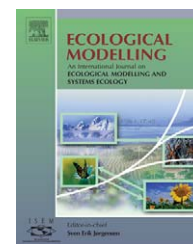


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Individual-based models as tools for ecological theory and application: Understanding the emergence of organisational properties in ecological systems[☆]

Broder Breckling^{a,*}, Ulrike Middelhoff^b, Hauke Reuter^a

^a University of Bremen, Centre for Environmental Research and Technology (UFT), Department 10: General and Theoretical Ecology, Leobener Str., D-28334 Bremen, Germany

^b University of Kiel, Ecology Centre, Olshausenstraße 75, D-24118 Kiel, Germany

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ABSTRACT

Individual-based models offer a structurally unique (and unifying) approach to ecological applications. Model results also provide an important input into ecological theory. The approach operates on the lowest organisational level considered in ecology (i.e. activities of individuals). Simulating the actions of single organisms allows to study how the properties of higher level ecological entities like swarms, populations, trophic networks and regional distribution patterns emerge. Unlike other approaches working on higher abstraction levels, individual-based models can represent structural–functional relationships similar to the pattern of available ecological knowledge. To demonstrate the range of applications of the approach we will address four issues using comprehensive data from two projects performed in Northern Germany.

First, a generic model structure for individual-based models operating on the basis of object-oriented programming is explained. It allows to capture a large variety of different ecological interactions.

In the second step, application examples from different fields of ecology are explicated. Plants and animals, active in terrestrial or aquatic environments, exhibit interaction types, which lead to self-organised structural–functional networks resulting from single organismic interactions. Spatial relations, dispersal, bio-energetics, plasticity of growth and form are topics which can be successfully dealt with in individual-based models. The wide range of qualitatively different interactions that can be represented is responsible for the importance the approach has gained in ecology.

In the third step, we show how the approach is used in a current research project to anticipate implications of genetically modified plants in agriculture. An individual-based model is used to simulate small-scale dispersal and persistence. The results are used for geostatistic extrapolation to the regional scale. Oilseed rape (*Brassica napus*) serves as an example. The model represents cultivation practice, feral populations and environmental characteristics.

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* Corresponding author. Tel.: +49 421 218 4200; fax: +49 421 218 7654.

E-mail addresses: broder@uni-bremen.de (B. Breckling), Uli@ecology.uni-kiel.de (U. Middelhoff), hauke.reuter@uni-bremen.de (H. Reuter).

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The fourth and final step discusses epistemological implications of individual-based models. It is concluded that a successful application of the approach requires detailed biological information about the represented species. This makes a leading involvement of field ecologists essential for model development. On the other hand, it also opens a theoretical access how to connect quantitative and qualitative aspects of cause–effect chains in ecology across different hierarchical levels. These aspects are discussed in relation to possible limitations of the approach.

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1. Introduction

Individual-based modelling (IBM) emerged in the 1970s complementing the prevailing application of differential equation-based approaches in ecological modelling. To deal with larger numbers of individuals in a model, the availability of simulation languages was necessary which could handle and process a very large amount of structured data. Without these technical options it was not reasonable to investigate the ecological importance and effects of differences between individuals. So far, population biology had focused on those aspects which were identical for all members of the population. Populations were described to be homogeneous. They were characterised quantitatively in form of a variable accounting for either biomass or number of individuals.

To consider at least some differences of population members, sub-groups were defined. Leslie (1945, 1948) proposed an approach to consider age-dependent developmental stages. The resulting matrix models are widely used in population modelling. Individual-based models drive this tendency of further differentiation towards an ultimate point, where each population member is represented with its specific characteristics regarded as relevant in the given context.

The first individual-based models were developed at the time when object-oriented programming became available. Among the first applications was a model describing territorial behaviour in dragon flies (Kaiser, 1976). Population structure analyses followed (Kaiser, 1979; Seitz, 1984). Both authors used SIMULA (Dahl et al., 1968), which was the first object-oriented programming (oop-) language.¹ During the 1990s, IBM (e.g. DeAngelis and Gross, 1992; Judson, 1994) became widely recognised as a modelling paradigm parallel to the emergence of SMALLTALK and C++ as programming languages.

The defining criteria for individual-based models are as follows: a population must be represented as a number of entities which are separately accessible and which need to have at least one (but normally more than one) quantitative or qualitative property which differs from each other—in addition to an individual identifier. The model must describe the change of these characteristics over time. Theoretically, a single column list where each row could store one bit of information symbolising different states of an individual together with the code to modify the states would do. However, for practical pur-

poses a more extended scheme is useful to analyse ecological interactions in detail.

In this contribution we outline such a scheme. Examples are shown how to apply this scheme in various fields. Furthermore, we present a recent research application demonstrating the integration of individual-based modelling into regional scale extrapolations. The context is biosafety research on genetically modified crops, focusing on the persistence and dispersal of oilseed rape (*Brassica napus*). In a concluding section, we point to more general application fields and to epistemological implications of individual-based modelling.

2. Generic model structure for individual-based models

In the context of ecosystem research at the University of Kiel (Müller, 1991; Müller and Fränze, 1991; Pöpperl et al., 1995) emerged the requirement to develop a unifying concept to describe terrestrial and aquatic plant as well as animal interactions (Breckling and Reiche, 1996; Breckling and Reuter, 1996; Breckling, 2002). Using the framework of object-oriented programming to represent an individual entity, we developed the structure in Fig. 1: a class hosts the general description of the modelled entity type, combining variables to store the individual state and the code to modify (update) the state. During simulation, objects are derived as instances from this class, which can interact with each other or with objects derived from other classes. In special cases, e.g. for modular organisms like plants, an object can be used equally well to specify the properties of a module of which the organism is a constituent

Class Organism

Declarations:

Variables characterising individual state
(e.g. location, biomass, age, alive)

Activity Procedures („methods“) to update states
(e.g. Movement, Growth, Reproduction)

Life Loop:

While alive do ...

