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Modeling invasion dynamics of Colorado potato beetle to test spatially targeted management strategy

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Abstract: The Colorado Potato Beetle (CPB), *Leptinotarsa decemlineata* (Say), one of the most destructive pests of potato, is currently spreading in northern Europe. The species is already numerous in Russia and the Baltic countries, so there is a substantial risk for massive aerial immigration to Finland. In Finland, CPB is a quarantine pest, so all infected sites are aggressively eradicated. In this paper, we will introduce a modeling framework which can be used for testing effectiveness of eradication scheme based on risk mapping, an unexplored option, for the case when a massive aerial immigration takes place and the current strategy without prioritizing will most likely fail.

We tackle the problem by introducing a spatially explicit population model that accounts for temporally varying resources for the growth, dispersal, and overwintering of the invaders. The neighborhood structure for dispersal is hierarchical, in order to mimic the stratified dispersal behavior of the beetle during invasions. To test a spatially targeted strategy we introduce here a concept of Key Cells. These cells connect one of more habitat clusters together facilitating further spread of CPB to new clusters. The number of adults that move to new sites is dependent on the resources beetles have for growth; the higher the value of Growth Index (GI) the more offspring and subsequently greater number of dispersers. As a result we have an ordered list of cells according to their capacity to push the spread onwards. By assigning a higher probability of detection and eradication to these key cells we can test whether the spatially targeted strategy would perform better than the strategy without prioritizing.

Our modeling work had two parts. First, we built CPB Response Model based on species ecology. This model is an input for computing annual growth, dispersal, and overwintering resource layers. Secondly, we built the CPB Invasion Model which follows the annual sub steps of immigration, dispersal, reproduction, detection, eradication, quarantine, and overwintering. The spread simulations can be run by iterating these sub steps for a desirable number of years. The monitored outputs are cell-specific population numbers, number of commercial fields invaded, and the overall number of invaded cells in the landscape.

Together, these two models provide a basis for a novel GIS-based Decision Support Suite. The predictive power of the CPB invasion model can be further enhanced by modeling the wind dispersal and overwintering mortality of the beetle with greater detail than in the current version. Overall, the main benefit of resource based approach is that it guides managers where to target surveillance and eradication measures in the mosaic landscape.

KEYWORDS: *Invasions, predictive modeling, management strategies, decision support tool*

1. INTRODUCTION

Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say), is the most destructive insect pest of potato and also causes severe losses in tomato and aubergine crops (EPPO/CABI, 1997). The beetle is present throughout Europe except for Britain, Ireland and Scandinavia, having its northern range limit in Russia (60˚N) (EPPO, 2006) (Figure 1). Since the last two aerial mass migrations to Finland in 1998 and 2002, a considerable amount of research has focused on studying the life history parameters of the beetle (e.g Boman et al., 2008A; Lyytinen et al., 2008) and economics of management strategies (e.g. Heikkilä & Peltola, 2007). Recently, Valosaari et al. (2008) investigated the effects of Bt-potato cultivation and longer quarantine as options to control the spread of the beetle.

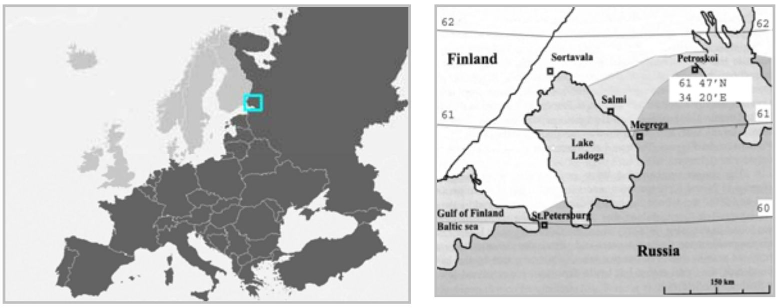

Figure 1. Left: Current European distribution of Colorado potato beetle (source: EPPO, 2006) dark = countries where CPB is present, light = countries where CPB is not present, the squared area is displayed at right. Right: CPB distribution around Lake Ladoga in Russian Karelia, dark = permanent populations, light = resent findings (Boman, 2008B, published with permission from Dr. S. Boman).

