Increased efficiency in the second-hand tire trade provides opportunity for dengue control

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ABSTRACT

Dengue fever is increasing in geographical range, spread by invasion of its vector mosquitoes. The trade in second-hand tires has been implicated as a factor in this process because they act as mobile reservoirs of mosquito eggs and larvae. Regional transportation of tires can create linkages between rural areas with dengue and disease-free urban areas, potentially giving rise to outbreaks even in areas with strong local control measures. In this work we sought to model the dynamics of mosquito transportation via the tire trade, in particular to predict its role in causing unexpected dengue outbreaks through vertical transmission of the virus across generations of mosquitoes. We also aimed to identify strategies for regulating the trade in second-hand tires, improving disease control. We created a mathematical model which captures the dynamics of dengue between rural and urban areas, taking into account the movement and storage time of tires, and mosquito diapause. We simulate a series of scenarios in which a mosquito population is introduced to a dengue-free area via movement of tires, either as single or multiple events, increasing the likelihood of a dengue outbreak. A persistent disease state can be induced regardless of whether urban conditions for an outbreak are met, and an existing endemic state can be enhanced by vector input. Finally we assess the potential for regulation of tire processing as a means of reducing the transmission of dengue fever using a specific case study from Puerto Rico. Our work demonstrates the importance of the second-hand tire trade in modulating the spread of dengue fever across regions, in particular its role in introducing dengue to disease-free areas. We propose that reduction of tire storage time and control of their movement can play a crucial role in containing dengue outbreaks.

1. Introduction

Dengue fever is among the most widespread vector-borne diseases, with approximately 2.5 billion people at risk and 50 million infections annually (World Health Organization, 2009). Dengue is endemic in over 100 tropical and subtropical countries (Gubler, 2002). It is also the fastest re-emerging disease (Cook and Zumla, 2008), imposing an economic burden alongside the impaired health of affected individuals. Two mosquito species are responsible for transmission of the virus via infective bites. The most common vector is *Aedes aegypti*, but the Asian tiger mosquito (*Aedes albopictus*) is increasingly important due to a rapidly ex-

panding global distribution encompassing most tropical regions (Belli et al., 2015; Rezza, 2012). *Aedes albopictus* began to spread worldwide in the 1970s thanks to marine transport of tires and other goods, leading to colonization of many areas of the world (Eritja et al., 2005). At a global scale *Aedes albopictus* continues to spread to naive regions due to commercial transport of used tires and climate change; the species is also showing signs of adaptation to colder climates (Benedict et al., 2007; Bonizzoni et al., 2013; Rochlin et al., 2013). There are four dengue virus serotypes (García-Rivera and Rigau-Pérez, 2006), and once an individual has been infected by one serotype they are permanently immune to that serotype but only temporarily immune to the others (Esteva and Vargas, 2003; García-Rivera and Rigau-Pérez, 2006).

Second-hand tires are widely traded both locally and globally. In countries with *A. aegypti* mosquitoes these often contain standing rain water and e.g. (Rezza, 2012; Yee, 2008), providing excellent larval habitats which are frequently infected with both species (Alves Honório et al., 2006; Higa et al., 2010). Tires have been an

important dispersal mechanism for both mosquitoes and dengue virus. *A. albopictus* originated in Asia but invaded the New World in the 1980s via imported used tires and bamboo plants (Belli et al., 2015; Gubler, 2002). It is now present in 20 countries in the Americas (Belli et al., 2015). International trade in used tires and bamboo has also been implicated in the introduction of *A. albopictus* to Europe (Medlock et al., 2012). There is also circumstantial evidence that the transportation of second-hand tires between urban areas has led to the introduction or re-emergence of dengue in areas previously free of disease (Belli et al., 2015; Kourí et al., 1998; Medlock et al., 2012).

According to Pan American Health Organization and World Health Organization (2014), *A. aegypti* was eliminated from the Americas in 1960. Subsequently several countries interrupted control measures and the mosquito began to spread again. Concurrently, social and economic changes in the Americas, which increased trade and migration, permitted re-infestation of the vector and dengue virus throughout South America. Due to economic development, Briseño-García et al. (1996) suggest that in Mexico there was correlation, if not causation, between the increase in the annual production of tires from 1960 to 1990 and dengue incidence. A direct relation between tire trade and dengue in Cuba was posited by Kourí et al. (1998). He mentions that from 1981 to 1996, Cuba lacked any dengue transmission. Reintroduction has now occurred in some areas; the municipality of Santiago de Cuba was reinfested in 1992 by *A. aegypti* transported in tires, followed by the return of dengue.

Two processes play an important role in the transportation of *Aedes* and dengue fever via tires. The first is the diapause phase in the mosquito life cycle, enabling eggs to survive long periods of unfavorable conditions, including desiccation (Thomas et al., 2012). Vertical or transovarial transmission of dengue also occurs, with infected females passing the virus to their e.g. (Esteva and Vargas, 2000; Günther et al., 2007; Martins et al., 2012; Murillo et al., 2014). Emerging adults are therefore able to transmit the disease without first interacting with an infected host (Cook and Zumla, 2008; Gubler, 1986), potentially causing outbreaks in dengue-free areas.

There is a large tradition in ecology of studying the possible and viable mechanisms of spread and colonization of species. Thus there is a broad literature describing different models and approaches to this problem (Gotelli and others, 1995; Levin et al., 2009; Loreau, 2010). For example, island-mainland models assume constant migration of individuals (MacArthur and Wilson, 2016) from an infinite mainland to an island. In contrast to this, in metapopulation models (Levins, 1969) there is no mainland but different patches. In this work we develop an explicit metapopulation model describing the colonization of *A. aegypti* between two areas of different ecological characteristics. In addition to this, we also analyzed the conditions that lead to the emergence or re-emergence of dengue caused by mobile reservoirs for disease. It should be noted that even if spread and colonization of species has been related with re-emerging zoonoses Bengis et al. (2004); Thompson (2000), there is little or none literature showing explicit dynamical models of this phenomena, as we do here. We assess the potential role of transportation of tires containing infected eggs in causing outbreaks in areas otherwise free of both vectors and dengue. We consider the spread of dengue caused by a single serotype.

Our mathematical model is based on two patches, representing a rural area with endemic dengue and an urban area which begins as dengue-free. We incorporate vertical transmission, diapause during transportation, and the efficiency of tire processing. Through this we generate scenarios in which (a) there is establishment of mosquitoes in an urban area from a rural area, (b) these lead to a dengue outbreak occurring in the urban area, (c) a per-
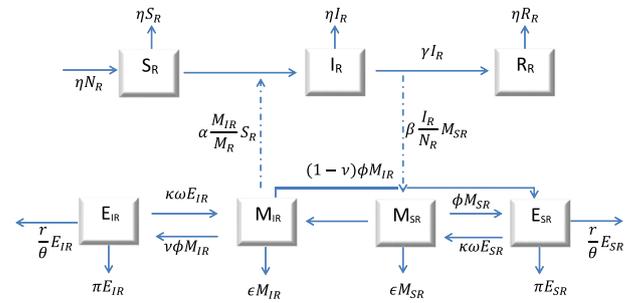

Fig. 1. Flowchart from rural dengue fever model. Elements of the upper row refer to segments of the human population, susceptible (S), infected (I) and recovered (R). The lower row refers to adult mosquitoes (M) or their eggs (E). Arrows represent transition rates between stages. See Tables 1 and 2 for definitions of terms.

