A Spatial Dynamic Model To Simulate Population Variations And Movements Within Fragmented Landscapes

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EXTENDED ABSTRACT

As the human population grows and its footprint on the landscape increases, land-use decisions play an increasing role in the extinction of plant and animal species. In order to reverse the current tendency of biodiversity loss, planners and land managers must consider the long-term impacts of their decisions on the persistence of living organisms.

This paper describes the development and application of a spatial dynamic model designed to help planners and managers assess the long-term repercussions of land-use development alternatives on the population dynamics and movement patterns of animal species.

This model, based on a cellular automata approach, is designed to incorporate life history traits of various species. It uses a spatial dynamic model (created under STELLA 7.0.1) distributed across the cells of GIS grids to simulate population demographics and spatial distribution within a landscape. The incorporation of the STELLA model equations within each grid cell and the calculation of simultaneous local interaction between cells, for all model variables is done through the use of the Spatial Modeling Environment (SME).

Applied to hypothetical species, over potential land-use change scenarios, our model showed development resulting in limited habitat losses (10%) could nonetheless lead to significant reductions in species population within a landscape (-49%). We therefore believe this model offers planners and managers the ability to anticipate possible repercussions of changes in local and regional land-use policies on sensitive animal species.

By simulating animal populations and their movements through the landscape, our model may help environmental managers develop landscape policies maximizing species survival, for example by placing corridors or roads over-paths at location allowing the maximum number of individuals to cross.

Animal species are highly adaptable and behavioral changes might be triggered by the increasing presence in their environment of human influenced landscapes. Consequently models that assume fixed behaviors may be of limited use. Our model, through the STELLA - SME interface, can be easily be adapted to account for different behaviors, so that it could be used to test the consequences of behavioral changes in species population dynamics and distribution.

Finally the outputs provided by the model, both in terms of quantitative values and display maps can represent a powerful tool in advocating policies for both specialists and non-specialist audiences.

This work also underscores the present lack of species-specific life history and habitat preference data and calls for more applied research on the processes governing species response and adaptability to environmental changes.

1 INTRODUCTION

Habitat loss and fragmentation result principally from human activities and in modern landscapes, urban sprawl plays a prominent role. Land-use policies drastically and permanently affect animal and plant populations by modifying the landscapes in which they evolved. The establishment of roads and suburban development leads to modification of species movement and migration patterns and can result in the isolation and potential extinction of local populations.

In order to help assess best development alternatives, managers and planners are increasingly seeking decision support tools based on modeling. Our model was developed as part of the Land use Evolution and impact Assessment Model (LEAM) project, which aims to predict land-use change and estimate its consequences based on socio-economical scenarios and land-use policies. Our model was designed to evaluate the impact of land-use change on animal movements and populations, based on land-use maps provided by the LEAM group.

Species respond in very different ways to modifications of their environments. Consequently, models designed to estimate species response to habitat fragmentation should be species-specific. Models focusing exclusively on habitat, while providing information on species location may fail to account for demographic processes, rescue effects or inbreeding depression that could trigger potential time lags in habitat use patterns and have dramatic long-term repercussions on the survival of species. Consequently, the use of population models as complements to habitat models could improve predictions of species response to environmental changes.

Population dynamic models based on cellular automata (CA) (Wolfram, 1984) have been shown to be more appropriate than partial differential equations for modeling populations within landscapes (Darwen et al., 1996). They have the capacity to handle complex boundaries and are very appropriate for modeling dynamic processes (Sirakoulis et al., 2000; Cannas et al., 2003). CA models usually associate to every cell of a grid a single discrete variable, its state, which limits the complexity of the considered population models. Our approach incorporates complex differential equation of population dynamics within a cellular automata model.

2 THE CONCEPTUAL MODEL

Our model is a CA that uses a combination of STELLA and SME (Maxwell et al., 2002), as described by Deal et al. (2000). Through this approach, the state of each grid cell can be defined as any of the parameters or variables of a dynamic population model, created under STELLA. The model requires several input grid maps, derived from land-use maps to calculate through the STELLA model equations, the state of each cell of the CA. As with other CA, our model can account only for local interactions between cells. To account for species habitat considerations at the landscape scale, such as habitat location, patch size or location of edges, the model can receive input maps from GIS-based models, such as the one defined by Aurambout et al. (in press).