The aim of this paper is to introduce the models that are needed to explore whether spatial targeting of control measures would increase the efficiency of eradication strategies. Although there is a wealth of research on the management of spatially structured invasions (e.g. for plants, see Grevstad, 2005; Whittle et al., 2007; for gypsy moth, see Tobin & Blackburn, 2007; Bogich & Shea, 2008) there seems to be a gap concerning how to eradicate an invader after a massive aerial migration. The general rule of thumb of first eradicating the new satellite colonies and then tackling the continuous area behind the frontline cannot be applied after a successful immigration of CPB since there will be no frontline but hundreds of small separate (satellite) colonies with independent resources for further spread.

To tackle this management problem, we introduce a spatially explicit population model (SEPM) that accounts for (1) spatio-temporal patterns of climatic resources, (2) habitat availability and (3) functional connectivity of the habitat, in the light of the dispersal modes of CPB (for the role of landscape connectivity see With et al., 1997). We base our modeling approach on the landscape ecological view that the local happening responses of individual organisms to the available resources result in the broad scale distribution (e.g. Turner et al., 2001). Since resources are not randomly distributed, we postulate that invaders should not be randomly controlled. So, we want to explore whether the strategy of first controlling the beetles at the sites (1) where their reproduction, dispersal, and overwintering are greatest, and (2) which serve as connectors between habitat clusters, could provide a basis for a new spatially targeted strategy. Thus, this paper introduces the models, in towards more regionally tailored advice, where eradication measures are targeted precisely and efficiently in both the space and time. Implementation and application of the models will be presented in further papers.

2. ANALYZING RESOURCES

Computing the resource indices

The land-cover types of CORINE land cover database that we assume to contain potato fields were: (1) Leisure facilities and small-scale horticultural production, (2) Non-irrigated field crops and (3) Land principally occupied by agriculture. The Information Centre of the Ministry of Agriculture and Forestry in Finland provided the location data on commercial potato fields in 2005. The habitat network for the CPB in Finland consists solely of potato since the abundance of the wild host plants for CPB is very low (Hämet-Ahti et al., 1998). Most of the commercial and small-scale domestic potato fields are situated in Southern and Central Finland but some production takes place in the north near the Arctic Circle.

We use human population density as a surrogate to describe the probability for logistic-aided dispersal since the geographic volume of transportation is not available (e.g. Gilbert, 2005). We define logistic-aided dispersal as any accidental transportation of the airborne beetles in vehicles. The cell-based probability for logistic-aided dispersal is given by Equation 2 at 'Simulating Spread'. The human population density data is provided by Statistics Finland with a cell size of 250 m x 250 m.

We assess the available resources with CPB Response Model (P1 in Figure 3). The spatial resolution of the Resource Sub Model (RSM) is 5 km x 5 km, which is the known annual maximum dispersal distance of CPB (Johnson, 1969). Seven site-specific resources in a grid are produced: 1) Growth Index, 2) Active Flight Index, 3) Overwintering Index, 4) Logistic-aided Dispersal Index, 5) Habitat Availability Index, (6) Commercial Potato Area Index, and 7) Connector Status of the cell (Table1). For all the temperature-based indices, a set of 30 annual layers is produced. The annual variation of these indices creates the dynamic resource base for CPB Invasion Model (P1 in Figure 3) whereas the Logistic-Aided Dispersal Index is constant over time and habitat-related indices are updated according to the quarantine measures used. The computation of Growth Index, Active Flight Index and Overwintering Index is based on the life history parameters of CPB (Table 2). Figure 2 clarifies the predicted life cycle of CPB in Finland.