Apply (call) Activity Procedures
(choose appropriate activity)
(update variables)

Hold [Delta t]

(i.e. detach this organism temporarily
to update others)

End life loop

End organism

Fig. 1 – Basic object structure for the simulation of an individual.

¹ For further backgrounds on SIMULA development see: <http://www.ifl.uio.no/adminf/tribute.html>. SIMULA is available for various platforms, among others the public domain. SIMULA-to-C compiler CIM (<http://www.ifl.uio.no/%7Ecim/cim.html>).

(internode, leaf, flower, etc.). In some cases it can be useful to represent a number of organisms which are almost identical as a single unit (super-organism) to save storage capacity. This may require a specification on how to add or remove (aggregate or dis-aggregate) individuals in such a unit. Since the number of organisms or entities to be dealt with can be very high, individual-based models tend to challenge the capacity limits of the simulation environment.

The class to describe the properties of an individual comprises a set of variables which specify the potential states of the individual considered as relevant. In addition, it contains a specification of the rules how to change these states. We call them activity procedures (or “methods” in oop-terminology). The third part organises the updating of the individual state variables. We specify this part within the class in the form of a loop, which is repeated as long as the organism exists as a living entity in the model run. Thus, among its state variables, the entity uses an additional Boolean operator which we call “alive”. While it is true, the update loop (“life loop”) is repeated. If “alive” is turned to “false”, the life loop is terminated and the particular organism (object) will be deleted.

In object-oriented programming with many concurrent objects, the timing of processes has high relevance, as full parallel processing is physically not possible.

On the level of the individual organism it is necessary to implement an algorithm to decide which of the possible activity procedures should be executed in a given situation. Different possibilities exist and should be specified according to the available knowledge and the necessary details. Two examples demonstrate the wide range of possibilities. *Cyclic activity control* denotes the regular execution of every activity procedure during each passage of the life loop. It may be applied in simple situations in which it is not necessary to decide between different activity procedures (e.g. schooling of fish, simple movement algorithms). Representing more complex behavioural patterns needs an elaborated decision algorithm. The *priority driven activity control* accounts for this case by assigning each possible activity a variable which indicates its execution priority. The activity with the highest value gets executed. By calculating the priority values in dependence of external and internal states as well as in relation to the time, an activity has not been executed; it is possible to represent complex behavioural patterns. This includes time–energy budgets and the analysis of trade-offs in the life history of individual organisms.

On the level of the whole program the simulation environment has to provide the updating of concurrent and interacting objects within a coherent simulation time frame. A structurally simple and highly efficient solution was provided by the SIMULA system class SIMULATION. It operates the following way: while a particular object is updated, it can access the states of any other object using a pointer (reference variable). It thus can adjust its own activity not only to its directly accessible internal variables but also to the state of any other object or system variables specified as relevant. After an update cycle is completed, the program control can switch to other objects. This is facilitated by a procedure called “HOLD”. Its execution detaches the current object and creates a so-called “EVENT”. An EVENT contains a time stamp specifying the simulation time interval after which the program execution should return

to the detached object. The class SIMULATION collects all “EVENTS” in an event queue. Each new element is sorted into the queue. After a current object is updated, the event handler removes the current event from the list and switches program control to the next object in the queue. The programmer only needs to specify the rule to determine the update interval for the objects (which can either be equidistant or vary according to the state of the object or other parts of the program). The event organisation is handled automatically in the background.

This scheme is highly flexible. It allows, for instance, the adjustment of an organism to external conditions. It is suitable to specify predator–prey interactions, schooling, diapause, behavioural shifts under varying conditions, the formation of colonies and the description of structural–functional development of modular organisms.

The programming skills to handle this approach can be acquired rather easily. An introduction to SIMULA is given by Pooley (1986). It is well possible that empirically working biologists use it after a relatively short training and specify their model so that it conforms well to the best standards of ecological knowledge and does not suffer from communication problems between computer scientists and field biologists. Some examples are shown to demonstrate the versatility of the approach.

3. Application examples of IBM in different ecological contexts

Plants and animals, which are active in terrestrial or aquatic environments, exhibit interaction types, which lead to self-organised structural–functional networks originating from single organismic (inter-) actions. Spatial relations, dispersal, bioenergetics, plasticity of growth and form are issues which can be successfully dealt with in individual-based models. To illustrate the wide application range of IBM, we start this overview using the outlined structure elements to describe a simplistic detail and then proceed to complex simulations.

3.1. A practical introduction to movement modelling: “snail trails”

Modelling the activity of animals frequently requires the development of a movement procedure. If an empirical basis for its specification exists, it usually consists of a recording of successive positions (co-ordinates) the organism had at certain points in time. This type of data is used to parameterise a procedure which generates similar patterns with respect to some statistical properties. This can be prepared as a task for group work in a training class. The class uses the original data to produce a functional algorithm.

In a few cases, organisms leave long-lasting traces of movement which can be used as templates for modelling. This avoids time-consuming data gathering. The larvae of miner flies (*Agromyzidae*) create typical irregular pattern on leaves when eating themselves through the leaf tissue (Fig. 2a). Comparable permanent traces are generated by snails grazing on