Fig. 2. Flowchart from urban dengue fever model. Elements of the upper row refer to segments of the human population, susceptible (S), infected (I) and recovered (R). The lower row refers to adult mosquitoes (M) or their eggs (E). Arrows represent transition rates between stages. See Tables 1 and 2 for definitions of terms.
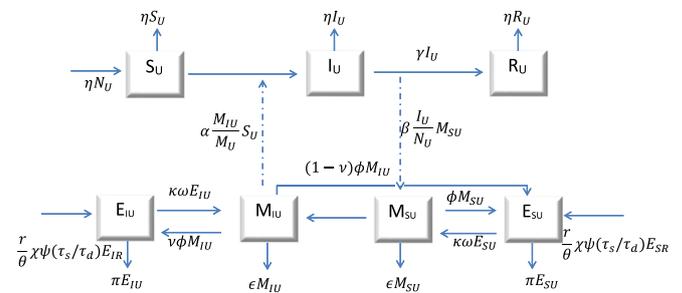
sistent disease state is created in the urban area due to continuous influx of infected eggs from rural area, and (d) an existing endemic infection is enhanced through additional input of infected vectors. In order to assess the potential for management, we present a case study of implementing a management program to reduce tire processing times. Our work demonstrates that, if effectively regulated, a reduction in the time that tires are stored could aid in dengue control.

2. Methods

Our model aims to capture the dynamics of dengue fever in both humans and female mosquitoes through tire movements at the landscape scale. Our rationale for doing so is that, without taking this into account, other measures focused on disease treatment and migration control may prove to be unexpectedly inefficient. We omit movement of infected mosquitoes, given that newly hatched *A. aegypti* only fly around 20 m from their point of emergence (Christophers, 1960), and we also omit movement of infected humans as we are only interested in the particular effects of tire movement.

The landscape is divided in a rural and an urban patch. Each patch contains a local human population. One system (Fig. 1) is used to model disease dynamics in the rural area, while another (Fig. 2) applies to the urban area. The systems in the two patches differ due to the transfer of eggs from rural to urban areas and in the values of parameters. Table 1 summarizes the model parameters.

The system of differential equations that model the dynamics of dengue in human and mosquito populations in the rural area is given by

$$\dot{S}_R = \eta N_R - \alpha \frac{S_R}{N_R} M_{IR} - \eta S_R,$$

Table 1
Model parameters.

Parameter	Description
η	Per-capita birth and natural mortality rates in humans
γ	Per-capita recovery rate
α	Effective biting rate, per day
C_a	Carrying capacity of hatcheries, where $a \in \{r, u\}$, and r is rural and u urban area
ϕ	Number of eggs laid per day for every female mosquito
ϵ	Per-capita mortality rate of adult mosquitoes
π	Per-capita mortality rate of immature stage mosquitoes
ν	Proportion of eggs that are infected by vertical transmission
ω	Development rate of immature to mature stages
κ	Fraction of mosquitoes that are female
$\frac{r}{\theta}$	Per-tire transportation rate
χ	Fraction of eggs that survive the transportation
$\psi(\tau_s/\tau_d)$	Fraction of eggs in tires that were able to continue their development before tire processing
τ_s, τ_d	Tire storage time and egg development time

Table 2
Parameter values for simulating the dynamics of dengue transmission in Puerto Rico based on literature sources.

Parameter	Value	Units	Reference
η	0.002	1/days	Estimated
γ	1/7	1/days	Adams and Boots (2010)
α	0.67	1/days	Adams and Boots (2010)
C_a	10,000 and 1000	eggs	Estimated
ϕ	10	1/days	Esteva et al. (2006)
ϵ	1/8	1/days	Adams and Boots (2010)
π	1/8	1/days	Adams and Boots (2010)
ν	0.3	proportion	Adams and Boots (2010)
ω	1/8	1/days	Adams and Boots (2010)
κ	0.5	proportion	Estimated
$\frac{r}{\theta}$	10, 20	1/days	Estimated
χ	0.1	proportion	Estimated
$\psi(\tau_s/\tau_d)$	0.64	proportion	Estimated using A.D.S. (2014)
τ_s, τ_d	90, 10	days	A.D.S. (2014); Esteva et al. (2006)

$$\dot{I}_R = \alpha \frac{S_R}{N_R} M_{IR} - (\eta + \gamma) I_R,$$

$$\dot{R}_R = \gamma I_R - \eta R_R,$$

$$\dot{M}_{SR} = \kappa \omega E_{SR} - \alpha \frac{I_R}{N_R} M_{SR} - \epsilon M_{SR},$$

$$\dot{M}_{IR} = \kappa \omega E_{IR} + \alpha \frac{I_R}{N_R} M_{SR} - \epsilon M_{IR},$$

$$\dot{E}_{SR} = \phi M_{SR}\left(1 - \frac{E_R}{C_r}\right) + (1 - \nu)\phi M_{IR}\left(1 - \frac{E_R}{C_r}\right) - \left(\pi + \omega + \frac{r}{\theta}\right) E_{SR},$$

$$\dot{E}_{IR} = \nu \phi M_{IR}\left(1 - \frac{E_R}{C_r}\right) - \left(\pi + \omega + \frac{r}{\theta}\right) E_{IR}. \tag{1}$$

The differential equations that model the dynamics of dengue disease in human and mosquito populations in the urban area are given by

$$\dot{S}_U = \eta N_U - \alpha \frac{S_U}{N_U} M_{IU} - \eta S_U,$$

$$\dot{I}_U = \alpha \frac{S_U}{N_U} M_{IU} - (\eta + \gamma) I_U,$$

$$\dot{R}_U = \gamma I_U - \eta R_U,$$

$$\dot{M}_{SU} = \kappa \omega E_{SU} - \alpha \frac{I_U}{N_U} M_{SU} - \epsilon M_{SU},$$

$$\dot{M}_{IU} = \kappa \omega E_{IU} + \alpha \frac{I_U}{N_U} M_{SU} - \epsilon M_{IU},$$

$$\dot{E}_{SU} = \phi M_{SU}\left(1 - \frac{E_U}{C_u}\right) + (1 - \nu)\phi M_{IU}\left(1 - \frac{E_U}{C_u}\right) - (\pi + \omega) E_{SU}$$
$$+ \cdots \frac{r}{\theta} \chi \psi\left(\frac{\tau_s}{\tau_d}\right) E_{SR}, \tag{2}$$

$$\dot{E}_{IU} = \nu \phi M_{IU}\left(1 - \frac{E_U}{C_u}\right) - (\pi + \omega) E_{IU} + \frac{r}{\theta} \chi \psi\left(\frac{\tau_s}{\tau_d}\right) E_{IR}.$$

Where $N_R = S_R + I_R + R_R$, $N_U = S_U + I_U + R_U$, $M_R = M_{SR} + M_{IR}$, $E_R = E_{SR} + E_{IR}$, $M_U = M_{SU} + M_{IU}$, $E_U = E_{SU} + E_{IU}$.

The total human populations in the rural and urban areas (N_R, N_U) are constant, given that the characteristic timescale of the disease is small (weeks) relative to that of human demographic processes (years). The susceptible human class S increases by the per-capita birth rate η multiplied by the overall population size N. Individuals become infectious (class I) according to the bite rate α of infected vectors M_I. The rate at which humans recover from infection, whereupon they become permanently immune (class R), is γ. The per-capita death rate η is identical for all classes, and to the birth rate. The consequence of this, is that the total population is constant (Brauer et al., 2008).

Mosquito populations increase through egg eclosion at the development rate ω and the total population is limited by a carrying capacity C_r in rural and C_u in urban areas. This is because mosquitoes exhibit density-dependent growth (Juliano, 2007) and at the same time it is ensured the stability of the model for a broad range of entomological parameters. Adult mosquitoes die with a rate ϵ. Female mosquitoes oviposit at a rate ϕ and the eggs have an intrinsic mortality rate π. If a female mosquito is already infected, a fraction ν of its oviposited eggs are infected (vertical transmission). Vectors become infected by biting infectious hosts (I) at the contact rate α. In contrast to humans, mosquitoes never recover from the disease. Our model only considers the fraction κ of mosquitoes that are female, as males do not transmit the disease.

