Large Scale Invasion of New Species and of Genetic Information

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Abstract: The spatial dynamics of the invasion of new species and genetic dispersal is studied under the presumption of rising temperature by using a coherent approach of coupled partial differential equations of the reaction diffusion type. The nonlinear reaction terms model the population dynamics, genetic exchange and competition. Temperature reaction norms of reproduction rates are conferred by a two allele system. The resulting non-linear initial boundary value problems are solved over geometries of heterogeneous landscapes. Geo-referenced model parameters, namely mean temperature, elevation, habitat suitability and land use, are imported into COMSOL Multiphysics from a geographical information system. The model is applied to the invasion of species at the scale of southern Germany. The nonlinearities of the interaction terms give rise to a richness of spatio-temporal dynamic patterns. Here we show how invasion processes in form of travelling waves are triggered by a temperature rise.

Keywords: Reaction-diffusion equations, biological invasion, genetic dispersal

1. Introduction

An "invasive species" is defined as a species that is non-native (or alien) to the ecosystem under consideration and whose introduction causes or is likely to cause economic or environmental harm or harm to human health (US Department of Agriculture). Changing environmental conditions and human activities have triggered species migration at a global scale causing biosecurity problems. Species range limits involve many aspects of evolution and ecology, from species distribution and abundance to the evolution of niches. Theory suggests several processes by which ranges are affected, including competitive exclusion, and Allee effects [1]. With the increasing concern about species conservation, a need exists for quantitative characterization of species' geographic range and their borders [2]. Particularly, with recent climate change several examples of range expansions have been reported [3], for instance in European butterflies [4]. Range retractions and extinctions occur as well but are often more difficult to detect [5] Range limits are correlated with a number of abiotic and biotic factors, including climate variables.

The aim of this study was to analyse the mechanisms of invasion of a new species or a genetic trait by means of a highly aggregated mathematical model. The model was devised to fulfil several purposes. It should

i) be amenable to a mathematical analysis for simple geometries,

ii) give insights to the mechanisms of invasion and colonization under spatially varying temperature profiles subject to a general temperature trend,

iii) be applicable in two dimensions at large landscape scales.

As an example we used a dragonfly species that invaded most of central Europe during the last century, *Crocothemis erythraea* [6].

2. Governing Equations

Notations

u_i: population density of species or biotype i
D: dispersion coefficient
u_s: density threshold for dispersal
$\beta(T)$: temperature (T) dependent growth rate
β_{max}: maximum growth rate
μ_i: mortality rate, the index refers to the species or biotype
a_{ij}: coefficient of competition between species (or biotype) i and species (or biotype) j
A_i: number of offspring of biotype i

m: > 2, determines the steepness of the threshold of the dispersion coefficient

The general form of a system of reaction diffusion equations for biological populations is given by

$$\frac{\partial u_i}{\partial t} = L[u] + f_i(u_1,...,u_n) \tag{1}$$

In the simplest case the spatial operator has the form

$$L[u] = \nabla \bullet D \nabla u \tag{2}$$

However, dispersal depends on species density, and the diffusion constant might have the following form exhibiting a threshold effect.

$$L[u] = D_0 \nabla \bullet \left[\left(\frac{u}{u_s} \right)^m \nabla u \right] \tag{3}$$

Thus, diffusion takes place only if a density threshold u_s is surpassed. Note that this nonlinearity in the diffusion term might cause numerical problems.

2.1 Competing species

The reaction terms describe temperature dependent population growth (1st term) and competitive interaction between different species (2nd term).

$$f_i(u_1,...,u_n) = \beta_i(T) u_i \frac{u_i}{u_i + K_i} - \mu_i u_i (1 + \sum_{j=1}^{n} \alpha_{ij} u_j) \tag{4}$$

$\beta_i(T)$ denotes the temperature response function of species "i". The equations include an Allee effect, i.e. reproduction is decreased at low population size. This is achieved by the term

$$\frac{u_i}{u_i + K_i},$$

which is controlling the growth rate in equation (3).

