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Modelling large scale invasion of new species under temperature change by reaction-diffusion equations

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Abstract: Due to human migration and climate change invasion of alien species has been observed in Europe. Recently, the mosquito *Aedes albopictus* has invaded the south of France. The spatial-temporal dynamics of invasion is studied in dependence of temperature and predation pressure of the resident ecosystem. The main elements population dynamics, predation and dispersal are combined in a coherent approach based on a system of coupled reaction diffusion equations for the aquatic and winged phase. The nonlinear reaction terms comprise a population dynamic model with temperature dependent reproduction rates and a predation term. The effect of temperature and predation pressure on travelling wave solutions is first investigated for a one dimensional model version. The nonlinearities of the interaction terms give rise to a richness of spatio-temporal dynamic patterns. In two dimensions, the resulting non-linear initial boundary value problems are solved over geometries of heterogeneous landscapes. Geo referenced model parameters such as mean temperature and human population density are imported into the finite element tool COMSOL Multiphysics from a geographical information system. The model is applied to the invasion of species at the scale of middle Europe. The results show that invasion is enhanced in urban regions with ephemeral habitats provided by temporary water bodies.

Keywords: Reaction-diffusion equations, biological invasion, range expansion, travelling waves, temperature dependence

1 Introduction

1.1 Introduction

Mosquitoes such as *Aedes aegypti* or *Aedes albopictus* are vectors of Dengue fever and Chikungunya disease respectively. (Dumont et al. 2008). Recently, *Aedes albopictus* has been colonizing parts of the Mediterranean coastal region in France since 2004 (Fontenille 2011). This species is the epidemic vector of the Chikungunya virus. Whereas *Aedes aegypti* colonizes permanent habitats, *Aedes albopictus* is a temporary water breeder occupying special ecological niches such as puddles, water tanks or even old tires holding water (Fontenille 2011). The respective virus is transmitted to mosquitoes by infested humans. It is the purpose of this study to analyse the range expansion of potential disease vectors in dependence of urban agglomerations providing temporary breeding sites and of temperature. The model is based on the Dengue disease model of Maidana and Yang (2008). We modified the mosquito part of the equations by adding a predation term and by introducing temperature dependent reproduction rates. The addition of the predation term produces an Allee effect, i.e. the decrease of per capita reproduction rate at low population densities (Figure 1.1). Besides environmental variables determining the ecological niche of a species Allee effects
are key features of range shifting dynamics and invasions (Taylor and Hastings 2005). The model equations can therefore be related to landscape features via the temperature and breeding sites with different strength of the Allee effect. By importing geographical information into a finite element tool enabling the solution of the underlying partial differential equations the simulation of invasion is thus possible at large landscape scale.

2 Model equations

Notations

\( A \): population density in aquatic phase  
\( M \): population density of winged phase (female adults)  
\( \mu_A \): mortality coefficient in aquatic phase  
\( \mu_M \): mortality coefficient of adults  
\( \beta \): predation rate  
\( \beta_{\text{max}} \): maximum predation rate  
\( K_s \): saturation constant of predators  
\( f(T) \): temperature response function of reproduction  
\( T \): temperature  
\( T_{\text{opt}} \): optimal temperature  
\( T_{\text{max}} \): lethal temperature  
\( T_{\text{min}} \): minimum temperature  
\( f(T) \): temperature response function of reproduction  
\( Q_{10} \): temperature coefficient  
\( C \): environmental capacity of aquatic phase  
\( D_0 \): coefficient of dispersion at optimal temperature  
\( \phi \): number of eggs laid per time  
\( \gamma \): emergence rate  
\( r \): proportion of females  
\( P(x,y) \): human population density  
\( P_{tr} \): threshold density

The parameter values are given in table 1 and in the Figure captions. The general form of a system of reaction diffusion equations is given by

\[
\frac{\partial u}{\partial t} = L[u] + f_1(u_1, \ldots, u_n)
\]

In our study, the spatial operator has the simple form

\[
L[u] = \nabla (D \nabla u)
\]

We consider a species (mosquito) with a life cycle comprising an aquatic phase (larvae) and a winged (adult) phase. It is assumed that the aquatic phase is subject to predator pressure.

\[
\frac{\partial A}{\partial t} = f(T)\phi (1 - \frac{A}{C})M - (\gamma + \mu_A)A - \frac{\beta A}{A + K_s}
\]

Note the dispersal of the winged phase is made temperature dependent.

\[
\frac{\partial M}{\partial t} = \nabla \cdot (D_0 f(T)\nabla M - \nabla M) + r \gamma A - \mu_M M
\]

Temperature response is described by the model of ONeill with the biological parameters Tmin, Topt, Tmax and Q10.

\[
f(T) = \left(\frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}}\right)^\beta \exp\left(\frac{p(T - T_{\text{opt}})}{T_{\text{max}} - T_{\text{opt}}}\right)
\]
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with \( p = \frac{1}{400} W^2 [1 + \sqrt{1 + \frac{40}{W}}] \) and \( W = (Q_{lo} - 1)(T_{max} - T_{opt}) \).

