Modelling the spread of ragweed: effects of habitat, climate change and diffusion

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Abstract. Ragweed (Ambrosia artemisiifolia L.) is an annual plant native in North America which has been invading Central Europe for 150 years. Caused by the warming of the European climate its spread process has accelerated in the last few decades. The pollen of ragweed evokes heavy allergies and – what probably counts even more – because of its bloom rather late in summer causes a second wave of allergy when other pollen allergies have decayed. We have reconstructed the invasion process of ragweed in Austria by collecting all records until the year 2005. Austria was subdivided into more than 2600 grid cells of $\approx 35\,\mathrm{km}^2$ each. Ragweed records were related to environmental descriptors (average temperatures, land use, etc.) by means of logistic regression models, and the suitability of grid cells as habitat for ragweed was determined. This enabled modelling of the diffusive spread of ragweed from 1990 to 2005. The results of the simulations were compared with the observed data, and thus the model was optimised. We then incorporated regional climate change models, in particular increased July mean temperatures of $+2.3\,^\circ\mathrm{C}$ in 2050, increasing considerably future habitat suitability. This is used for predicting the drastic dispersal of ragweed during the forthcoming decades.

1 Introduction

The spread of plants, animals and men, of infections, money and even cultural ideas is of interest for everybody. The issue becomes particularly interesting in a changing world. Changes are fast today, in some respects probably faster than at any time in human's earlier history: climate change including man-made, migration of people, or change of the communication means starting with the rapid replacement of the native languages by poor English.

That is the reason why many "diffusionists" (physicists or chemists working in the field of diffusion), having studied diffusion, i.e., the spread, of particles in gaseous, liquid or solid media, sooner or later begins considering problems of the above type. But even though his/her general thinking is adapted to transfer the ideas originating from problems in one narrow field of diffusion to other problems in physics or chemistry, the diffusionist is faced with problems that are of a "strange" type as soon as she/he tackles problems outside the "hard natural sciences", problems that usually cannot be dealt with analytically. To our knowledge this was for the first time emphasised by J.G. Skellam [1], a British bio-mathematician, who described by diffusion equations "of a new type" the dispersal of the muskrat (Ondatra zibethica L.) in Europe after its introduction from North America in the years 1905 to 1927.

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An additional problem for the diffusionist is that often no experiments can be performed, conclusions have rather to be drawn from observations alone. Experiments are obviously not allowed, or at least highly problematic for the spread of infections, of people and of alien species, i.e., introduced species originating from a foreign region. This again distinguishes diffusion problems outside the natural sciences from such problems in physics or chemistry. Problems in these "hard natural sciences" are friendlier to the researcher: there are no ethic problems, there are no health problems, the parameters can be varied and often the systems can be chosen in a "clinically pure state", i.e., without all the baffling details which arise from a scenario involving living beings, and therefore the development can be treated analytically.

Skellam described the dispersal or spread of the muskrat by adding a growth term in Fick's diffusion equation, and was able to model the linear time dependence of the radius of dispersal of the muskrats. Since this seminal work several other biological dispersal phenomena have been described by diffusion equations. Probably most attention was gained by the description of the "demic diffusion" of Neolithic farmers in Europe, first undertaken by A.J. Ammerman and L.L. Cavalli-Sforza in the 1970s [2]. These authors made use of the so-called Fisher equation, i.e., a Fickian diffusion equation supplemented by a logistic growth term (i.e., growth to saturation). The result was a "wave of advance" with a diffusion front, starting from the Near East and reaching the western borders of Europe after 4000 years. More recently these equations have been reworked several times and supplemented by taking into account the mixture of the invaders with the Palaeolithic population roaming through Europe before that wave of advance from the Near East had arrived [3]. Even pure "cultural diffusion" of the Neolithicum, i.e., diffusion just of the new technique of agriculture nearly without diffusion of people has been discussed [4]. In addition, diffusion of colonists on other continents was modelled by diffusion equations with logistic growth, to mention only the work of J. Steele et al. [5] on the dispersal of the Palaeoindians after crossing the Bering street about 14000 years ago down to the southernmost part of South America in the surprisingly short time span of obviously less than 2000 years.