The number of tires transported from the rural to the urban area per unit time is r and θ is the mean number of tires in the

rural area. Hence rE_{IR}/θ is the rate of infected egg movement from rural to urban areas and rE_{SR}/θ is the rate of susceptible egg movement also from rural to urban areas. During transportation a fraction χ of eggs survive. τ_s is the storage time before tire processing and τ_d represents the egg development time. As we assume that eggs stay in diapause stage during transportation and start its development once the tires arrive to the storage places, the fraction of eggs in the tires that are able to hatch as adults before being killed by tire recycling should be a function of τ_s/τ_d, i.e. $\psi(\tau_s/\tau_d)$. ψ should be a function such that when $\tau_s = 0$ then $\psi = 0$, while when τ_s is greater than the development time τ_d, ψ should approach one. The total number of tires in the rural area remains constant, but this is not true of the urban area. Thus, we would expect the effect of tire transportation on disease dynamics in the rural area to be limited. We also assume no substantive changes in the tire trade at the timescale of the model dynamics.

The model explicitly takes into account the movement and storage time of tires. Our study focuses on the necessary conditions for four possible outcomes. This conditions are obtain by the analysis of the stationary state. Scenario *I* considers the establishment in the urban area of mosquitoes from a rural area where both areas are disease-free. In Scenario *II* a dengue outbreak emerges in the urban area as a consequence of the joint introduction of the mosquito and the virus in infected eggs. Scenario *III* induces or enhances a persistent disease state in the urban area through the constant introduction of infected mosquito eggs. Finally, in Scenario *IV*, we consider how regulation of the market in second hand tires could act as a dengue control measure. To demonstrate the impacts on dengue spread we calculate the secondary dengue cases generated in the urban area as the result of a single case in rural area. This quantity can be used as a preliminary measure of the impact of controlling the movement of tires during dengue outbreaks. Finally we apply our model to a specific study of the tire management system in Puerto Rico using data from the Solid Waste Authority (A.D.S., 2014).

3. Results

3.1. Scenario I: Establishment of mosquitoes in an urban area

Initial state: Mosquitoes only present in rural area; no disease.

If initially there were no mosquitoes in the urban area, the transportation of a single batch of tires can lead to the introduction of mosquito eggs from rural to urban areas. In order to obtain the conditions when establishment of an adult population of mosquitoes in an urban area might occur, we determine the *urban net reproductive rate* (derived in Appendix A) R_M^u by means of the next generation matrix (Diekmann et al., 1990). The next generation matrix is a main element used in the formal mathematical procedure to obtain R_M^u. This quantity may change in different environmental and ecological conditions due to the change of insect development. Thus, if $R_M^u > 1$, then the population of mosquitoes is able to establish itself from a small number of eggs, while if adverse environmental conditions cause $R_M^u < 1$, then the mosquito population will eventually become extinct.

We are interested in the conditions that allow establishment of mosquitoes in a disease-free area area. First, we find the condition that allows the immigration of viable eggs and then the condition in the urban area to sustain a mosquito population. In a single batch of N_T tires, the number of viable eggs that arrive in the urban area is given by

$$\frac{\omega}{\pi+\omega}\psi\left(\frac{\tau_s}{\tau_d}\right)\chi N_T \frac{E_R^*}{\theta} = \frac{\omega}{\pi+\omega}\psi\left(\frac{\tau_s}{\tau_d}\right)\chi N_T \frac{R_M^r - 1}{R_M^r}\frac{C_r}{\theta}$$

where $\frac{\omega}{\pi+\omega}$ is the probability of an egg hatching into an adult mosquito, E_R^* is the stationary number of eggs in the rural area (see

Appendix B), R_M^r is the *rural net reproductive rate* (see Appendix B), and $\chi\psi(\frac{\tau_s}{\tau_d})$ is the fraction of eggs that survive before the tire processing cycle completes. Like the urban net reproductive rate, the rural net reproductive rate is an indicator for the long-term persistence of mosquitoes in the rural area, that is, the average number of offspring that a female mosquitoes produces during her lifetime. Thus, $\frac{E_{R^*}}{\theta}$ is the number of eggs per tire, which multiplied by the batch size N_T determines the number of transported eggs. Then $\chi\psi(\frac{\tau_s}{\tau_d})N_T\frac{E_{R^*}}{\theta}$ is the number of eggs that survive tire transportation and processing, which is then multiplied by probability of hatching $\frac{\omega}{\pi+\omega}$ to obtain the number of emerging adult mosquitoes in the urban area. Then, the introduction of the species happens if

$$\frac{\omega}{\pi+\omega}\frac{N_T}{\theta}\chi\psi\left(\frac{\tau_s}{\tau_d}\right)\frac{R_M^r - 1}{R_M^r}C_r > 1 \tag{3}$$

The establishment of the mosquito population in the urban area will occur if in addition to the previous condition, the following is also met:

$$R_M^u = \frac{\kappa\omega\phi}{\epsilon(\pi+\omega)} > 1 \tag{4}$$

This condition indicates that an urban mosquito population is sustainable. R_M^u can be interpreted in terms of the model parameters as follows: ϕ/ϵ is the average number of eggs laid by a single female mosquito, $1/(\pi+\omega)$ is the average time of survival of an immature mosquito, and $1/\omega$ is the average time spent in development, then $\kappa\omega/(\pi+\omega)$ is the probability that an egg will succeed to become an adult mosquito, and finally ϕ/ϵ is the average number of eggs oviposited by a single female mosquito. Expression (3) shows the importance of limiting the batch size and not only the tire transport rate. As a single big batch of tires could be enough to introduce a species even if the average tire transportation rate tend to zero.

On the other hand, if tire recycling becomes an established market with a constant flux of tires from the rural to the urban area, then the expected waiting time T_M before the introduction of a mosquito species from the rural to the urban population is given by the inverse of the rate of egg introduction

$$T_M = \left[\frac{\omega}{\pi+\omega}r\chi\psi\left(\frac{\tau_s}{\tau_d}\right)\frac{R_M^r - 1}{R_M^r}\frac{C_r}{\theta}\right]^{-1} \quad \text{for} \quad R_M^r > 1 \tag{5}$$

The expression inside the square parenthesis is similar to the second expression of (3) but N_T is replaced by the tire introduction rate *r*. Thus this expression represents the rate of introduction of successful eggs and its inverse is the average time before introduction of a single egg. This two different cases, single batch and constant rate, give different insights about two important aspects of tire transportation.

3.2. Scenario II: A dengue outbreak occurs

Initial state: Mosquitoes and dengue only present in the rural area, but urban environmental conditions suitable for an outbreak.

If continuous introduction of tires takes place from a dengue-endemic rural area to the urban area, a dengue outbreak might be precipitated by transportation of infected eggs. In order for this to happen the conditions in Eqs. (3) and (4) must be met, also *basic reproductive number without vertical transmission must be greater than one*, that is, $R_0^u > 1$. Its value is given by $R_0^u = \sqrt{\frac{\alpha}{\epsilon}\frac{\beta N}{(\eta+\gamma)M^*}}$ (derived in Appendix C). In this case vertical transmission is omitted as its effect is negligible at the beginning of an outbreak (see Adams and Boots, 2010). Thus, in addition to (3), the condition

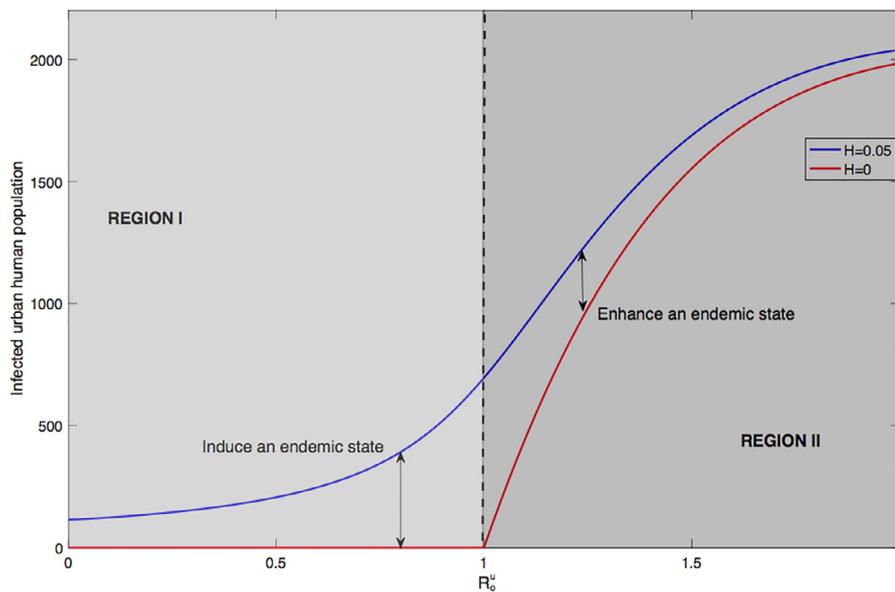$$\sqrt{\frac{\alpha}{\epsilon}\frac{\beta N}{(\eta+\gamma)M^*}} > 1 \tag{6}$$

Fig. 3. Input of tires can enhance a dengue endemic state or induce a persistent one. Steady-state number of infected humans as a function of basic reproductive number R_o. It is possible to induce a dengue-persistent state even though $R_0^u < 1$ (Region I) if there is a continuous flow of tires from an endemic rural area. If the disease is already endemic, tire transport of eggs will enhance the endemic state (Region II). $H = \frac{r}{\theta} \chi \psi \left(\frac{\tau_s}{\tau_d} \right)$ represents variation in the flow of tires.

must also be meet.