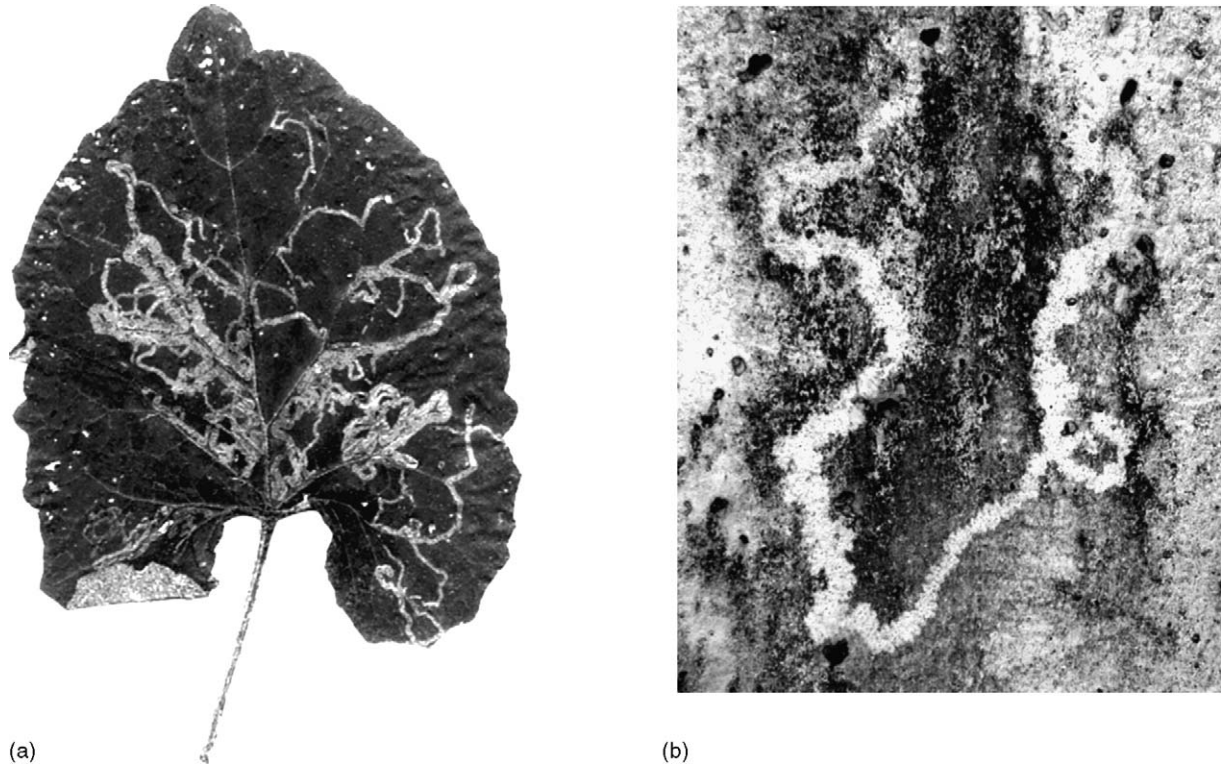


Fig. 2 – Movement patterns of miner flies and snails: (a) leaf mines can be used as movement traces to specify an algorithm producing a similar pattern. (b) Snails having grazed algae on concrete surface can be used for the same purpose. While traces of leaf miners can be handled after magnifying a photocopy of the leaf, the snail trails may be drawn on a transparency directly from the site where it was found, or from a photography.

algae which have grown on solid substrate surfaces (Fig. 2b). Photographs or drawings of other traces would do equally well. First part of the task is to re-draw a typical selection of such a trace and turn it into a set of points. Using a circle with a fixed radius, successive points are marked and connected by a straight line. The original trail is thus replaced by a polygon. Next, the successive angles between the lines are measured and assigned to a frequency distribution. For a quick result, we use 30° classes and ignore auto-correlations of successive steps. The obtained frequency distribution of angles is used to generate a similar pattern (Fig. 3) simply by choosing successive angles with the same frequency distribution as the observed one. The angle and the circle radius determine the polar co-ordinates of the successive locations. While the analysis used a comparatively short track interval, longer tracks can be generated by simulation. Now the long-term implications of this movement behaviour are accessible.

Structured random components play an important role in most animal movement patterns. Finally, it is necessary to mention the aspects of the observed pattern which are not included in the model but might be integrated in a further refinement process: auto-correlations, response to environmental structures, etc. The aim of this exercise is to demonstrate to students that they are able to specify a stochastic procedure adapted to empirical data, offering a starting point for further progress.

3.2. Schooling

The modelling of fish schools is a good example to demonstrate how individual interaction leads to the formation of a self-organised macroscopic structure. Schooling emerges as individuals adapt their movements to the direction and speed of visible neighbours (Reuter and Breckling, 1994). If schooling individuals use changes in local environmental characteristics (e.g. local food density variations) as factors to adapt their speed (Fig. 4), the whole school can function as a sensor changing direction towards preferred locations (Kils, 1986). Statistical investigations have shown that in a certain range of patterns, schooling fish are more successful in finding food patches compared to solitary ones (Breckling et al., 1997). In a parameter combination adapted to herrings (*Clupea harengus*) and in an environment containing approximately 25% of favourable patches with a diameter of around 10–20 body lengths, simulations revealed that schooling individuals stay on average about 20% longer in the favourable habitat compared to non-schooling fish. Besides this, schooling can have other advantages like predator avoidance (e.g. Magurran, 1990).

3.3. Dispersal modelling

To analyse schooling, we focused entirely on repeated execution of a movement procedure for each individual. Dispersal

