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Modelling individual movements in heterogeneous landscapes: potentials of a new approach

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Abstract

This paper deals with modelling methods for spatially explicit simulations of animal movements in heterogeneous landscapes. Within this context technical and methodical limitations of grid-based models are discussed followed by examining the sparse use of Geographical Information Systems (GIS). Then a new approach is presented which is distinguished by two essential features to overcome the constituted limitations: (1) an irregular grid (similar to a quadtree) for modelling heterogeneous, patchy landscapes on a wide range of spatial scales and (2) the object-oriented approach for modelling individual movements in a vector-based manner independently of the resolution of the underlying grid. This sophisticated approach is embedded in a modelling framework which provides methods for model definition, simulation handling and flexible model evaluation. Finally, general potentials and links to modelling results of this approach are given. © 1997 Elsevier Science B.V.

Keywords: Landscape ecology; Individual-based; Movement models; Telemetry; GIS; Object-orientation

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1. Introduction

The effect of spatial patterns on the temporal dynamics of animal movements is of special importance for both, theoretical concepts and conservation measures. It is the concept of metapopulations which assumes that a defined exchange of organisms between isolated local populations can increase their survival probability (e.g. Hanski, 1989, 1991; Frank and Berger, 1996). A favoured conservation measure which focuses on this defined exchange of organisms is the connection of habitats by means of corridors (e.g. Saunders and Hobbs, 1991; LaPolla and Barrett, 1993; Lindenmayer and Nix, 1993; see Dawson, 1994 for a critical review; Andreassen et al., 1996; Tischendorf and Wissel, 1997). Such exchange of organisms is based on their movements across more or less fragmented and there-

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fore heterogeneous landscapes. However, it turns out to be a difficult task to improve our knowledge and understanding about the influence of landscape structures on animal movements.

Animal movements remain difficult to record despite sophisticated methods for tracking individual organisms, e.g. telemetry, are available. Such observations are limited to a small number of individuals in just one landscape configuration. They are time consuming, expensive and labour intensive. It is furthermore difficult to transfer the results of such tracking studies to new or changed landscape structures and to other scales, which is necessary in particular for landscape-related conservation measures.

It seems likely that simulation models could play an important rule in transferring singular results from empirical research to other landscape structures on different spatial and temporal scales. However, as far as I know appropriate modelling methods are hardly available despite the tremendous progress in hard-and software development. Individual movements in landscapes are commonly modelled with regular grids like the well-known cellular automata (Hogeweg, 1988; Phipps, 1992; Molofsky, 1994; Ruxton, 1996; Jeltsch et al., 1997). Despite clear advantages of this approach, it is beset with cardinal shortcomings if movements of organisms across heterogeneous landscapes should be modelled. The underlying technical and methodical limitations will therefore be discussed.

Geographical Information Systems (GIS) are powerful tools for modelling landscapes (see e.g. Burrough, 1988; Coulson et al., 1991). Surprisingly, they have hardly been used for simulation models in the context of this paper up to now. GIS's provide different spatial data models (usually vector and grid) and sophisticated algorithms for landscape modelling purposes. They at least seem to provide ideal prerequisites for providing landscape models which could in turn be linked with dispersal models. However, this task is combined with various problems which will be the second focus of the initial discussion.

The evaluation of these modelling approaches motivated me to look for new ways to overcome technical problems and to provide more compatibility between empirical data and model parameters. A new approach is portrayed which is distinguished by two separated parts: an efficient spatial data model (an irregular grid) and object-oriented individual models. The combination of these parts permits simulation experiments to investigate effects of spatial patterns on animal movements on a wide range of spatial and temporal scales. The presented approach is embedded in a sophisticated modelling framework with a graphical user interface.

Lastly, I will discuss potential fields of application of this approach. Instead of showing a modelling example I refer to results which are published separately.

