number of non-infected mosquitoes observed between t_i and t_f. In particular, I_c takes into account the number of non-infected mosquitoes that persist after the release of *Wolbachia*-carrying mosquito, and I_0 is the number of non-infected mosquitoes in a scenario where the release does not occur. Therefore, E_k measures the reduction in the wild population due to the introduction of the invasive (infected with a *Wolbachia* strain) mosquitoes. The indices k distinguish the different scenarios. In the four scenarios shown in Fig. 3, $t_i = t_s$ (t_s is the time when the first release is performed) and $t_f = t_s + 730$ (t_f is two years after the first release), and the values obtained for E_k are: (i) $E_1 = 56.8\%$, (ii) $E_2 = 57.1\%$, (iii) $E_3 = 61.3\%$, and (iv) $E_4 = 62.3\%$. Observe that the value of this index depends on the time at which it is measured. The mean prevalences (and the minimum and maximum values) of the infection in each scenario are: (i) 57.9% (54%-89%), (ii) 58.3% (55%-86%), (iii) 62.9% (59%-83%), and (iv) 64.1% (55%-82%). Moreover, the mean prevalences during the last 30 days in each experiment are 55%, 57%, 61%, and 62%. Remember that infection prevalence is measured as

$$P = \frac{N_w}{N_w + N_u}.$$

Fig. 4 shows, for the four scenarios, how the ratio of infected (N_w) to non-infected (N_u) mosquitoes at the time of the release (t_s) affects the efficacy of the technique. In all cases, the curves have a sigmoid shape, and the efficacy, given by the continuous lines, does not achieve 70%. The efficacy value of 50% is highlighted in each panel. For the strategy of a single release, to achieve 50% efficacy, the number of infected mosquitoes released must be at least five times the number of non-infected ones, if the release is done during the period of the year when the population is lower. On the other hand, if it is done during the period when the population is higher, the number of infected mosquitoes released must be at least four times the number of non-infected ones. In the case of four releases, if the release is done during the unfavorable period, the number of infected mosquitoes released must be four times the number of non-infected ones to achieve 50% of efficacy; and if it is done during the favorable period the number of infected mosquitoes released must be two times the number of non-infected ones. For one and four releases, a significant value of efficacy can be seen when $N_w/N_u(t_s)$ is smaller than one, and the mean prevalence of infection measured over the last 30 days (see dashed lines) is almost zero. In both cases, an asymptotic value of 60% for the prevalence is observed, which is achieved before four releases are conducted.

Fig. 5 shows how the mean temperature impacts the dynamics of both populations. In all cases, a total of 3×10^3 mosquitoes were released in four batches of the same size during the favorable period for the mosquito population. Panels (a), (b), (c), and (d) were composed following the mosquito dynamics at the temperatures of 18, 22, 28, and 32°C, respectively (with a standard deviation of 3°C). The dotted lines show the mosquito dynamics without a control, where control means the replacement or suppression of the wild population by the *Wolbachia*-carrying one. From these figures, we can infer that the optimum temperature for the wild mosquitoes is around 28 °C; at this temperature, the wild mosquito population can achieve high levels year-round. Control efficacy was measured as in Fig. 4. From left to right, and top to bottom,