The values of the resource indices can be examined in multiple spatial scales. Spatial exploration of resource analyses includes mapped resource layers and spatial resource profiles of each cell either separately or in the form of descriptive focal or zonal statistics. This model is very flexible since a wide variety of scenarios can be explored by changing the CPB response parameter values, climate, habitat network, and any combinations of these. However specialist knowledge on the ecology of the modeled species is needed to change existing response parameter values and in building the necessary response sub model file.

Table 2. Response parameters of CPB

Life History Parameter	Value	Literature Source
Emergence from diapause	60-90 DD above +10 ° C	Ferro et al.(1999)
From emergence to egg-laying	51-70 DD above +10 ° C	Ferro et al.(1999)
Degree days for 1 generation	300 DDs above +10 ° C	Boman et al. (2008B)
Fecundity	30 - 200	EVIRA (2008)
Flight take-off threshold	+15 ° C	Caprio (1987)
Diapause induction 1) Min daily temperature 2) Average weekly temperature 3) Triggering day length	 < +12 ° C < +12 ° C < 15.00 h	Sutherst et al. (1991)
Winter mortality	0.7 (mean)	EPPO/CABI (1997)
Rate of superdiapausing	2 %	Tauber M.J & Tauber C.A (2002)
Superdiapause mortality Survive to begin 2nd winter Mortality during 2nd winter	 54.4 % 55.0 %	Ushatinskaya R.S. (English version 1976)

Table 1. Source data and resource indices computed by the Resource Sub Model

Resource Layers, Data Source	Output	Function	Inputs
30 annual layers **years 1971-2000** **FMI**	**1. Growth Index** **GI**	Seasonal accumulation of degree days	
	Degree days	Sinusoidal	Daily min and max temperature Day length
	Fecundity	Exponential	Degree days
30 annual layers **years 1971-2000** **FMI**	**2. Active Flight Index** **AFI**	Seasonal accumulation of flight take-off -days& favorability	
	Favorability	Linear above the threshold	Daily maximum temperature
30 annual layers **years 1971-2000** **FMI**	**3. Overwintering Index** **OWI**	Seasonal accumulation of winter mortality	
	Winter Mortality	Linear above the threshold	Mean daily temperature
1 layer **year 2005** **Statistics Finland**	**4. Logistic-Aided Dispersal Index** **LADI**	Scaled function that uses local mean of human population density as parameter	Human population density
1 layer **year 2000** **CORINE**	**5. Habitat Availability Index** **HAI**	Suitable habitat as percentage of the total cell area	Size and location of the selected CORINE land use classes
1 layer **year 2005** **Ministry of Agric**	**6. Commercial Potato Area Index** **CPAI**	Area of commercial potato fields at the cell	Size and location of commercial potato fields
1 layer **year 2000** **CORINE**	**7. Connector Status Index** **CSI**	Local sum	Number of linked clusters

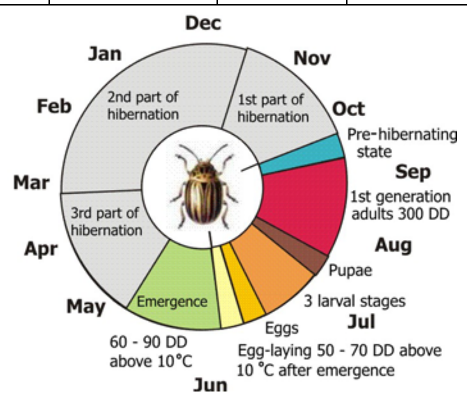

Figure 2. Life cycle model of CPB in Finland

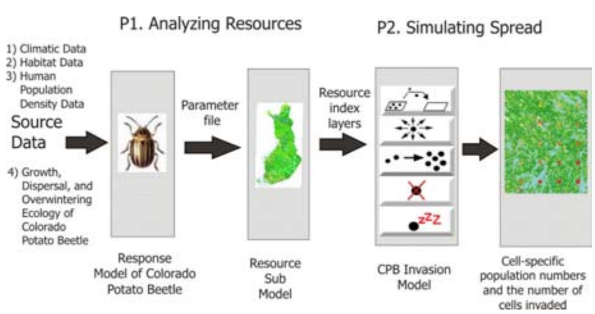

Figure 3. Flow of the modelling task with two phases

Finding and ranking the key cells

To extract key cells first a threshold value is assigned for the Habitat Availability Index, for example 0.10 to form a binary map of the landscape. Next the scores are computed for each cell (i,j) as a function (1) of the 30-year average Growth Index (GI, range: 0-100) and the Connector Status Index (CSI, range: 0.01-1.00)

