Invasion-analysis of stage-structured populations in temporally-varying environments

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June 19, 2018
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*Master’s Thesis in Engineering Physics, 30 ECTS* at the Department of Physics, Umeå University

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Abstract

Climate change may cause epidemic threats as species spreading human diseases invades previously unpopulated areas. A species can establish in new areas if they fulfills an invasion criterion. Two common invasion criteria are the long-term exponential growth-rate, $r$, and the basic reproduction number, $R_0$, that measures the population’s exponential growth in time and growth between generations respectively. Previous work have determined the long-term exponential growth-rate of the mosquito *Aedes aegypti*, a vector spreading dengue, zika and yellow fever, in Europe. However, in epidemiology $r$ is rarely used as invasion criterion, which makes their results difficult to communicate and interpret. A more commonly used invasion criterion is the basic reproduction number $R_0$. From this number, public health receives information about high-risk areas where they can vaccinate the population and prevent the mosquitoes from establishing by reducing breeding habitats. Here we extend the previous work by developing a method to calculate $R_0$ for *Aedes aegypti* and verify it by the results from previous studies. Using $R_0$ as invasion criterion we then predict the global distribution of *Aedes aegypti* during different climate change scenarios in the 21st century. One related to high emissions of greenhouse gases, RCP8.5, and one to low emissions, RCP2.6. We predict that the distribution of *Aedes aegypti* will expand towards higher latitudes at great speed during the 21st century assuming the high emission scenario RCP8.5. Assuming the low emission scenario RCP2.6, the distribution will not reach higher latitudes at the end of the 21st century. In Europe, the distribution covered 1.8% in the beginning of the 20th century and at the end of the 21st century the distribution will cover 10% assuming RCP8.5 and 2.0% assuming RCP2.6. This work underlines the importance of reducing global warming and to take other preventive actions to avoid major epidemic outbreaks. Since we also provide instructions and software to calculate both $r$ and $R_0$ for stage-structured models in periodic environments, we anticipate that this work will support more studies of this kind to better understand the epidemic threats from climate change.

Keywords: *Aedes aegypti*, Global distribution, Basic reproduction number, Long-term exponential growth-rate, Invasion criterias, Stage-structured models, Periodic environment, Global plotting program, Algorithms, Software
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1 Introduction

The world around us is rapidly changing. As the population and consumption increases, we use more energy, manufacture more cars and travel more often. This behavior has tremendous effects on the earth’s ecosystems as the emissions of greenhouse gases increase the surface temperature and new infrastructure decrease the access to natural habitats. Beginning in the 1950’s, these changes has accelerated in a trend that the world has never seen before (Steffen et al., 2015).

The changing environment does not only affects our human behavior, it also affects the wild species of our planet. Overall, these changes have a negative impact on species since the mean abundance decreases rapidly (Steffen et al., 2015). However, these changes are not necessarily bad for all species, some may actually benefit from this. An increasing surface temperature may enable species preferring higher temperatures to invade previously unpopulated areas. These climate related invasions may also be true for species spreading human diseases, known as vectors.

A common vector is mosquitoes, most feared for spreading malaria and dengue. The worrying part of the spread of dengue mosquitoes is that most people get self-limiting symptoms by the first infection, while by the second infection the risk of developing more serious symptoms increases with death as a potential outcome (Ranjit and Kissoon, 2011). Due to the self-limiting symptoms of the first dengue infection, it is possible that the mosquitoes are already here, reproducing, with a potential epidemic outbreak ahead, we just haven’t noticed them, yet. Detecting the mosquitoes by manual field work is almost impossible in a large-scale and this is where simulations comes in. By predicting where the mosquitoes might be, now and in the future, one can concentrate the manual resources to likely (high-risk) areas, verifying the presence of the mosquitoes.

One way to predict where the mosquitoes might be is by calculating an invasion criterion that says if introduced mosquitoes will survive or go extinct. Two common invasion criteria is the long-term exponential growth-rate, \( r \), and the basic reproduction number, \( R_0 \), that measures the population’s exponential growth in time and growth between generations respectively. Little is known of the future distribution of \( Aedes aegypti \), a vector spreading dengue, zika and yellow fever (Kurane, 2010). However, a recent study from Liu-Helmersson et al. (2018) predicts the long-term exponential growth rate, \( r \), of these mosquitoes in Europe under different climate-change scenarios. In epidemiology however, \( r \) is rarely used as an invasion criterion, which makes their results difficult to communicate and interpret. A more commonly used invasion criterion is the basic reproduction number \( R_0 \). So, to predict and communicate the global threats, there is a need for a global study that uses the basic reproduction number as invasion criterion instead.

In this thesis, we implement the stage-structured demographic models from Liu-Helmersson et al. (2018) to verify their results of the long-term exponential growth rate of these mosquitoes across Europe under different climate-change scenarios. To illustrate the solutions, we provide a software that plots solutions on global maps. Then, a corresponding method for calculating the basic reproduction number, \( R_0 \), for this stage-structured population in a temporally-varying environment is developed and implemented. We then go beyond this...
study, predicting the mosquito invasion globally. This work will hence facilitate the communication of the results so that the potential epidemic threats will reach more. This is of importance since it can work as an incentive to reduce global warming, and by communicating the threat, it can lead humans to take other preventive actions to avoid major epidemic outbreaks.

In the next section, we begin with presenting the stage-structured mosquito model. In appendix A we present additional information of the model parameters. Then we present the method for calculating both $r$ and $R_0$ for stage-structured models in periodic environments. In appendix B and C we present additional theory to these methods and algorithms with corresponding software available on Github. We then present some information of how we used these methods in our simulations. After that we present the main ideas behind the plotting program that we constructed to illustrate the solutions. This software is also available on Github. In the following section we present the results from the simulations with $r$ for *Aedes aegypti* in Europe and compare them to previous studies. Then we show that $R_0$ produce similar results before we use it in our future predictions of the global distribution of *Aedes aegypti*. At the end of this thesis, we conclude by future perspectives.
2 Method

2.1 Mosquito model

In this model, we use three stages of *Aedes aegypti*: larvae, pupa and female adults. Let us denote them by $L$, $P$ and $A$ respectively. The flowchart of this system is shown in figure 1.

![Flowchart of mosquito model](image)

**Figure 1:** Modeled life cycle of *Aedes aegypti*. The modeled life cycle of *Aedes aegypti* where we only consider females. The transition rates are denoted $\sigma_A$ from female adults via eggs to larvae, $\sigma_L$ from larvae to pupae and $\sigma_P$ from pupae to female adults. The mortality rates are denoted $\mu_A$ for female adults, $\mu_L$ for larvae and $\mu_P$ for pupae. The original image is from ENVIS Centre on Climate Change and Public Health (2016).

