A Geographic Automata Model of Colorado Beetle in a Novel Environment

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EXTENDED ABSTRACT

Developing reliable methods for predicting advance of potentially harmful invaders in a novel environment remains a persistent challenge to epidemiological and ecological modelers. The dominating demographic approaches handle space only implicitly and the spatio-temporal variation in the resources for invaders growth, reproduction, and spread are widely missed.

Here we introduce a geographic automata based spread model for Colorado Beetle that attempts to capture both the inter-seasonal variation in environment and the spread dynamics. Spread is modeled with active, wind-aided, and logistic-aided dispersals. With the model the resource base of the invader can be explored using the resource profiles of summers and winters, categorized by their temperature sums and regimes respectively. We use a case study of hypothetical aerial invasion of Colorado Beetle in Finland to demonstrate how the model can be used for exploration and prediction of invasion dynamics.

The simulation model consists of a spatial seasonal resource array and of a spatial abundance level of beetles. During simulation several spatio-ecological metrics are updated. These metrics help the user to compare seasonal changes in location and area of invasion pattern, perforation rate of the pattern, and occurrence probabilities (OP) of the invading species. Occurrence probability gives an estimate of relative abundance of the invader in the situations where detailed individually based estimates are not feasible. Because an invader's impact is correlated with its abundance, a surrogate model is thereby generated by relating the invader's abundance to environmental variables and their inter-seasonal fluctuations. Hanski and Gilpin (1997; Hanski 1999) are in the same line finding that efforts to explain and predict occurrence patterns on the basis of species-specific resource requirements may have a high probability of success. Such a model, like the one we introduce here, could elucidate which part of the potential habitat will be most prone to permanent establishment of an invader. Lack of precision should not be a deterrent to developing predictive models where none exists. Crude predictions can be refined as additional data become available. Even though the problems of *a priori* modeling, such as validation and verification, do arise, in many cases it is the only approach we can use in order to get at least a glimpse to the future.

These future events can be explored, for instance, by studying the differences in location, area, and perforation rate of the invasion pattern and by comparing occurrence probabilities of the species in multiple spatial and temporal scales in selected area. The user is also able to explore directional speeds with emerging primary and secondary progression zones for a selected area. The metrics aid the user in exploring the evolution of an invasion pattern at different scales and compare the regional differences in spreading rates between selected areas.

Consequently, the aim of this study is to enter the field of *a priori* modeling and develop GIS-based software for exploration of the resource base of potential invader and for simulation of its potential spread in Finland. In addition our objectives are firstly to identify and rank the most risk prone areas where resource for growth, dispersal, and overwintering are most favorable from season to season. These are the areas where establishment of the beetle is most likely to happen if a mass migration takes place and the eradication measures fail. Secondly, our objective is to develop a model with which the resource base of the invader under current and future climates can be explored using the resource profiles of different temperature-categorized summers and winters at several scales. Thirdly, our objective is to provide the user with the metrics which would aid their exploration of the evolution of an invasion pattern at different scales and to compare the regional differences in spreading rates between selected areas.

1. INTRODUCTION

Developing reliable methods for predicting advance of potentially harmful invaders in a novel environment remains a persistent challenge to epidemiological and ecological modelers. Perhaps the simplest approach has been to ignore spatial effects by modeling movement as either a diffusive process (e.g. Andow et al., 1990; Okubo, 1980) or as simple transfer functions (e.g. Fahrig and Merrim, 1985). Although these models provide a synoptic picture of landscape dynamics they do this by handling space only implicitly. In addition, these models miss spatio-temporal variation in the resources for invaders growth, reproduction, and spread. Altogether, these models fail in predicting potential spread of a novel species since they ignore heterogeneity of landscape along not to mention the temporal variability in the resources available for an invader.

Every expansion is a combined effect of population growth and diffusion (see Figure1). Conventionally, diffusion and spread has been modeled by ecologists with partial differential equations. In this study we will develop a Geographic Automata (Benenson and Torrens, 2004) model to capture the spatial and temporal heterogeneity of resource base available for an invader. This guarantees that both spatially and temporally varying environment and spatially explicit and temporally varying resource base are explicitly included into the simulation model.