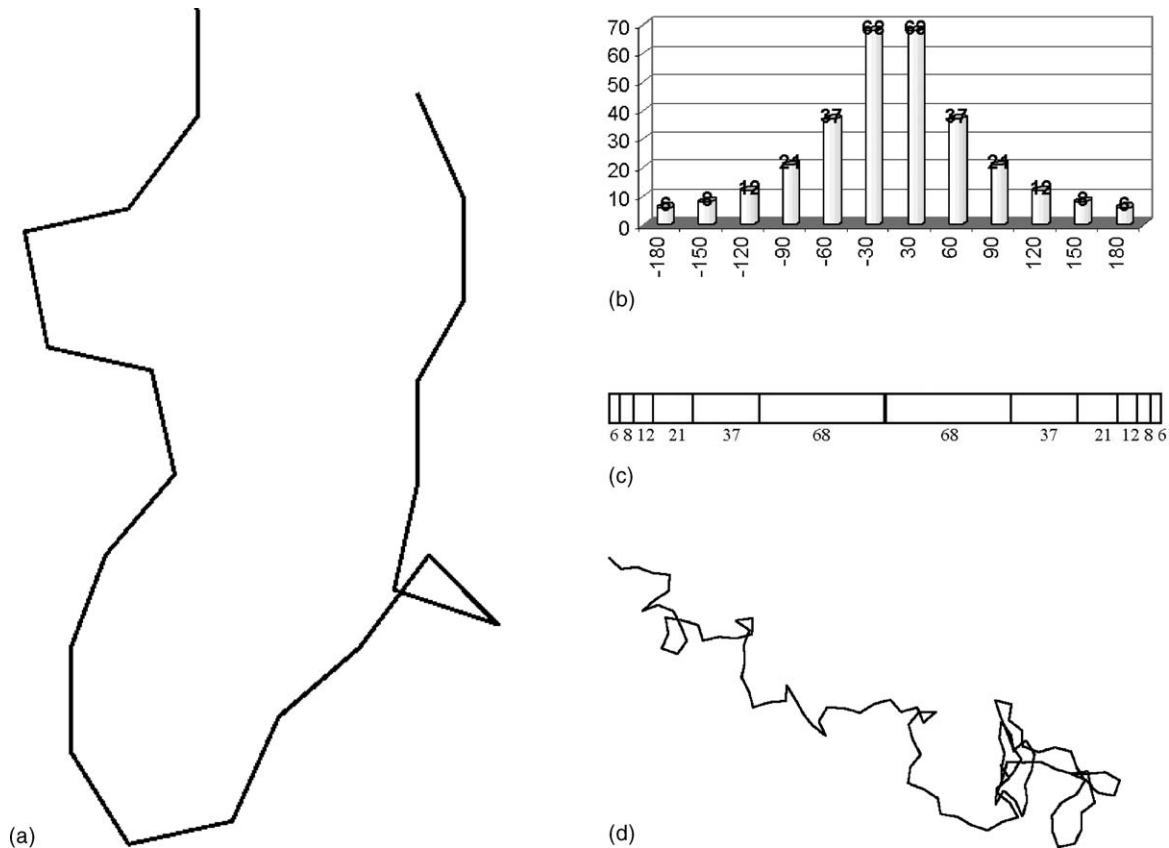


Fig. 3 – Steps to produce a movement procedure: (a) a circle is used to mark successive points (of the snail trail shown in Fig. 2b). The points are connected to a polygon and successive turning angles are measured. (b) The obtained frequency distribution of angles (here: in 30° classes from a longer trail than shown in (a)) can be implemented in a random procedure. (c) Drawing an evenly distributed number from the interval produces a similar frequency, which is used to produce the simulation results. (d) Employing the described procedure it is now possible to create longer, statistically similar movement tracks and analyse their implications.

analysis in the context of population projections requires additional activities to be considered. The “life loop” of an individual must at least consist of movement, orientation (adaptation of movement to local environmental conditions), survival probability and reproduction. Using the mainly forest-dwelling ground beetle *Carabus parallelepipedus* as an example, Reuter (2001) has tested various landscape structures for colonisation results. Crucial factors are transition probabilities between different types of land cover, directional priorities (orientation towards dark silhouettes while being in an open landscape) and the extent of random directional changes (Fig. 5). Combining these factors, Reuter (2001) and Jopp and Reuter (in press) gave an explanation for the low-to-moderate success of this species to colonise fragmented forest habitats (Fig. 6).

3.4. Bioenergetics

A further aspect was included in a fish model for roach (*Rutilus rutilus*) developed by Hölker (2000) for a typical Northern German freshwater lake (see also Hölker and Breckling, 2001, 2002, 2005). The approach combined a diurnal movement pattern between littoral and pelagial, feeding efficiency, bio-energetics

and growth, thus a combination of behaviour and biomass development. The model results demonstrated that the differences caused by diurnal changes of the preferred habitat, random marginal differences in food accessibility and positive feedback increasing existing differences through size-dependent swimming speed (larger fish move faster, reach the preferred habitat sooner and stay longer in advantageous parts of the lake) can explain characteristic asymmetries in cohort size spectra (Fig. 7). The size spectrum of a cohort (fish of the same age in a particular water body) is not only influenced by genetic differences. It can be equally well explained by an interplay of environmental, behavioural and energetic influences, even if the initial size is identical.

3.5. Modular organisms

Modular organisms like higher plants, corals and sponges pose a specific challenge to capture the relation of functional dynamics and structural development in a model. Middelhoff (2000), Middelhoff and Breckling (2005) and Eschenbach (2000, 2005) have used the object-oriented approach to analyse the growth of alder trees. The models of long-term structural development (decades) were parameterised using short-term

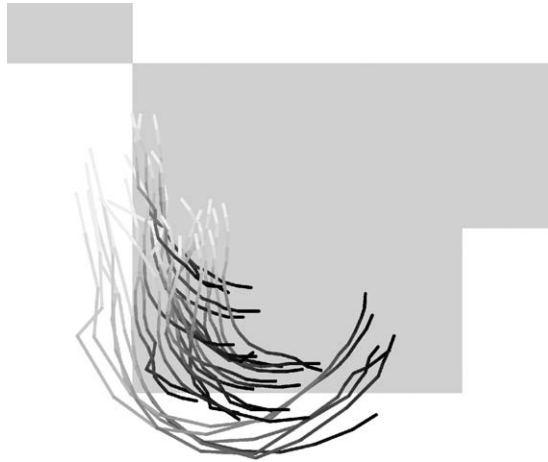


Fig. 4 – Traces of a fish school in a heterogeneous environment: the grey shaded area is a part of the environment with higher food density where individuals move more slowly. Coming from the upper left some individuals enter the food patch and slow down. To keep the school together, primarily those individuals still outside the food patch change direction (turn left and up). As a result the whole school enters the food patch. As an emergent property this phenomenon occurs if the speed difference between preferred and non-preferred parts of the habitat is sufficiently large. The effect also works for gradients.

measurement (days, months). Long-term studies on how the overall structure of the organism emerges require a model capable of generating long-term results based on short-term dynamics. Allocation rules and matter transport could be analysed by using the shape of the tree for additional calibration (Fig. 8). It is interesting to note that a strict validation is not possible since long-term functionality (over a few decades) cannot be measured directly. However, a consistent parameterisation matching the observable shape of the trees is indeed possible. Thus, the model can narrow the plausible range of uncertain parameters.