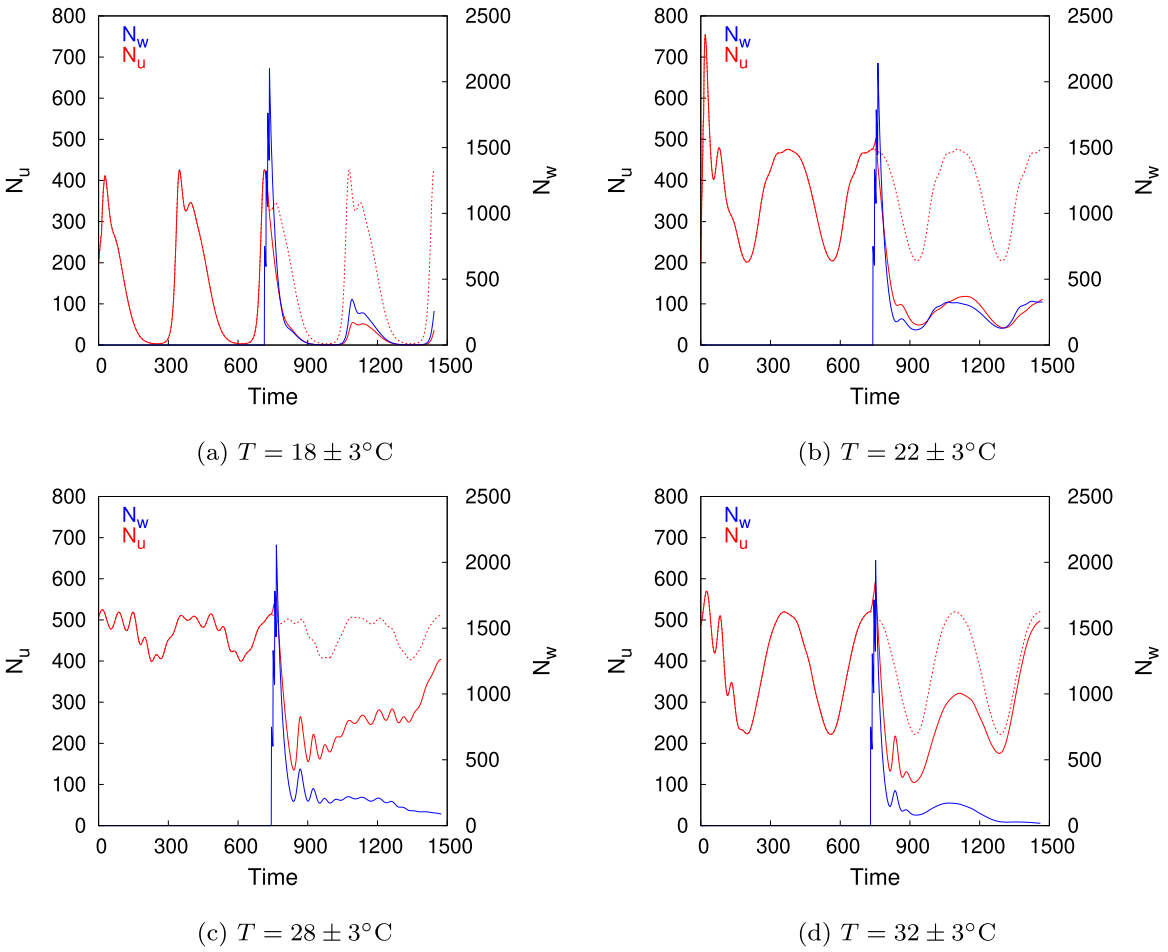


Fig. 5. Temporal evolution of both mosquito populations before (dashed lines) and after the release of *Wolbachia*-carrying mosquitoes (continuous lines). In red, is shown the dynamic of the non-infected mosquito population, and in blue is shown the dynamic of the infected one. Each panel has considered a scenario of daily temperature as described on the label.

the efficacy (prevalence) was 71.5% (87.3%), 70.3% (75.4%), 43.3% (19.1%), and 30.7% (3.9%). In the last two panels, although an efficacy higher than 30% was obtained, the infected mosquito population could not persist in the long term.

3.2.2. Infection traits impacted by temperature

Fig. 6 shows that the ratio of infected to non-infected mosquitoes necessary to achieve 50% efficacy increases as the temperature increases, until reaching 27 °C. After that, the efficacy is less than 50%, and the figure shows the minimum number of $N_w/N_u(t_s)$ to achieve the maximum efficacy. Remember that the mosquito-infected release strategy is the same as in Fig. 5. In general, extreme temperatures - low or high - cause a decrease in the mosquito populations, while intermediate temperatures allow an increase in the mosquito population. The increase in temperature affects the fitness of the infected mosquitoes more than the non-infected ones. Besides, a temperature increase also increases the infection loss rate. Therefore, to maintain the same efficacy, the ratio of infected to non-infected mosquitoes at the time of release must increase as the temperature increases. Differently from the observed non-linear increase in the ratio of infected to non-infected mosquitoes, the prevalence seems to decrease linearly as the temperature increases.