The model requires four grid map inputs with identical geographical extent and cell size to estimate animal populations and their movement pattern in the landscape: (1) land-use map; (2) habitat map, (3) genetically connected entity (GCE) map and (4) myopia map.

The land-use map uses the 1992 National Land Cover Data (NLCD) classification scheme, to which two classes, roads and highways, were added. The habitat map and the GCE map are output maps generated by the habitat fragmentation model described by Aurambout et al. (in press). The habitat map locates suitable habitat patches for hosting at least one individual of the species of interest and classifies it as either edge or core. The GCE map represents suitable habitat patches that can potentially exchange individuals and thus are considered "genetically connected entities". Each grid cell located within a suitable habitat patch is given a value equal to the total habitat area of the genetically connected entity, to which it belongs, while other cells are given a null value.

The myopia map is generated from the habitat map and provides for each cell an indication of its distance to suitable habitat. Cells located within suitable habitat patches are given a value of one, while others are given a value corresponding to their respective distance, in cells, from suitable habitat.

At each step of the model run, the four input rasters are used by the STELLA models within each grid cell to calculate their respective "state".

The model runs on a discrete monthly time step, and cycles on a yearly (12 + x month) basis. The spatially static part of the population dynamic occurs during the first twelve time steps of every year. Movement is decoupled from the population dynamic and can continue after the twelfth month, for a number of time steps (x) defined by the user and equal to the average number of cells than can be migrated by a dispersing individual during one single season. This approach was chosen to avoid the potential overlap of generations among migrating animals that could occur for species moving more than twelve cells in a season (i.e. juveniles of year n+1 dispersing while juveniles of year n are still migrating).

3   POPULATION MODEL

We articulated our population model around three successive life stages (stocks), accounting for cubs, juveniles and adults. The content of each stock is modified through input and output flows, which function is controlled through converters accounting for species-specific life history traits. This model was designed to simulate population demography and movement of non-flying species which suitable habitat can be identified as limited patches. At the first time step of every simulation, populations of cubs, juveniles, and adults are initialized within suitable habitat cells, based on values specified by the user.

Cubs represent a spatially static phase of the population model. They appear during the breeding season as a result of Juveniles and Adults sexual reproduction, which only occurs in cells of suitable habitat. We made no distinction between male and female; every individual able to secure territory was assumed to reproduce. A proportion of the cubs die before reaching the juvenile stage and the remaining cubs become juveniles during the cubs independence season.

Juveniles and Adults represent mobile phases during which movement out of and into their cells is possible. However, Adults tend to remain in their cell as long as it remains suitable for them, while a fixed proportion of Juveniles emigrate annually during the juvenile migration month. Both Adults and Juveniles can reproduce sexually. A proportion of Juveniles die before reaching adulthood and the remainder becomes Adult during the Juveniles' sexual maturation season. Once reaching adulthood, an individual of the species remains in the adult stock until it moves out of the cell or dies.

Our model is based on the hypothesis that any cell of suitable habitat can provide a fixed amount of food and shelter for the focal species. Therefore the carrying capacity (K) of each suitable habitat cell was defined as the quotient of cell size divided by the average home range for the species. In order to account for social species that tolerate the presence of other conspecifics on their territory, a territoriality coefficient parameter was defined, corresponding to the number of individuals sharing the same home range. This parameter was then used as a multiplier to the carrying capacity value to estimate the maximum number of individuals per cell. K was associated with a negative feedback on the reproduction rate of adults and juveniles and with a positive feedback on the death rates of all life stages. Our focal species was unable to reproduce or feed in non-suitable habitat cells, and moved from cell to cell until reaching suitable habitat. The K value of these cells, therefore had no influence on the dynamic of crossing populations and was set to a value equal to ten times the K of suitable cells (to avoid any potential limitation of K on moving populations). Island biogeography theory suggests a decrease of suitable habitat patch area leads to a smaller hosted population that is more vulnerable to extinctions resulting from environmental or demographic changes, human disturbance and reduction in genetic variation (Hanski, 1997; Bunnell, 1999). However, much uncertainty remains on the long-term effect of habitat fragmentation, concerning potential time lags in habitat use pattern, demographic responses, and genetic changes. To account for the potential impact of inbreeding due to genetic isolation of small populations, we incorporated an estimate of genetic degeneration. We defined a minimum viable population as the minimum number of individuals in a population necessary to avoid the negative effects of inbreeding depression. Genetic degeneration was expressed as a graphical function taking values between 0 and 1 based on the ratio of the potential population hosted within each genetically connected entity (obtained from the GCE map) divided by the minimum viable population. This genetic degeneration parameter was associated with both a negative feedback, (cub birth rate), and a positive feedback (cub, adult and juvenile death rates).

