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Individual-based modelling in ecology: what makes the difference?

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Is individual-based modelling really a new approach in ecology? A large part of the uncertainty surrounding this question is a consequence of imprecisely delimited boundaries between classical and individual-based modelling. Genuine 'individual-based' models describe a population made up of individuals that may differ from one another; they also describe changes in numbers of individuals rather than in the population density, and take resource dynamics explicitly into account. Individual-based models that fulfil these criteria will not characterize ecological systems as 'stable' systems in their ideal form, with equilibrium states represented by points in the phase space.

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Individual-based modelling is on the way to becoming an established discipline in ecological modelling^{1–6}. Is this only because we have high-performance computers on almost every desk, so that individual-based modelling is now open to everyone? Or is individual-based modelling really a new approach that may lead to a different view of many questions in ecology?

Based on recent publications^{3,6,7}, one may be led to think that there is a gradual transition between the classical models of theoretical population biology and individual-based models. This would render

individual-based modelling a new technique only. However, ecological systems described from the perspectives of individual organisms do not appear to be simple dynamic systems⁸. This has important consequences for the dynamics and other properties of ecological systems. Like Huston *et al.*¹, we believe that individual-based modelling really makes a basic difference compared to the classical way of modelling. Nevertheless, these differences will become clear only when 'individual-based' models are properly defined.

A large part of the uncertainty about whether individual-based modelling con-

stitutes a new approach is a consequence of imprecisely delimited boundaries between classical and individual-based modelling. Therefore, we will first introduce four criteria that help define this boundary.

Classification criteria

The often-used differentiation of individual-based ecological models into so-called *i*-state and *i*-distribution models⁷ reflects only a rather technical aspect of the model structure. These are but two different numerical ways to describe individuals in the model. Similarly, two approaches have been used for a long time in statistical physics. In this field, they are complementary and yield the same results. Thus, from the biological point of view as well as in terms of the potential of the model to explain and predict dynamics of the system, this classification yields hardly any important information.

The classification of ecological models can be much more meaningful when based on some biologically important attributes of the models. There are four appropriate classification criteria: (1) the degree to which the complexity of the individual's life cycle is reflected in the model; (2) whether or not the dynamics of the resources (like food, space or habitat quality) is explicitly taken into account; (3) the use of real or natural numbers in representing the size of a population; and (4) the extent to which variability of individuals of the same age is considered. Most models of theoretical ecology describing dynamics of ecological systems may be classified according to these criteria.

Assumptions of ecological models

Basic models used in classical mathematical ecology, as for example the logistic equation and the Lotka-Volterra models, describe features of an average individual. In addition, they assume an extremely simple life cycle of this average individual. Nothing is said about the life cycle of the modelled organism except birth, death and the number of offspring. For instance, development, metabolism and ageing of individuals, their behaviour or the amount of resources used during their lifetime are not explicitly taken into account. Instead, an average individual is born, immediately produces offspring, and dies shortly afterwards. This is a life cycle of 'zero complexity', so to speak.

A second class of models, usually called models with age, stage or size structure, are based on the description of more-complex life cycles: reproduction and mortality depend on age, stage or size of the individual. Individuals are grouped into classes in these models, but within each class individual variability is still neglected. Instead, features of an average individual in each class are considered. Often it remains unclear whether this averaging of individual properties is based on biological assumptions or only on the need for mathematical convenience.

There is another class of models that includes more-complex life cycles, but is still based on an average individual. The models by Kaiser⁹, one of the pioneers of individual-based modelling, belong to this class. In Matessi's¹⁰ model, individuals have a sigmoid growth curve identical for each individual, and production of offspring is proportional to the final weight. Kooijman and Metz¹¹ (also see De Roos *et al.*¹²) analyze the effect of chemical stress on populations by modelling the impact of pollutants on the growth of individuals. In the 1980s, the term 'physiologically structured populations' was introduced in books edited by Metz and Diekmann⁷ and Ebenman and Persson¹³. This term well reflects what we wish to emphasize here – that life cycles often are so complex that different stages may differ more than individuals of different species, thereby complicating the simple relationships between model parameters and population dynamics as depicted in most classical models.