All this work had to be done with a very limited data set, since in all cases dispersal phenomena in earlier time have been described, in periods which lacked any contemporary observation. This pertains not only to the prehistoric spread of men but also to the dispersal of the muskrat which was long over when Skellam modelled it. We know only of one analytical treatment of an extensive data set of a present day dispersion phenomenon, namely the dispersal of one-dollar bank notes throughout the United States mirroring human travel and perhaps even the spread of infectious diseases [6].

An appropriate method to model ongoing dispersion phenomena, which we can follow every day and where we rely on detailed information and plenty of data, is stochastic computer simulation. This will be applied in the present paper for the analyses of the observed spread and the prediction of the future spread of an invading alien plant. An extensive paper on the method of calculating the dispersion is under preparation [7].

2 The common ragweed

Common ragweed (*Ambrosia artemisiifolia L.*), see Fig. 1, is an annual plant which has first been unintentionally brought to Europe in the mid-18$^{\text{th}}$ century. Since then it has invaded large parts of SE and SW Europe, where it has greatly increased in range and abundance since the mid of the 20$^{\text{th}}$ century. In Austria, the invasion was delayed and ragweed has so far only colonised the warmest parts of the lowlands of eastern and south-eastern Austria. As a pioneer species it grows preferably in disturbed ruderal habitats (the surroundings of human settlements, roadsides), but also in agriculturally used areas like maize and soy bean fields [8]. Its pollen evokes heavy allergies and because of the pollen's spread rather late in summer this causes a second wave of allergy when other pollen allergies have decayed. Being particularly interested in the spread of ragweed in our home country Austria, we will consider the progressive extension of the ragweed's habitat due to climatic change in order to predict its dispersal ("diffusion") in this country in the coming decades. We are aware of the limitations

Fig. 1. (Colour online) common ragweed (*Ambrosia artemisiifolia L.*) (taken from [9]).

due to the limited area considered, but in absence of data pertaining to one and the same geographic grid in different countries we undertake the endeavour in order to start and show the direction how to proceed. We hope that our attempt will serve as a basis when standardised data will become available for a larger area covering more than one country.

Ragweed is a uniquely suited paradigm for studying its dispersal in Austria due to at least three aspects:

(a) Ragweed is an annual plant with fast succession of generations which enables the plant to rapid response to climatic changes as they appear to occur currently.

(b) Ragweed is a conspicuous species whose invasion is extraordinarily well documented; hence, accurate distribution data for Austria are available.

(c) Ragweed is presently rapidly spreading in Austria.

3 Simulation of progressive infestation of Austria by ragweed from 1990 to 2005

The method we use is a type of stochastic cellular automaton method, utilising a modified version of the procedure applied by Gilbert et al. [10]. Austria (Fig. 2) is subdivided into 2612 grid cells (about $35\,\mathrm{km}^2$ each), and for each cell it is registered whether and in which year ragweed has been found there. As seen in Fig. 3 the records become progressively numerous after 1960, particularly during the two last decades. We therefore decided to design an optimised model which simulates the increase in infestation from 1990 to 2005 (Fig. 4).

Our procedure is an iterative algorithm (Fig. 5) with the empirically determined infestation status of Austria in 1990 as starting configuration $\Theta_{t=0}$. In the configurations, an infested cell is represented by 1 (marked black in the figure) and a non-infested one by 0 (white). We use habitat suitability matrices h_t (Fig. 6), based on the bioclimatic envelope of the species in Austria. By relating probabilities of occurrence at a given location to climate and environmental conditions at this site, i.e., mean July temperatures, relief index, main streets and land use index in a logistic regression model, an optimal habitat model is calculated [12].