2. State of the art

2.1. Grid-based models

Grids divide a continuous two-dimensional space into discrete units of equal size and shape, i.e. cells. Each cell can easily be selected by indices because of its defined position in a matrix. By this arrangement cells relate descriptive information, e.g. state variables and transition rules both, to each other (by fixed neighbourhood relationships) and to the area they cover. In this way information about landscape features and individuals can be placed in a spatial context. Movements of individuals are commonly expressed by rules that either assign individual positions to other cells or change cumulative cell state variables which describe a spatial class of individuals. Such movement rules can be influenced by landscape features associated with cells. For example, movements can be restricted to cells that are explicitly defined as habitat (e.g. Soulé and Gilpin, 1991; Johnson et al., 1992a; Schippers et al., 1996). In general, the grid-based approach involves the following advantages:

- Grids provide a clear arranged and fixed spatial structure which is binding on landscape and movement modelling.
- Fixed neighbourhood relationships between cells facilitate the description of local interactions by state transition rules.

These and perhaps other reasons I did not consider encourage models to use grids for a wide spectrum of spatial explicit simulation models. However, the use of grid-based models is restricted because of various shortcomings: (1) the size of a grid appropriate for simulation models is limited for two reasons: memory capacity and simulation time. Simulation time is most crucial, because at each time step at least one iteration over the whole grid is necessary. Thus simulation time is directly proportional to the grid size. That is why grid-based models seldom exceed 10.000 cells. Such models can express either a high resolution (fine grain) or a large extent. However, organisms often perceive larger scale sectors (differences between extent and grain; Wiens, 1989) which may lie beyond the limits of grid based models. (2) The fixed spatial structure implies an equal resolution for both landscape features and individual movements. There is little elbow-room to model movements with resolutions that differ from that of the grid. However, it is the resolution of the modelled movements which determines the interactions with the underlying landscape configuration. Model results can differ if movements are modelled on different resolutions within the same landscape representing grid (see Tischendorf, 1995, pp. 80). Hence, it is difficult or impossible to look for such influences and to carry out systematic investigations into the influence of movement modelling on different scales. (3) Modelling of movement is possible only in terms of cell jumps. The necessary rough discretization of step sizes and step angles makes model parameters incompatible with the vector-based description of movements, which is a typical output of empirical tracking studies (e.g. Baars, 1979) and has also been used for the mathematical analysis of movements (Kareiva and Shigesada, 1983; Marsh and Jones, 1988; McCulloch and Cain, 1989). Because of this incompatibility, comparison of results as reached by the different methods is difficult.

2.2. GIS

GIS's are powerful and complex tools for landscape modelling (e.g. Burrough, 1988; Coulson et al., 1991). The most important feature of GIS's is that they link spatial data models (usually grid and vector) to a database management system and therefore relate descriptive information to space. Based on this approach GIS's support model description, visualisation and conversion between different spatial data models as well as the combination of different descriptive data layers (called overlay). With these and other features they are appropriate for descriptive landscape modelling and evaluation.

Surprisingly, GIS's are hardly used for simulation models, especially for analysing the effect of spatial patterns on movement processes. But this is conceivable by combining GIS's with models of individual movements as, e.g. realised by Schippers et al. (1996). The observed clear rejection of GIS's in ecological modelling may have different reasons. At first I presume that the complexity of tools like GIS's deters modellers or biologists for the following reasons:

- they are difficult to handle;
- of large settling-in periods;
- of the arising inhibition thresholds of 'non-GIS educated people'.

Secondly, because GIS's are mostly commercial products they are expensive and implementation details are mostly protected. Spatial data structures often are hidden or binary encoded as for instance in ARC/INFO. This implies that the modeller has to use GIS's own commands (mostly integrated into a macro language such as AML for ARC/INFO) if he wants to gain access to the spatial data. In using common programming languages, an interface (something like a precompiler for 'embedded AML') would be necessary (see e.g. Ostendorf and Boyns, 1996 for one possible solution).

A third reason becomes perceptible if we look at the plane spatial data models which GIS's are based on, in particular the vector data model. Vectors describe points which are summarised to lines describing patch (polygon) boundaries or linear features as e.g. roads. In contrast to grids, patches are here described by their boundaries and not by arranged discrete parts (cells) of a continuous space. The selection of spatially related descriptive information by point coordinates (such as a position of an individual) becomes only possible by relating them to all boundary coordinates of the whole vector data model. Because individual movements are modelled in discrete steps, the crossing of linear features (e.g. boundaries) requires the calculation of an intersection between movement path and boundary which is a time-consuming task. For these reasons vector-based landscape models are not appropriate for the combination with simulation models despite the clear advantage that they are technically scale-independent.