3.2.3. The effect of the bacteria strain

The parameters related to the infection, ξ and q, were studied in a scenario of daily temperature variation. Each pair (ξ, q) represents a unique strain. As an example, the mean daily temperature data in Niterói, Rio de Janeiro, Brazil from 2020 to 2022 was used. Missing data were predicted to be the means observed in the last three years. Importantly, the temperature data displayed here were collected from meteorological stations (National Institute of Meteorology) and may not reflect the temperature that the mosquito, especially in the aquatic phase, feels. The microclimatic conditions at breeding and resting locations can be affected by direct exposure to the sun, by the amount of water in the breeding habitats, etc [36].

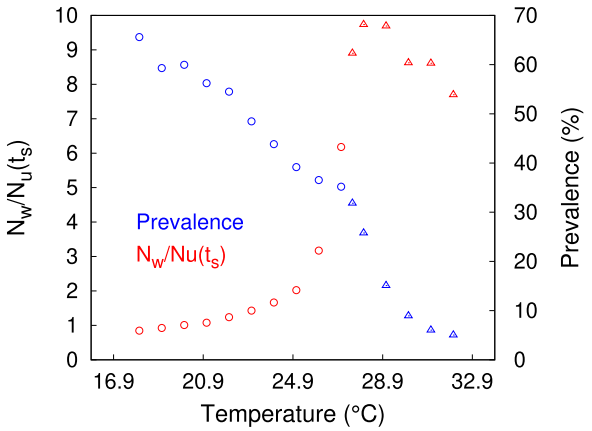


Fig. 6. The ratio of infected to non-infected mosquito population (in red) and the prevalence of infection (in blue) as a function of temperature. The ratio $N_w/N_u(t_s)$ corresponds to a reduction of 50% (in $\odot$), and of $< 50\%$ (in $\triangle$) on N_u population. The prevalence is measured during the last thirty days of simulation.

Fig. 7 shows the daily temperature data and the dynamics of both non-infected and infected mosquito populations. Four releases were done (a total of 3×10^4 infected mosquitoes) at 7-day intervals, starting at day 100. The difference between panels (c) and (d) consists of the bacteria strain used during the release. Here, the question to be addressed is: how does the chosen strain impact the efficacy of the technique? The assumption is that only the traits related to maternal inheritance and cytoplasmic incompatibility vary among strains. Observe that both strains are able to suppress the wild population for some period, but the strain with parameter values $\xi = 0.99$ and $q = 0.95$ was more efficient in reducing the wild population and persisted longer.

Fig. 8 shows the dependence of the efficacy of the *Wolbachia*-carrying mosquito release technique to suppress the wild population as a function of the mosquito's infection parameters q and ξ, which depend on the bacteria strain used to infect the mosquito. As expected, the increase in ξ leads to an increase in efficacy. Moreover, for a fixed value of ξ, the efficacy increases as q increases.

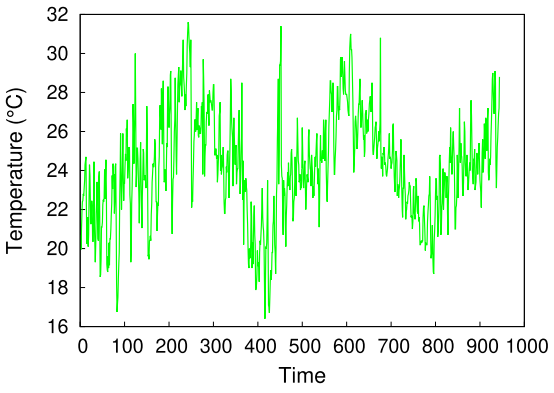
Finally, Fig. 9 shows the dependence of the prevalence of the infection as a function of the same parameters. High values of q and ξ are able to maintain the infection in the population for longer periods of time; on the other hand, lower values require new introductions of *Wolbachia*-infected mosquitoes in order to mantain the prevalence of the infection so that it blocks, for example, dengue virus transmission.