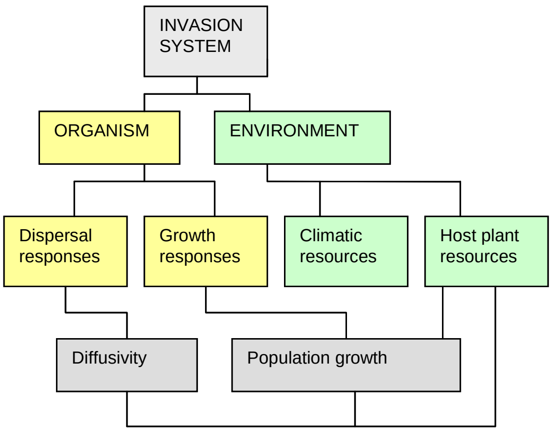

Figure 1. The concept of expansion

Predicting the pattern of spread of an invading species belongs methodologically to a priori modeling. There are international conventions on how to assess the potential of entry and establishment of an exotic species possessing a pest status (IPCC, 2001) but there are no scientific or regulatory conventions on how to predict the spread of an invader once the immigration has successfully happened. Predictive models of further dispersal after successful immigration of an invader are sparse. Consequently, national authorities lack predictive tools to help them prioritize most risk prone areas of the virgin habitat network and decide where they can most effectively allocate limited resources.

Colorado Beetle, *Leptinotarsa decemlineata* (Say) is one of the most severe pests of potato in the world. Colorado beetle possesses a suite of life history strategies which allows it to survive and proliferate in an unstable habitat by distributing its reproduction and dispersal effectively in space and time. Nowadays there exists a wealth of accumulated literature on Colorado beetle's ecology which provides a unique opportunity to cease for our synthesizing modeling task.

In this paper we develop a model of invasion dynamics based on literature on the ecology of Colorado Beetle and existing environmental data on the target area (Finland). We first develop a Spatial Resource Inventory Model (SRIM) with which we analyze the resource basis available for the beetle. We then use the context of geographic automata methodology to build the Resource-constrained Geographic Automata Model (RGAM) with which we are able to simulate spread of the beetle within its novel habitat network. Below we focus on introduction of the model leaving the actual implementation and application for future work.

2. MATERIALS

2.1. Habitat data

The best available habitat data sources for modeling the Colorado beetle were deemed to be the CORINE Land Cover raster database and the Finnish Commercial Potato Production Data. The spatial resolution of CORINE is 25 m x 25 m. The land cover types that were assumed to contain potato fields were: Leisure facilities and small-scaled horticultural production, Non-irrigated field crops and Land principally occupied by agriculture. The Finnish commercial potato field data is maintained by the Ministry of Agriculture and Forestry Data Service Centre and it covers all field plots which have more than 0.5 acres commercial potato production.

2.2. Weather data

A grid of daily mean temperatures and rainfall covering a 30-year period of 1971-2000 was provided by the Finnish Meteorological Institute. The spatial resolution of the data set is 10 km x 10 km. The daily minimum and maximum temperatures that are needed by the Spatial Resource Inventory Model (SRIM) were computed from this data using correlations between the daily mean temperature and the daily minimum and maximum temperature. The correlations were obtained using regression analysis on a climate dataset that contains daily minimum, maximum, and mean temperatures. The climate dataset was obtained from the website of the Prudence project (http://prudence.dmi.dk/) and it is developed by the Swedish Meteorological and Hydrological Institute. The equations that were derived using the data from summer months in one grid point in Finland are:

$$t_{\min} = 0.886t - 0.024 \quad (r^2=0.93) \qquad (1)$$

$$t_{\max} = 1.088t + 0.65 \quad (r^2=0.97) \qquad (2)$$

The daily rainfall data was used to estimate wet and dry stresses during growing seasons and during winter diapauses (see The Model). Since during the winter the rainfall can either be genuine rain or come down as snow we kept record for the thickness of snow cover using sub model for a snow melt.

Despite of our efforts on data acquisition we still miss the regional data on prevailing wind directions and speeds for July and August which both are needed for the simulation of invasion dynamics with the Resource-constrained Geographic Automata Model (RGAM). In case this data will remain unavailable we will model the wind as stochastic component in the forth-coming simulations.

2.3. Logistic Data

We use a surrogate parameter to capture the available logistic resources of each cell. According to studies of Gilbert et al. (2005) human population density can be used as an effective indicator of logistic activities of the geographic area studied and thus can effectively operate as a surrogate when detailed logistic networks and their volumes are not available.

2.4. Soil Data

The geological survey of Finland maintains a 1:20,000 scale vector soil database of Finland, which can be used to determine the average clay content within the grid cells for modelling the stresses experienced by the beetles during their dormancy in the soil.