The characteristic waiting time before the introduction of infected female mosquitoes T_o, is given by

$$T_o = \left[\frac{\kappa \omega}{\pi + \omega} r \chi \psi \left(\frac{\tau_s}{\tau_d} \right) \frac{E_{IR}^*}{\theta} \right]^{-1} \qquad (7)$$

where $r \chi \psi \left(\frac{\tau_s}{\tau_d} \right)$ is the number of successfully imported eggs per unit time, $\frac{\kappa \omega}{\pi + \omega}$ is the probability of an egg hatching into a female mosquito before death by natural causes, and $\frac{E_{IR}^*}{\theta}$ is the fraction of infected eggs in the tires. Thus the expression represents the effective rate of introduction of infected female mosquitoes.

In the case of introduction of a single batch of N_T tires, in addition to conditions (3) and (6), the following must be satisfied:

$$\frac{\kappa \omega}{\pi + \omega} N_T \chi \psi \left(\frac{\tau_s}{\tau_d} \right) \frac{E_{IR}^*}{\theta} > 1 \qquad (8)$$

This is similar to T_o (Eq. (7)) but r is replaced by the batch size N_T. Thus condition (8) represents the requirement that the number of eggs that hatch must exceed one.

3.3. Scenario III: Persistent dengue states can be induced and enhanced

Initial state: Mosquitoes and dengue only present in the rural area, and urban environmental conditions unfavorable for an outbreak.

There may be situations in which $R_0^u < 1$, and therefore dengue infestation in the urban area is not self-sustaining, but where continuous introduction of infected eggs in tires from an endemic rural area can induce a persistent disease state in the urban area. This state is not maintained by the intrinsic dynamics of the disease in the urban area and will cease if the introduction of infected eggs is interrupted (see Figs. 3 and 4).

In this situation, the expected number of active dengue cases in the urban area is given by the stationary state I_U^* that is determined as

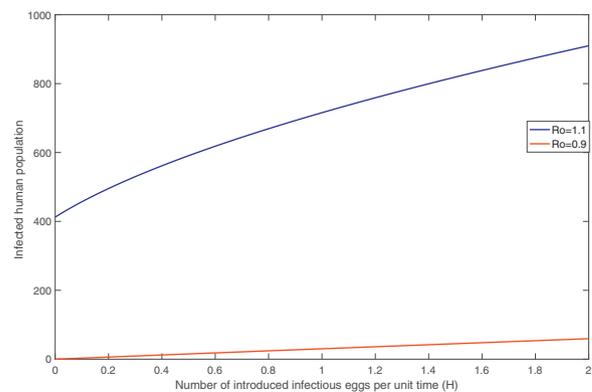$$I_U^* = \frac{M_{IU}^*}{M_{IU}^* - N_U \frac{\eta}{\alpha}} \qquad (9)$$

Fig. 4. Stationary level of infection in the urban population with increasing introduction of eggs. Dengue cases increase as the number of introduced infected eggs per unit time H is increased. Red line $R_0^u < 1$ (intrinsically non-endemic state) and blue line $R_0^u > 1$ (endemic state). The parameter H is given by $\frac{r}{\theta} \chi \psi \left(\frac{\tau_s}{\tau_d} \right)$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

where M_{IU}^* represent the stationary state of the infected mosquitoes in the urban area (see Appendix H).

Where dengue is already endemic in the urban area, the continuous importation of tires can enhance the number of infected people (see Figs. 3 and 4). The number of infections at any given time is given by Eq. (9) when $R_0^u > 1$ in Eq. (H.1).

3.4. Scenario IV: Regulation of the second hand tire market as a dengue control measure

We now analyze the response of the infected human population with respect to tire movement. If tires are processed immediately, or at least soon after arrival to the urban area such that $\tau_s << \tau_d$, introduction of dengue fever does not occur.

In the rural area, diminishing the number of eggs by removal from the rural area reduces the basic reproductive number in rural area R_0^r (see Appendix D); this means that the number of dengue cases is reduced. This is due to the increase in r while holding all other parameters constant.

In addition to this, if a large enough number of exported tires is maintained, then the *net reproductive rate* could shift from $R_M^r > 1$ to $R_M^r < 1$, meaning that the rural mosquito population could no longer sustain itself. If it takes too long before the mosquito population cease to exist, dengue can remain for some period of time before vanishing. If dengue remains in this situation in rural areas then the risk of introducing infected eggs into the urban area will persist unless tires are processed immediately. The maximum storage time τ_s which still prevents dengue introduction can be estimated by ensuring that the expected latency before introduction of an infected female mosquito (Eq. (7)) is greater than the extinction time of the vector in the rural area. In this work we have assumed that diapause ends when the eggs enter the urban area; the eggs thence continue their development, allowing some time before hatching.

When $R_M^r < 1$ we can use the Jacobian matrix of the vector demography (Appendix B.1) to obtain the expected extinction time. This is the time taken for the linearized system describing the dynamics of the mosquitoes to reach a population size of zero. The variable R_M^r can also be interpreted as the number of successful offspring that a female mosquito produces during its lifespan. The inverse of the smallest absolute value from its eigenvalues is an estimator of extinction time. Thus, the following condition should be met to reduce the risk of dengue dispersal in an established market where tires are continuously imported to the urban area:

$$T_o < \left| \frac{1}{2} (\gamma + \sqrt{\xi}) \right|^{-1} \quad \text{and} \quad R_M^r = \frac{\kappa \omega \phi}{\epsilon (\pi + \omega + r/\theta)} < 1$$

where $\gamma = -(\epsilon + \pi + \omega + r/\theta)$, $\xi = \gamma^2 - 4\Xi$ and $\Xi = \epsilon (\pi + \omega + r/\theta)(1 - R_M^r)$ (see Appendix B). This simultaneously works as a control measure in the rural area.

In order to assess the impact of interventions in the tire trade on disease dynamics, we can calculate the secondary human infections in the urban disease free area caused by human infections in the rural area at the beginning of an outbreak $R_{r \to u}$ (see Appendix F). There will be one initial case of dengue virus in the urban area related to tire transportation for each $1/R_{r \to u}$ cases in the rural area, where

$$R_{r \to u} = \frac{\alpha \kappa \omega r \chi}{\epsilon (\omega + \pi)(\theta(\omega + \pi) + r)} \psi \left(\frac{\tau_s}{\tau_d} \right) \frac{\nu \phi}{\epsilon} \frac{\beta}{(\eta + \gamma)}.$$

Thus, $R_{r \to u}$ gives the number of cases in urban area which are derived from an infected person in the rural area.

3.5. Case study

One of the main barriers for dengue eradication in Latin America is the problem of stored tires (Cantanhede and Monge, Lima, 2002). These are favorable sites for the breeding of multiple vector insects, with implications for disease transmission and human health. Used tires are one of the sites in which *A. aegypti* females deposit their eggs, becoming an important pathway for their proliferation and thus causing outbreaks of dengue in tropical and subtropical countries (Cantanhede and Monge, Lima, 2002). Conditional on successful introduction, an endemic disease state can arise in areas where the environmental conditions are suitable (Cantanhede and Monge, Lima, 2002).