At each time step t a spread probability $S(x,\Theta_t)$ is calculated for each non-infested cell x. This probability depends on the infestation status of the cells surrounding x. Multiplying the spread probability matrix and the habitat suitability matrix h_t pointwise, we receive a matrix of total infestation probabilities at time t. These probabilities are compared to uniformly distributed pseudo random numbers on $[0,1]$. If the probability in a cell is larger than the random
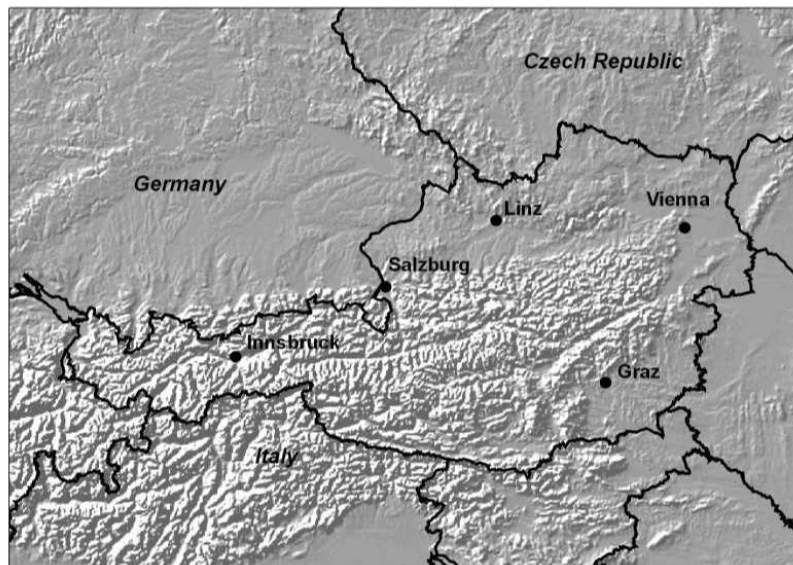
Fig. 2. Map of Austria showing the lowlands, alpine areas and inner-alpine valleys (taken from [11]).
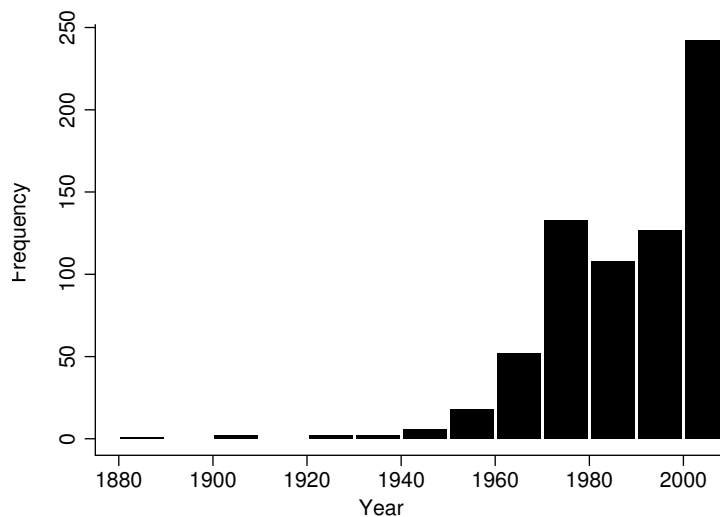

Fig. 3. Frequency of records of ragweed in Austria between 1880 and 2005 (taken from [12]).

number, the cell is taken as infested for time step $t + 1$, in the opposite case as non-infested. Now the procedure is performed for the next time step $t + 1$ and so on. The result for the year 2005 is compared to the observed infestation matrix of Austria, represented by 2612 grid cells.