$$score_{i,j} = GI_{i,j} \times CSI_{i,j} \qquad (1)$$

The range of CSI is as follows: 0.01 means that the cell is not connecting any clusters, 0.25 for 1 cluster, 0.50 for 2 clusters, 0.75 for 3 clusters, and 1.00 for 4 clusters. Consequently, the minimum score is 0 and the maximum 100. Then, the cells are ordered by their scores and ranked. Figure 4 shows four cells that are ranked in Table 3. The Growth Index describes how much thermal accumulation the cell offers for reproduction. A high value means that there will be many offspring (dispersers). These cells also have high Active Flight Index values since warm weather means that the threshold temperature for active flight take-off is reached on many days per season. Overall, finding the Key Cells depends on the approach. If we know how many cells we can have under surveillance and eradication, we take, for example, the first 500 cells from the list and assign them as Key Cells. As can be seen, any changes, whether climatic or habitat-related, as well as the threshold for binary map, have an effect on the order of the cells.

Table 3. Example of ranking

Cell ID	Growth Index 30 year average	Connector Status Index	Score	Rank
1001	17	0.25	4.25	3
1103	20	0.25	5.00	2
1206	15	0.25	3.75	4
1325	24	0.25	6.00	1

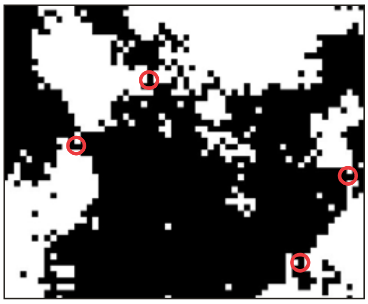

Figure 4. Four cells, each of which connects one cluster to the central one.

3. SIMULATING SPREAD

The spread of the CPB is simulated on the two-dimensional lattice of square cells with the resolution of 5 km x 5 km. Each cell is characterized by its resource indices that both represents temporally varying resource base and also constrain the spread to cells where habitat is available. The simulation consists of scripts representing life-history and management events that are placed in a recursive loop so that the simulation can be run for the desired number of years (Figure 5, see also P2 in Figure 3). The scripts can be executed in Geoinformatica which is an open-source platform for analyzing, processing, and modeling of geospatial data built on FOSS (Jolma, 2007).