Some Latin American countries, such as Costa Rica and Peru, have banned the import of used tires (Cantanhede and Monge, Lima, 2002). This is due to the perceived danger to public health, in addition to concerns regarding road safety and protection of the environment. Costa Rica does not possess the necessary technology to treat used tires without causing environmental pollution (Cantanhede and Monge, Lima, 2002).

In Puerto Rico the accumulation of discarded tires in *gomeras* and facilities around the island represent an environmental and
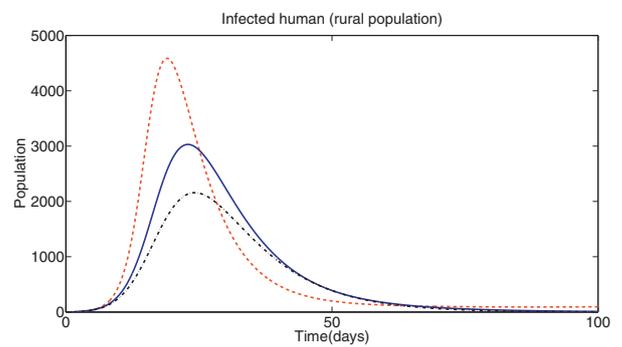

Fig. 5. Dynamics of dengue infection in rural areas under three scenarios. Red dashed line shows the population size of infected humans when there is no transportation of tires. Blue solid line shows the infected population when tire transportation takes place ($r/\theta = 10$). Black dash-dot line shows the infected population when tire transportation rate is increased ($r/\theta = 20$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

health crisis (A.D.S., 2014). The country has therefore implemented a tire management program. According the Solid Waste Authority (ADS), around 18,000 tires are discarded every day; this amounts to 4.7 million tires a year. Despite the tire management program, it is not possible to collect all discarded tires. Among the major public health risks of excessive accumulation of tires is the spread of pests and diseases such as dengue.

A total of 6766 confirmed cases of dengue were reported in Puerto Rico in 2013 (A.D.S., 2014). For this reason the authorities have decided to reduce the disposal of tires. They have introduced authorized solid waste facilities in which the accumulation of tires is permitted for up to 90 days. The law also allows local governments to collect used tires voluntarily and temporarily. The collection and transport of discarded tires is carried out by official vehicles (A.D.S., 2014).

In this section we use the data provided by ADS to estimate $\Psi(\tau_p/\tau_d)$ and make an estimation of the program benefits in the reduction of dengue cases. We also employ our model to analyze the implications of tire management for dengue transmission in this specific geographical context. We use the number of discarded tires and processed tires per *gomera* reported by ADS to calculate the parameter r representing the rate of tire transportation from rural to urban areas. In order to do so we merge all urban populations into a single population, and the same for rural populations, i.e. we have used the homogeneous mixing hypothesis. This approximation leads to an overestimation of disease cases because it is assumed that there are more interactions between the populations than occur in reality. Thus the estimates given by this analysis represent a worst case scenario, but also provide the starting point for a geographically-structured model.

Figs 5 and 6 show the populations of infected humans in rural and urban areas. In Fig. 5 the infected population in rural areas with no transportation of tires (red dashed line) demonstrates that the disease is endemic. If transportation of tires takes place, the infected population in rural areas declines by 9.8% (blue solid line). So, in this situation tire transportation acts as another mortality rate.

Puerto Rico has instituted a program to recover used tires. Fig. 6 shows the comparison between number of infected people depending on whether the tires are handled appropriately. The blue line depicts the infected population in the absence of a recycling program ($\Psi(\tau_s/\tau_d) = 1$). The recycling program recovers and processes 36% of tires in the three temporary storage centers ($\Psi(\tau_s/\tau_d) = 0.64$). Our model suggests that the tire recycling program may have reduced the number of dengue cases considerably.
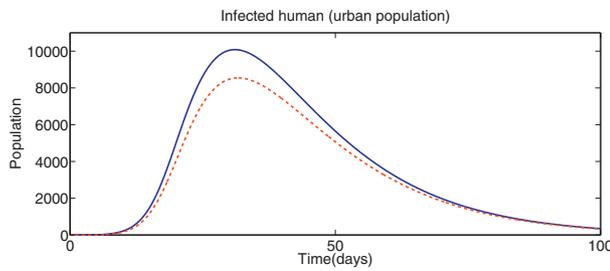
Fig. 6. Dynamics of dengue infection in urban areas, indicating the impact of the tire recycling program. Blue solid line shows the outbreak dynamics with unregulated transport of tires, red dashed line shows the predicted urban outbreak given the existence of this program. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Compared to the case with no recycling program, the program reduced the number of infected people in urban areas by 13.0% (red line).

4. Discussion

The trade in second-hand tires, if unregulated, can under certain circumstances be an important factor in the generation of dengue outbreaks. Tire movement can both trigger epidemics and sustain disease states through continuous reintroduction. Regulation can help to avoid these impacts and reduce the availability of mosquitoes hatcheries. Thus tires are an important component of disease dynamics whenever environmental conditions are conducive to a dengue epidemic.

Discarded tires are believed to be one of the most productive hatcheries of the *Aedes* mosquitoes which transmit dengue fever (Alves Honório et al., 2006), with many eggs transported whilst in a diapause state. As a result of vertical transmission across generations, infected mosquitoes can pass the virus to their offspring, and therefore a new generation of infective vectors emerge, able to transmit the disease without first feeding on an infected individual. Evidence also exists of vertical transmission of Zika and Chikungunya viruses by *A. aegypti* and *A. albopictus* (Agarwal et al., 2014; Ferreira-de-Brito et al., 2016; Niyas et al., 2010; Thangamani et al., 2016), extending the implications of our model to other vector-borne diseases. Our model therefore has important consequence for the spread of a range of emerging diseases. Even in hostile environmental conditions, the resistance of *Aedes* eggs to desiccation, combined with vertical transmission of the virus, is likely to facilitate the persistence and spread of disease.

Our model demonstrates that the movement of tires containing mosquito eggs has the potential to transfer both vector and virus from rural to urban regions, and with a sufficient rate of input, can induce a persistent dengue state in the urban area even if environmental conditions or control measures such as fumigation and hatchery elimination would otherwise cause it to be eradicated. Management of the tire trade to reduce their storage time is a potential strategy for reducing spread of the disease, and we demonstrate using an empirical case study from Puerto Rico that even a modest program of tire collection can lead to major declines in the disease burden experienced in urban areas. Tires left in the open are productive *A. aegypti* hatcheries (Alves Honório et al., 2006; Higa et al., 2010; Yee, 2008), increasing the risk of dengue transmission. There is also evidence that tire transportation has led to the introduction of dengue in areas previously free of disease (Belli et al., 2015; Kourí et al., 1998; Medlock et al., 2012).

The model explicitly takes into account the movement and storage of second-hand tires, typically from rural to urban areas for processing, a common feature of their trade. Thus, this study can help to guide tire-trade policy. The particular policy can be strengthened or relaxed depending on local conditions with respect to the scenarios analyzed above.

Our model can be used as the basis for evidence-based policy-making in a range of contexts with appropriate parametrization. Practical issues such as the frequency of fumigation campaigns, limits to the batch sizes of tires, and regulations concerning the storage time and conditions of tires, can all have quantifiable impacts on disease dynamics. Incorporating these actions as model extensions would inform effective investment of limited resources. Most importantly, we show that control of dengue transmission in urban areas provides insufficient protection of public health when tire movement continues as a source of constant reintroduction.

The homogeneous mixing assumption for the rural area and the urban area is likely an overestimation of cases in our model. In order to improve accuracy of the predictions it would be necessary to build and spatially explicit model where different rural areas with its interactions are taken into account. In addition to this, the model analyses the impact of tire movement alone. Extending the model in order to take into account human migration can guide more complex policies of simultaneous interventions on tire trade and human mobility.