3. THE MODEL

3.1. Analyzing Dynamic Resource Base

Responses of an invader are described with multiple indices which reflect growth, dispersal and overwintering responses of the species to various environmental stimuli (see table1). The leading principle in selection of values for Response Model of Colorado beetle has been to use the worst-case scenario in order not to underestimate the resources offered by the novel environment since underestimation in the context of quarantine pest spread predictions may have much more severe consequences.

The indices are categorized into three groups: growth-related indices, dispersal-related indices, and stress indices respectively. The conceptual basis of indices is partially analogous to that used in CLIMEX software (Sutherst et al., 2004) with exception that the focus of Spatial Resource Inventory Model (SRIM) is on inter-seasonal variation in resource base compared with long-term averaged establishment assessed in CLIMEX. The other two differences are that SRIM contains a new family of indices, dispersal-related indices, to capture dispersal resources offered by the new environment. The second difference of SRIM compared to CLIMEX is the handling of stresses. Compared to the annual stress indices of CLIMEX, SRIM uses a seasonal concept and further divides Cold, Heat, Wet and Dry Stresses to their summer and winter analogs. With seasonal indices SRIM is able to keep track on changes on the resource base of any given location between seasons.

In short, the various species-specific physiological and behavioural responses are transformed to a concise model of growth, dispersal, and overwintering of Colorado beetle (see appendix1). In the next phase, the environmental Response Model of Colorado beetle is used together with habitat and weather data to analyse seasonal resources for Colorado beetle in its novel environment. Briefly, we look the new environment for an invader through its species-specific physiological and behavioural responses. The Table 1 introduces the resource indices of SRIM and a brief description of the functions.

Table 1. The resource indices of the Spatial Resource Inventory Model (SRIM)

Index	Function	Parameters
Growth Index	Sinusoidal	Temperature Index Stress Indices
Temperature Index	Trapezoidal	4 thresholds
Diapause Index	Step function	Diapause -1 Non-Diapause +1
Overwintering Index	Seasonal accumulation of overwintering stresses during the diapause	Diapause Index Stress Indices
Habitat Availability Index	Proportion of suitable habitat area of the total area of the cell	Selected Land use classes of Commercial potato fields
Active Flight Index	Seasonal accumulation of flight take-off days and their favourability	Active Flight Take-off Temperature Index Diapause Index
Active Flight Take-off Temperature Index	Trapezoidal	4 thresholds
Wind-Aided Dispersal Index	Proportion of Active Flight Take-off Days when wind speed exceeds the threshold.	Windy Flight Take-off Days Active Flight Take-off Days Wind speed threshold
Logistic-Aided Dispersal Index	Zonal mean	Human population density

The Spatial Resource Inventory Model (SRIM) computes the resources for each season in a grid: 1) Growth Resources (Growth Index), 2) Dispersal Resources (Active Flight Index, Wind-aided Dispersal Index, and Logistic-aided Dispersal Index), 3) Overwintering Resources (Overwintering Index), and 4) Host Plant Resources (Habitat Availability Index). In addition it provides mapped stress indices for summer and winter season respectively (table 2.). Statistical classification methods can be used to compute the resource profiles at several scales (local, focal, areal, and global) in different temperature-categorized summers and winters. The operation of SRIM is easily tractable because it considers the mechanisms affecting growth, dispersal, and overwintering explicitly. Another advantage of SRIM is that it can be used as an explorative tool independently from the spread simulation tool.

Table 2. The stress indices of the Spatial Resource Inventory Model (SRIM)

Index	Function	Parameters
Summer Cold Stress (SCS)	Linear below the threshold	SCS Degree-day Threshold SCS Accum. Rate
Winter Cold Stress (WCS)	Linear below the threshold	WCS Temperature Threshold WCS Accum. Rate
Summer Heat Stress (SHS)	Linear above the threshold	SHS Temperature Threshold SHS Accum. Rate
Winter Heat Stress (WHS)	Linear above the threshold	WHS Temperature Threshold WHS Accum.Rate
Summer Dry Stress (SDS)	Linear below the threshold	SDS Moisture Threshold SDS Accum. Rate
Winter Dry Stress (WDS)	Linear below the threshold	WDS Moisture Threshold WDS Accum.Rate
Summer Wet Stress (SWS)	Linear above the threshold	SWS Threshold Soil Moisture SM SWS Rate
Winter Wet Stress (WWS)	Linear above the threshold	WWS Moisture Threshold Daily Rainfall RF Snow Cover SC Snow Melt SM WWSAccum.Rate