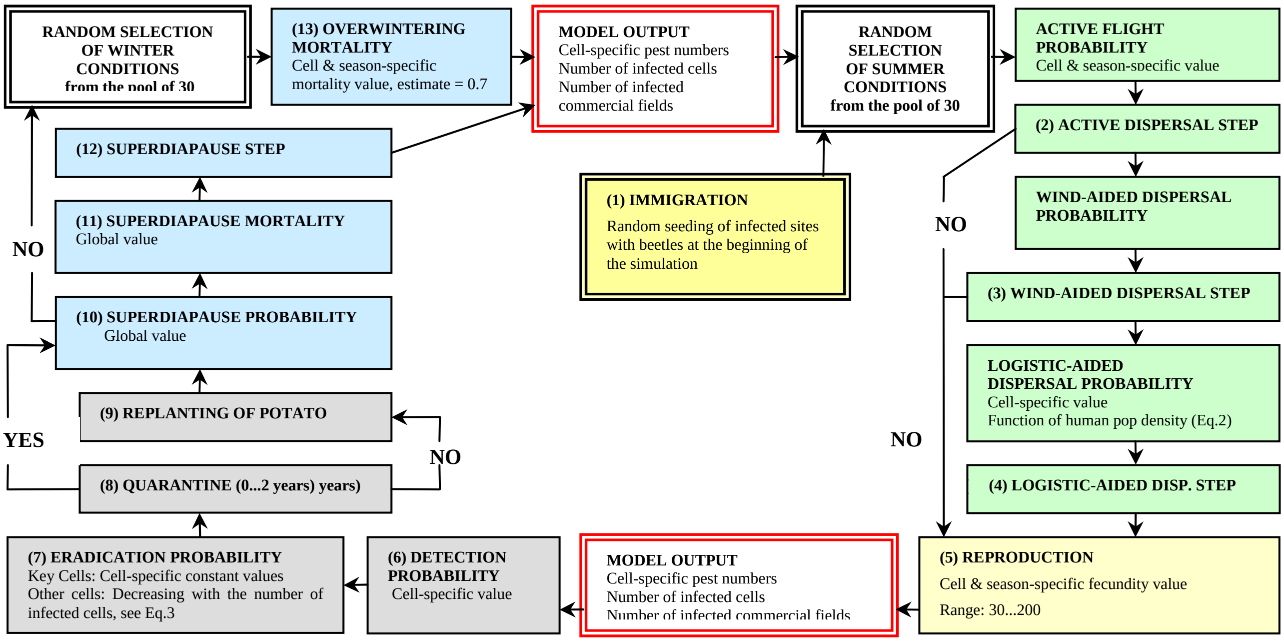

Figure 5. The schematic representation of the CPB Invasion Model. The stages of the model are represented as boxes where the life-history process or management process is given.

At the beginning of the first modeled year (Figure 5.1) the landscape is randomly seeded with beetles representing the typical situation after an aerial immigration. Beetles that land on non-habitat cells are considered to die since the cell size exceeds the search radius of the beetle. Next, a random year from the array of 30 years (1971 -2000) is selected so that the correct values for temperature-related indices can be obtained. After this step the number of beetles that would disperse is randomly distributed to one of the eight neighboring cells (Moore neighborhood) with the probability given by Active Flight Index (of the randomly selected year). If the beetle disperses (Figure 5.2) it has a random probability to be carried further to one of the 16 next-to-neighbor cells by wind (Figure 5.3) or a cell-based probability by logistics (Figure 5.4). The probability for logistic-aided dispersal at cell (i,j), $\Pr(\mathrm{LADI})_{i,j}$, is computed as a function of human population density ($\mathrm{hpop}_{i,j}$) of the cell by assuming that there have to be 7000 residents to reach 0.50 probability that the beetles would be accidentally transported to next-to-neighbor cells (2). The shape of the function is assumed to follow the general trend that the logistic activity, here the probability for accidental transportation, increases very conservatively in relation to human population density.

$$\Pr(\mathrm{LADI})_{i,j} = -\frac{1.0}{1+\left(\dfrac{hpop_{i,j}}{7000}\right)^2} + 1 \qquad (2)$$

After the dispersal steps, individuals die if they do not find viable habitat. If the probability for Active Flight is zero, the individuals stay in the home cell and reproduce there with a probability based on Growth Index (of the randomly selected year). Those who disperse will reproduce at the destination cells accordingly. To keep the model simple we assumed a linear relationship between the annual Growth Indices and the number of offspring so that the minimum GI equals 30 and the maximum to 200 offspring (Figure 5.5). The number of offspring represents those who survive to the adult stage and are capable of overwintering. The cell-specific beetle densities and proportion of infected cells are taken as the model output at this stage (Figure 5). After the beetles have reproduced, the fields are inspected and each individual beetle has a detection probability that increases with population size (Figure 5.6). If the detection probability is allowed to decrease, then more and more infected cells remain undiscovered and the overall number of invaders in the landscape does not decrease as effectively as the successful eradication of discovered infestations would indicate. In the Key Cells, the detection probability has a fixed value (0.8) throughout the simulation. If at least one beetle is found, the crop is destroyed and the beetles die at the cell-based probability called eradication efficiency. In the Key Cells, eradication probability is a fixed high value (0.9) representing the current eradication estimate of national authorities (Evira, 2008) during the last two immigration events; elsewhere the eradication probability decreases (3). When the number of infected cells (nic) exceeds a threshold value of 250, the eradication probability sharply drops and is only 0.50 when the number of infected cells is 500 (Figure 5.7).