4 POPULATION MOVEMENT

In this model, movement occurs in two instances: (1) during the juvenile dispersal season and (2) when the population of suitable habitat cells exceeds its carrying capacity. This approach accommodates the documented behavior in many species, where juveniles reaching sexual maturity are rejected by their parents and forced to search for new territories. Therefore, every year, during the juveniles' migration month, a proportion of the juveniles was allowed to move out of their habitat cell. Both adults and juveniles are also likely, at any time step, to leave their cell if the population of breeding individuals surpasses the cell's carrying capacity. In this circumstance the excess of juveniles move out first, followed by the excess of adults. Once out of their suitable habitat cell, juveniles and adults continue to move at every time step until they reach another, non-overpopulated, suitable habitat cell. Individuals failing to find suitable habitat within a particular time period, will either starve or be killed by predators. To account for this phenomenon and avoid species moving beyond unrealistic distances, dispersal was allowed to occur during a limited number of time steps (the dispersing period) following the juvenile migration month, after which all migrating individuals not reaching suitable patches were killed. The dispersal period, calculated by dividing the average dispersal distance by the grid cell size, was added to 12 to obtain the number of months per model iteration.

The effect of habitat viscosity on the spread or movement of organisms is typically ignored. Many treat animal dispersal as random patterns (Sirakoulis et al., 2000) or assume dispersal in all direction as equiprobable (Berec, 2002). In our model, the proportion of the cells' population dispersing to each of its eight neighboring cells is determined, by a dispersal module influenced by two factors: (1) the nature of the neighboring cells surrounding the target cell and (2) its distance to suitable habitat (myopia).

Certain species have the capacity to sense their immediate surrounding environment and preferentially choose, based on their specific life history traits, to cross or avoid certain land-uses instead of others. To include this behavior in the model, each land-use is weighted according to its degree of attractiveness. These values are used, in the movement sub-model to calculate the proportion of the moving population that will emigrate in each direction, depending on the land-use types present in each of the eight surrounding cells. Species having different sensory capacities may perceive their environment in different ways. Therefore, the nature of the immediate surrounding habitats may not be the only parameter influencing species decision in their choice of dispersal direction.

Animals may be able to sense suitable habitat patches from distance and direct their movement towards them with minimal regard to the nature of the matrix that separates them. This potential behavior was incorporated into our movement sub-model by adding a "distant attraction" module. This module, based on the myopia map, attributes to each grid cell a parameter indicating its distance (in cells) and direction to the nearest suitable habitat patch. The immediate neighbor cells around each target cell are given a "direction" value of one if their myopia value is equal to the minimum of the eight neighbors, and zero otherwise. Based on these direction values, migration occurs only towards neighboring cells having positives values. Most species have limits in the distance at which they can sense suitable habitat, therefore we defined a suitable habitat diffusion distance beyond which myopia values are considered identical and do not influence the direction of species migration.

The migration path of most species may be influenced by a combination of adjacent habitat attraction and distant attraction. Therefore, the effects of both modules were integrated in the movement sub-model. Since, both modules might not have the same weight in influencing species movement, a "habitat attractivity" coefficient was added. This coefficient modifies the weight of distant attraction compared to the influence of immediately adjacent land-uses. If an animal is located within an environment composed of identical land-uses, its capacity to sense distant suitable habitat might increase (pay less attention to immediate land-use and focus on distant attractor) or decrease (disoriented and focus on land-use). Therefore a "homogenous landscape influence" coefficient was added to balance the effect of immediate land-use. The final proportion of emigrating population in each direction is defined in Equation 1.