3.2. From Resources to Spread Predictions

The invasion simulation model computes predictions of the location, shape and intensity of the invasion. The resolution (5 km x 5km grid) of the model follows the seasonal maximum dispersal distance by active flight that is 5 km (Johnson, 1969; Sandru & Suteu, 1969 in Bartlett, 1979). The spatial neighborhood of each grid cell is considered both as (i) eight adjacent cells (active flight during the season) and as (ii) 16 next-to-neighbor cells (wind-aided flight or logistic-aided dispersal). In the invasion theory, this kind of dispersal model is called stratified dispersal since it has two distinct mechanisms operating at the same invasion event (Shigesada & Kawasaki, 2001).

During each simulation step (one year) the population growth, active flight, wind-aided, and logistic-aided dispersal, and overwintering are computed. A year is divided into summer, which is the growing season for reproduction and dispersal, and winter, which is the hibernating time. The simulation is based on transition rules for the grid cells. The grid cells divide the space and the values associated with the cells represent the resources and the beetles in the area of the cell. The transition rules describe how the resources and beetles in a cell change as a function of time and the resources and beetles in the cell and its neighbors.

The climate input data for the model is prepared from the historical climate data assuming there is no correlation between years and between winter and a summer. The climate input time series is generated by selecting seasons randomly from the existing climate data.

3.3. Summer transition step

During the summer transition step each cell interacts with its 8 neighboring and 16 next-to-neighbor cells though active and vector-aided dispersal mechanisms. If the vector-aided dispersal dominate there can emerge new satellite populations further away from the front. The transition function for summer is the following:

$$OP_{i,j}^{t+1} = \left[\left(GI_{i,j}^{t} - AFI_{i,j}^{t} - LADI_{i,j}^{t} \right) OP_{i,j}^{t} \right] \left[\sum_{i=1}^{8} \frac{1}{8} AFI_{i}^{t} \left(\sum_{i=1}^{8} GI_{i}^{t} OP_{i}^{t} \right) \right] \left[\sum_{i=1}^{16} \frac{1}{16} WAFI_{i}^{t} \left(\sum_{i=1}^{16} GI_{i}^{t} OP_{i}^{t} \right) \right] \quad (3)$$

where
OP is Occurrence Probability,
GI is Growth Index,
AFI is Active Flight Index,
WAFI is Wind-Aided Flight Index, and
LADI is Logistically-Aided Dispersal Index.

The summer step has thus two components: 1) Growth at the given cell and Dispersal out of the cell either by active or wind-aided flight or by logistic-aided dispersal and 2) Growth at the both neighborhoods; AFI-reachable adjacent cells and WADI and LADI-reachable next-to neighbor cells. The first component describes growth and dispersal events of the season at the given cell and the second component describes the growth and dispersal events of the season at the two defined neighborhoods. The given location donates dispersers to the neighboring 25 cells and the 25 neighboring cells donate a proportion of their dispersers to the given location. Each of the adjacent cells contributes with 1/8 to the next state of the given cell whereas the next-to-neighbors contribute only with 1/16. In addition, the contribution of the super-diapausing beetles emerging randomly from the soil call further adjustments to the current summer transition function.

3.4. Winter transition step

During the winter dormancy neither growth nor any interaction with beetles living at the neighboring or next-to-neighboring cells happens. Consequently, the winter transition step is purely local operation at the given location only. We simply compute a new value for Occurrence Probability as a function of overwintering index:

$$OP_{i,j}^{t+1} = OP_{i,j}^{t} OWI_{i,j}^{t} \quad (4)$$

where
$OWI_{i,j}^{t}$ is the overwintering index at time step t at cell (i,j).

If the overwintering index is one, it means that the dormancy has succeeded optimally and the new Occurrence Probability of the cell is the same as previously. If, however, the overwintering index drops down to zero the Occurrence Probability should logically become zero - but this is not always the case. If there are super-diapausing adults in the soil ("beetlebank"), the Occurrence Probability decreases drastically but not to "true" zero. This state is called "false" zero because although no beetle can be found above the ground there might still be an underground reserve. Thus, we cannot say that the population has gone extinct. Only if by the third summer there are no emerging adults we can assign Occurrence Probability of the given cell to zero and consider the beetle locally extinct.