The natural mortality rates are denoted by $\mu_i$ and the stage-transition rates by $\sigma_i$, where the index $i \in \{L, P, A\}$ indicates from which stage the transition goes, including mortalities. All of these parameters depend on climate conditions, such as temperature and precipitation, explicitly and hence implicitly on time (see appendix A for additional information of the model parameters). The dynamics of the mosquito stages is given in matrix form as

$$
\begin{bmatrix}
\frac{dL}{dt} \\
\frac{dP}{dt} \\
\frac{dA}{dt}
\end{bmatrix} =
\begin{bmatrix}
-\sigma_L - \mu_L & 0 & \sigma_A \\
\sigma_L & -\sigma_P - \mu_P & 0 \\
0 & \sigma_P & -\mu_A
\end{bmatrix}
\begin{bmatrix}
L \\
P \\
A
\end{bmatrix},
$$

(1)

or

$$
\frac{dx}{dt} = M(t)x
$$

(2)
if we denote $x \equiv [L, P, A]^T$ and the parameter matrix with $M(t)$.

### 2.2 Long-term exponential growth-rate

The long-term exponential growth-rate $r$ for a stage-structured model like equation 2 can be calculated by assuming that the environment is periodic. This means that if we want to calculate $r$ over the 1950s, we assume that the environment in the 1950s is repeated before and after, over and over again. Let’s denote the period of the environment by $T$. With this assumption, $r$ can be calculated from the fundamental solution of equation 2,

$$\frac{dF}{dt} = M(t)F$$  \hspace{1cm} (3)

from $t_0$ to $t_0 + T$ with the identity matrix as initial condition (for further information see appendix B). Let’s denote this solution $F(t_0 + T, t_0)$. The elements $F_{ij}(t_0 + T, t_0)$ can be interpreted as the number of individuals of type $i$ at time $t$ that one individual of type $j$ at time $t_0$ has given rise to, including descendants. This equation only has a closed form solution if $M$ is constant, then

$$F(t, t_0) = \exp(M \cdot (t - t_0))F(t_0, t_0) = \exp(M \cdot (t - t_0))I.$$  \hspace{1cm} (4)

Since this generally is not the case, we have to solve equation 3 numerically. We start with discretizing time into $N + 1$ time steps with $\Delta t = \frac{T}{N}$,

$$t_k = t_0 + k\Delta t \quad k = 0, 1, \ldots, N.$$  \hspace{1cm} (5)

If we then assume that $M$ is constant on each time interval,

$$M(t) = M_{kc} \quad t \in [t_k, t_{k-1}],$$  \hspace{1cm} (6)

we can approximate $F$ at each time from the exponential solution in equation 4 as

$$F(t_k, t_0) \approx \exp(M_{kc}\Delta t)F(t_{k-1}, t_0).$$  \hspace{1cm} (7)

By taking $M$ as the average between the time steps

$$M_{kc} = (M(t_k) + M(t_{k-1}))/2,$$  \hspace{1cm} (8)

we get an approximation of the fundamental solution from $t_0$ to $t_0 + T$ as

$$F(t_0 + T, t_0) \approx \prod_{k=1}^{N} \exp\left(\frac{(M(t_k) + M(t_{k-1}))\Delta t}{2}\right).$$  \hspace{1cm} (9)
Knowing $F(t_0 + T, t_0)$ we can calculate $r$ as

$$r = \log(\lambda)/T,$$

where $\lambda$ is the dominant real eigenvalue of $F(t_0 + T, t_0)$, further information is found in appendix B.

### 2.3 Preconditioning of the basic reproduction number

A general definition of the basic reproduction number $R_0$ in periodic environments, here with period $T$, was suggested by Bacaër and Guernaoui (2006). They propose that $R_0$ can be deduced from

$$\int_0^\infty A(t, \tau)w(t - \tau)d\tau = R_0w(t),$$

where $A(t, \tau)$ is a $n \times n$ matrix function and $w(t)$ a $T$–periodic vector function (the full definition is given in appendix B). The element $A_{ij}(t, \tau)$ represents the expected number of individuals of type $i$ born per unit of time at time $t$ by one individual of type $j$ that was born at time $t - \tau$. To clarify, in the mosquito model adults give rise to larvae, hence $A_{11}(t, \tau)$ can be thought of as the number of adults at time $t$ that one larva that was born at time $t - \tau$ has given rise to, times the rate that adults give rise to larvae at time $t$. So, for this case one can note that $A_{11}(t, \tau)$ can be expressed as the birth-rate at time $t$ times the $(3, 1)$ element of the matrix solution from $t - \tau$ to $t$. However, since $R_0$ describes the growth-rate per generation, we need to remain on the same generation when counting the expected number of adults that the larva has given rise to. Therefore, the matrix solution should be obtained without descendants, i.e with $\sigma_A(t) = 0$, let’s denote this solution $F^A(t, t - \tau)$. Otherwise, $\sigma_A(t)$ is not replaced by zero. Knowing $F^A(t, t - \tau)$ we can express $A_{11}(t, \tau)$ as

$$A_{11}(t, \tau) = \sigma_A(t)F^A_{31}(t, t - \tau).$$

Since $R_0$ is a scalar that maps the population from one generation to the next one it is equal for all stages, therefore it is enough to look at one stage only (a more detailed explanation of $R_0$ is found in appendix B). This reduce equation 11 to a scalar function, i.e $A \to A$ and $w \to w$. In the mosquito case, we can choose to look at the larvae which implies that $A(t, \tau) = A_{11}(t, \tau)$, hence

$$A(t, \tau) = \sigma_A(t)F^A_{31}(t, t - \tau).$$

To solve equation 11 to get $R_0$ we first use a similar approach as Bacaër and Guernaoui (2006) to rewrite the equation to integrals from 0 to $T$. If we start with changing variables $\theta = t - \tau$, we have
\[
\int_{-\infty}^{t} A(t, t - \theta) w(\theta) d\theta = R_0 w(t).
\] (14)

We can then split the integral and use the periodicity of \( w(t) \) and \( A(t, t - \theta) \) (the environment) to go from an infinite integral to an integral from 0 to \( T \):

\[
R_0 w(t) = \int_{0}^{t} A(t, t - \theta) w(\theta) d\theta + \int_{-\infty}^{0} A(t, t - \theta) w(\theta) d\theta =
\]

\[
\int_{0}^{t} A(t, t - \theta) w(\theta) d\theta + \sum_{n=0}^{\infty} \int_{0}^{T} A(t, t - \theta + (n + 1)T) w(\theta) d\theta =
\]

\[
\int_{0}^{T} A(t, t - \theta + (n + 1)T) w(\theta) d\theta + \int_{T}^{\infty} A(t, t - \theta + (n + 1)T) w(\theta) d\theta =
\]

\[
\sum_{n=0}^{\infty} \int_{0}^{t} A(t, t - \theta + nT) w(\theta) d\theta + \sum_{n=0}^{\infty} \int_{t}^{T} A(t, t - \theta + (n + 1)T) w(\theta) d\theta.
\] (15)

If we then define

\[
\hat{A}(t, \tau) = \sum_{n=0}^{\infty} A(t, \tau + nT),
\] (16)

we have that

\[
\int_{0}^{t} \hat{A}(t, t - \theta) w(\theta) d\theta + \int_{t}^{T} \hat{A}(t, t - \theta + T) w(\theta) d\theta = R_0 w(t).
\] (17)

Since we now have reduced this problem such that it only includes terms of \( w \) on the interval \([0, T]\), this problem is getting suitable for a numerical approach.