The outcome of this algorithm depends heavily on the used spread probability function S, which in our case was implemented as either an equi-distribution, a Gaussian or a superposition of two Gaussians (each depending on certain parameters, i.e., width, height, ...). Repeated simulations with different parameters are performed according to this algorithm, and the outcome of each simulation is judged with respect to its quality. On the basis of this judgement a genetic algorithm determines new parameters for the next set of simulations. This procedure is repeated until the genetic algorithm has found parameters which reproducibly yield good results. A single Gaussian spread probability function turned out to be sufficient in the frame of the achievable agreement of simulated and observed infestation.
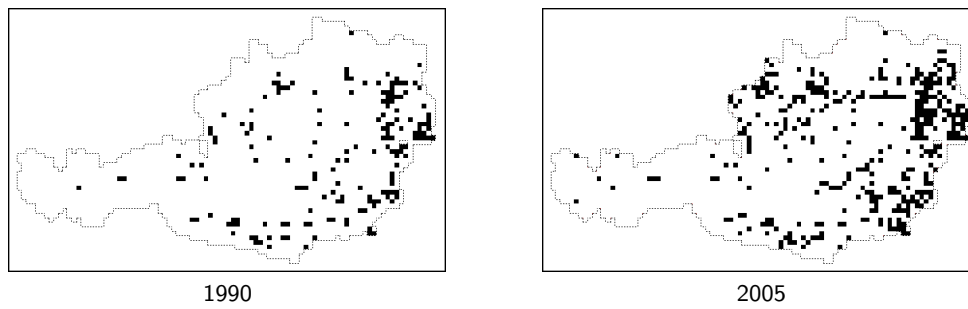
Fig. 4. Cumulative grid distribution map of ragweed in Austria in the year 1990 (left) and 2005 (right). The black rectangles indicate grid cells with at least one record (taken from [12]).
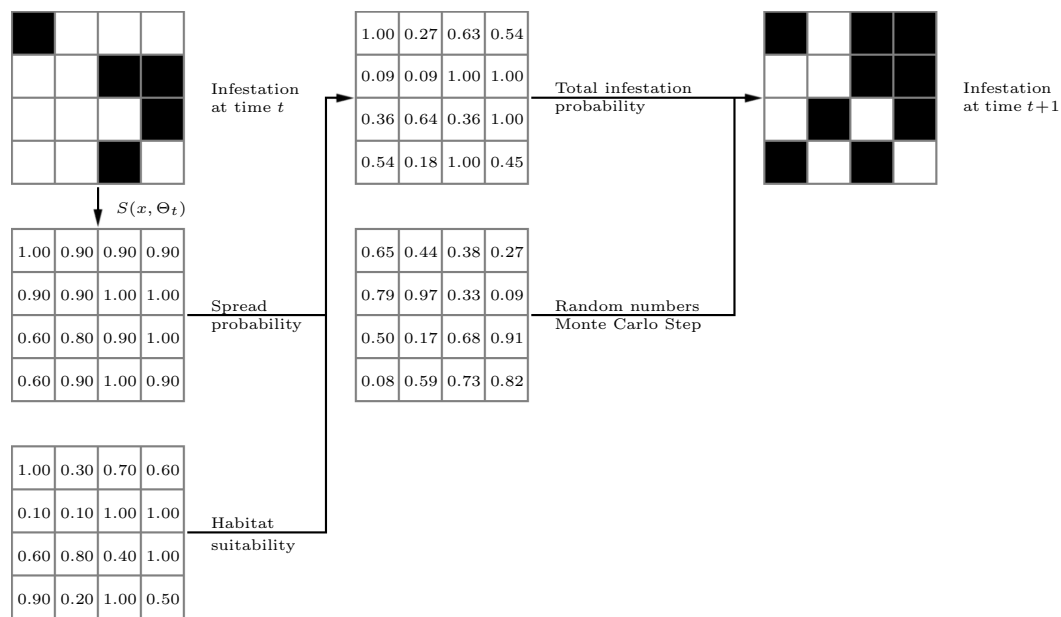

Fig. 5. Algorithm for determining the infestation status at time $t + 1$, given the infestation status Θ_t by ragweed at time t and the habitat suitability matrix h_t. An infested grid cell is symbolised as black, a non-infested one as white. For detailed explanation see text.

4 Prediction for spread under changing climates

In the next step we took into account climate change. The model elaborated by Gobiet et al. [13] predicts an increase of the mean July temperature for Austria by $2.3\,°C$ in 2050. Computing the habitat suitability matrix for the year 2050 with this predicted temperature increase alters habitat quality considerably, making large areas more accessible for future invasion of ragweed (Fig. 6).

Predictions for the coming years are now straightforward. By linearising the increase in the habitat quality for the years between 2005 and 2050, the respective suitabilities are calculated. These new suitability values are then used for spread simulations in the same way as was done for the period 1990 to 2005. Fig. 7 shows the as-simulated spread of ragweed in terms of infestation probability for the years 2030 and 2050.