$$\Pr(\mathrm{Erad})_{i,j} = \frac{0.9}{1+\left(\dfrac{nic-250}{250}\right)^2} \qquad (3)$$

When the infected cell is put into quarantine, the beetles that survive the control measures stay there during the next growing season but are unable to reproduce and die (Figure 5.8). After a quarantine step, the landscape structure is updated, since the cells in quarantine are not part of the habitat network in the following growing season. When the quarantine period ends, the cell is replanted with potato and becomes available for CPB (Figure 5.9). Those beetles that are not detected or escape the control measures will enter winter diapause in September. A small proportion of the beetles enter a superdiapause with a probability of 0.02 and they hibernate for 2 years (Figure 5.10). Those that fall into a regular winter diapause die during the winter with a cell-based probability depending on the harshness of the winter (Figure 5.13). The probability for overwintering mortality varies annually so we first randomly select the year from the array of 30 (1971-2000) to derive the correct cell-based probabilities. Those beetles that fall into superdiapause are physiologically better protected from the temperature extremes and about half of them survive to the beginning of the 2nd winter, followed by 55 % mortality during the 2nd winter (Fig.5.11). Consequently, about 0.05% of the undiscovered or escaped emerge in their 2nd spring (Figure 5.12). At the beginning of the next growing season, the beetles emerging from the superdiapause mix with the overwintered individuals within the cell forming the spring population. If no new immigration is initialized, the simulation loop begins with the random selection of year that would follow the steps from number 2 to 13 again.

The choice of incorporating temporal variability in the form of 30 annual Growth Index, Active Flight Index, and Overwintering Index Layers ensures that the inherent spatial autocorrelation is preserved. If climate had been modeled as a randomly varying stochastic variable and dispersal as a temperature-independent random walk, as Valosaari et al. (2008) have done, the site-specific reproduction, dispersal, and overwintering rates would not have been captured. If the goal of the modeling is to assess the efficiency of management strategies at a finer than national scale, then both spatial heterogeneity and periodic variation of invaders' resources need to be integrated into the models. In spite of the increased complexity, this approach facilitates testing of a wide variety of management options for the local, regional, or national efficiency, as well as the production of demographic, distributional, and pattern metrics of multiple spatial scales.

4. OUTLINE OF GIS-BASED DECISION SUPPORT SYSTEM

In tandem, the Resource Sub Model and CPB Invasion Model may in the future provide a GIS-based Decision Support Suite for evaluation and design of management strategies to control quarantine species. It could further guide the management decisions by pinpointing areas and sites where to target the eradication efforts in case not all sites can be treated with equal efficiency. The quantitative assessment of resources and the ability to extract Key Cells might become a valuable additional tool. Even if the use of Key Cells in the management did not ensure rapid eradication, it would most certainly help to confine the beetle within a tolerable geographical extent for later eradication measures. The development of an operational GIS-based Decision Support System (DSS) would need close co-operation with the national authorities, so that the cost of different control strategies could be taken into account. Some other basic tools are also listed in Figure 6.

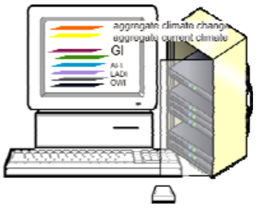

Figure 6. The GIS-based DDS for management of quarantine pests should contain the following functionalities:

- browsing of resource layers
- computation of new layers
- creation of new species files
- running climate and habitat change scenarios
- running cost analyses
- tools for spatial queries
- tools to make reports, maps, charts etc.
- tools for book-keeping of conducted management actions

5. DISCUSSION AND CONCLUSIONS

The models presented here are a step towards developing GIS-based software to explore resource bases of invaders and to simulate their spread. The main benefit of CPB invasion model is that it keeps track of invader responses in both space and time. Invasion models that account for both spatial configuration and periodic changes in growth and dispersal responses are still scarce. However, such accounting is of necessity if we want to manage the invader in a spatially targeted fashion. The use of the resource sub model means that the CPB invasion model is more generally applicable since the environmental and landscape conditions do not have to be the same. The user first assesses annual resources and the habitat structure and then simulates the spread in a desired geographical area.