**2.4 Numerical approach of the basic reproduction number**

To obtain \( R_0 \) from equation 17 we need to be able to evaluate \( \hat{A} \). Expanding \( \hat{A} \) we have

\[
\hat{A}(t, \tau) = \sum_{n=0}^{\infty} A(t, \tau + nT) = \sigma_A(t) \left( \sum_{n=0}^{\infty} F^A(t, t - \tau - nT) \right).
\] (18)

Since the initial value of \( F^A \) is the identity matrix, one can shift its initial value by multiplying \( F^A \) with a constant matrix from the right. This works since
a constant matrix multiplication from the right does not change the original equation, i.e let $\hat{F} = F^A C$, then $\hat{F}(t_0, t_0) = I C$ and

$$\frac{dF^A}{dt} = M(t)F^A,$$ (19)

which is equivalent to equation 48 if one multiply both sides with $C^{-1}$ from the right. This implies that we can factorize the solution, i.e look at the solution from a time $t_0$ to a time $t_2$ with an as a solution from an intermediate time $t_1$ to $t_2$ with a solution from $t_0$ to $t_1$ as initial condition,

$$F^A(t_2, t_0) = F^A(t_2, t_1)F^A(t_1, t_0).$$ (20)

Using this possibility to change initial conditions the addends in equation 18 can be expressed as

$$F^A(t, t - \tau - nT) = F^A(t, t - \tau)F^A(t - \tau, t - \tau - nT).$$ (21)

Again, using the possibility to factorize $F^A$ we can express last term in equation 21 as

$$F^A(t - \tau, t - \tau - nT) = \prod_{k=1}^{n} F^A(t - \tau - (k - 1)T, t - \tau - kT).$$ (22)

Since the factors only considers one period $T$ and the environment is $T$-periodic, all factors will be equivalent. Hence, we can express them as

$$F^A(t - \tau - (k - 1)T, t - \tau - kT) = F^A(t - \tau, t - \tau - T) \quad k = 1, 2, ..., n, \quad (23)$$

which gives

$$F^A(t - \tau, t - \tau - nT) = F^A(t - \tau, t - \tau - T)^n.$$ (24)

Inserting this into equation 18, we get $\hat{A}$ as

$$\hat{A}(t, \tau) = \sigma_A(t) \left( F^A(t, t - \tau) \sum_{n=0}^{\infty} F^A(t - \tau, t - \tau - T)^n \right)_{31}. \quad (25)$$

Since $\sigma_A(t) = 0$ when calculating $F^A$ and the identity matrix is the initial condition, pupae and female adults cannot give rise to any new larvae or pupae, hence $F^A$ will be lower triangular. With these conditions, one larva or pupa cannot give rise to more than one adult, hence $0 \leq F^A_{31} \leq 1$. Since the eigenvalues of a lower triangular matrix is the diagonal entries, all eigenvalues of
\( F^\Lambda(t - \tau, t - \tau - T) \) are less or equal to one in magnitude, which is the necessary condition for that the geometric series converges to

\[
\sum_{n=0}^{\infty} F^\Lambda(t - \tau, t - \tau - T)^n = (I - F^\Lambda(t - \tau, t - \tau - T))^{-1}. \tag{26}
\]

This would also be true if we chose to look at another stage in equation 13, such as pupae or adults. By using cofactor expansion on the determinant eigenvalue equation, one can see that the eigenvalues will be the diagonal elements for these matrices as well which will be less than or equal to one in magnitude.

Inserting equation 26 into equation 25 we find that

\[
\hat{A}(t, \tau) = \sigma_A(t) \left( F^\Lambda(t, t - \tau)(I - F^\Lambda(t - \tau, t - \tau - T))^{-1} \right)_{31}, \tag{27}
\]

which is affordable to calculate since it is finite in time. Knowing \( \hat{A}(t, \tau) \) it is possible to obtain \( R_0 \) from equation 17 by discretization of time

\[
t_k = k\Delta t \quad k = 0, 1, 2, \ldots, N, \tag{28}
\]

where \( \Delta t = T/N \) and then solve equation 17 for all \( t = t_k \) using a quadrature rule. Then one ends up with \( N + 1 \) equations

\[
\sum_{l=k}^{N} W_{kl} \hat{A}(t_k, t_k - t_l + T)w(t_l) = r_0 w(t_k), \quad k = 0, \tag{29}
\]

where \( V_{kl} \) and \( W_{kl} \) are weights for the quadrature rule. This can be written as an eigenvalue equation

\[
\hat{A}\tilde{w} = r_0 \tilde{w} \tag{30}
\]

where \( \hat{A} \) is a non-negative \((N + 1) \times (N + 1)\) matrix, \( \tilde{w} \) is a \((N + 1)\) column vector and \( r_0 \) is the spectral radius of the eigenvalue problem with the relation

\[
r_0 \xrightarrow{N \to \infty} R_0. \tag{31}
\]
The final part of the problem is then to fill the matrix $\tilde{A}$. From equation 20 it is possible to see that if one knows $F^A$ on each interval, then one can express $F^A$ at all times as matrix products, i.e

$$F^A(t_k, t_l) = \prod_{m=l+1}^{k} F^A(t_m, t_{m-1}).$$

(32)

Since solving the matrix differential equation often takes longer time than matrix multiplications, this is useful.