4. Discussion

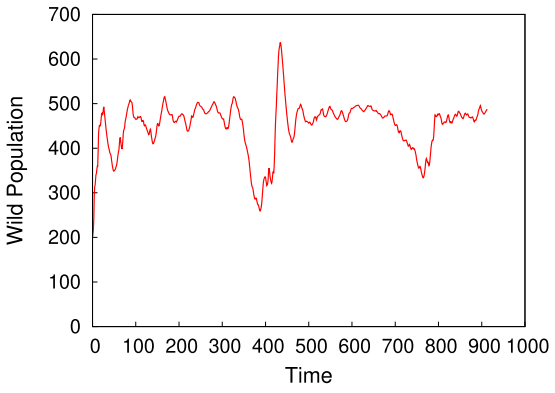
The technique of releasing *Wolbachia*-carrying mosquitoes to suppress or replace a wild mosquito population that, in the case of *Ae. aegypti*, does not naturally carry the infection has proven to be efficient in diminishing or blocking the transmission of dengue and other arboviruses around the world [10–12]. As this *Wolbachia*-carrying mosquito comprises a new symbiont, the establishment of the infection in the population of *Ae. aegypti* still suffers from a series of difficulties [37,38], such as (i) following the evolution of the host-symbiont interaction to monitor the feasibility of the technique; (ii) controlling the impact of cofactors, such as temperature, on bacteria density inside the mosquito's body; (iii) assessing the impact of carrying the bacteria on mosquito fitness; (iv) choosing a bacteria strain that promotes high virus blockage, etc. Here, we explore and discuss some of these issues.

We start from a fixed scenario of temperature variation, where we can identify favorable and unfavorable periods for mosquito proliferation (Fig. 2). Then we vary the number of releases and the starting time of release (Fig. 3). Supposing that a wild population is already established in the environment where release of *Wolbachia*-carrying mosquitoes will be conducted, and there are no constraints to prevent mating among individuals, the results show that the best period for releasing the infected mosquitoes, for the strategy of a single batch, is when the wild population is approximately at its maximum level, i.e., during the favorable period. Furthermore, multiple introductions separated by seven days were more efficient than a single introduction (Fig. 4), which is in accordance with [39].

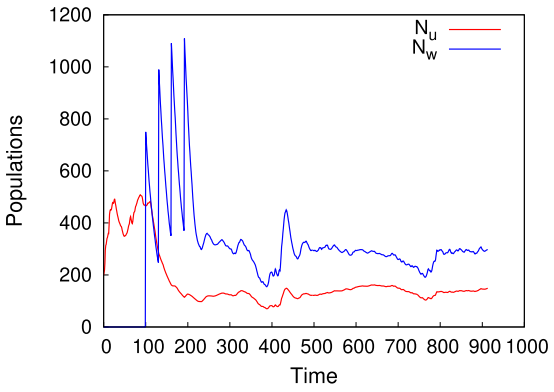
Currently, the releases of *Wolbachia*-carrying mosquitoes are augmentative, which involves mass rearing and periodic release following an inoculative seasonal basis. But the number of mosquitoes released, and the periodicity, depend on several decisions related, for example, to the cost-effectiveness of vector control, and the objective of the control: population replacement, population suppression or population replacement followed by suppression. This affects the selection of the bacterium strain, or accurate sex sorting. Besides, the number of *Wolbachia*-infected mosquitoes released depends on the native mosquito population density, and the size of the release area. Furthermore, landscape heterogeneity can impede mosquito dispersal, jeopardizing the control techniques [40,41].