4. RESULTS

Spatial exploration of resource analyses includes, for example, mapped resource layers and spatial resource profiles. In addition the user can explore invasion pattern dynamics, for instance, compare seasonal changes in location, area, and perforation rate of the invasion pattern and occurrence probabilities of the invading species. In addition, a set of difference maps of all the output variables can also be explored for multiple spatial and temporal scales. The user can also extract directional speeds with emerging primary and secondary progression zones for a selected area. Another kind of structural exploration is potentially also available for users. This is the study of explicit "skeleton" geometry of the invasion patterns, which are extracted by the method invented by Rosenfeld and Kak (Rosenfeld & Kak 1978 in Clarke et al. 1994).

5. DISCUSSION

We have to live in an incomplete and complex world. In the middle of seemingly un-reducible complexity of invasion dynamics it is good to remember that all models are caricatures and crude simplifications of complex systems. In this respect our Spatial Resource Inventory Model (SRIM) and its results-using Resource-constrained Geographic Automata Model (RGAM) are no exceptions, on the contrary. Our aim was to develop as spatially explicit, easily tractable, explainable and interpretable model as possible. The main question is whether our models have captured main features of importance for the invasion phenomenon, in our case that of the invasion event of a potential new insect species into the novel area where resources for its growth, dispersal, and overwintering form a spatially and temporally varying mosaic.

Any spatial model like our invasion model here is restricted by its spatial and temporal scale it has. Due to this fact, we would like to emphasize that we are full aware of the deficiency of the resource model to fully capture the resource base realistically. For instance, at a landscape level, topography has an effect on thermal accumulation (degree-day accumulation). In addition, we have totally ignored the biotic template. In practice, more biotic components than just host plant availability have direct effects on the success of establishment of a potential invader. These other components, like predators, parasitoids, competing species and pathogens can cause either permanent or temporal exclusion of the invading species from some locations where other resources for growth, reproduction, dispersal, and overwintering are met. The other missing component is evolution. Adaptability of local strains can produce situations where prevalence of some characteristic response pattern changes. Regarding Colorado Beetle it is of high importance to know if Russian beetles have become more cold-tolerant, or are able to develop from egg to adult in shorter time or with lower degree-day accumulation than reported in the current literature. In addition to evolution of geographically more adapted strains, also individuals in each population show variation in their response to temperature, humidity, wind, and soil type. This means that when calculating the response indices for growth, dispersal, and overwintering we always have a range of responses instead of just one fixed response. In practice this means that some adults will take-off for flight already at + 18 ºC while some wait for days till the temperature exceeds +25 ºC. In the framework of our modelling task we could in the future study the effects of this variation to the outcome of invasion predictions.

The lack of these precisions should not however be deterrent to developing predictive models where none exists. Crude predictions can be refined as additional data become available. Despite the challenges of a priori modeling, especially verification difficulties, this kind of modeling is the only choice available to explore potential future invasion scenarios and the exquisite spatio-temporal evolution of invasion patterns.

Finally, we conclude that the field of invasion ecology would greatly benefit from the kind of collaboration, which has taken place among disciplines of spatial ecology and geoinformatics in this study. It is the combined effect of spatial ecologists and specialists on geographic information science that could open novel avenues for future research and eventually make this kind of applied geoinformatics a thriving tributary of spatial ecology.

6. CONCLUSION

In the above we have introduced a three step modeling framework. At first, we built the growth, dispersal, and overwintering Response Model of Colorado Beetle following the Spatial Resource Inventory Model (SRIM) to analyze the projected seasonal growth, dispersal, and overwintering resources available for Colorado Beetle after potential immigration to a novel habitat network. As an output from resource analyses we created a spatially and temporally varying resource base for each location. Now we could import the dynamic resource base to Resource-constrained Geographic Automata Model (RGAM) to simulate the spread of Colorado Beetle. But in order for GA to work we needed also the transition rules; for summer and winter step respectively.

Although the procedure needs a response model for resource analyses before we are able to use the actual Geographic Automata on spread we still find the method quite straightforward to apply. It follows the concept of expansion (see Figure1) by keeping track of the responses of the organism in its new environment. As you might remember every expansion is a combined effect of population growth and diffusion. By building a procedure, which describes the growth and diffusion responses of Colorado Beetle with temporally varying resources we have captured the general concept of expansion. Furthermore our modeling framework facilitates a straightforward multiple-lined avenue for spatial exploration of several scales. This is something the traditional modeling approaches of diffusion equations (e.g. Andow et al., 1990; Okubo, 1980) or simple transfer functions (e.g. Fahring and Merrim, 1985) are not able to provide.

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