There are multiple options of how to factorize $F^A$, to avoid unnecessary calculations we need to look at the patterns in $\tilde{A}$. For simplicity, let’s define $\tilde{A} \equiv L + U$ where $L$ is a lower triangular matrix corresponding to the sum from $l = 0$ to $l = k$ and $U$ is a upper triangular matrix corresponding to the sum from $l = k$ to $l = N$ in equation 29, then

$$L_{kl} = \begin{cases} V_{kl} \tilde{A}(t_k, t_k - t_l) & k > 0, \ l \leq k, \\ 0 & \text{otherwise}, \end{cases}$$

$$U_{kl} = \begin{cases} W_{kl} \tilde{A}(t_k, t_k - t_l + T) & k < N, \ l \geq k, \\ 0 & \text{otherwise}. \end{cases}$$

(33)

If we expand the terms of $\tilde{A}$ that appears in $L$ and $U$ we have

$$\tilde{A}(t_k, t_k - t_l) = \sigma_A(t) \left( F^A(t_k, t_l)(I - F^A(t_l, t_l - T))^{-1} \right)_{31}$$

(34)

and

$$\tilde{A}(t_k, t_k - t_l + T) = \sigma_A(t) \left( F^A(t_k, t_l - T)(I - F^A(t_l - T, t_l - 2T))^{-1} \right)_{31}.$$ 

(35)

Since the environment is periodic

$$F^A(t_l - T, t_l - 2T) = F^A(t_l, t_l - T),$$

(36)

which we can factorize as

$$F^A(t_l, t_l - T) = F^A(t_l, t_0) F^A(t_0, t_1 - T) = F^A(t_l, t_0) F^A(t_N, t_l).$$

(37)

The terms in the inverse is hence the same for both matrices and changes column-wise in $\tilde{A}$, let’s define it as

$$F_{TI} \equiv (I - F^A(t_l, t_0) F^A(t_N, t_l))^{-1}. $$

(38)
In $L$, the diagonal elements contain the initial condition of $\mathbf{F}^\Lambda$ (the identity matrix) while the subdiagonal elements only considers one time step. For the rest of the elements $\mathbf{F}^\Lambda$ is elongated with one time step each row, hence it is suitable to express these terms recursively

$$
\mathbf{F}^\Lambda(t_k, t_l) = \mathbf{F}^\Lambda(t_k, t_{k-1})\mathbf{F}^\Lambda(t_{k-1}, t_l) \quad k \geq 1, \quad l < k - 1.
$$

(39)

This gives

$$
L_{kl} = V_{kl} \sigma_A(t_k) \begin{cases} 
(F_T)_{31} & k > 0, \quad l = k, \\
\mathbf{F}^\Lambda(t_k, t_l)F_T & k > 0, \quad l = k - 1, \\
\mathbf{F}^\Lambda(t_k, t_{k-1})\mathbf{F}^\Lambda(t_{k-1}, t_l)F_T & k > 1, \quad l < k - 1, \\
0 & \text{otherwise}.
\end{cases}
$$

(40)

In $U$, we can use the periodicity to factorize the terms of $\mathbf{F}^\Lambda$ as

$$
\mathbf{F}^\Lambda(t_k, t_l - T) = \mathbf{F}^\Lambda(t_k, t_0)\mathbf{F}^\Lambda(t_N, t_l),
$$

(41)

where $\mathbf{F}^\Lambda(t_k, t_0)$ appears in the first column of $L$ and $\mathbf{F}^\Lambda(t_N, t_l)$ appears at the last row of $L$, this gives

$$
U_{kl} = W_{kl} \sigma_A(t_k) \begin{cases} 
\mathbf{F}^\Lambda(t_N, t_l)F_T & k = 0, \quad l < N, \\
\mathbf{F}^\Lambda(t_k, t_0)F_T & k < N, \quad l = N, \\
\mathbf{F}^\Lambda(t_k, t_0)\mathbf{F}^\Lambda(t_N, t_l)F_T & 1 < k < N, \quad l < N, \\
0 & \text{otherwise}.
\end{cases}
$$

(42)

Defining the matrix in this way makes it suitable to to fill $\mathbf{A}$ column wise. Since in both $L$ and $U$, we have matrix products were we are only interested in the 3,1-element. To get this element, we only needs row 3 of the first matrix and column 1 of the last matrix, which reduces the number of calculations. An algorithm that uses this is found in appendix C, which can be used for other stage-structured models as well.

### 2.5 Information about the simulations

Since the mosquito model is dependent on temperature and precipitation, we have used monthly CRU TS3.25 temperature and precipitation data and interpolated into daily for the past. For the future, we have used daily data averaged from the five ISIMIP models for two emission scenarios, one high emission (RCP8.5) and one low emission (RCP2.6).
For the $R_0$ future predictions we needed to reduce the computational time for each grid point as much as possible since we have a lot of grid points for different climate scenarios during several decades. Therefore we restricted ourselves to use only the endpoints of each time interval, hence

$$V_{kl} = \Delta t \begin{cases} 1 & k > 0, \quad 0 < l \leq k \\ 0 & \text{otherwise} \end{cases}$$

$$W_{kl} = \Delta t \begin{cases} 1 & k > 0, \quad k < l \\ 0 & \text{otherwise} \end{cases} . \quad (43)$$

For the same reason, we also implemented an adaptive power iteration method for the eigenvalue problem that used more iterations near the critical value $R_0 = 1$. We have used MATLAB for all implementations.

### 2.6 Global plotting program

To illustrate the solutions for the mosquito model we needed a global plotting program. The main idea behind the plotting program was to triangulate the land areas with the solutions points as nodes, then to interpolate the solution over each triangle.

To achieve this, the MATLAB-program first loads the coastal coordinates then uses a Winkel-Tripel projection (Kessler, 2000) on them. This can be seen in figure 2 a) for the whole world. If we are only interested in a certain area between some latitudes and longitudes, it can be chosen as in figure 2 b). For the selected area, the program locates all solution points inside this land area, seen in figure 2 c). Then, the program interpolates the solution from these points to the other points needed to describe this land area, i.e points at boundaries, shown in figure 2 d). Knowing the solutions on all points, a Delaunay triangulation is performed with the restriction that all triangles must be inside the land area, this is shown in figure 2 e). The solutions is then interpolated on each triangle using a specified colorbar, which can be seen in figure 2 f). The program is written as general as possible, which enables the user to specify certain areas, colorbar-, add a grid and to calculate the area with values above a certain threshold.
Figure 2: Illustrates how the plotting program works. a) the coastal coordinates plotted with a Winkel-Tripel projection and b) the possibility to specify a certain area between latitudes and longitudes of the globe. c) the points with solution inside the land area and d) additional points in red needed to describe this area. e) a Delaunay triangulation of the points with the constraint that all triangles must be inside the land area and f) a solution interpolated over these triangles.
3 Results and Discussion

3.1 Verification of the long-term exponential growth-rate

Calculating the $r$ for the mosquito *Aedes aegypti* during each decade between 1901-2099 in the city of Athens, we find close to identical results as Liu-Helmersson et al. (2018). In figure 3, one can see a comparison of the results. These results illustrates the change in the *Aedes aegypti* distribution, the only decade in the 20th century when the climate in Athens was habitable for the mosquitoes was during 1931-1940. In the 21st century however, the climate in Athens will be habitable for the mosquitoes during all decades.