2.2 Genetic spread

Dispersal of genetic information involves population dynamic- and genetic processes. For a diploid species with three different genotypes (AA, Aa, aa) fertility rates as derived from Hardy–Weinberg Theory [7, 8] are

$$\begin{aligned}
f_1(\vec{u}) &= \beta_1(T)\frac{1}{u}\left(u_1 + \frac{1}{2}u_2\right)\left(A_1u_1 + \frac{1}{2}A_2u_2\right) - \\
&\quad \mu_1 u_1 (1 + \sum\nolimits_{j=!}^{3} \alpha_{1j} u_j) \\
f_2(\vec{u}) &= \beta_2(T)\frac{1}{u}\left(u_3 + \frac{1}{2}u_2\right)\left(A_1u_1 + \frac{1}{2}A_2u_2\right) + \\
&\quad \frac{1}{u}\left(u_1 + \frac{1}{2}u_2\right)A_3u_3 - \mu_2 u_2 (1 + \sum\nolimits_{j=!}^{3} \alpha_{2j} u_j) \\
f_3(\vec{u}) &= \beta_3(T)\frac{1}{u}\left(u_3 + \frac{1}{2}u_2\right)\left(A_3u_3 + \frac{1}{2}A_2u_2\right) - \\
&\quad \mu_3 u_3 (1 + \sum\nolimits_{j=!}^{3} \alpha_{3j} u_j)
\end{aligned} \tag{5}$$

with $u = u_1 + u_2 + u_3$ and $\vec{u} = (u_1, u_2, u_3)$.

2.3 Temperature Reaction Norm

Temperature response of growth rates is modelled by the O'Neill function [9], which is parameterized by the biological meaningful parameters T_{min}, T_{opt}, T_{max} and Q_{10}. For an example see Fig. 1.

$$\beta(T) = \beta_{i\max}\left(\frac{T_{\max} - T}{T_{\max} - T_{opt}}\right)^p Exp\left(\frac{p(T - T_{opt})}{T_{\max} - T_{opt}}\right) \tag{6}$$

with $p = \frac{1}{400} W^2 [1 + \sqrt{1 + \frac{40}{W}}]^2$

and $W = (Q_{10} - 1)(T_{\max} - T_{opt})$.

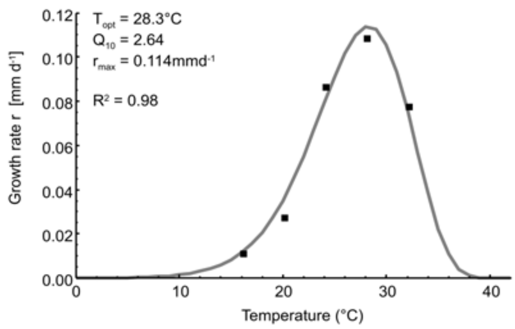

Figure 1. Temperature response of a recent invader in central Europe, the dragonfly *Crocothemis erythraea*. The dots depict measured values of growth rates, the grey line the fitted response curve.

3. Use of COMSOL Multiphysics

In order to simulate dispersal at the landscape scale, geographical information has to be linked with finite element methods. These comprise temperature fields and landscape structures (Fig. 2). Geo referenced temperature data of southwestern Germany 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 km^2 [10]. The temperature data were interpolated within COMSOL Multiphysics by use of the two dimensional linear interpolation option in the function menu (Fig. 3). Landscape structures were exported as shape files from ARCGIS and imported into the COMSOL environment using the „Export to CAD“ tool from ArcToolbox.

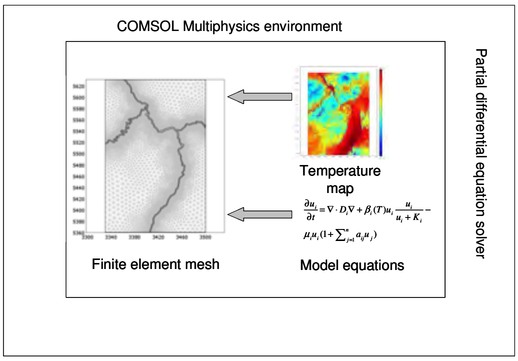

Figure 2. Linking geographical information and finite element methods.

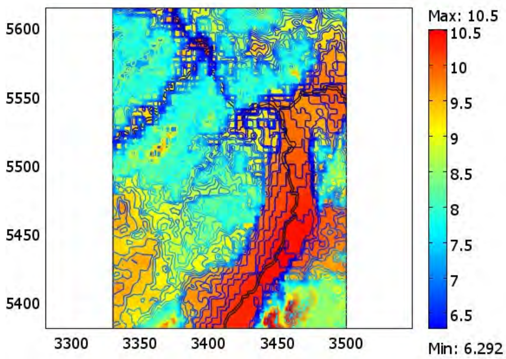

Figure 3. Temperature map of south west Germany and east France as derived from interpolation of WorldClim global climate data base. Interpolation was performed within COMSOL.