3. The new approach

3.1. Landscape modelling with an irregular grid

To overcome the named shortcomings I developed a hierarchical spatial data model—a grid with cells of different size (Fig. 1(b)). This data model can be applied to patchy landscape models in which patches are considered as homogeneous units bounded by clear border lines. Similar data models, known as quadtree, are used to store big raster images efficiently (see Foley et al., 1990; pp. 550–554). The irregular grid combines the advantages of regular grids with those of the vector-data model. It provides a high resolution within a large extent (scale sector, see Wiens, 1989) and permits easy selective access to spatially related descriptive information because cells are arranged in a fixed hierarchical order. The final shape of an irregular grid depends on initial vector or coordinate-based structural information-the configuration of the landscape model (Fig. 1(a)). This corresponds with a digital draft for which a graphic editor has been provided within the modelling framework. An interface to GIS data sets (grid and vector) is planned.

Fig. 2 provides a general idea about the recursive data structure of the irregular grid. The basic object 'cell' contains two coordinate pairs defining its lower left edge and its upper right edge. In addition it holds a link to a single linked list of smaller cells which divide the space further. This subdivision is triggered only by boundary coordinates of the digital draft (Fig. 1(a)). Each cell object contains identical algorithms that work equally at different levels and at every place in the hierarchy. In this way an object 'root-cell' (a square that covers the whole area and is the top of the hierarchy) evolves into an irregular grid which corresponds with the initial structural information (Fig. 1(b)). Afterwards spatial related descriptive information (landscape features such as vegetation type) have to be assigned to all cells of the irregular grid. Firstly, all cells belonging to one homogeneous unit (patch) have to be combined to clusters. This can be done interactively by selecting a cell with a mouse click. A flooding algorithm scans the whole hierarchy and collects all cells belonging to that patch which covers the

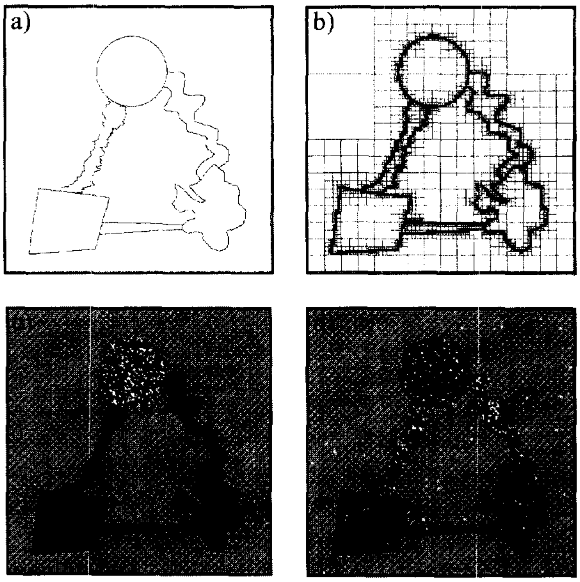

Fig. 1. (a) The spatial configuration of a patchy landscape model has to be provided in a digital form. This can either be done using the graphic editor of the modelling framework or by importing GIS-data sets (planned). (b) Based on the information from (a), a corresponding irregular grid is generated which provides not only a high resolution within a large extent but also easy and fast selective access to spatial descriptive information. With it scale-problems of grid-based landscape models are overcome. (c) The complete landscape model after assigning different descriptive information (marked by different grey scales) to the patches (cell-clusters). Crosses mark the initial positions of the individuals within a patch. (d) The spatial distribution of the individuals after simulation. The final positions are the result of the movements and the interactions with the underlying landscape model.