Equation 1

$$Pn = \frac{I \times Wn + Mn \times Ha}{\sum\limits_{N}^{s}(I \times Wi + Mi \times HA)}$$

Pn: proportion of a cell population emigrating to Northern neighbor; *Wn*: weight of the land-use situated North of the target cell; *Wi*: weight of the land-use situated in the ith direction of the target cell; *Mn*: myopia attraction from the North; *Mi*: myopia attraction from the ith direction; *Ha*: habitat attractivity coefficient; *I* : coefficient of homogenous landscape influence >1 or < 1 if the eight cells neighboring cells have identical land-use values to each other; =1 otherwise

Various land-uses present different environments and the death toll associated with the crossing of each cell might be dependent on its land-use. Therefore we allowed the user to define, specific adult and juvenile migration death rates for each considered land-uses, corresponding to the proportion of individuals that might die while crossing a particular habitat cell. This migration death rate, contrary to the population death rate, is applied at every time step to the flow of animals (both adults and juveniles) entering the target cells and therefore affects every migrating individual.
The model was evaluated on a two-dimensional controlled environment and produced spatial dispersal patterns consistent with our specifications.

5 APPLICATION OF THE MODEL

We applied our model to a fictitious land-use raster to assess its ability to provide information to planners on the dynamic response of species to landscape alterations. Initially free from human impacts (Fig. 1a), this landscape was altered to simulate the development of roads and highways (Fig. 1b). The effects of these landscape changes were considered for a fictitious forest specialist species, assumed to have a home range of one cell, a dispersal distance of 8 cells, minimum viable population of 5000 individuals and known life history specificities. We also assumed edge habitat, extending 60 meters into forested patches to be a long-term population sink, while core patches acted as sources.
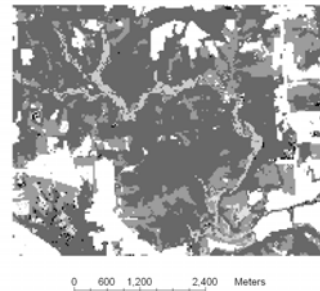

a
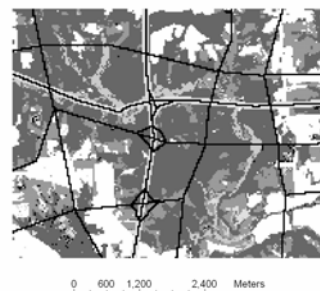
b

Figure 1: Land-uses of the initial and modified maps, each composed of 29530 30 x 30m cells. The initial land-use map (a) represents a semi-natural landscape with limited human disturbance, while the modified land-use map (b) displays the same landscape crossed by 7 roads (black lines) and 2 highways (black lines surrounded by a 30 meter buffer.

The consequences of development on populations of the species were investigated by examining the populations of breeding individuals within each habitat cell. The averaged variations of the total breeding population accumulated for all landscape cells during a 15 year period (Fig. 2), shows a population decrease during the first six years, corresponding to the model's stabilization phase, followed by a plateau at the model's steady state. This was the case for both initial and changed conditions. However, we observe a very significant difference in the total population between the two runs. The population supported in the changed landscape is only one-half (48.7%) of that present in the initial configuration. This difference, also induced by the land-use modification, cannot totally be explained by the observed loss of only 10.7% of the forested habitat.
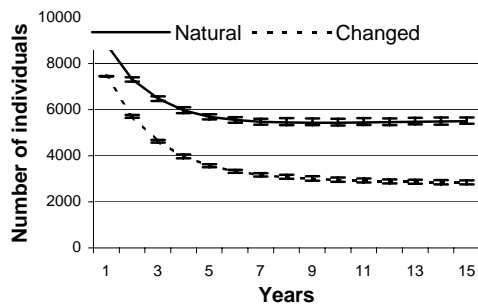
Figure 2: October predictions for 15 years of model runs (30 run average) of the total breeding population for the initial and modified maps. The paired t test for these two populations is P=0.01 (t=3.689>2.624).