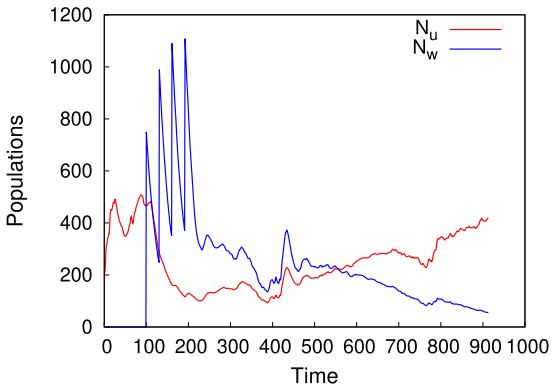
(a) From 2020 to 2022



(b) non-infected one



(c) $\xi = 0.99$ and $q = 0.95$



(d) $\xi = 0.99$ and $q = 0.8$

Fig. 7. In (a) temperature versus time, in (b) the temporal dynamics of the non-infected population, and in (c) and (d) the temporal dynamics of non-infected and infected populations for two different sets of parameters related to the infection's traits.

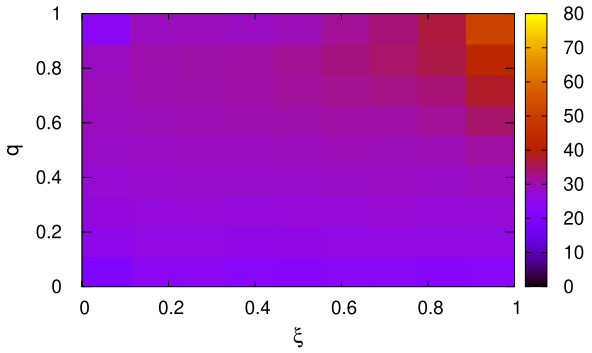


Fig. 8. Plot of $\xi \times q \times E$, respectively, the parameters that measure the maternal inheritance, the cytoplasmic incompatibility, and the efficacy of control. E is estimated by the reduction of wild mosquitoes during a set-up period of time, and it is shown in different colors. The scale of colors is shown on the right of the panel; cold to warm colors represent E from 0% to 80%.

Taking the best scenario, i.e., four releases of infected mosquitoes, separated by seven days, done during the favorable period for mosquito population, Fig 4 shows that increasing the ratio of infected mosquitoes to non-infected ones raises the efficacy. However, from Fig. 4(b) it is clear that increasing $N_w/N_u(t_s)$ above four raises the cost of the technique without significantly increasing its efficacy. Besides, the proportion of mosquitoes released to achieve $\geq 50\%$ efficacy depends on several parameters such as temperature, maternal inheritance, cytoplasmic incompatibility, etc. (Figs. 5 to 8). Overall, extreme temperatures affect both mosquito populations because they increase mosquito mortality and infection loss rates, and decrease oviposition, and development rates (Fig. 1). On the other hand, the increase on both maternal inheritance and cytoplasmic incompatibility correlates with the increase in the infection prevalence in the mosquito population, which impacts the trans-

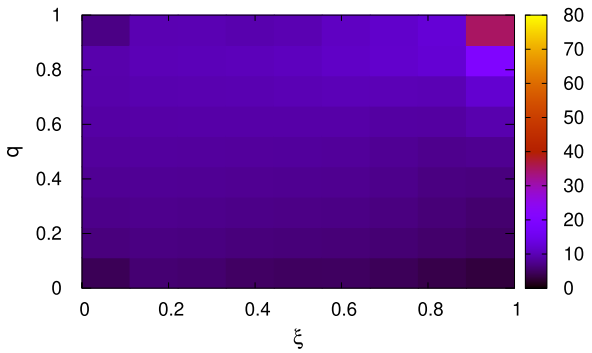


Fig. 9. Plot of $\xi \times q \times P$, respectively, the parameters that measure the maternal inheritance, the cytoplasmic incompatibility, and the prevalence of the infection. P is the ratio between the number of *Wolbachia*-carrying mosquitoes and the total mosquito population, and it is shown in different colors. The scale of colors is shown on the right of the panel; cold to warm colors represent P from 0% to 80%.