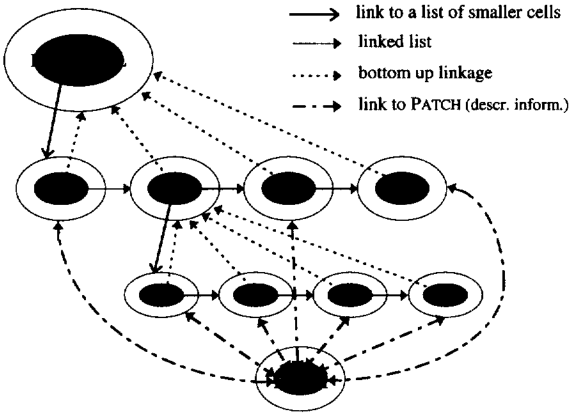

Fig. 2. Principle scheme of the object-oriented data structure for the irregular grid. Cells either are linked to a list of smaller cells (refinement, higher resolution) or are linked to a patch object which holds the descriptive information of the landscape model. The process of refinement is triggered by the boundary coordinates as provided by the digital landscape configuration (Fig. 1(a)). By linking a cluster of different sized cells to one patch object its descriptive information gets precisely the spatial dimension of that area which is covered by the cells of the cluster.

initial mouse click position. Then a patch object which holds the descriptive information can be assigned to this cluster (see Fig. 2). Fig. 1(c) shows an example of a complete landscape model.

The size of an irregular grid (in terms of numbers of cells) only depends on the complexity of the initial structural information. The huge reduction of cells considerably reduces memory capacity and simulation time. Landscapes with fine grain (complex boundary forms) and large extents can be modelled with it. Thus the irregular grid is an efficient solution of the restrictions as discussed initially. However, cells are no longer appropriate as place holders for individual positions for two reasons: cells differ in size and neighbourhood relationships are ambiguous. This implies a separate model for individual movements.

3.2. *Object-oriented modelling of individual movements*

Individuals are modelled object-oriented. An object itself can be regarded as a model because it combines state variables and methods (methods are also called procedures or functions, e.g. Meyer (1988), Silvert (1993). State variables of an object can only be changed by its methods which in turn provide the objects entire functionality. Different objects can communicate with each other by exchanging information about their respective state. Thus the actual functionality of one object may depend on the current states of other objects. In this way the behaviour of modelled individuals can be related to other individuals and to environmental objects such as a landscape model.

As mentioned above, using the irregular grid requires spatial independence of the individual models. Therefore the state of an individual model (object) contains at least one coordinate pair defining its spatial position within the landscape model. An individual 'moves' if a method of it changes these coordinates. Even these movement methods (of the object) have to be related to the individuals environment to take external influences on the actual movement decision into account.

Real movements of organisms in landscapes are influenced manifold. It is hardly possible to model all these influences separately. Some theories exist for the different movement motivations on different spatial and temporal scales (e.g. Ims, 1995). However, not all of them can be considered simultaneously for a movement model. So far I will refer to three distinct influences which can be treated separately in a movement model.

Firstly, the movement pattern itself is commonly described as a sequence of probabilistic discrete steps expressing the way an individual may walk under homogeneous conditions. It can be quantified by measuring the distance and the turning angle between two consecutive positions (e.g. Kareiva and Shigesada, 1983). Tracking studies usually record real movements by measuring these two parameters after equidistant time intervals. The accumulation of these measurements shows frequency distributions for step sizes and step angles (e.g. Baars, 1979; Wallin and Ekbom, 1988). This stochasticity subsumes the organisms movement ability and the impact of fine grained heterogeneity which allows the use of these two parameters for modelling movements on a theoretically homogeneous background. This has been done for the analytical treatment of movement patterns (e.g. Kareiva and Shigesada, 1983; Marsh and Jones, 1988; McCulloch and Cain, 1989) and in a discrete manner for grid-based simulation models (e.g. Soulé and Gilpin, 1991; Johnson et al., 1992a,b; Schippers et al., 1996).

Secondly, individual movements are strongly influenced by the spatial distribution of resources. Individual movement decisions therefore have to be related to spatial information as provided by the landscape model. The required selective access to spatially related information is done by projecting the individuals position onto the landscape model. That cell of the irregular grid which covers the requested position will be selected and provides a link to the corresponding patch object (see Fig. 2) which in turn provides the local descriptive information. Hence, individual and patch objects 'communicate' by means of the spatial relationship between individual positions and the irregular grid. In this way movement patterns of the modelled individuals (and other factors such as probabilistic mortality rates) can be related to patches and can therefore differ within the entire landscape model. Additionally, boundary encounters can trigger special behavioural rules as for instance turning back reactions or probabilistic crossings as a measure of boundary permeability (e.g. see Stamps et al., 1987). Such boundary encounters are detected if two subsequent positions of the moving individual identify different patch objects. There are almost no technical limits in modelling boundary reactions. However, little is known and quantified about what organisms perceive as a boundary and how they react. This should not deter to use initial (null) hypotheses which in turn could be tested in field experiments.