Appendix A. Urban net reproductive rate

In the following we determine the urban net reproductive rate, for this we consider the equations for mosquitoes in urban area, that is $\dot{M}_{SU}$, $\dot{M}_{IU}$, $\dot{E}_{SU}$ and $\dot{E}_{IU}$. Also $\dot{M} = \dot{M}_{SU} + \dot{M}_{IU}$ and $\dot{E} = \dot{E}_{SU} + \dot{E}_{IU}$, then we have the following system:

$$\dot{M} = \kappa\omega E - \epsilon M,$$

$$\dot{E} = \phi M - (\pi + \omega)E + \frac{r\chi}{\theta}\psi\left(\frac{\tau_s}{\tau_d}\right)E_R. \qquad (A.1)$$

We calculate the mosquito urban net reproduction rate using the method of Diekmann et al. (1990). The system (A.1) can be defined as $\dot{\mathfrak{x}} = \mathfrak{F} - \mathfrak{V}$:

$$\dot{\mathfrak{x}} = \begin{pmatrix} \dot{M} \\ \dot{E} \end{pmatrix}, \quad \mathfrak{F} = \begin{pmatrix} \kappa\omega E \\ 0 \end{pmatrix},$$

$$\mathfrak{V} = \begin{pmatrix} \epsilon M \\ (\pi + \omega)E - \phi M\left(1 - \frac{E}{C}\right) - \frac{r\chi}{\theta}\psi\left(\frac{\tau_s}{\tau_d}\right)E_R \end{pmatrix}.$$

The Jacobian matrices F and V, associated with $\mathfrak{F}$ and $\mathfrak{V}$, respectively, at the vector free equilibrium $M^* = 0$, $E^* = 0$ are

$$F = \begin{pmatrix} 0 & \kappa\omega \\ 0 & 0 \end{pmatrix}, \quad V = \begin{pmatrix} \epsilon & 0 \\ -\phi & (\pi + \omega) \end{pmatrix},$$

$$V^{-1} = \begin{pmatrix} \frac{1}{\epsilon} & 0 \\ \frac{\phi}{\epsilon(\pi+\omega)} & \frac{1}{\pi+\omega} \end{pmatrix},$$

$$K = FV^{-1} = \begin{pmatrix} \frac{\kappa\omega\phi}{\epsilon(\pi+\omega)} & \frac{\kappa\omega}{\pi+\omega} \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues of K are 0 and $\frac{\kappa\omega\phi}{\epsilon(\pi+\omega)}$, so the mosquito urban net reproductive rate is given by

$$R_M^u = \frac{\kappa\omega\phi}{\epsilon(\pi+\omega)}$$

The meaning of the parameter R_M^u is the average number of mosquitoes produced by a single mosquito during her lifetime in the urban area.

Appendix B. Rural net reproductive rate

In the following we determine the vector demography, we start with rural net reproductive rate, for this we consider the equations for mosquitoes in rural area, that is $\dot{M}_{SR}$, $\dot{M}_{IR}$, $\dot{E}_{SR}$ and $\dot{E}_{IR}$. Also $\dot{M} = \dot{M}_{SR} + \dot{M}_{IR}$ and $\dot{E} = \dot{E}_{SR} + \dot{E}_{IR}$, then we have the following system:

$$\dot{M} = \kappa\omega E - \epsilon M,$$

$$\dot{E} = \phi M - (\pi + \omega + \frac{r}{\theta})E. \tag{B.1}$$

We calculate the net reproductive rate using the method of (Diekmann et al., 1990). We write the system (B.1) as $\dot{\mathfrak{x}} = \mathfrak{F} - \mathfrak{V}$:

$$\dot{\mathfrak{x}} = \begin{pmatrix} \dot{M} \\ \dot{E} \end{pmatrix}, \quad \mathfrak{F} = \begin{pmatrix} \kappa\omega E \\ 0 \end{pmatrix}, \quad \mathfrak{V} = \begin{pmatrix} \epsilon M \\ (\pi+\omega+\frac{r}{\theta})E - \phi M\left(1-\frac{E}{C}\right) \end{pmatrix}.$$

The Jacobian matrices F and V, associated with $\mathfrak{F}$ and $\mathfrak{V}$, respectively, at the vector free equilibrium $M^* = 0$, $E^* = 0$ are

$$F = \begin{pmatrix} 0 & \kappa\omega \\ 0 & 0 \end{pmatrix}, \quad V = \begin{pmatrix} \epsilon & 0 \\ -\phi & (\pi+\omega+\frac{r}{\theta}) \end{pmatrix},$$

$$V^{-1} = \begin{pmatrix} \frac{1}{\epsilon} & 0 \\ \frac{\phi}{\epsilon(\pi+\omega+\frac{r}{\theta})} & \frac{1}{\pi+\omega+\frac{r}{\theta}} \end{pmatrix},$$

$$K = FV^{-1} = \begin{pmatrix} \frac{\kappa\omega\phi}{\epsilon(\pi+\omega+\frac{r}{\theta})} & \frac{\kappa\omega}{\pi+\omega+\frac{r}{\theta}} \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues of K are 0 and $\frac{\kappa\omega\phi}{\epsilon(\pi+\omega+\frac{r}{\theta})}$, so the rural net reproductive rate is given by

$$R_M^r = \frac{\kappa\omega\phi}{\epsilon(\pi+\omega+\frac{r}{\theta})}.$$

Where R_M^r is the average number of mosquitoes produced by a single mosquito during her lifetime in rural area. On the other hand, the system (B.1) has two stationary states $E^* = M^* = 0$ and $M^* = \frac{C\kappa\omega}{\epsilon}\left(\frac{R_M^r-1}{R_M^r}\right)$, $E^* = C\left(\frac{R_M^r-1}{R_M^r}\right)$.

Linearization around the trivial stationary solutions requires calculation of the Jacobian matrix around the equilibrium point (0, 0)

$$\mathbf{DF(0, 0)} = \begin{pmatrix} -\epsilon & \kappa\omega \\ \phi & -(\pi+\omega+\frac{r}{\theta}) \end{pmatrix}.$$

This obtains the following characteristic polynomial:

$$\lambda^2 + (\epsilon + \pi + \omega + \frac{r}{\theta})\lambda + \epsilon(\pi+\omega+\frac{r}{\theta})(1-R_M) = 0$$

whose roots are of the shape

$$\lambda_\pm = \frac{1}{2}\left(\gamma \pm \sqrt{\xi}\right)$$

where $\gamma = -(\epsilon + \pi + \omega + \frac{r}{\theta})$, $\xi = \gamma^2 - 4\Xi$ and $\Xi = \epsilon(\pi+\omega+\frac{r}{\theta})(1-R_M)$.

Appendix C. Basic reproduction number without vertical

In the following we calculate the basic reproduction number in urban area. The infected classes in the urban model are I_U, E_{IU} and M_{IU}, so the matrices $\mathfrak{F}$ and $\mathfrak{V}$ take the following shape:

$$\mathfrak{F} = \begin{pmatrix} \alpha\frac{S_U}{N_U}M_{IU} \\ 0 \\ \alpha\frac{I_U}{N_U}M_{SU} \end{pmatrix} \quad \mathfrak{V} = \begin{pmatrix} (\eta+\gamma)I_{IU} \\ (\pi+\omega)E_{IU} - \frac{r}{\theta}\chi\psi(\tau_s/\tau_d)E_{IR} \\ \epsilon M_{IU} - \kappa\omega E_{IU} \end{pmatrix}$$

The Jacobian matrices are

$$F = \begin{pmatrix} 0 & 0 & \alpha\frac{S_U}{N_U} \\ 0 & 0 & 0 \\ \alpha\frac{M_{SU}}{N_U} & 0 & 0 \end{pmatrix} \quad V = \begin{pmatrix} (\eta+\gamma) & 0 & 0 \\ 0 & (\pi+\omega) & 0 \\ 0 & -\kappa\omega & \epsilon \end{pmatrix}$$

$$V^{-1} = \begin{pmatrix} \frac{1}{(\eta+\gamma)} & 0 & 0 \\ 0 & \frac{1}{\pi+\omega} & 0 \\ 0 & \frac{\kappa\omega}{\epsilon(\pi+\omega)} & \frac{1}{\epsilon} \end{pmatrix}$$