![Graph](image)

**Figure 3:** *Aedes aegypti* decadal $r$ in Athens during 1901-2099. Comparison between a) our results and b) the result from Liu-Helmersson et al. (2018). Model parameters are based on interpolated monthly temperature and precipitation data from CRU TS3.25 for the past (with coastal correction of 1.34 °C (Liu-Helmersson et al., 2018)) and an average of the five ISIMIP RCP8.5 and RCP2.6 models for the future.

Predicting the future scenarios for Europe, we find, as well Liu-Helmersson et al. (2018), that already in 2051-2060, *Aedes aegypti* may invade major parts of southern Europe assuming the high emission scenario RCP8.5. In figure 4 one can see that the results corresponds well. One can however note that our plot has higher resolution and that the color scales is slightly different. In our plot the blue colors correspond to negative growth-rate and red to positive, while Liu-Helmersson et al. (2018) uses green colors to indicate areas with close to positive growth-rates.
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Figure 4: Aedes aegypti decadal $r$ in Europe for RCP8.5 during 2051-2060. Comparison between a) our results and b) the result from Liu-Helmersson et al. (2018). Model parameters are based on interpolated monthly temperature and precipitation data from an average of the five ISIMIP RCP8.5 models.

For the results above, we have used monthly data interpolated into daily. This means that we will not have larger variations in weather between days that one sometimes see in reality. However, since there are daily data available for the future climate models that recreates these variations, we can see how this approximation effects the result. In the figure 5, one can see that in general this approximation works well but that it slightly overestimates the growth-rate in some areas, e.g southern France.

Figure 5: Aedes aegypti decadal $r$ in Europe for RCP8.5 during 2051-2060. Comparison between a) interpolated monthly data and b) daily data. Model parameters are based on data from an average of the five ISIMIP RCP8.5 models.

The other approximation we use is that we average the climate predictions by the different models instead of treating them separately and average the results. In figure 6 one can see that overall the results are similar but when averaging the models the result will be overestimated in some areas, e.g the boundary to the northern parts of Europe as well as parts of central Europe and Balkans.
3.2 Verification of the basic reproduction number

To verify that our model of $R_0$ works, we chose a constant environment and calculated the theoretical value of $R_0$. We then calculated $R_0$ numerically for different periods and time steps. In figure 7 one can see that with longer period one needs more time steps to reach the theoretical value.

Since $R_0 > 1$ when $r > 0$, we also verify the results for $R_0$ by comparing it to $r$. In figure 8 one can see a comparison between $R_0$ and $r$ for the city of Athens. The figure shows that $R_0 > 1$ coincides with $r > 0$. 

Figure 6: *Aedes aegypti* decadal $r$ in Europe for RCP8.5 during 2051-2060. Comparison between a) averaging the climate models and b) treating each model separately and average the result. Model parameters are based on interpolated monthly data from the five ISIMIP RCP8.5 models.

Figure 7: $R_0$ in a constant environment. The solid line shows the theoretical value and the dashed lines the solution for different periods and time steps. Model parameters are based on a chosen temperature of 14°C and precipitation of 15 mm/day.
Figure 8: Decadal $R_0$ and $r$ for \textit{Aedes aegypti} in Athens during 1901-2099. Comparison between $R_0$ (dashed blue lines) and $r$ (solid red lines) for each decade in the 20th and 21st century in Athens. Model parameters are based on interpolated CRU TS3.25 monthly temperature (with coastal correction of 1.34°C (Liu-Helmersson et al., 2018)) and precipitation data for the past. For the future they are based on an interpolation of monthly data from an average of the five ISIMIP RCP8.5 models and ISIMIP RCP2.6 models.

3.3 Predictions of global distribution during climate change

During the 20th century, we only see minor changes in the habitable areas of \textit{Aedes aegypti} in Europe. Figure 9 shows that during 1901-1910 there are almost no habitable areas but during 2001-2010 there are some areas around southern Spain and Italy where the mosquitoes might be present. Since our calculations predicts if introduced mosquitoes would survive or go extinct, it really shows the habitable areas of the mosquitoes. With todays global trade and travel, we assume that mosquitoes will be introduced and therefore our results should show a prediction of the actual distribution of the mosquitoes.

Figure 9: \textit{Aedes aegypti} decadal $R_0$ in Europe during 1901-1910 and 2001-2010. Comparison between $R_0$ during a) 1901-1910 and b) 2001-2010. Model parameters are based on interpolated monthly data from CRU TS3.25.
Looking into the future we see major differences in the distribution in Europe. In figure 10 we see that assuming the low emission scenario RCP2.6, the distribution is restricted to southern Spain and Portugal but assuming the high emission scenario RCP8.5 major parts of southern Europe will be affected.

![Figure 10: Aedes aegypti decadal $R_0$ in Europe for RCP2.6 and RCP8.5 during 2021-2030, 2051-2060 and 2091-2099. Comparison between $R_0$ for RCP2.6 to the left and RCP8.5 to the right for three decades, 2021-2030 (a) and b)), 2051-2060 (c) and d)) and 2091-2099 (e) and f)). Model parameters are based on daily temperature and precipitation data from an average of the five ISIMIP RCP2.6 and RCP8.5 models.]

To visualize the differences, figure 11 shows the percentage of the area in the European plots above with $R_0 > 1$. The figure clearly shows that assuming RCP2.6 the distribution will be restricted to 2% of Europe throughout this century while assuming RCP8.5 the distribution will increase to cover 10% of
Europe which may cause major epidemic problems.

![Graph showing decadal $R_0 > 1$ areas in Europe for Aedes aegypti](image)

**Figure 11: Area with decadal $R_0 > 1$ in Europe for Aedes aegypti in Europe during 1901-2099.** Percentage of the area with $R_0 > 1$ for three decades in the past 1901-1910, 1951-1960 and 2001-2010 and three decades in the future 2021-2030, 2051-2060 and 2091-2099. Model parameters are based on interpolated monthly data from CRU TS3.25 for the past and an average of daily data from the five ISIMIP RCP8.5 and RCP2.6 models for the future.