Thirdly, organisms interact by avoiding or attracting each other. In this cases individual movements become density-dependent. Such interactions are difficult to deal with using the represented approach because individuals are freely located in space without any arrangement. The calculation of distances or neighbourhood relationships is time consuming because the position of each individual must be compared with those of all others. Furthermore, simulation results based on reciprocal individual interactions may be sensitive to the sequence of activated individuals during one single time step. To avoid such potential artefacts the states of all individuals can be updated synchronously which is realised by holding an additional state (buffer). Beside this applied pseudoparallel approach there are different ways of dealing with this general problem (Gorlen et al., 1990; Ahrens et al., 1992; Maley and Caswell, 1993).

The modelling framework provides predefined objects for individual models which are fitted out with all mechanisms necessary to model the discussed aspects. A species specific model arises either by defining predefined objects interactively or by deriving more specific objects from them (see e.g. Folse et al., 1989; Maley and Caswell, 1993 for object-oriented mechanisms).

3.3. *Model analysis*

A modelling framework generally supports model specification, simulation management and model analysis. The model analysis should be flexible with respect to model specifics and the question to be ascertained. Therefore modelling frameworks are commonly equipped with mechanisms which permit the selective choice of evaluation measurements to be recorded during the simulation run. Such 'observing data structures' are designed to 'observe' a specific aspect of the whole model state by recording a certain evaluation measurement. This approach is advantageously because the model and its analysis are clearly separated and 'data cemeteries' are avoided or at least better arranged by reducing the simulation data output.

It is of particular importance for spatial models to aggregate the huge amount of information produced by simulation runs. The simulation of individual movements within a heterogeneous landscape changes the distribution of all individuals within the landscape model (Fig. 1(c, d)). Theoretically the biography of each modelled individual can be recorded. This would produce a huge amount of data which is difficult to handle and to analyse. Hence individual states have to be aggregated for which I see two general ways:

landscape-related and population-related aggregation.

The presented modelling framework provides observing data structures which can be selectively activated before the simulation run. Activated observers are than linked with objects of the model (patch or individuals) and communicate with them during simulation. There are two observer classes reflecting the landscape-related and population-related aggregation of the whole model state. The following observer objects record information selected by features of the landscape model.

- number of individuals inside a patch-patch observer;
- number of boundary encounters from within a patch-crossing observer;
- number of individuals that leave a patch-emigration observer;
- number of individuals walking into a patch-immigration observer;
- histogram, based on the number of time steps after which individuals immigrate into a patch-time observer.

The other class of observer objects records population related information:

- number of all individuals, size of the whole population-population observer;
- mean distance walked by all individuals-distance observer;
- histogram across distances walked by all individuals during simulation-distance frequency observer;
- histogram across angles between two consecutive steps for all individuals-step angle observer;
- histogram across turning angles, differences between step angles of the first and the last step of all individuals-turning angle observer.

Additionally, one observer records all positions of the modelled individuals-track observer. It can be used to show individual tracks after simulation.

In addition to these implemented observers further objects can and will easily be added using mechanisms of the object-oriented approach.

4. Potentials

The inherent observation level of the portrayed approach tempts to construct very complex dispersal models. Biologists often want to see 'realistic' models taking a lot of species specifics into account. There are almost no limits to realising a certain complexity. However, too much complexity may obstruct the view of essential relationships. This section provides some hints for examining generic relationships with this approach and focuses on the advantages of the intrinsic compatibility with empirical tracking data.

4.1. Pattern-oriented modelling

It is the spatial complexity of landscape structures and individual movements which complicates their consistent quantitative description. This in turn makes it difficult to obtain results with a certain generality. I will therefore concentrate on the potentials of pattern oriented models as introduced by (Grimm, 1994; Grimm et al., 1996).