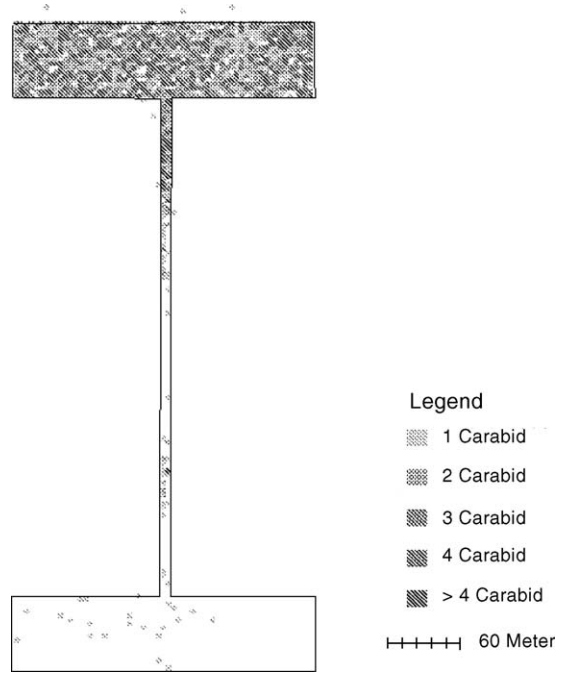


Fig. 6 – Dispersal of *Carabus parallelepipedus* in a simulated habitat after 11 simulated years (two forests connected by a hedgerow, the upper one colonised, the lower one empty. Outside the solid line: open field). The beetles move faster in open fields but suffer a higher mortality. The model demonstrates that colonisation even along hedgerows of only a few hundred meters can take several years (Reuter, 2001).

3.6. Complex behavioural and energetic studies analysing reproductive success

Individual-based models are suitable to study complex networks linking physiology, behavioural strategies, time budgets and spatial and temporal variability of the environment with the performance of the organisms. Combining empirical investigation and modelling, it was found for a passerine bird (European robin, *Erithacus rubecula*) that the reproductive

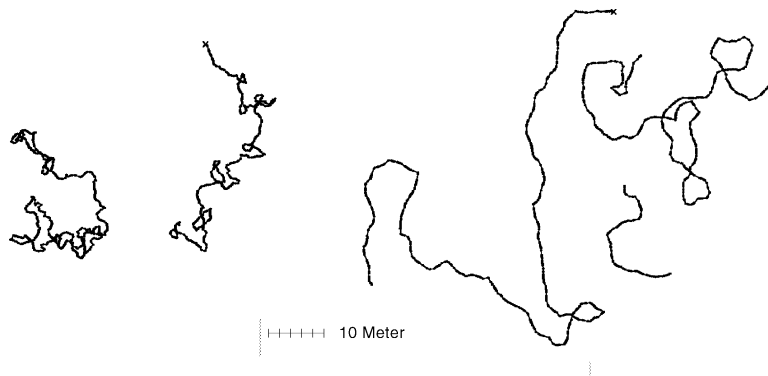


Fig. 5 – Simulated traces of *Carabus parallelepipedus* inside forest habitat (left) and on open field (right). The parameterisation was done according to telemetric data and trap catches.

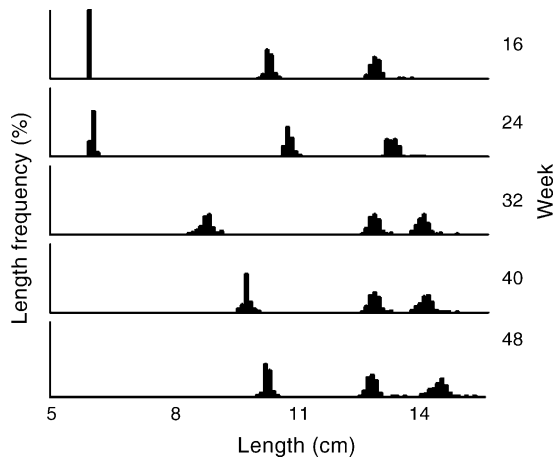


Fig. 7 – Simulated size spectrum of a roach cohort starting with identical length and biomass. The differentiation emerges as a result of size-dependent foraging efficiency in a heterogeneous habitat (Hölker and Breckling, 2005).

success is influenced by a very high individual variability (Reuter and Breckling, 1999; Grajetzky, 2001) at the beginning of the breeding phase. Small changes in weather conditions and seasonality of food availability (emergence of particular insects) have a long-lasting impact. The couples even within the same habitat are frequently not in the same phase of the reproductive cycle. Thus, the vulnerability to short-term environmental fluctuations differs greatly. However, having studied the decision pattern of starting a breeding cycle, the natural variability could be well represented by a model (Fig. 9) (Reuter and Breckling, 1999). Models of this type can be utilised in sensitivity analyses crossing different hierarchical (or organisational) levels.



Fig. 8 – Simulation of alder trees: identical parameters were used except for assimilate transport efficiency. This allows to discuss plausible ranges for long-term effects based on short-term interactions (Eschenbach, 2005).