Looking back at the distribution globally, we see in figure 12 that already in the beginning of the 20th century, the distribution covered major parts of the lower latitudinal areas and that the distribution has expanded towards higher latitudes until the beginning of the 21st century, e.g South Africa and Australia. Looking at the maps we also see that our calculations predict that Aedes aegypti might be present in some areas with low precipitation, i.e parts of Australia. This might show a weakness of the mosquito model. Since larvae and pupae of the Aedes aegypti is dependent on water, areas where the mosquitoes does not have access to water should be excluded. We have not verified if our predictions of the distribution is restricted to areas with access to water, further investigation on this is needed. But since the main food of Aedes aegypti outside the rain forest is humans (Siriyasatien et al., 2010) and humans often live close to water supplies, this issue could be addressed by including population density into the mosquito model as described by Liu-Helmersson et al. (2018).
Looking at the future scenarios, we again see large differences between the climate scenarios. In figure 13 one can see that the expansion towards higher latitudes is much more restricted for RCP2.6 than for RCP8.5, e.g China and Australia. The figure also shows that a great part of north Africa with a predicted distribution will assuming RCP8.5, lack a distribution in the future since the climate will be too extreme for *Aedes aegypti*.
Figure 13: Aedes aegypti decadal $R_0$ globally for RCP2.6 and RCP8.5 during 2021-2030, 2051-2060 and 2091-2099. Comparison between $R_0$ for RCP2.6 to the left and RCP8.5 to the right for three decades, 2021-2030 (a) and (b)), 2051-2060 (c) and (d)) and 2091-2099 (e) and (f)). Model parameters are based on daily temperature and precipitation data from an average of the five ISIMIP RCP2.6 and RCP8.5 models.

The expansion we mentioned earlier can also be visualized by the maximum latitudes that are habitable. Figure 14 shows a great increase for the northern hemisphere during the 20th century but more is to come assuming RCP8.5, on the southern hemisphere we see an even worse increase. On the other hand, assuming RCP2.6 this will not expand further in the north and in the south they will increase but then withdraw. Connecting the historical and future predictions, the historical shows an overestimation. The reason for this could be the overestimation we saw when comparing the results from monthly and daily data in figure 5.
Figure 14: Boundaries of $R_0 > 1$ for *Aedes aegypti* during 1901-2099. The a) northern and b) southern boundary of $R_0 > 1$ for three decades in the past 1901-1910, 1951-1960 and 2001-2010 and three decades in the future 2021-2030, 2051-2060 and 2091-2099. Model parameters are based on interpolated monthly data from CRU TS3.25 for the past and an average of daily data from the five ISIMIP RCP8.5 and RCP2.6 models for the future.

Looking at the percentage of the area that were habitable, we see a great increase during the 20th century in figure 15. For the future scenarios, we see a great decrease assuming RCP8.5 and a slight increase assuming RCP2.6. This might at first seem counterintuitive, but as seen in figure 13, the reason for this is that assuming the RCP8.5 major parts that were habitable will become inhabitable during the 21st century, especially in north Africa.

Figure 15: Area with decadal $R_0 > 1$ globally for *Aedes aegypti* during 1901-2099. Percentage of the area with $R_0 > 1$ for three decades in the past 1901-1910, 1951-1960 and 2001-2010 and three decades in the future 2021-2030, 2051-2060 and 2091-2099. Model parameters are based on interpolated monthly data from CRU TS3.25 for the past and an average of daily data from the five ISIMIP RCP8.5 and RCP2.6 models for the future.
4 Conclusions

We predict that the habitable areas of *Aedes aegypti* will increase towards higher latitudes. The difference between the high and low emission scenario is significant, where the high emission scenario shows a much greater increase. Thus reducing global warming is essential to decrease the spread of *Aedes aegypti*. If the emissions continue to increase, the distribution of *Aedes aegypti* will cause major epidemic problems in the 21st century as it extends to areas with large populations.

In the following months, we will extend this study, highlighting the epidemic threat by predicting the human population at risk of *Aedes aegypti* during the 21st century. By including population density into the model we will also exclude areas where the mosquitoes does not have access to food and water. However, one question still remaining after this study is if the withdraw we see of *Aedes aegypti* in north Africa during the 21st century will be true even for other insects, such as pollinators. If so, how will this effect the humans living in these areas?
References


Brännström, Å. (2018). Personal communication. Professor at the Department of Mathematics and Mathematical Statistics, Umeå University.


A Model Parameters

The behavior of the model parameters is presented in the figures below. One should note that the transition from female adults via eggs to pupae, $\sigma_A$, is fairly complicated but assuming that there is no density dependence and that there are full access to food, it is given by $\sigma_a = \phi q f$, where $\phi$ is the oviposition rate, $q$ the fraction of eggs hatching with a fraction $f = 1/2$ becoming female. For a more detailed explanation we refer to the supplementary of Liu-Helmersson et al. (2018).

![Figure 16: Temperature dependence of $\sigma_l$ and $\sigma_p$. The temperature dependence of the transition rate from a) larvae to pupa and from b) pupa to adults.](image1)

![Figure 17: Temperature dependence of $\Phi$ and $q$. The temperature dependence of a) the oviposition rate and b) the egg hatching fraction that is used to describe the transition from female adults to larvae.](image2)
Figure 18: Temperature and precipitation dependence of $\mu_l$ and $\mu_p$. The temperature and precipitation dependence of the mortality rates for a) larvae and b) pupae.

Figure 19: Temperature dependence of $\mu_a$. The temperature dependence of the female adult mortality rate.
B Invasion Criteria

Ecological systems can usually be described by a system of ordinary differential equations, written in matrix form we have

\[
\frac{dx}{dt} = Mx. \tag{44}
\]

The solution to the matrix differential equation above is given by the matrix exponential as

\[
x(t) = \exp(M \cdot (t - t_0)) x(t_0). \tag{45}
\]

If one instead have a similar system as in equation 44 but with coefficients that depends on time,

\[
\frac{dx}{dt} = M(t)x, \tag{46}
\]

then a general closed form solution similar to equation 45 does not exist. However, if the coefficients (or the environment) varies periodically with period \(T\), then equation 46 will, according to Floquet theory (Klausmeier, 2008) have a solution of the form

\[
x(t) = \sum_{i=1}^{n} c_i \exp(\mu_i t) p_i(t) \tag{47}
\]

where \(c_i\) are constants, \(\mu_i\) are Floquet exponents and \(p_i\) are periodic functions with period \(T\). Since the solution is given by sum of periodic functions, each multiplied with an exponential term, the long-term behavior of the system is determined by the Floquet exponents \(\mu_i\) (Klausmeier, 2008). To find the Floquet exponents, one can calculate the fundamental solution of equation 46,

\[
\frac{dF}{dt} = M(t)F, \tag{48}
\]

from \(t_0\) to \(t_0 + T\) with the identity matrix as initial conditions. We denote this solution \(F(t_0 + T, t_0)\). This matrix equation behaves like the vector equations 44 and 46. So, in similarity \(F\) is given as in equation 45 if \(M\) is constant. Otherwise it does not have a closed form solution. The interpretation of the element \(F_{ij}(t, t_0)\) is the number of individuals of type \(i\) at time \(t\) that one individual of type \(j\) at time \(t_0\) has given rise to. This means that if we know \(F(t, t_0)\) we can express the population as