The second criterion for classifying models is the question of whether resources are modelled explicitly. This question mainly concerns models of a single population. Resource dynamics may be modelled explicitly, or implicitly by using the concept of carrying capacity. It is important to differentiate between these two kinds of modelling. Kozłowski¹⁴ argues convincingly that, for most types of biotic or abiotic resources, an implicit represen-

tation of the resources is not sufficient. Regulation of population depends not only on population density, but also on the resource level. Only by explicit modelling of resource dynamics will the mutual relationship between population and resource become clear.

Natural or real-number representation of the size of a population is the third criterion for classifying existing ecological models, which allows us to separate models into two different classes. In most population and community models, population density (N) is used as a state variable, that is, N is a real number. There is also a small group of models where the number of individuals in the population is used; N is then a natural number. Within the framework of classical ecological modelling, the commonly used justification for the two approaches is that the first category comprises models describing large populations, whereas the second deals with small populations. For example, stochastic models of population dynamics addressing the problem of extinction of small populations assume that N is a natural number. Density was introduced in ecological models as a state variable for mathematical convenience only, using the argument that, for large numbers of individuals, the discreteness of individuals may be neglected. But this argument is 'scale-free'. Individuals interact with other individuals only within a limited time horizon and spatial domain. Therefore, what constitutes the population for a single individual may often be a rather low number of individuals. Moreover, interactions between individuals take place on a short timescale, so the number of individuals that interact with a given individual may even be much smaller.

The final and most important criterion for the differentiation of population and community models is whether differences among individuals are taken into account – even if the individuals are of the same age. There are two possible sources of differences in even-aged individuals. First, they may be casual differences. This means, for instance, that all individuals have the same probability of producing one offspring, but it is impossible to predict which one will reproduce in a given short time interval. In this sense, individual variability is introduced in some stochastic population models, but these models usually use extremely simple life cycles and consider no resource dynamics. We argue that casual variation is simply a rare component of individual variability. This kind of variation can appear only when resources are in adequate supply, and only random factors are important, for example, change in the weather.

Secondly, differences among individuals may be caused by other than random

factors. For instance, they may be an effect of competition between individuals. There are many models both for plant and animal populations that describe the development of differences among individuals resulting from competition. For example, analyses of changes in frequency distributions of body weights in even-aged plant and animal populations in relation to the population density and resources are frequent^{15,16}. The frequency of different patterns of changes in the shape of weight distributions even received a kind of statistical description. Latto¹⁷ found that the variance of the distribution of final weights and the skewness of this distribution both increased with population density and deteriorating food conditions for 30% of the fish populations and for 10% of the bird and mammal populations analysed. Competition is a more important source of individual variability than mere casual variation. The development of differences between individuals in resource use, weight, position in hierarchy, and behaviour in even-aged populations owing to competition, is well documented for many fish species^{18–21}. Models describing the development and change in individual variability within single generations can be iterated and thereby produce models of population dynamics incorporating not only more-complex life cycles of individuals but also differences among them^{22–24}.

'Narrowly defined' individual-based models

It is a widely held view that individual-based models begin where the life cycle of an individual is described in more detail than in classical models. Thus, individual-based models would include those that do not consider differences among individuals, deal with changes in the population density rather than with numbers of individuals, or take resources only implicitly into account. However, the degree of complexity in the description of a life cycle is not a good discriminant because it does not allow for a meaningful differentiation among the different kinds of models. Models that somehow deal with individuals, but that do not fulfil all four criteria above, differ only more or less gradually from classical models, and should therefore be called 'individual-oriented' models. This is because they still do not place the individual in the centre of interest. They still adhere to a description at the population level and still abstract from the fact that real populations are built of real individuals who differ from each other, and whose differences may change in reaction to biotic and abiotic factors. We adhere to a narrower classification of ecological models. Genuine 'individual-based' models (we call them 'narrowly defined' individual-based models) describe

a population made up of individuals that may differ from one another, take into account the complexity of the individual's life cycle, describe changes in numbers of individuals rather than in the population density, and also take resource dynamics explicitly into account.

A shift of the emphasis to individuals in ecological modelling was possible because of the development of computers. We do not say that theoretical ecologists did not think of individuals earlier. However, the assumptions of classical ecological models speak for themselves – only an average individual is considered, and thus only features characteristic of the population as a whole. Classical models are simpler and typically allow for analytical solutions. This raises the question of whether it pays to use the more costly individual-based approach? The answer depends on whether individual-based models allow for more than classical models, that is, for better understanding, prediction and, in turn, better management. There is no answer to this important question as yet, but the question itself is rarely asked in the first place – maybe because of the imprecisely delimited boundaries between individual-based and other models.