Another example of model application integrating a wider interaction network was provided by Reuter (2001). In Nordic environments of the boreal and arctic region some small mammals, in particular rodents, exhibit pronounced semi-regular population cycles. The driving forces of these cycles with their characteristic outbreak dynamics are well investigated; however, a clear ranking of the underlying causes is still under debate. The importance of various factors has been discussed, among which are foodweb interactions with the largest impact, focusing on predators (Nordahl, 1995; Hanski and Henttonen, 1996; Turchin and Hanski, 2001; Klemola et al., 2002) as well as on limitations caused by the rodent food (e.g. Jedrzejewski and Jedrzejewska, 1996; Selas, 1997). For both hypotheses there is empirical support (for detailed references see Reuter, 2001). Including energetics, migration, environmental heterogeneity and predators in an individual-based model, it could be shown that both, bottom-up and top-down control, can trigger cyclic dynamics (Reuter, 2005). However, their impact is not constant. There are irregular shifts in the contribution of top-down and bottom-up regulation. This might explain why in short-term observations both have been found as relevant.

These models have been based on object-oriented modelling and the exemplified fundamental structure of individual-based models. The represented spatial extent of the models was limited to just a few square kilometres. The next example shows an extension of this approach employing an extrapolation to cover larger areas.

4. Risk-analysis of genetically modified organisms: oilseed rape as an example for integrated model application

We applied the individual-based modelling approach in biosafety research to anticipate the dispersal and survival of

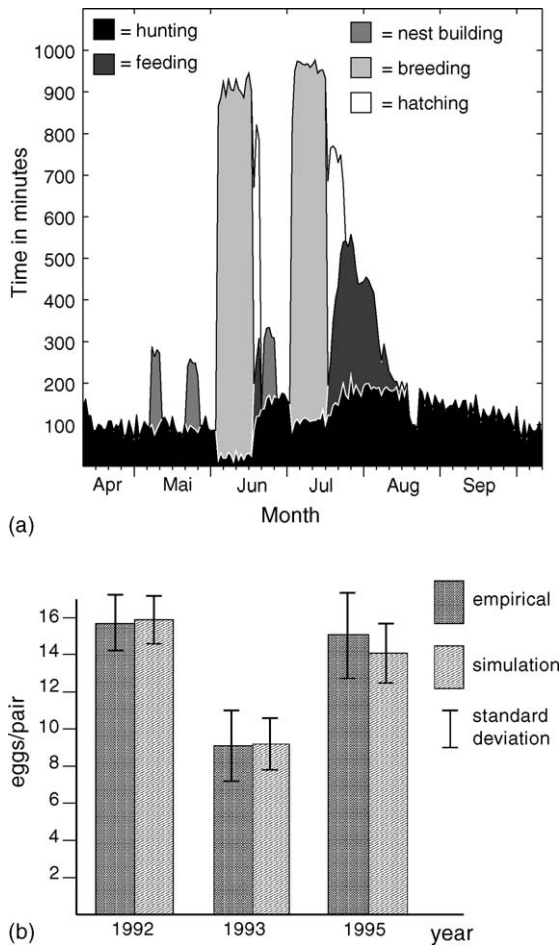


Fig. 9 – Simulations of the reproduction phase of European robins (*Erithacus rubecula*): (a) time budgets of a female individual spent on particular activity types. (b) Reproductive success of robins, empirical data from a beech forest in the Bornhöved Lakes region (Germany, Schleswig-Holstein) and simulation result. The model combines behaviour, time budgets, environmental structure and energetics to simulate breeding success (Reuter and Breckling, 1999).

genetically modified organisms. Statements valid for larger areas are not achievable on a purely empirical base as every possible combination of factors cannot be accessed. To extrapolate local empirical findings in time and space, it is necessary to use modelling and geostatistics. The approach has been developed in a co-operation between biologists, geographers, physicists and agronomists (Breckling et al., 2003).

Oilseed rape (*Brassica napus* L.) is an old crop plant originating from Southern Europe. There, we also find the centre of diversity of closely related species. In Canada and the USA, genetically engineered varieties are on the market which are resistant to herbicides. Herbicide resistance (HR) is intended to simplify weed control and allow erosion reducing non-tillage systems. However, there are a number of undesirable side effects.

Oilseed rape hybridises with several wild relatives (OECD, 1997), some of which are agriculturally relevant weeds or even

food plants. A high proportion of seed shedding occurs during harvest which leads to volunteer growth in the next crop of the rotation. The seeds may persist up to 10 years or more in the soil seed bank (Schlink, 1994, 1998) and can cause weed problems (volunteers) in subsequent crop rotations. Oilseed rape also grows frequently outside cultivated areas (feral populations). Recently, it was found in Germany that old varieties which ceased to be cultivated almost 20 years ago can still be found as feral plants along roadsides and at ruderal sites.² Cross-pollination by bees or wind between adjacent fields can cause crop contamination between transgenic and conventional fields.

What would be the implications of a commercialisation of this transgenic crop in a region with small-scale agriculture and a heterogeneous spatial pattern? This was the question investigated by the Project “Generische Erfassung und Extrapolation der Raps-Ausbreitung” (GenEERA, Generic Recording and Extrapolation of Oilseed Rape Dispersal) dealing with Northern Germany where a focus of rapeseed cultivation is located. The processes necessary to simulate oil seed rape survival and dispersal cover a wide range of spatial and temporal scales as well as different organisational levels. Simulation of level crossing interactions and feedback processes is the domain of individual-based models. We therefore developed an individual-based model Generic Transgene Movement and Persistence (GeneTraMP, Middelhoff and Breckling, 2003) that enables a detailed investigation of oilseed rape persistence and dispersal on a field-to-field scale. The model integrates existing knowledge on biological fundamentals and transgene spread over space and time. The development of cultivated, volunteer and feral oilseed rape as well as wild relatives is calculated for typical spatial units covering 1 km². The model includes the following processes and components:

- Spatial structure and land cover types relevant for oilseed rape establishment, e.g. farmland, roads, road margins, ruderal sites and settlements (as data input derived from digital maps in form of grid maps with a spatial resolution of 10 m × 10 m).
- Specification of genotypes (one to several loci) and species (*B. napus*, *B. rapa*, *Raphanus raphanistrum*, *Sinapis arvensis*, *Diploaxis tenuifolia*, *D. muralis*).
- Phenological development and reproduction of oilseed rape and related species in relation to soil conditions (land cover type) and depending on climate (as input data derived from an ontogenetic model, based on climate data).
- Local and regional processes of pollen transfer (by insects and/or wind) and seed dispersal (partly as input data).
- Crop rotation and crop management like sowing, tillage, herbicide management and harvest (specified by input data).
- Local variation of seed losses, feral plant sizes and reproduction, self-fertilisation rates, harvest losses as well as seed persistence (allowed range of variation specified by input data).

² Presented by A. Dietz-Pfeilstetter 16-6-2004 at the Biosafety Conference in Berlin, see <http://www.biosicherheit.de/pdf/statusseminar2004/poster05.pdf> (in German).

GeneTraMP represents individual seeds and plants (volunteers, ferals) as well as cohorts of plants (population of oilseed rape crop on a field) that are located in a spatially explicit model environment. Due to local and climatic conditions, seeds persist and the model plants develop and interact. As a result, gene flow and persistence can be recorded for simulated periods of many years, thus taking into account a wide range of different conditions (e.g. spatial arrangements and crop rotations). We used existing and validated models for the representation of the ontogenesis of oilseed rape (Habekotté, 1996) and of seed persistence processes as well as management practices (Colbach et al., 2001). For the parameterisation of processes like pollen dispersal, we used results of previous studies (e.g. Rieger et al., 2002; Treu and Emberlin, 2000). The occurrence frequencies of oilseed rape as volunteers during crop rotation and of feral plants outside cultivated areas in Northern Germany were adjusted according to the data of Menzel et al. (2003).

The local dynamics of oilseed rape could be represented accurately with the described model. For an extrapolation to the landscape level, running the model for various scenario conditions was required. To determine the relevant parameter ranges and to identify representative landscape subsets, an analysis of regional information was essential. In this context we used spatial information data for land cover (Coordinated Information on the Environment, CORINE), meteorological data of the German Weather Service (DWD, temperature, wind, precipitation and sunshine) to compile a climate classification and agro-statistical information (Statistisches Bundesamt, 1999) to analyse regional differences in crop rotation. The synoptic evaluation of these data allowed the determination of eight representative model regions. Remote sensing data (Landsat) were used to detect the regional distribution of oilseed rape cultivation (Fig. 10). The individual-based model was simulated for all combina-

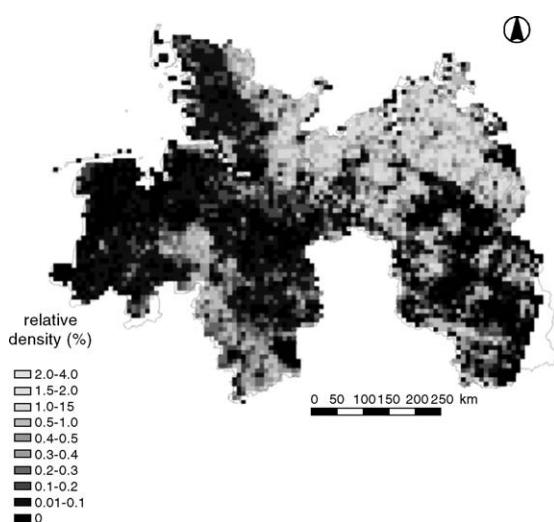


Fig. 10 – Density of oilseed rape cultivation in Northern Germany 2001 derived from an evaluation of remote sensing images (Laue, 2004). The greyscale displays the fraction of cultivated oilseed rape of the total area (% 25 km^{-2}) on a $5 \text{ km} \times 5 \text{ km}$ grid. The spatial configuration of cultivation is important for the probability of interaction processes.

tions of relevant parameters occurring in the area for which the up-scaling was intended and the results were stored in a database. The final step of up-scaling required a selection of the model run with the closest match of the boundary conditions of each local site of the extrapolation area. This could be determined based on the available regional data sets. Fig. 11 shows the result the accumulation of transgenic seeds in the soil seed bank as an example for the up-scaling process.

The results obtained so far in the project network GeneEERA (Breckling et al., 2003) show that it is possible to combine available data on different scales to predict major processes of transgene dispersal on the landscape level; however, further issues (e.g. gene flow into related species, gene-stacking, coexistence and economic issues) are still to be worked out and extracted.

It can be seen that the accumulation processes will take roughly a decade (2–3 crop rotation cycles). Persistence times in the wild can be expected to be also in the order of magnitude of decades. Comparing the relevance of the different escape pathways, we found that the contamination level of conventional seeds turned out to be of major importance, since this will spread the transgenes also among conventional crop populations. For oilseed rape it can be concluded that large-scale averages may remain under the current legal contamination threshold of 0.9%. However, transgene elimination in case of an exit scenario would take several decades—if possible at all. To what extent feral populations may lead to additional interactions remains an issue for further model evaluations.