4. Results

4.1 Traveling wave solutions for linear and nonlinear dispersion

The mode of dispersal is determined by the dependence of the coefficient of dispersal on density. If the coefficient is constant, traveling wave solutions are obtained with smooth wave fronts as shown in Fig. 4. This behavior is drastically changed in the case of the nonlinear dependence of dispersion on population density (Eq. 3). The wave fronts are sharp and dispersal is slower than in the previous case (Fig. 5). This nonlinearity causes numerical problems and requires fine mesh sizes and hence long computer time.

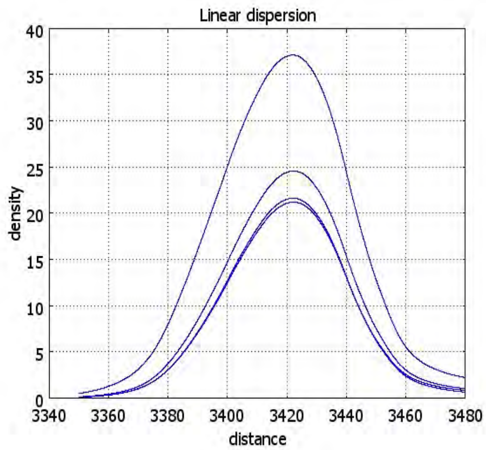

Figure 4. Traveling wave fronts for constant dispersion parameter.

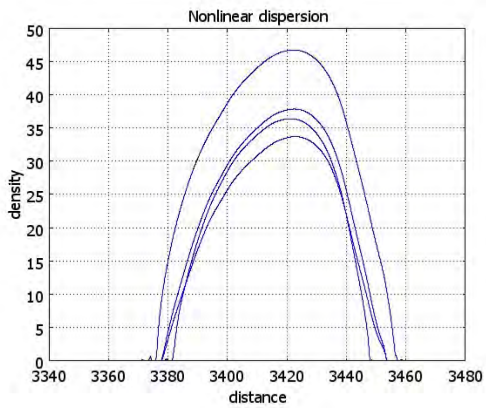

Figure 5. If the dispersion parameter depends in a nonlinear way on population density (Eq. 3) sharp wave fronts occur.

4.2 Invasion of species

The upper Rhine valley plays an import role as a route for invasion of species from the south, since it is linked via the Bresse and the Rhone valley to the Mediterranean. The valley is surrounded by the Vosges and Black Forest so large temperature gradients at short distances occur (Fig. 3). Two species are considered: an indigenous species with a mean annual temperature optimum of 8 °C and an invading species with an optimum temperature of 11.5°C. The following scenario is considered. Initially, both species are distributed in a narrow region at the southern end of the Rhine valley. Their spatial temporal dynamics is followed for several years without any change in temperature. After the establishment of the populations, temperature is slowly increased. The simulations are based on equations 2, 4, and 6. The COMSOL program is set up for both species simultaneously, which are coupled via the competition term in equation (4).

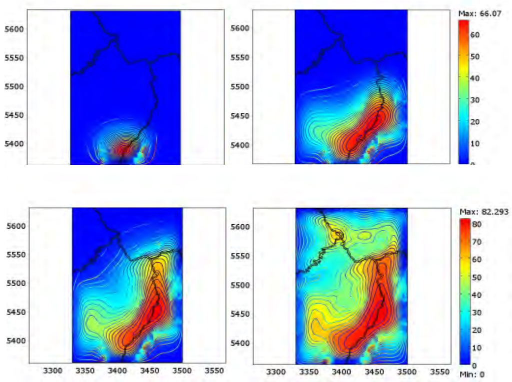

Figure 6. Invasion of a species with a high optimal temperature.

Figure 6 shows a sequence of spatio-temporal dispersal patterns. Starting from a focal region in the south (Fig. 6, first row left), the species migrates to the north via the warm Rhine valley (Fig. 6 first row right and second row left). After a general temperature increase, the species starts to colonize also the mountainous regions (Fig. 6 second row right).

The case of a species with a lower temperature optimum is shown in Fig. 7. Starting from two foci in the Vosges and Black Forest mountains (Fig. 7, first row left) the population is spreading over the mountainous areas (Fig. 7 first row right and second row left). After a temperature increase, this species is replaced by the invader with the higher optimal temperature.