The classical view of ecological systems

Classical mathematical ecology confirmed and developed a view of the dynamics of ecological systems ('balance of nature'), which is well established in ecological thinking, and even became a part of the language of journalists and politicians. According to this view, ecological systems are deterministic dynamic systems characterized by states of 'stable' equilibria. This means that the world we observe is in a state of equilibrium, or is approaching this state after a disturbance. This extremely simple picture of the state of ecological systems, characterized by point equilibria in the phase plane, is so deeply rooted in ecologists' minds that almost all analysis of ecological systems performed by theoretical ecologists is confined to equilibrium states of the systems. Non-equilibrium approaches in ecology are relatively rare²⁵.

It is known, of course, that equilibria do not cover the whole range of solutions of the model equations. Attractors may be more complicated geometrical objects, such as closed curves (in case of oscillations representing limit cycles) or 'strange attractors', which yield deterministic chaos. The latter properties of classical models are referred to as a kind of complication of the ideal stable world. Moreover, many ecologists claim that deterministic chaos does not occur in nature.

The world seen from the perspective of classical stochastic models looks only

Box 1. Regulation in narrowly defined individual-based models

Assume that generations do not overlap, and that all individuals are identical. Each individual has the same amount of resources and converts these resources into the same number of offspring. Initially, when the amount of resource is such that each individual can produce more than one offspring, the population is exponentially increasing. Gradual shrinking of resources, however, leads to the situation in which individuals are able to produce only one offspring. This restriction concerns all individuals, as they are identical and share resources evenly. Then the number of individuals in the population will be constant. When resources are becoming even more scarce, the amount of resources that an individual receives as a result of even partitioning is not sufficient to produce even one offspring. At that moment, the population will die. Therefore, a population made up of identical individuals can only grow exponentially and then go extinct, also exponentially.

The dynamics are different when the population consists of individuals that differ with respect to the amount of resources they can obtain as a result of competition. The initial phase of population growth will be similar. But when resources are becoming scarce, only weaker individuals will not be able to reproduce. Superior individuals that can secure sufficient amount of resources will continue reproduction. If the differentiation of individuals takes place in each generation and unexploited resources regenerate, this provides a mechanism enabling survival through the phase of low resources. The cost of this, however, is oscillations in numbers.

In classical models, regulation takes place because the density of the population, which is a real number, can take equilibrium values. At the equilibrium, the rate of change in density equals zero. This effect does not exist in narrowly-defined individual-based models. Instead, we assume differences among individuals, but this mechanism of regulation is imperfect.

slightly different. It brings about the important problem of population extinction, but the mean solution still reminds us of the solution to a corresponding deterministic model. Individual-oriented models, containing descriptions of even very complex life cycles but referring only to an average individual, do not provide anything new – they yield the same picture of ecological systems dominated by the equilibrium view.

Łomnicki²² examines another class of individual-based models. He assumes discrete generations and uneven resource partitioning owing to competition between individuals. However, the analyzed variable is population density, and thus a real number. It has been shown that this model, although it contains differences among individuals, can also generate solutions of the type of a stable equilibrium point. This result was confirmed by Uchmański²⁶ for the model version with overlapping generations. Using models of this kind, Łomnicki shows that individual differences, especially those caused by the contest competition, promote 'stability' of ecological systems^{22,27,28}. Begon and Wall²⁹ introduce individual differences to the classical model of competition between two species. They get a coexistence of these species in situations where one of them was competitively excluded in the model without individual differences.

As one can see, there is a tendency among theoretical ecologists to think that individual-based models will support the equilibrium picture of ecological systems, which was produced by models of classical theoretical ecology. However, critics of Łomnicki's view argue that such a univocal relationship between individual variability and population stability cannot be defended, since all depends on the type of the model and on the situation described by the model^{30–32} (these papers

describe models for changes in population density with differences among individuals but without considering resources explicitly).