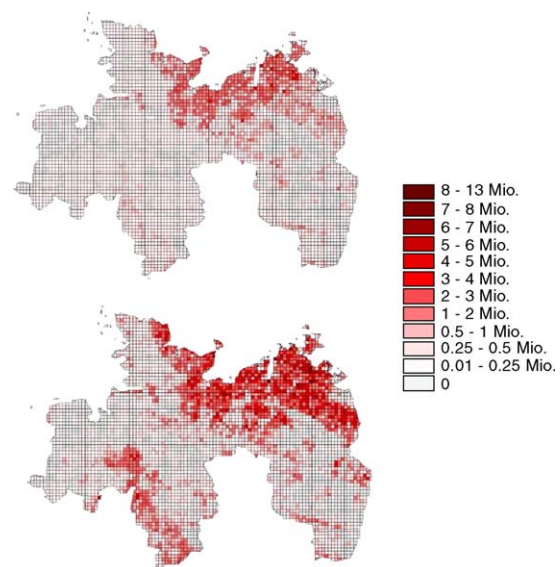


Fig. 11 – Visualising model results for Northern Germany: extrapolation of the oilseed rape soil seed bank development after simulating the effects of crop rotation and meteorological influences on gene flow with time (seed persistence, volunteer numbers). (Above) Seed bank after 5 years of cultivating transgenic oilseed rape with a market share of 10% (randomly distributed) and (below) a subsequent increase of the market share to 50% for another 5 years. Resolution: $5 \text{ km} \times 5 \text{ km}$, seeds per hectare of farmland.

5. Epistemological implications of individual-based models

Once having developed a basic structure that can capture the activities of individuals, a wide spectrum of different ecological relations becomes accessible for modelling. IBMs open a field in which conventional mathematical generalisations are not well applicable. The approach considerably expands the range of questions which can be investigated in an algorithmic form (Huston et al., 1988). Though the models can be kept highly generic and adaptable to specific situations, most of the results are site specific. Their special feature is to investigate the contribution of individual variation to aggregated results. IBMs connect different integration levels and help to analyse emergent phenomena (Hölker and Breckling, 2002a,b; Reuter et al., 2005). The overall modelling strategy largely conforms to artificial life or agent-based approaches.³

On the basis of examples in Sections 3 and 4 it is obvious that the domain of individual-based models are situations in which structured populations, spatial heterogeneity, and local interactions lead to a complex interplay of feedback processes across several integration levels. They may help in the search for solutions to problems where the outcome of individual interaction is decisive for overall results and additionally, abstraction from low level processes is not possible without an unacceptable reduction in model accuracy. But the detailed, mainly, rule-based representation may induce limitations and drawbacks. In contrast to ‘traditional’ equation-based models, IBMs have no consistent mathematical structure. This poses high demand on the documentation of models and makes communication about model processes difficult, e.g. to re-implement a model. Often a high number of parameters are necessary to specify processes, which in turn requires detailed biological knowledge. Additionally, common critique indicates that the high number of parameters will lead to an increased inherent susceptibility to internal errors (Pascual and Levin, 1999) and a high sensitivity to small parameter changes (Conroy et al., 1995; Hartway et al., 1998). Both arguments neglect some of the basic features of IBMs. Parameters usually have a direct biological significance and are often closely related to empirical investigations. This limits the range of plausible values considerably. On the other hand, we can state a shift in driving forces. The highly parameter-dependent configurations in equation-based models are partly replaced by the increasing importance of relations between model elements (Reuter et al., 2005). This decreases parameter sensitivity.

Both equation-based and individual-based models address different aspects of ecological processes. The respective limitations and strengths have to be considered when choosing the appropriate approach for an investigation.

We will now briefly outline how individual-based modelling as developed within ecology fits into the general development of formal scientific approaches.

Scientific analysis attempts to explain phenomena as a result of preceding causes. Identical causes yield identical

effects. The relationship needs to be precisely defined and quantitatively calculable. It excludes voluntarism as a part of cause–effect relations (determinism). This view gave rise to the development of classical mechanics as a basic scientific paradigm (Prigogine and Stengers, 1984; Prigogine, 1980). The discovery of chaotic dynamics (Lorenz, 1963; May, 1976; see Gleick, 1987) in deterministic equations showed intrinsic limitations of determinism. The “validity” of a deterministic relationship might require infinite precision and is thus, strictly speaking, a purely theoretical construct (and not an ontological issue). The deterministic paradigm captures only a very limited part of phenomena. It is, however, scientifically indispensable—comparable to rational numbers which may approximate but not exhaust real numbers.

The finding of chaotic dynamics demonstrated a *mechanistic* way to amplify infinitesimal differences to the macroscopic level and functionally connect microscopic and macroscopic description levels (Gleick, 1987; see also Peitgen et al., 2004; Flake, 2000). Since the deterministic paradigm lost its prevalence in the microscopic domain of quantum physics, it is now limited to characterise “simple cases”.

Individual-based models play a comparable role in ecology as chaos research does in physics. Individual-based models ended the dominance of the view that relevant issues in ecology could be described on the population level in abstraction of the ecologically active entities (Lomnicki, 1988). IBMs allow to study how the outcome of single actions may be amplified to the population, food web or ecosystem level, and how the overall result emerges from an overlay of the underlying activities. This complements the analysis of classical deterministic processes. Looking at the details that are calculated in IBMs, it is possible to study “historical” processes in the sense that it can be traced, how single actions can, under certain conditions, lead to altered system developments on higher aggregation levels—exactly the same as what was called the “butterfly effect” (Gleick, 1987) in chaos research: the flap of a butterfly wing in Hawaii can be causally linked to the occurrence of a hurricane in Florida.

The individual approach requires the application of object-oriented (or agent-based) modelling techniques and thus depends crucially on the availability of an efficient technical infrastructure (Langton, 1995; Maes, 1990).

Using IBM, model development becomes a less abstract and mathematical exercise than differential equation modelling on the population level has been. The specification of individual actions according to a behavioural repertoire requires the involvement of extended and specific biological knowledge. While in conventional modelling it is common practice that a modeller with a background in computer science is advised by a field scientist about which assumptions to implement in a model, the individual-based approach also encourages the reverse: an experienced programmer advises the field scientist how to optimise the model structure in which the latter formalises his biological expertise.

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³ E.g. SWARM, http://wiki.swarm.org/wiki/Main_Page.

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