\[
x(t) = F(t, t_0)x(t_0). \tag{49}
\]
Knowing $F(t_0 + T, t)$ we can calculate the Floquet exponents as

$$\mu_i = \log(\lambda_i)/T \tag{50}$$

where $\lambda_i$ is the eigenvalues of $F(t_0 + T, t_0)$ (Klausmeier, 2008). According to Perron-Frobenius theorem, this matrix will have a non-negative eigenvalue $\lambda$ greater than or equal to all other eigenvalues with a corresponding non-negative eigenvector. So, this will be the dominant term and thus determine the long-term exponential growth-rate of the population as (Brännström, 2018)

$$r = \log(\lambda)/T. \tag{51}$$

Hence, $r$ will be a measure of exponential growth-rate per time. In the long run it will map the population exponentially from one time to another, i.e. let $x(t)$ be the population at time $t$, then the population at a later time is

$$x(t + \tau) \approx \exp(r\tau)x(t). \tag{52}$$

Thus an $r > 0$ indicates that an introduced species will grow and an $r < 0$ indicates that they will go extinct. This type of measure, stating if a species can invade another area is called an invasion criterion.

Another invasion criterion is the basic reproduction number, $R_0$, that measures the growth-rate per generation. In other words, $R_0$ will in the long run map the population from one generation to the next one, i.e let $x_n$ be the population at generation $n$, then the population at the next generation is

$$x_{n+1} \approx R_0 x_n. \tag{53}$$

Thus an $R_0 > 1$ indicates that an introduced species will grow and an $R_0 < 1$ indicates that they will go extinct. With constant parameters or a constant environment, in other words $M$ is independent of time, then it is possible to calculate $R_0$ analytically. This could be done by starting with one individual of a stage, then calculate the probable number of new individuals of the next generation of this stage that this individual will give rise to (Brännström, 2018).

Let’s take the mosquito model as an example. We start with one larva, then the probability that this larvae becomes a pupa is $\sigma_l/\left(\sigma_l + \mu_l\right)$, using similar reasoning for the other stages we find

$$R_0 = \frac{\sigma_l}{\sigma_l + \mu_l} \frac{\sigma_p}{\sigma_p + \mu_p} \frac{\sigma_a}{\mu_a}. \tag{54}$$

On the other hand, if the parameters depend on time then this is not possible. In this case, we use the assumption of a periodic environment and turn to Bacaër and Guernaoui (2006) that have proposed a general definition of $R_0$ in periodic environments. They propose that for a $n \times n$ nonnegative, continuous matrix function $A(t, \tau)$, where the elements $A_{ij}(t, \tau)$ represents the expected number
of individuals of type $i$ born per unit of time at time $t$ by one individual of type $j$ that was born at time $t - \tau$. There exists a unique real number $R_0$ such that there exists a nonnegative, nonzero, continuous and $T$–periodic vector function $w(t)$ such that

$$\int_0^{\infty} A(t, \tau)w(t - \tau)d\tau = R_0 w(t)$$  \hfill (55)

if $A(t, \tau)$ is $T$–periodic with respect to $t$ for all $\tau$ and $\int_0^{\infty} A(t, \tau)d\tau$ is finite for all $t$. For a more detailed description of the biological interpretation of this equation we refer to the follow-up paper of Bacaër and Dads (2012).
C  Algorithms

In this section we provide algorithms to calculate \( r \) and \( R_0 \) for stage-structured models in periodic environments. The codes we used in our simulations together with the plotting program is available on Github.

C.1  Long-term exponential growth-rate

Algorithm 1 Long-term exponential growth-rate

1: procedure \( r(Nt,T,t_0,params) \)
2: Calculates the long-term exponential growth-rate for a system
3: \( \frac{dx}{dt} = M(t)x \)
4: where the matrix solution \( F \) to from the system from \( t_0 \) to \( t \) with
5: \( F(t_0) = F_0 \) (empty should imply \( F_0 = I \)) is given by the function
6: \( F(t,t_0,Nt,F_0,\text{params}) \)
7: \( M(t) \) is given by the function \( M(t,\text{params}) \)
8: \( Nt \) is the number of time steps,
9: \( T \) is the period of the environment,
10: \( t_0 \) is the initial time,
11: \( \text{params} \) contains necessary information about the environment
12: set \( F = F(t_0 + T,t_0,Nt,[],\text{params}) \)
13: calculate \( r \) as the spectral radius of \( F \)
14: return \( r \)
Algorithm 2 Matrix solution

1: procedure $F(t, t_0, Nt, F_0, params)$
2: Calculates the matrix solution to
3: $\frac{dF}{dt} = M(t)F$ from $t_0$ to $t$ with $F(t_0) = F_0$
4: where $M(t)$ is given by the function $M(t, params)$
5: $t$ is the final time,
6: $t_0$ is the initial time,
7: $Nt$ is the number of time steps,
8: $F_0$ is the initial condition (empty implies identity matrix),
9: $params$ contains necessary information about the environment
10: set the step length $\Delta t = (t - t_0)/Nt$
11: save half the step length $\Delta t_2 = \Delta t/2$
12: set $M_1 = M(t_0 + \Delta t, params)$
13: if $F_0$ is empty then
14: set $F_0$ to the identity of the size of $M_1$
15: set $F = \exp((M(t_0, params) + M_1)\Delta t_2) \cdot F_0$
16: for $i = 2$ to $Nt$ do
17: set $M_2 = M(t_0 + i\Delta t, params)$
18: update $F = \exp((M_1 + M_2)\Delta t_2) \cdot F$
19: set $M_1 = M_2$
20: return $F$
Algorithm 3 Improved matrix solution

1: procedure $F(t, t_0, N_t, F_0, params)$
2: Calculates the matrix solution to
3: \[ \frac{dF}{dt} = M(t)F \] from $t_0$ to $t$ with $F(t_0) = F_0$
4: where $M(t)$ is given by the function $M(t, params)$
5: $t$ is the final time,
6: $t_0$ is the initial time,
7: $N_t$ is the number of time steps,
8: $F_0$ is the initial condition (empty implies identity matrix),
9: $params$ contains necessary information about the environment
10: \[ t \]
11: \[ t_0 \]
12: \[ N_t \]
13: \[ F_0 \]
14: \[ params \]
15: \[ \Delta t \]
16: \[ M_1 \]
17: \[ M_2 \]
18: \[ D_1 \]
19: \[ D_2 \]
20: \[ i \]
21: \[ M_3 \]
22: \[ M_4 \]
23: \[ D_3 \]
24: \[ \Delta t_2 \]
25: \[ M_5 \]
26: \[ M_6 \]
27: \[ \Delta t \]
28: \[ F \]
29: \[ V \]
30: \[ D \]
31: \[ V^{-1} \]
32: \[ F_0 \]
33: \[ F \]
34: \[ \Delta t \]
35: \[ F_0 \]
36: \[ F \]
37: \[ F \]
38: \[ F_0 \]
39: \[ F \]
40: \[ F \]
41: \[ F_0 \]
42: \[ F \]
43: \[ F \]
44: \[ F \]
45: \[ F_0 \]
46: \[ F \]
47: \[ F \]
48: \[ F \]
49: \[ F \]
50: return $F$