Non-equilibrium ecology

Do narrowly defined individual-based models produce results other than the results of the classical models? It is difficult to answer this question. When resources are in adequate supply, each individual will produce a similar number of offspring. The population follows an exponential growth, and no difference exists between the classical description using properties of an average individual and the narrowly defined individual-based model, since all individuals are alike in this case. Differences are likely to appear only when resources are in short supply. In the classical models, limited resources account for the reduction of reproduction of an average individual. In the models with different individuals, the weakest individuals will mainly feel the consequences of resource limitation^{22–24}.

Classical models show a large variety of dynamic behaviours that seem to cover a complete range of possibilities. It is easier to state what will *not* be produced by the narrowly-defined individual-based models. These models will not, for instance, characterize ecological systems as 'stable' systems in their ideal form, with equilibrium states represented by points in the phase space. The discreteness rooted deep at their base, issuing from the fact that we count individuals (their number can equal 0, 1, 2, ...), which, in addition, differ from one another, will produce only a kind of 'imperfect regulation' of ecological systems. This means that a perfect, fine-tuned 'balance of nature' is not to be expected. Instead, more or less wide fluctuations in numbers of individuals will occur, which additionally may be amplified by the effects related to interactions

Box 2. Non-equilibrium models in ecology

Non-equilibrium ecological models are used to explain the existence of the systems that according to the equilibrium theory should be subject to the competitive exclusion principle. It is assumed that a high species diversity in the communities of competing species can be maintained through disturbances. They interrupt the process of exclusion of inferior species, and by doing this they maintain the system far from the state of equilibrium which is characterized by small species diversity^{5,38}. These disturbances can be caused by: (1) predators feeding on the dominant competitor; (2) random environmental fluctuations that temporarily can attenuate the effect of density-dependent factors; (3) directional changes in the mean values of parameters characterizing the environment. A high species diversity can also be maintained due to the fact that the scale of the time of competitive exclusion of species is long and comparable to the scale of the time of speciation and immigration of new species to the system.

Classical ecology assumes that ecological systems are equilibrium systems. Non-equilibrium ecological models assume that they are permanently far from equilibrium. In contrast, narrowly defined individual-based models show that a single population can be a non-equilibrium system: their dynamics are characterized by oscillations, they may have no point equilibria and locally go extinct. The reason is imperfect regulation described in Box 1.

As the analysis of narrowly defined individual-based models shows, the time to extinction of a population depends on the character of interactions among individuals and on their life cycle. Oscillations are violent and the population dies out in a short time if individuals compete only once in their life³³. The amplitude of oscillation is decreasing and the lifetime is increasing practically *ad infinitum* if individuals compete many times over their lifetime²³.

with the resource that is modelled explicitly. In many cases, local populations will sooner or later be subject to extinction (Box 1).

These features of population dynamics, which, after Huston⁵, can be designated as inherently non-equilibrium properties, are observed in narrowly defined individual-based models of animal populations^{23,24,33}. They can be also observed in some forest models^{34,35}, which are not far away from what we call narrowly defined individual-based models.

Narrowly defined individual-based models make it possible to analyse factors that increase population survival time and damping number oscillations. Classical mathematical ecology states that ecological systems are intrinsically stable, and only external factors disturb their stability^{36,37}. Instead, the narrowly defined individual-based models show that so-called 'intrapopulation factors' can be the cause of destabilization, weak regulation of local population and its extinction. They also prove that life cycles of individuals (that is, the simple fact that individuals, after all, do something during their lifetime) and the way individuals interact one with another are very important for predicting the dynamics of the whole population (Box 2).

Complexity and limited generality are often quoted as the main limitations of individual-based modelling. In our opinion, these shortcomings may be overcome by taking our orientation from real patterns observed in nature³⁹. If individual-based models have the potential to induce a paradigm shift in ecology towards an 'ecology of individuals', then we will need more models of this type. There is great deal of data and knowledge concerning the ecophysiology and behaviour of individuals of numerous animal and plant species that could be transformed into some general pattern⁴⁰ and then used in different

kinds of individual-based models of population dynamics.

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The shape of evolutionary developmental biology

The Shape of Life: Genes, Development, and the Evolution of Animal Form

by Rudolf A. Raff

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For many biologists, evolution of body plans has always brought to mind that old saying about the weather: everyone talks about it, but nobody ever seems to do anything about it. No longer. In recent years, months, and even weeks, there has been a flurry of important discoveries that have contributed significantly to our conceptual and factual understanding of the evolution of animal body plans, their defining characteristics, and the origin of the higher taxa that they represent^{1–3}. Thus, it is hard to imagine a new volume more timely than this one.