We evaluated the Jacobian matrices at the disease free equilibrium $S_U = N_U$, $M_{SU} = M_U$, $E_{SU} = E_U$, $I_U = M_{IU} = E_{IU} = 0$. The eigenvalues of $K = FV^{-1}$ since the basic reproduction number is the spectral radius. The maximum of the eigenvalues of K will be the basic reproduction number.

$$K = \begin{pmatrix} 0 & \frac{\alpha\kappa\omega}{\epsilon(\pi+\omega)} & \frac{\alpha}{\epsilon} \\ 0 & 0 & 0 \\ \frac{\alpha N}{(\eta+\gamma)M^*} & 0 & 0 \end{pmatrix}$$

There are three eigenvalues, one of them is zero, the other is smaller, so the maximum is

$$R_0^u = \sqrt{\frac{\alpha N}{(\mu+\gamma)M^*}\frac{\alpha}{\epsilon}}.$$

The basic reproduction number without vertical transmission in urban area R_0^u is the expected number of secondary cases produced by a single infection in a completely susceptible urban population

Appendix D. Basic reproduction number in rural area

We calculated the basic reproduction number in rural area using the next generation matrix method $\dot{\mathfrak{x}} = \mathfrak{F} - \mathfrak{V}$ (Diekmann et al., 1990). The infected classes in the rural model are: I_R, E_{IR} and M_{IR}. The information is separated into two matrices, the first one corresponding to new infection and the second corresponding to disease progression, that is

$$\dot{\mathfrak{x}} = \begin{pmatrix} \dot{I} \\ \dot{E}_{IR} \\ \dot{M}_{IR} \end{pmatrix}$$

$$\mathfrak{F} = \begin{pmatrix} \alpha\frac{S_R}{N_R}M_{IR} \\ \nu\phi M_{IR}\left(1-\frac{E_R}{C_r}\right) \\ \alpha\frac{I_R}{N_R}M_{SR} \end{pmatrix} \quad \mathfrak{V} = \begin{pmatrix} (\eta+\gamma)I_{IR} \\ (\pi+\omega+\frac{r}{\theta})E_{IR} \\ \epsilon M_{IR} - \kappa\omega E_{IR} \end{pmatrix}$$

The Jacobian matrices are

$$F = \begin{pmatrix} 0 & 0 & \alpha \frac{S_R}{N_R} \\ 0 & -\frac{\nu\phi M_{IR}}{C_r} & \nu\phi\left(1 - \frac{E_R}{C_r}\right) \\ \alpha \frac{M_{SR}}{N_R} & 0 & 0 \end{pmatrix}$$

$$V = \begin{pmatrix} (\eta + \gamma) & 0 & 0 \\ 0 & (\pi + \omega) + \frac{r}{\theta} & 0 \\ 0 & -\kappa\omega & \epsilon \end{pmatrix}$$

$$V^{-1} = \begin{pmatrix} \frac{1}{(\eta+\gamma)} & 0 & 0 \\ 0 & \frac{\theta}{\theta(\pi+\omega)+r} & 0 \\ 0 & \frac{\theta\kappa\omega}{\epsilon(\theta(\pi+\omega)+r)} & \frac{1}{\epsilon} \end{pmatrix}$$

We evaluated the Jacobian matrices at the disease free equilibrium $S_R = N_R$, $M_{SR} = M_R$, $E_{SR} = E_R$, $I_R = M_{IR} = E_{IR} = 0$. Then we found the eigenvalues of $K = FV^{-1}$; from this we need the maximum of the eigenvalues of K, which is the basic reproductive number.

$$K = \begin{pmatrix} 0 & \frac{\alpha\theta\kappa\omega}{\epsilon(\theta(\pi+\omega)+r)} & \frac{\alpha}{\epsilon} \\ 0 & \frac{\nu\phi\theta\kappa\omega}{\epsilon(\theta(\pi+\omega)+r)}\left(1 - \frac{E}{C_r}\right) & \frac{\nu\phi}{\epsilon}\left(1 - \frac{E}{C_r}\right) \\ \frac{\alpha N}{M^*\eta+\gamma} & 0 & 0 \end{pmatrix}$$

There are three eigenvalues, one of them is zero, the other is smaller, so the maximum is

$$R_0^r = \frac{1}{2}\frac{\nu\phi\kappa\omega\theta}{\epsilon(\theta(\pi+\omega)+r)}\left(1 - \frac{E_R^*}{C_r}\right)$$
$$+ \frac{1}{2}\sqrt{\left(\frac{\nu\phi\kappa\omega\theta}{\epsilon(\theta(\pi+\omega)+r)}\left(1 - \frac{E_R^*}{C_r}\right)\right)^2 + \frac{4\alpha}{\epsilon}\frac{\alpha N}{(\eta+\gamma)M^*}}.$$

The basic reproduction number in rural area R_0^r is the expected number of secondary cases produced by a single infection in a completely susceptible rural population

Appendix E. Basic reproduction number in urban area

To calculate the basic reproduction number in urban area we consider the infected classes in the urban model, that is I_U, E_{IU} and M_{IU}, so the matrices $\mathfrak{F}$ and $\mathfrak{V}$ take the following form:

$$\mathfrak{F} = \begin{pmatrix} \alpha \frac{S_U}{N_U} M_{IU} \\ \nu\phi M_{IU}\left(1 - \frac{E_U}{C_u}\right) \\ \alpha \frac{I_U}{N_U} M_{SU} \end{pmatrix} \quad \mathfrak{V} = \begin{pmatrix} (\eta+\gamma)I_{IU} \\ (\pi+\omega)E_{IU} - \frac{r}{\theta}\chi\psi(\tau_s/\tau_d)E_{IR} \\ \epsilon M_{IU} - \kappa\omega E_{IU} \end{pmatrix}$$

The Jacobian matrices are

$$F = \begin{pmatrix} 0 & 0 & \alpha \frac{S_U}{N_U} \\ 0 & -\frac{\nu\phi M_{IU}}{C_u} & \nu\phi\left(1 - \frac{E_U}{C_u}\right) \\ \alpha \frac{M_{SU}}{N_U} & 0 & 0 \end{pmatrix}$$

$$V = \begin{pmatrix} (\eta+\gamma) & 0 & 0 \\ 0 & (\pi+\omega) & 0 \\ 0 & -\kappa\omega & \epsilon \end{pmatrix}$$

$$V^{-1} = \begin{pmatrix} \frac{1}{(\eta+\gamma)} & 0 & 0 \\ 0 & \frac{1}{\pi+\omega} & 0 \\ 0 & \frac{\kappa\omega}{\epsilon(\pi+\omega)} & \frac{1}{\epsilon} \end{pmatrix}$$

We evaluated the Jacobian matrices at the disease free equilibrium $S_U = N_U$, $M_{SU} = M_U$, $E_{SU} = E_U$, $I_U = M_{IU} = E_{IU} = 0$. We found the eigenvalues of $K = FV^{-1}$; the maximum of the eigenvalues of K is the basic reproduction number.

$$K = \begin{pmatrix} 0 & \frac{\alpha\kappa\omega}{\epsilon(\pi+\omega)} & \frac{\alpha}{\epsilon} \\ 0 & \frac{\nu\phi\kappa\omega}{\epsilon(\pi+\omega)}\left(1 - \frac{E_U}{C_u}\right) & \frac{\nu\phi}{\epsilon}\left(1 - \frac{E_U}{C_u}\right) \\ \frac{\alpha N}{(\eta+\gamma)M^*} & 0 & 0 \end{pmatrix}$$

There are three eigenvalues, one of them is zero, the other is smaller, so the maximum is

$$R_0^u = \frac{1}{2}\frac{\nu\phi\kappa\omega}{\epsilon(\pi+\omega)}\left(1 - \frac{E_U^*}{C_u}\right)$$
$$+ \frac{1}{2}\sqrt{\left(\frac{\nu\phi\kappa\omega}{\epsilon(\pi+\omega)}\left(1 - \frac{E_U^*}{C_u}\right)\right)^2 + \frac{4\alpha}{\epsilon}\frac{\alpha N}{(\eta+\gamma)M^*}}$$

The basic reproduction number in urban area R_0^r is the expected number of secondary cases produced by a single infection in a completely susceptible urban population.