By variation of the parameter \( Q_{lo} \) the whole spectrum of response curves ranging from stenothermal to eurythermal forms can be generated.

3 Analysis of the homogeneous part

The homogeneous part of the model is amenable to a stability analysis. Stationary solutions are easily obtained by inserting \( M_S = \frac{r \gamma A}{\mu M} \) into the right hand side of equation (2) yielding

\[
P(A) = f(T') \phi (1 - \frac{A}{C}) \frac{r \gamma A}{\mu M} (\gamma + \mu_A) \frac{A}{A + K} - \frac{\beta A}{A + K}
\]

Due to the predation term, the population dynamics is subject to a strong Allee effect, i.e. the per capita growth rate is negative in some interval (Figure 1.1). This equation has the three stationary solutions

\( A_{s1} = 0 \)

the minimal viable population size

\( A_{s2} = -\frac{1}{2r \gamma \phi f(T)} (C \gamma \mu_M + C \mu_A \mu_M - C r \gamma \phi f(T) + K r \gamma \phi f(T) - W) \)

and the maximum density

\( A_{s3} = -\frac{1}{2r \gamma \phi f(T)} (C \gamma \mu_M + C \mu_A \mu_M - C r \gamma \phi f(T) + K r \gamma \phi f(T) + W) \)

with

\[
W = \sqrt{C^2 (\gamma + \mu_A)^2 \mu_M^2 + r \gamma \phi f(T)(-2C (2 \beta + (C + K_s)(\gamma + \mu_A)) \mu_M + (C + K_s)^2 r \gamma \phi f(T))}
\]

Figure 1: Analysis of stationary solutions. 1.1 Per capita growth rate as a function of aquatic population density revealing a strong Allee effect, i.e. negative values
below a threshold 1.2 Bifurcation diagram with predation pressure as bifurcation parameter 1.3. Bifurcation diagram with temperature bifurcation parameter 1.3 Bifurcation surface with both temperature and predation pressure as bifurcation parameters.

The stationary solutions are controlled by temperature T and predation pressure $\beta$. Both parameters determine the regions of viability. Figure 1.2 shows the stationary solutions as a function of the predation pressure $\beta$. Figure 1.3 shows the stationary solutions for constant predation pressure as a function of temperature T and Figure 1.4 shows a three dimensional plot of the solution surfaces. Bifurcations occur at two temperatures ($\beta$ fixed) and at two values of $\beta$ (T fixed). The upper solution surface is locally stable, the lower surface is unstable separating the regions of attraction of the upper solutions from the zero plane, which in a certain region is locally stable.

4 Travelling wave solutions in one dimension

It has long been established that reaction diffusion equations with population dynamic reaction terms may possess traveling wave solutions (Fisher, 1936). Since the population dynamic terms are controlled by temperature and predation pressure (parameter $\beta$) the region of existence for traveling wave solutions and the wave velocity depend on these parameters. The predation pressure is a decisive parameter for the range expansion of a species. Dispersal of temporary water breeders such as Aedes aegypti or Aedes albopictus is therefore facilitated in regions of high human population densities with its numerous temporary waters such as puddles that last more than three days, sagging or plugged roof gutters, discarded tires holding water, litter, bird baths, inlets to sewers and drainage systems holding stagnant water and any other possible containers or pools of standing water (Reiter 2010, Wikipedia). The effect of predation pressure on the range expansion is demonstrated in Figure 2. Left of the origin, a high predation pressure prevails giving rise to a high Allee effect, in the right of the origin, predation pressure is low. In accordance with the general theory (Hadeler and Rothe 1975, Richter et al. 2012) Traveling waves are attenuated in the section of high predation pressure, i.e. in regions with non temporary waters with established ecosystems.

Figure 2: Travelling waves occur in regions of low predation pressure (right part of origin) and are attenuated in regions with high predation pressure (left part of origin).
5 Large scale dispersal

5.1 Coupling Geographical Information with a finite element tool

For the simulation of dispersal at landscape scale, the finite element tool COMSOL Multiphysics (www.comsol.de) is used and linked to a geographical information system providing temperature and population density data and landscape structure.

Geo referenced temperature data of central Europe were imported from the WorldClim global climate data base (www.worldclim.org). WorldClim is a set of global climate layers with a spatial resolution of 1 km². The temperature data were interpolated within COMSOL Multiphysics by use of the two dimensional linear interpolation option in the function menu. Landscape structures were exported as shape files from ArcGIS and imported into the COMSOL environment using the „Export to CAD“ tool from ArcToolbox. The modelling concept is presented in figure 3. In the following simulations the invasion of two mosquito species were studied with respect to their ability to occupy the ecological niche of temporary waters in urban settlements. According to Fontenille (2011) Aedes albopictus prefers these habitats whereas Aedes aegypti prefers more natural habitats. Predator pressure was made dependent of human population density which reflects urban areas providing ecological niches for temporary breeders. Equation 8 states that at low human population densities natural habitats prevail with predation pressure \(\beta_{\text{max}}\) whereas in urban areas above a density threshold \(P_{tr}\) predation pressure decreases.