mission of diseases such as dengue by decreasing it (Figs. 8 and 9). When the infection traits are not optimized, as through a wrong choice of the bacterial strain, large numbers of mosquitoes, and probably multiple introductions are necessary to maintain a high incidence of infection over the long run.

In this context, different *Wolbachia* strains have been released in population replacement programs, with varying levels of success. We will highlight three strains: *w*AlbB, *w*MelPop, and *w*Mel. All of them have the key features related to the infection, which are cytoplasmic incompatibility, maternal transmission, and pathogen blocking. The strains differ in the ability to resist high temperatures, and in the fitness cost imposed by carrying the symbiont. In particular, *w*Mel is unstable in high temperatures, and therefore a reduction of infection features is expected in tropical ambient temperatures, which can limit the capacity of this strain to invade natural populations and halt arbovirus transmission [17]. On the other hand, *w*AlbB is more resistant to heat and antibiotics than the other two strains and therefore is likely to be stable in different environments. On the other hand, infected females hatching from resting eggs become infertile. This fitness cost can impact the invasion and persistence of this strain in locations with long dry seasons [42]. Finally, although strong pathogen blocking is observed for *w*MelPop, the severe fitness cost to the host makes stable population replacement unlikely to occur, when using this strain [41].

Assuming that a relationship between temperature and infection loss exists, such as the relationship given by Eq. 7, it is important to discuss the impact of temperature variation on the efficacy of the technique (Fig. 6). As the temperature increases, a higher ratio of infected to non-infected mosquitoes is needed to maintain the same efficacy, until a threshold (around 28.9°C) is achieved. After that, the efficacy diminishes. On the other hand, the prevalence always decreases with the increase in temperature.

Finally, to develop a more reliable model for use in real scenarios, one would need specific laboratory and field data assessing the impact of abiotic factors on infection traits and mosquito entomological parameters. Furthermore, the results shown depend on the chosen functions (Equations (4)-(8)), so we need to know the characteristics of the local population of mosquitoes to make the best choice of the period of the year for the infected-mosquito release, the best ratio of infected to non-infected mosquitoes used and the best bacterial strain to promote the infection. Although the level of rainfall was not considered, it probably affects mosquito abundance, by changing mosquito mortality or varying the carrying capacity.

5. Conclusion

A non-autonomous time-delayed differential system, with time-varying delay, is proposed to reproduce the temporal dynamics of two mosquito populations, differing in that one is *Wolbachia*-free and the other is *Wolbachia*-carrying. The effects of temperature on both mosquito entomological parameters and the infection traits were analyzed. The results showed that the efficacy of this technique depends on several parameters such as (i) the ratio of infected mosquitoes to non-infected ones during release, (ii) the period of the year when infected mosquitoes are released, (iii) the periodicity of mosquito releases, and (iv) the bacteria strain used to infect the mosquito. In summary, four releases at 7-day intervals are more efficient than one, during the favorable period when the mosquito population is high is the best time to implement the release, and increasing the strength of cytoplasmic incompatibility and maternal inheritance can optimize the efficacy. High temperatures can jeopardize the efficacy of the technique by both increasing the ratio of infected to non-infected mosquitoes to achieve persistence of the infection and by diminishing the prevalence of the infection in the population in the long run. Although one can find in the literature a general idea of how abiotic and biotic factors affect mosquito dynamics and infection traits, the interaction among them is not trivial. Here, we propose a framework to predict how this interaction impacts the replacement of the wild mosquito population with an infected one that is not able to transmit dengue.

Data availability

No data was used for the research described in the article.

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