The creation of roads and highways (Fig. 3a, b) led to (1) the conversion of core into lower quality edge habitat, as well as (2) the separation of the initially connected landscape into four genetically isolated patches (where populations fell below the 5000 inbreeding threshold in three of the four patches), creating an on-going genetic degeneration effect (responsible for the continuing population decrease after year six) and (3) an increased death rate of juveniles crossing roads during dispersal. These factors therefore have a major influence on the species long term response. As a result, our approach provides information of significant value that cannot be obtained by direct extrapolations from land-use maps and therefore represent a valuable complement to habitat models outputs.
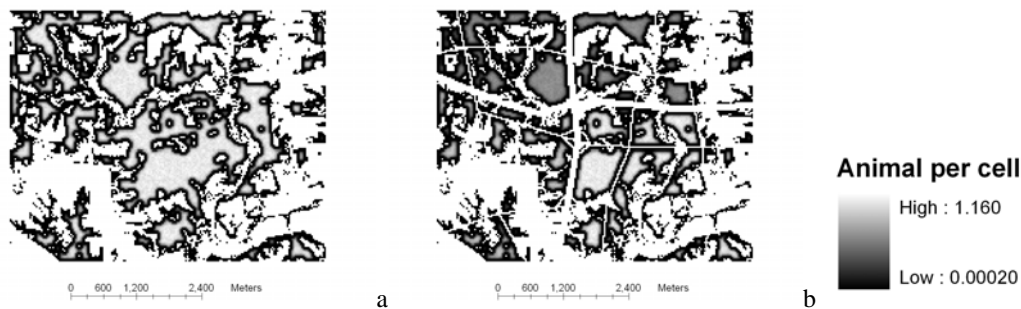
Figure 3: Spatial pattern of the total breeding population distribution and abundance after 15 years of model run, for (a) the initial and (b) modified landscapes.

5.1 Effect of cell size

The cell size of rasters to which the model is applied, and its relationship with the territory size of a considered species, has a determinant influence on the accuracy and validity of the produced results. If the cell size becomes too small, the number of moving individuals becomes meaningless and only a portion of the actually dispersing population will be considered to move, thereby biasing the model's predictions. Consequently, for the model to be used to investigate population dynamics or source-sink interactions within a landscape, its cell size should be equivalent to the average territory of the focal species.

However, landscape modifications, although minimal at the scale of a species' home range, can have dramatic consequences on its movement and behavior (for example the passage of a highway in the middle of the grizzly bear home range (Gibeau et al., 1998)). In certain cases, it may be useful to model movements at a lower scale resolution. To accommodate this purpose, our model can be decoupled from the population sub-model and accept a lower cell size. Used at a local scale, the model can indicate the likelihood of a species being present in the landscape. Nevertheless, by increasing the gird resolution and therefore increasing the number of cells through which the species disperses, the number of tracks they leave quickly decreases with distance away from the suitable habitat patches. This makes interpretation of movement patterns very difficult beyond 100 cells.

6 CONCLUSION

We demonstrated our model could provide useful information concerning the dynamics of species population movements and their spatial distribution during dispersal. Its validity could not be estimated by comparing experimental results with real case study however; the major challenge to our model's application to real case

scenarios remains the lack of specific data concerning species life history characteristics. For most species, surprisingly little is known about their essential life characteristics. Very little data are, to our knowledge, available concerning the dispersal distance of animals and their preferential movement path. Furthermore, the dispersal phase of juveniles, on which most of the population spatial dynamics depends, remains greatly unstudied.

Consequently, there is an important need for more accurate and intensive data collection on species life history traits, as well as applied research investigating long-term spatial population behavior at a large spatial scale. Finally, as the human footprint increases across landscapes, studies should focus on species responses to humanized landscapes rather than to "pristine" locations.

The parameter values required by our model (land-use weights, migration distance, specific land-use death rates, etc.) which, to our knowledge, are not yet available in the literature could be obtained empirically. Most population movement studies, to date, investigated the location of animals on a semi-daily or daily basis. While providing information on where an individual was, they did not determine how it got there. However, through the use of GPS and GIS technology, animal movement patterns could be plotted within minutes and could provide insights on species movement patterns. Experiments involving animal release and dispersal tracking within controlled landscapes could also prove to be very instructive to determine species habitat preference.

7   ACKNOWLEDGEMENT

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