The basic reproduction number of the complete model is the maximum of the two numbers, basic reproduction number in rural area and basic reproductive number in urban area.

$$R_0 = \max\{R_0^r, \ R_0^u\}$$

Appendix F. Number of transmissions from rural to urban area

To evaluate transmission from rural to urban dengue cases, we utilized the basic reproduction number of rural and urban area. The desired parameter is the number of infections an individual in the rural population would generate in the urban population through the movement of infected tires. For this we assume that dengue is endemic in the rural population. The infected classes in the full model are: $I_R, E_{IR}, M_{IR}, I_U, E_{IU}, M_{IU}$. The information is separated into two matrices, the first one corresponds to new infections $\mathfrak{F}$ and the second to disease progression $\mathfrak{V}$, that is

$$\mathfrak{F} = \begin{pmatrix} \alpha \frac{S_U}{N_U} M_{IU} \\ \nu\phi M_{IU}\left(1 - \frac{E_U}{C_u}\right) \\ \alpha \frac{I_U}{N_U} M_{SU} \\ \alpha \frac{S_R}{M_R} M_{IR} \\ \nu\phi M_{IR}\left(1 - \frac{E_R}{C_r}\right) \\ \alpha \frac{I_R}{N_R} M_{SR} \end{pmatrix} \quad \mathfrak{V} = \begin{pmatrix} (\eta+\gamma)I_{IU} \\ (\pi+\omega)E_{IU} - \frac{r}{\theta}\chi\psi(\tau_s/\tau_d)E_{IR} \\ \epsilon M_{IU} - \kappa\omega E_{IU} \\ (\eta+\gamma)I_{IR} \\ (\pi+\omega)E_{IR} + \frac{r}{\theta}E_{IR} \\ \epsilon M_{IR} - \kappa\omega E_{IR} \end{pmatrix}$$

The Jacobian matrices are

$$F = \begin{pmatrix} 0 & \alpha\frac{S_U}{N_U} & 0 & 0 & 0 & 0 \\ \alpha\frac{M_{SU}}{N_U} & 0 & 0 & 0 & 0 & 0 \\ 0 & \nu\phi\left(1-\frac{E_U}{C_u}\right) & -\frac{\nu\phi M_{IU}}{C_u} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \alpha\frac{S_R}{N_R} & 0 \\ 0 & 0 & 0 & \alpha\frac{M_{SR}}{N_R} & 0 & 0 \\ 0 & 0 & 0 & 0 & \nu\phi\left(1-\frac{E_R}{C_r}\right) & -\frac{\nu\phi M_{IR}}{C_r} \end{pmatrix}$$

$$V = \begin{pmatrix} (\eta+\gamma) & 0 & 0 & 0 & 0 & 0 \\ 0 & \epsilon & -\kappa\omega & 0 & 0 & 0 \\ 0 & 0 & (\pi+\omega) & 0 & 0 & -\frac{r}{\theta}\chi\,\psi\,(\tau_s/\tau_d) \\ 0 & 0 & 0 & (\eta+\gamma) & 0 & 0 \\ 0 & 0 & 0 & 0 & \epsilon & -\kappa\omega \\ 0 & 0 & 0 & 0 & 0 & (\pi+\omega+\frac{r}{\theta}) \end{pmatrix}$$

$$V^{-1} = \begin{pmatrix} \frac{1}{(\eta+\gamma)} & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{\epsilon} & \frac{\kappa\omega}{\epsilon(\pi+\omega)} & 0 & 0 & \frac{\kappa\omega r\chi}{\epsilon(\pi+\omega)(\theta(\pi+\omega)+r)}\psi\left(\frac{\tau_s}{\tau_d}\right) \\ 0 & 0 & \frac{1}{(\pi+\omega)} & 0 & 0 & \frac{r\chi}{(\pi+\omega)(\theta(\pi+\omega)+r)}\psi\left(\frac{\tau_s}{\tau_d}\right) \\ 0 & 0 & 0 & \frac{1}{(\eta+\gamma)} & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{\epsilon} & \frac{\kappa\omega\theta}{\epsilon(\theta(\pi+\omega)+r)} \\ 0 & 0 & 0 & 0 & 0 & \frac{\theta}{\theta(\pi+\omega+r)} \end{pmatrix}$$

We evaluated the Jacobian matrices at the disease free equilibrium, then found $K = FV^{-1}$. To get the number of disease transmissions from the rural to urban area we obtained K^3 with this matrix. In the column for the infectious rural population the following is obtained:

$$R_{r\to u} = \frac{\alpha\kappa\omega r\chi}{\epsilon(\omega+\pi)(\theta(\omega+\pi)+r)}\psi\left(\frac{\tau_s}{\tau_d}\right)\frac{\nu\phi}{\epsilon}\frac{\alpha}{(\eta+\gamma)}$$

Appendix G. Summary of reproduction number

- Urban net reproductive rate.

$$R_M^u = \frac{\kappa\omega\phi}{\epsilon(\pi+\omega)}$$

- Rural net reproductive rate.

$$R_M^r = \frac{\kappa\omega\phi}{\epsilon(\pi+\omega+\frac{r}{\theta})}$$

- Basic reproduction number without vertical transmission in urban area.

$$R_0^u = \sqrt{\frac{\alpha N}{(\mu+\gamma)M^*}\frac{\alpha}{\epsilon}}$$

- Basic reproduction number in urban area.

$$R_0^u = \frac{1}{2}\frac{\nu\phi\kappa\omega}{\epsilon(\pi+\omega)}\left(1-\frac{E_U^*}{C_u}\right)$$
$$+\frac{1}{2}\sqrt{\left(\frac{\nu\phi\kappa\omega}{\epsilon(\pi+\omega)}\left(1-\frac{E_U^*}{C_u}\right)\right)^2+\frac{4\alpha}{\epsilon}\frac{\alpha N}{(\eta+\gamma)M^*}}$$

- Basic reproduction number in rural area.

$$R_0^r = \frac{1}{2}\frac{\nu\phi\kappa\omega\theta}{\epsilon(\theta(\pi+\omega)+r)}\left(1-\frac{E_R^*}{C_r}\right)$$
$$+\frac{1}{2}\sqrt{\left(\frac{\nu\phi\kappa\omega\theta}{\epsilon(\theta(\pi+\omega)+r)}\left(1-\frac{E_R^*}{C_r}\right)\right)^2+\frac{4\alpha}{\epsilon}\frac{\alpha N}{(\eta+\gamma)M^*}}$$

- Number of transmissions from rural to urban area

$$R_{r\to u} = \frac{\alpha\kappa\omega r\chi}{\epsilon(\omega+\pi)(\theta(\omega+\pi)+r)}\psi\left(\frac{\tau_s}{\tau_d}\right)\frac{\nu\phi}{\epsilon}\frac{\alpha}{(\eta+\gamma)}$$

Appendix H

The stationary state of infected mosquitoes in the urban area M_{IU}^* is found from the solution of the following quadratic equation:

$$(R_o^u)^2(\eta+\gamma)\left(\frac{\eta+\gamma}{\beta}+N_u\right)(M_{IU}^*)^2$$
$$-(\eta+\gamma)\left((R_o^u)^2\left(\frac{\kappa\omega}{\beta}E_{IU}^*+N_UM_U\right)-\eta N_U\right)M_{IU}^*$$
$$-\frac{\kappa\omega}{\epsilon}\eta N_U E_{IU}^* = 0 \tag{H.1}$$

and E_{IU}^* is given by

$$E_{IU}^* = \frac{r\chi\,\psi\left(\frac{\tau_s}{\tau_d}\right)}{\theta(\omega+\pi)}E_{IR}^*$$

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