A landscape pattern can be defined as a quantifiable aspect of the spatial landscape structure. Here spatial relationships between different components of the whole structure are calculated. The spatial pattern analysis results in so called landscape indices (O'Neill et al., 1988; Li and Reynolds, 1994; McGarial and McComb, 1995; McGarial and Marks, 1995; Riitters et al., 1995) which describe different aspects of the spatial landscape structure. Landscape based models can be defined as pattern oriented if simulation results are analysed against such landscape indices.

In reality movements of organisms lie between random walk and straight movement paths and produce some kind of typical pattern. A movement pattern on a homogeneous background can therefore be described by two probability distributions as already described in Section 3.2. The step length distribution describes the stochasticity of the velocity of the moving individual. The convolution of the movement path is expressed by the step angle distribution. Movement models can be regarded as pattern oriented if simulation results are analysed against such generic movement characteristics rather than against a lot of species specific movement features.

The concentration on generic characteristics as well for landscapes as for movements leads to clear models with a small number of parameters and evaluation measurements. Such pattern oriented models can provide general insights into the consequences of the complex spatial interactions between movements and landscape structures. There are two promising results obtained by such pattern oriented models. Firstly, we have shown that the number of boundary encounters of moving individuals inside patches enhances linearly with increasing perimeter:area ratios of these patches (Tischendorf, 1995; Tischendorf et al., 1997). This relationship only depends on the mean velocity of the modelled individual movements. This finding in turn explains the typical asymptotic increase of the transition probability (by moving individuals through corridors) with increasing movement corridor width (Tischendorf and Wissel, 1997) as initially found by (Soulé and Gilpin, 1991). Such generic results may also serve as initial hypothesis for empirical studies. In particular the experimental design of tracking studies or the preliminary selection of key factors can be supported by this kind of pattern oriented models.

4.2. Bridge between tracking studies and conservation management

Telemetry has become the key method for tracking single individuals because small and lightweight transmitters are increasingly available and the disturbing impacts by human observers are minimised. Despite this technical progress tracking studies are restricted for different reasons. Technical equipment is expensive, the realisation is time consuming and labour intensive and it is difficult (and sometimes restricted for conservation reasons) to catch individuals and attach transmitters. Therefore, tracking data are generally limited to a small number of individuals and document organisms movements only within one landscape configuration during a short period of time. On the other hand conservation measures change landscape structures (increase habitats or create movement corridors) which in turn may and should influence the movements of affected species. The consequences of such measurements are hardly foreseeable.

Here, models of individual movements within heterogeneous landscapes could build a bridge between the singularity of the empirical results and the requirements of conservation measures. For this purpose tracking data have to be analysed against the underlying landscape structure, e.g. movement steps recorded within equal patch types should be summarised to patch specific movement patterns. Tracking data can then be fitted with probability distributions which in turn define the movement patterns to be modelled. The first simulations should be carried out on a landscape model which corresponds with the research area of the empirical study. If the simulation confirms the movement dynamics as observed in reality the landscape model can be changed and repeatedly combined with the individual movement models. Such simulation experiments may support the discussion about conceivable consequences of changed landscape structures on individual movements.

5. Summary

It is the purpose of this paper to stimulate the discussion about methods for landscape related dispersal models. In the first part technical restrictions of grid based approaches as well as the problem of coupling simulation models and GIS's are discussed. As a consequence of this discussion a new modelling approach which overcomes some of the current technical and methodical restrictions is portrayed. The portrayed modelling framework combines a landscape model with individual-based movement models and supports a flexible simulation management. It is the landscape model which is distinguished by its efficient spatial data model-the irregular grid. It provides the prerequisite for landscape models with a high spatial resolution within a large extent. The spatially explicit individual models are implemented object-oriented. Their movements are described vector-based to enhance compatibility with tracking data and analytical treatments of movement processes. Because of the spatially selective communication between individual models and the landscape model behavioural rules can directly be related to the spatial context of individual positions. There exists a wide field of potential applications for this kind of modelling which is basically founded on the increasing availability of tracking data and the digital representation of landscape data in GIS's. This modelling framework is written in C + + and is consequently implemented object-oriented on a SUN workstation.

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