Ragweed will spread considerably during the coming decades: the eastern lowlands of Austria will be infested to a high degree and even large inner-alpine valleys will become increasingly occupied. But there is good news as well: the dispersal is relatively slow, it will be by far not as fast as to invade all suitable habitat, as can be seen by comparison of Fig. 6, right (habitat
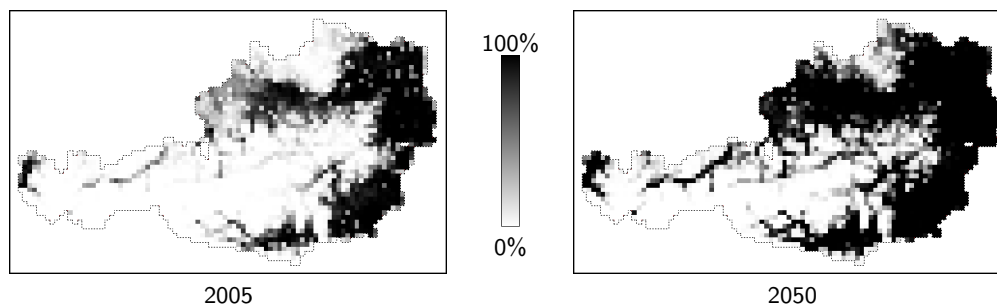
Fig. 6. Habitat suitability of the 2612 grid cells of Austria for the year 2005 resulting from a logistic regression which takes into account land curvature, land use, main streets and average July temperature. Actual values for 2005 (left) and predicted values for 2050 (right) [13]. Degree of grey tones indicates degree of habitat suitability.
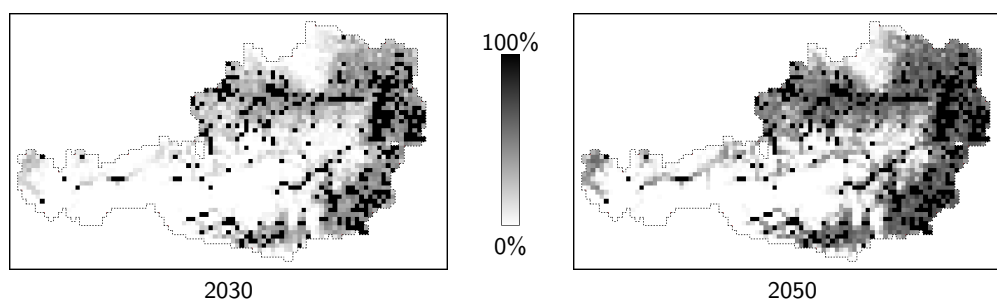

Fig. 7. Simulated infestation probability of ragweed for the years 2030 (left) and 2050 (right). Grey tones indicate the infestation probability for the respective cell.

suitability for 2050) and Fig. 7, right (predicted range for 2050). This is a message encouraging measures for the slowing down of ragweed's dispersal.

5 Comparison with the dispersal of an insect

It is most interesting to compare the spread of an alien plant species like ragweed with the spread of newly introduced alien animal species. The spread of the latter often appears to be faster with the reasons being diverse.

Of particular current interest, and thus particularly attractive for studying, is the spread (dispersal, diffusion) of the horse chestnut leaf-miner moth (*Cameraria ohridella*). Introduced to Central Europe in the 1980ies, it has spread very rapidly and often reaches high population densities, especially in urban areas. Its larvae forage exclusively in leaves of horse chestnut (*Aesculus hippocastanum*). With progressing summer, the leaves of the horse chestnut trees become dotted with brown patches and cause the trees to shed their leaves long before they would normally do so. The progress of the infestation of the horse chestnut trees is not a simple diffusion front, but small population islands appear well in advance of the continuous diffusion front which are later on "swallowed" by the progressing front.

M. Gilbert et al. [10] have treated the dispersal of the moth with a cellular automaton method different from ours. These authors do not consider a habitat but rather regard all places in Europe as equally well suited for the spread of the leaf-miner moth. On the other hand they found a most interesting additional process which governed the rate of spread. The pre-states (the larvae) of the moth are transported incidentally by human traffic over huge distances which allows the diffusion front to advance at a much faster rate than if the moth would have to spread by flight only. The authors assume that this long-range transport is positively related

to density of transport ways (roads, railway lines), which in turn should be coupled to human population density. Thus, where in our case the variations in habitat suitability have a large impact on the spread of ragweed (because of the spatially very inhomogeneous geography of Austria), Gilbert et al. focus on the enhanced diffusivity introduced by human traffic.

6 Conclusions and outlook

Understanding the spread of an alien species like ragweed opens the chance to design and implement adequate mitigation measures in early phases of spread. In case of ragweed it is highly indicated to prevent or at least slow down the spread because of the disastrous allergenic reaction caused by its pollen. Modelling the dispersal should help to do so.

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