Like all *a priori* models, CPB invasion model is also very difficult to verify. However, validation of the model can be achieved by examining the three sources of uncertainty according to Higgins et al. (2003). The *model uncertainty* is due to uncertainty in the representation of resources (Table 1) and in processes forming the CPB invasion model (Figure 5). The *parameter uncertainty* concerns the life history parameters of Colorado potato beetle (Table 2) that are derived from the literature. This uncertainty can be tackled by iteratively refining the values when new information on ecology of beetle becomes available. The *inherent uncertainty* can also be present if there are such underlying stochastic processes that reduce the information content of the mean forecasts. The spatial accuracy of predictions can be further enhanced by modeling wind-aided dispersal (Figure 5.3) with directional probabilities that are based on the dominant wind directions in June and August, when beetles disperse. The relationship between the prevailing wind direction of summer months and CPB spread was already reported by Tower (1906) over 100 years ago. Also, overwintering mortality (Figure 5.13) could be refined by adding the effects of snow cover and soil types on beetle survival.

Moreover, in this study we have computed only two components from the large set of available landscape metrics (see Turner et al., 2001). We have described the habitat network with cell-based Habitat Availability Index and Connector Status Index, but the characterization of the landscape can be done at multiple scales. In general, we should explore how managers could benefit from the use of landscape indices in the same way they nowadays use meteorology in their work. From the management point of view it would also be important to work towards some general rules in managing invasions that start with aerial mass migrations. At the moment we do not know how to most effectively eradicate a quarantine pest that has hundreds of separate colonies in a vast geographic area. Our solution in this paper has been to identify where growth and dispersal of the populations are greatest and apply control in a spatially targeted -fashion according to this ranking. However, to develop prioritizing and decision algorithms for successful management of invasive species remains a research challenge.

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REFERENCES

Bogich, T. and Shea, K. (2008), A state-dependent model for the optimal management of an invasive metapopulation. *Ecological Applications*, 18(3), 748–761.

Boman, S. (2008A), Quantitative genetic approach for assessing invasiveness: geographic and genetic variation in life-history traits. *Biological Invasions*, 10, 1135-1145.

Boman, S. (2008B), Ecological and genetic factors contributions to invasion success. The northern spread of the Colorado Potato Beetle (*Leptinotarsa decemlineata*). Doctoral Thesis. Jyväskylä University Printing House, Jyväskylä. (50pp.)

Caprio, M.A. (1987), Flight initiation behavior and host plant attraction in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). M.S. thesis, Michigan State University, East Lansing.

EPPO/CABI, (1997), *Leptinotarsa decemlineata*. - In: Smith, I.M., Scott, P.R. & Holderness, M. (eds.), Quarantine pests for Europe, 2nd ed. *Data sheets on quarantine pests for European Union and for the European and Mediterranean Plant Protection Organization*, 352-357. CABI International, University Press, Cambridge.

EPPO (2006), Distribution Maps of Quarantine Pests for Europe, *Leptinotarsa decemlineata*. Available at: http://pqr.eppo.org/datas/LPTNDE/LPTNDE.pdf.

Evira, (2008), Koloradonkuoriaisesiintymät Suomessa 1998-2005. - Available at: http://www.evira.fi/attachments/ kasvintuotanto_ja_rehut/ kasvintarkastus/karanteenituhoojat/kolorado/koloradonkuoriainen_1998_2005.pdf

Ferro, D.N., Alyokhin, A.V. and Tobin, D.B. (1999), Reproductive and dispersal behavior of the overwintering Colorado potato beetle (Coleoptera: Chrysomelidae). *Entomologica Experimentalis et Applicata*, 91, 443-448.