11: set the step length $\Delta t = (t - t_0)/N_t$
12: save half the step length $\Delta t_2 = \Delta t/2$
13: set $M_1 = M(t_0 + \Delta t, params)$
14: \[ if \] $F_0$ is empty \[ then \]
15: \[ set \] $F_0$ to the identity of the size of $M_1$
16: \[ set \] $F = \exp((M(t_0, params) + M_1)\Delta t_2) \cdot F_0$
17: \[ if \] $N_t = 1$ \[ then \]
18: \[ return \] $F$
19: \[ set \] $M_2 = M(t_0 + 2 \cdot \Delta t, params)$
20: \[ set \] $D_1$ to boolean if $M_1$ is diagonal
21: \[ set \] $D_2$ to boolean if $M_2$ is diagonal
22: \[ for \] $i = 3$ to $N_t - 1$ \[ do \]
23: \[ set \] $M_3 = M(t_0 + i\Delta t, params)$
24: \[ set \] $D_3$ to boolean if $M_3$ is diagonal
25: \[ if \] $D_1$ and $D_2$ and $D_3$ \[ then \]
26: \[ set \] $M_4 = 2M_2 + M_1$
27: \[ set \] $M_5 = M_3$
28: \[ else \]
29: \[ do \] an eigendecomposition s.t $VDV^{-1} = (M_2 + M_1)\Delta t_2$
30: \[ if \] $(M_2 + M_1)\Delta t_2$ is not a defective matrix \[ then \]
31: \[ update \] $F = V \exp(D)V^{-1} \cdot F$
32: \[ else \]
33: \[ update \] $F = \exp((M_2 + M_1)\Delta t_2) \cdot F$
34: \[ set \] $M_1 = M_2$
35: \[ set \] $D_1 = D_2$
36: \[ set \] $M_2 = M_3$
37: \[ set \] $D_2 = D_3$
38: \[ update \] $F = \exp((M_2 + M_1)\Delta t_2) \cdot F$
39: \[ return \] $F$
C.2 Basic reproduction ratio

Algorithm 4 Basic reproduction number

1: procedure R0(Nt, T, t0, j, i, V, W, params)
2: Calculates the basic reproduction number for a system
3: \[
\frac{d x}{d t} = M(t) x
\]
4: where the matrix solution \( F \) to from the system from \( t_0 \) to \( t \) with
5: \( F(t_0) = F_0 \) (empty should imply \( F_0 = I \)) is given by the function
6: \( F(t, t_0, Nt, F_0, params) \)
7: \( M(t) \) is given by the function \( M(t, params) \)
8: \( Nt \) is the number of time steps,
9: \( T \) is the period of the environment,
10: \( t_0 \) is the initial time,
11: \( params \) contains necessary information about the environment
12: 
13: set \( A = AT(Nt, T, t0, params) \)
14: 
15: calculate \( R \) as the spectral radius of \( A \)
16: return \( R \)
Algorithm 5 Matrix for the eigenvalue problem

1: procedure AT($N_t, T, t_0, j, i, V, W, params$)
2:   Calculates the matrix $\tilde{A}$ defined from the equation
3:   $\int_{t_0}^{t} \dot{A}(t, t - \theta)w(\theta)d\theta + \int_{t}^{T} \dot{A}(t, t - \theta + T)w(\theta)d\theta = R_0w(t)$ s.t
4:   $\dot{A}\tilde{w} = r_0\tilde{w}$ using the right points in the quadrature
5: where the matrix solution $F$ to from the system from $t_0$ to $t$ with
6: $F(t_0) = F_0$ (empty should imply $F_0 = I$) is given by the function
7: $F(t, t_0, N_t, F_0, params)$
8: $M(t)$ is given by the function $M(t, params)$
9: $N_t$ is the number of time steps,
10: $T$ is the period of the environment,
11: $t_0$ is the initial time,
12: $j$ is the chosen state,
13: $i$ is state that develops to stage $j$,
14: $V$ is the weight matrix for the lower triangular part,
15: $W$ is the weight matrix for the lower triangular part,
16: $params$ contains necessary information about the environment
17:
18: set the step length $\Delta t = T/N_t$
19: set $n$ as the size of $M(t)$
20: allocate for a matrix $F_i$ of size $n(N_t \times 1)$
21: allocate for a matrix $F_0$ of size $n(N_t \times 1)$
22: set $t_i = t_0$
23: set $temp = I_n$
24: for $k = 0$ to $N_t - 1$ do
25:   set $t_f = t_i + \Delta t$
26:   set $temp2 = F(t_f, t_i, 1, [\ ], params)$
27:   fill $F_i$ blockwise with $temp2$
28:   update $temp$ as $temp2$ times $temp$
29:   fill $F_0$ blockwise with $temp$
30:   set $t_i = t_f$
31:
32: allocate for a matrix $A$ of size $(N_t + 1 \times N_t + 1)$
33: set $temp2 = I_n$
34: set $temp = I_n$
35: for $l = N_t$ with step $-1$ to $0$ do
36:   if $l < N_t$ then
37:     set $temp$ as block $l$ of $F_i$
38:     set $temp2$ as $temp2$ times $temp$
39:   if $l > 0$ then
40:     set $F_Tl$ as column $j$ of the inverse of ($I_n$ minus block $l - 1$ of $F_0$
41:     times $temp2$)
43: else
44:     set $F_Tl$ as column $j$ of the inverse of ($I_n$ minus $temp2$)
45:     for $k = l + 1$ to $N_t$ do
46:       set $A[k, l]$ as row $i$ of $temp$ times $F_Tl$ times $V[k, l]$
47:       if $k < N_t$ then
48:         update $temp$ as block $k$ of $F_i$ times $temp$
49:       set $temp$ as $temp$ times $F_Tl$
50: set $A[0, l]$ as $temp[i]$ times $W[0, l]$
for $k = 1$ to $l - 1$ do

  set $A[k, l]$ as row $i$ of block $k - 1$ of $F_0$ times $temp$ times $W[k, l]$

if $0 < l < Nt$ then


for $k = 0$ to $Nt$ do

  set $temp$ as $\Sigma_1(t_0 + k\Delta t, params)$

for $l = 0$ to $Nt$ do

  set $A[k, l]$ as $temp$ times $A[k, l]$

return $A$