\[
\beta(x, y) = \beta_{\text{max}} \exp\left(-\left(\frac{P(x, y)}{P_{tr}}\right)^n\right) \tag{8}
\]

5.2 Effect of temperature on dispersal

In the following scenarios the dispersal of a temporal breeder population is simulated under the mean actual temperature and under a temperature rise of 2°C.
The population disperses from two foci within two urban regions situated in the warm Rhine valley: the region of Basel and the region of Frankfurt. The simulations demonstrate that temperature exerts a large influence on the propagation. The propagation speed is less at lower temperature and mountainous regions cannot be crossed.

Figure 4 Dispersal of a population at the actual temperature distribution. Starting from two foci in the urban centres Frankfurt (upper focus) and Basel (lower focus) the population disperses slowly and does not colonize mountainous regions.
5.3 Effect of habitat preference on dispersal

In this scenario, the dispersal of two populations with different habitat preferences is analysed. We consider a population which prefers ephemeral habitats such as *Aedes albipictus* and a population which prefers more natural habitats with an established ecosystem. According to equation 8, ephemeral habitats are related to urban areas providing temporary breeding sites with no established aquatic ecosystem. In the simulation, the upper Rhine valley was considered, which is a region of suitable temperature and is to a high degree urbanized. For the species preferring urban habitats invasion proceeds in two stages: in the beginning dispersal patterns follow the urban densities and subsequently, other areas with higher predation pressure are also colonized once threshold densities are surpassed (Figure 6.2). The comparison between the two species (Figure 6) demonstrates the importance of temporary habitats for the invasion of *Aedes albipictus* and similar species.

Figure 5 Dispersal under a temperature increase of 2°C. Dispersal proceeds faster and also mountainous areas are colonized.

Figure 6 Dispersal of two populations with different habitat preference. 1) Preference of natural habitats 2) Preference of ephemeral habitats in urban areas.

6 Conclusions and Recommendations

In our study we demonstrate that spatial explicit simulation of the invasion of species with different environmental requirements, here temperature response and urban habitat with low predation pressure, is feasible even at large scales by importing landscape covers from a GIS into a finite element solver environment. The analysis of the spatially homogeneous part of the model and the spatial simulations over real landscapes show that range expansion can be conceived as a nonlinear threshold process. Once a density threshold is surpassed, dispersal is triggered in form of a travelling wave which is distorted by landscape features such as elevation which determines the ambient temperature and urbanisation (Figure 6), which determines the quality of the habitat. The speed of the wave front is dependent on the ambient temperature and the strength of the Allee effect. Simulations of future warming (Figure 5) show that increasing temperature may alter the distribution range of a species drastically, as suggested by the study of Caminade et al. (2012). The interaction of a temperature increase and Allee effect as expressed by the predation pressure render the upper Rhine valley a hazardous area for the invasion of *Aedes albopictus*. From the simulation results it is evident that the best precaution against the invasion of *Aedes albipictus* and similar
species is the avoidance of temporary waters in urban areas. In the next step the model will be extended to the potential spread of chikungunya and dengue disease by adding equations for the human population and their interaction with the disease vectors (Dumont et al. 2008). Furthermore control strategies, such as the release of sterile males as proposed by Fontenille (2011) will be implemented into the model.

Table 1: Model parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Standard value</th>
<th>Dimension</th>
<th>Range</th>
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<tbody>
<tr>
<td>$\mu_A$</td>
<td>0.01</td>
<td>1/day</td>
<td>fix</td>
</tr>
<tr>
<td>$\mu_M$</td>
<td>0.01</td>
<td>1/day</td>
<td>fix</td>
</tr>
<tr>
<td>$\beta_{max}$</td>
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<td>1/day</td>
<td>0.1-1.2</td>
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<tr>
<td>$K_i$</td>
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<td>[1]</td>
<td>0.01-0.001</td>
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<tr>
<td>$\phi$</td>
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<td>1/day</td>
<td>fix</td>
</tr>
<tr>
<td>$\gamma$</td>
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<td>1/day</td>
<td>fix</td>
</tr>
<tr>
<td>$r$</td>
<td>0.5</td>
<td>[1]</td>
<td>fix</td>
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<td>$T_{max}$</td>
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<td>°C</td>
<td>fix</td>
</tr>
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<td>$T_{opt}$</td>
<td>17</td>
<td>°C</td>
<td>15-20</td>
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<tr>
<td>$Q_{10}$</td>
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<td>fix</td>
</tr>
<tr>
<td>$C$</td>
<td>1 (normalized)</td>
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<tr>
<td>$D$</td>
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<td>km²/year</td>
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<td>$P_{tr}$</td>
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<td>#/km²</td>
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<tr>
<td>$n$</td>
<td>4</td>
<td>[1]</td>
<td></td>
</tr>
</tbody>
</table>

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