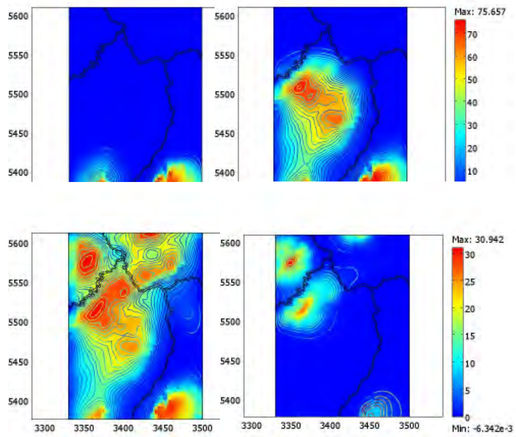

Figure 7. Invasion of a species with a low optimal temperature.

4.3 Genetic Dispersal

This simulation is based on equations 2, 5 and 6. Three biotypes are considered whose optimal temperatures slightly differ. The parameter optimum temperature is subject to genetic transfer by means of the Hardy-Weinberg mechanism (Eq. 5).

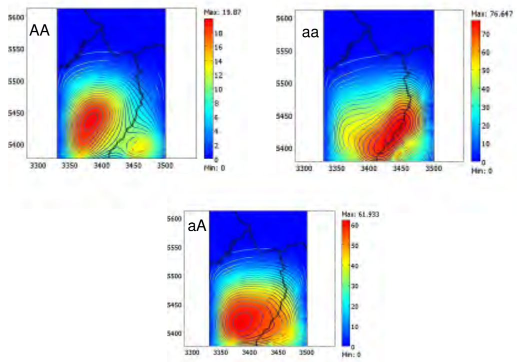

Figure 8. Dispersal of biotypes of one species differing with respect to their temperature optima. Genotype AA has a low optimal temperature, genotype aa has a higher optimal temperature and the heterozygote aA lies somewhere in between.

According to their temperature response curves the different biotypes occupy different areas. Because of the genetic variation this species is insensitive against a climatic change in a certain temperature range.

5. Discussion

Reaction diffusion equations are capable of modelling dispersal of interacting populations or biotypes in dependence of temperature and other environmental variables.

A temperature rise is able to trigger invasion of a new species or of genetic information in form of travelling waves. Species with a large variation of temperature response curves have a large tolerance range with respect to temperature increase.

By importing landscape covers from a GIS into the COMSOL Multiphysics environment and interpolation of geo-referenced temperature data simulation of dispersal at large scales is feasible.

Further research needs are related to the embedding of COMSOL simulations into parameter estimation schemes.

6. References

1. Sexton, J. P., McIntyre, P. J., Angert, A. L. and Rice, K. J., Evolution and ecology of species range limits, *Annual Review of Ecology, Evolution and Systematics* **40**: 415-436 (2009)
2. Fortin, M.-J., Keitt, T. H., Maurer, B. A., Taper, M. L., Kaufman, D. M. and Blackburn, T. M., Species' geographic ranges and distributional limits: pattern analysis and statistical issues, *Oikos* **108**: 7-17 (2005)
3. Parmesan, C., Ecological and evolutionary responses to recent climate change, *Annual Review of Ecology, Evolution and Systematics* **37**: 637-669.
4. Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. and Warren, M., Poleward shifts in geographical ranges of butterfly species associated with regional warming, *Nature* **399**: 579-583 (1999)
5. Thomas, C. D., Franco, A. M. A. and Hill, J. K., Range retractions and extinction in the face of climate warming, *Trends in Ecology and Evolution* **21**: 415-416 (2006)
6. Ott, J., The expansion of Crocothemis erythraea (Brullé, 1832) in Germany - an indicator of climatic changes. In: Tyagi, B. K. (ed.) Odonata: Biology of dragonflies. Scientific Publishers (India), pp. 201-222 (2007).
7. Nisbet R. M., Gurney W. S. C., Metz J. A. J., Stage structured Models applied in Evolutionary Ecology. In: *Applied Mathematical Ecology* (eds Levin SA, Hallam TG, Grass LJ), pp. 428-449. Springer-Verlag, Berlin Heidelberg (1989)
8. Richter, O., Spatio-temporal patterns of Gene Flow and Dispersal under Temperature Increase. *Mathematical Biosciences* **218**: 15-23 (2009)
9. Spain J. D. in *BASIC Microcomputer Models in Biology*. Addison-Wesley, London Amsterdam Don Mills Ontario (1982)
10. Jones and A. Jarvis, Very high resolution interpolated climate surfaces for global land areas, Intern*ational Journal of Climatology* **25**: 1965-1978 (2005)

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