Gilbert, M., Guichard, S., Freise, J., Gregoire, J.C., Heitland, W., Straw, N., Tilbury, C, and Augustin, S. (2005), Forecasting *Cameraria ohridella* invasion dynamics in recently invaded countries: from validation to prediction. *Journal of Applied Ecology*, 42, 805-813.

Grevstad, F. (2005), Simulating control strategy for a spatially structured weed invasion: *Spartina alterniflora* (Loisel) in Pacific Coast estuaries. *Biological Invasions*, 7, 665-677.

Hastings, A., Hall, R.J., and Taylor, C.M., (2006), A simple approach to optimal control of invasive species. *Theoretical Population Biology*, 70, 431-435.

Heikkilä, J. and Peltola, J. (2007), Phytosanitary measures under uncertainty. In: Oude Lansink, A.G.J.M. (ed.), New approaches to the economics of plant health, pp. 147-161. Wagening UR Frontis Series 20.

Higgins, S.I., Clark, J.S., Nathan, R., Hovestadt, T., Schurr, F., Fragoso, J.M.V., Aguiar, R., Ribbens, E., and Lavorel S. (2003), Forecasting plant migration rates: managing uncertainty for risk assessment. *Journal of Ecology*, 91, 341-347.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. and Uotila, P. (eds.) (1998), Retkeilykasvio (4th ed.), Museum of Natural History, Plant Division, Helsinki.

Johnson, C.D. (1969), Migration and dispersal of insects by flight. Methuen, London.

Johst, K., Brandl, R., and Eber S. (2002), Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos*, 98, 263-270.

Jolma, A. (2007), Geoinformatica: a modeling platform built on FOSS. In: ISESS 2007, Prague, Czech Republic, May 22 - 25, 2007.

Lyytinen, A., Lindström, L., and Mappes, J. (2008), Genetic variation in growth and development time under two selection regimes in *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata*, 127, 157-167.

Sutherst, R.W., Maywald, G.F. and Bottomley, W. (1991), From CLIMEX to PESKY, a generic expert system for pest risk assessment. *EPPO Bulletin*, 21, 595-608.

Tauber, M.J. and Tauber, C.A. (2002), Prolonged dormancy in *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) a ten-year field study with implications for crop rotation. *Environmental Entomology*, 31(3), 499 - 504.

Tobin, P. and Blackburn, L., eds. (2007), Slow the spread: a national program to manage the gypsy moth. Gen. Tech. Rep. NRS-6. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 109 p. USDA. 2007. Slow the spread: a national program to manage the gypsy moth.

Tower, W.L. (1906), An investigation of evolution in Chrysomelidae beetles of the genus Leptinotarsa. Carnegie Institute, Washington D.C.

Turner, M.G., Garner, R.H., and O'Neill, R.V. (2001), Landscape ecology in theory and practice - pattern and process. Springer Science+Business Media, LLC. (401pp.)

Ushatinskaya, R.S. (1966), Prolonged diapause in Colorado potato beetle and conditions of its formation, pp. 168-200. In: Arnoldi K.V (ed.), Ecology and physiology of diapause in the Colorado potato beetle. Izdatel'stvo "Nauka", Moskva. (English translation 1976). Indian National Scientific Documentation Centre, New Delhi.

Valosaari, K-R., Aikio, S., and Kaitala, V. (2008) Spatial simulation model to predict the Colorado potato beetle invasion under different management strategies. *Annales Zoologici Fennici*, 45, 1-14.

With, K., Gardner, R., and Turner M. (1997), Landscape connectivity and population distributions in heterogeneous environments. *Oikos*, 78, 151-169.

Whittle, A.J., Lenhart, S., and Gross, L., (2007), Optimal control for management of invasive plant species. *Mathematical Biosciences and Engineering*, 4, 101-112.