The book is a triumph. In an engaging narrative, Raff summarizes a wealth of information from contemporary developmental biology, molecular genetics and paleontology that is pertinent to a mechanistic explanation of the evolution of animal form. Moreover, this information and the accompanying important insights into the developmental basis of evolutionary change are woven together into a coherent story. A vast range of topics are considered: *Hox* genes, Ediacaran fauna, jaws, Baron Cuvier, morphological novelty, key innovations and marsupial frogs are just a few examples. In achieving this breadth of treatment, Raff reveals himself to be a true, modern naturalist; his fascination and passion for the natural world emerge as strongly as his scientific curiosity.

The book is organized around two related themes: the origins of the major animal body plans during the great Cambrian radiation more than 500 million years ago, and the developmental basis of their subsequent evolutionary modification, which continues

to the present. To Raff, an essential feature of the origin of body plans is the evolution of morphological novelty, which may define any of several different taxonomic categories. Thus, he does not (as have some authors) restrict body plans to phylum-level differences in anatomy (although characteristic features of body plans are typically most conspicuous at this level). Nor does he postulate the existence of qualitatively different developmental mechanisms that underlie differences in the scale of body plan disparity among various taxonomic categories. Indeed, the implicit suggestion that virtually all instances of morphological evolution in animals derives from perturbation of a common set of developmental genetic processes and principles is among the book's most significant contributions to ongoing debates in evolutionary theory regarding the nature of evolution above the species level, or macroevolution. Building on the theme of biological order developed earlier, and in much greater depth, by Riedl⁴, Raff cites modularity as the pre-eminent characteristic of metazoan ontogeny – 'the attribute that most strongly facilitates evolution'.

Together with dissociation, duplication and divergence, and co-option, modularity defines a set of 'principles of evolvability', which may account for phenomena ranging from heterochrony in direct-developing sea urchins to lactose biosynthesis in mammals.

Raff offers a balanced, realistic view of many current research directions and paradigms in the study of development and evolution; his assessments will cause celebration and consternation to members of both camps. For example, in the nearly 20 years since Gould⁵ rekindled modern interest in the evolutionary significance of changes in developmental rates and timing, a considerable segment of evolutionary and comparative biologists have come to manifest a virtual preoccupation with heterochrony as a pre-eminent mechanism and mode of evolutionary change in development. Yet Raff, while conceding the pervasiveness of heterochronic changes in ontogenetic pattern and agreeing that such changes may offer important insights into underlying developmental processes, clearly regards this extreme em-

phasis on heterochrony as undeserved, and, in some instances, even unhelpful. Indeed, 'the uncritical attribution of so many of the phenomena observed in the evolution of development to heterochronic 'mechanisms' may be inhibiting a more penetrating investigation of the subject.'

He is equally sober in his discussion of the strengths and weaknesses of the 'model systems' approach so beloved by most contemporary developmental biologists – while extremely effective as a paradigm for exploration of basic and common developmental processes, such an approach may have considerable liabilities and biases when employed in a comparative context. To Raff, comprehensive investigation of the relation between evolution and development requires that one's phylogenetic analyses be as rigorous and appropriate as analyses of developmental process and mechanism.

Finally, Raff devotes considerable and deserved attention to homology. Many people working at the interface of evolution and development continue to employ drastically different (in some cases, incompatible) meanings of the word. Such a disparity in terminology (and underlying concepts of similarity and difference) will only become more problematic as research programs continue to converge from disparate academic origins. However, this must be resolved, and in such a way that recognizes both the historical nature and hierarchical organization of biological processes. Raff favors a 'traditional historical and morphological' definition. And while many people (including us) may agree with him, the issue is far from resolved. Everyone must also remain keenly aware of the potentially confounding effects of homoplasy (parallel or convergent evolution) on assessments of homology, and acknowledge that homoplasy can occur in a vast range of features, from the feeding apparatus that defines major body plans⁶ to proteins⁷.

Many authors have cited the current widespread and intense interest in comparative aspects of ontogeny as heralding the birth of a new field of evolutionary developmental biology^{8–10}. Although it will be another several years before these bold claims can be assessed objectively, *The Shape of*