

## References

- 1 Knowlton, N. *Annu. Rev. Ecol. Syst.* 24 (in press)
- 2 Van Moorsel, G.W.N.M. (1983) *Mar. Ecol. Prog. Ser.* 13, 273–283
- 3 Ayre, D.J., Veron, J.E.N. and Duffy, S.L. (1991) *Coral Reefs* 10, 13–18
- 4 Gattuso, J.-P., Pichon, M. and Jaubert, J. (1991) *Coral Reefs* 9, 173–182
- 5 Knowlton, N., Weil, E., Weigt, L.A. and Guzmán, H.M. (1992) *Science* 255, 330–333
- 6 Marsden, J.R. (1992) *Bull. Mar. Sci.* 51, 14–18
- 7 Knowlton, N. and Keller, B.D. (1985) *Bull. Mar. Sci.* 37, 893–904
- 8 Nizinski, M.S. (1989) *Bull. Mar. Sci.* 45, 174–188
- 9 Duffy, J.E. (1992) *Mar. Ecol. Prog. Ser.* 90, 127–138
- 10 Knowlton, N., Weigt, L.A., Solórzano, L.A., Mills, D.K. and Bermingham, E. (1993) *Science* 260, 1629–1632
- 11 Jackson, J.B.C. and Cheetham, A.H. (1990) *Science* 248, 579–583
- 12 Mladenov, P.V. and Emson, R.H. (1990) *Mar. Biol.* 104, 265–274
- 13 Palumbi, S.R. and Metz, E.C. (1991) *Mol. Biol. Evol.* 8, 227–239
- 14 Matsuoka, N. and Hatanaka, T. (1991) *Zool. Sci.* 8, 121–133
- 15 Avise, J.C. and Ball, R.M., Jr (1990) *Oxf. Surv. Evol. Biol.* 7, 45–67
- 16 Van Veghel, M.L.J. and Bak, R.P.M. (1993) *Mar. Ecol. Prog. Ser.* 92, 255–265
- 17 Kojis, B.L. (1986) *Mar. Biol.* 91, 291–309
- 18 Willis, B.L., Babcock, R.C., Harrison, P.L. and Wallace, C.C. (1992) *Abstr. 7th Int. Coral Reef Symp., Guam* 109
- 19 Templeton, A.R. (1989) in *Speciation and Its Consequences* (Otte, D. and Endler, J.A., eds), pp. 3–27, Sinauer Associates
- 20 Connell, J.H. (1978) *Science* 199, 1302–1310
- 21 Goreau, T.F. (1959) *Ecology* 40, 67–90
- 22 Weil, E. and Knowlton, N. *Bull. Mar. Sci.* 54 (in press)
- 23 Zlatarski, V.N. and Estalella, N.M. (1982) *Les Scléractinaires de Cuba*, Editions de l'Académie Bulgare des Sciences
- 24 Morse, D.E., Hooker, N., Morse, A.N.C. and Jensen, R.A. (1988) *J. Exp. Mar. Biol. Ecol.* 116, 193–217
- 25 Morse, A.N.C. (1992) *Abstr. 7th Int. Coral Reef Symp., Guam* 72
- 26 Tsuchiya, M. and Nishihira, M. (1985) *Galaxea* 4, 37–48
- 27 Buss, L.W. and Jackson, J.B.C. (1979) *Am. Nat.* 113, 223–234
- 28 Hughes, D.J. and Jackson, J.B.C. (1992) *Bull. Mar. Sci.* 51, 443–465
- 29 Cheetham, A.H. and Jackson, J.B.C. (1992) *Paleontol. Soc. Spec. Publ.* 6, 55
- 30 Blank, R.J. and Trench, R.K. (1985) *Science* 229, 656–658
- 31 Rowan, R. and Powers, D.A. (1992) *Proc. Natl Acad. Sci. USA* 89, 3639–3643
- 32 Buddemeier, R.W. and Fautin, D.G. (1993) *BioScience* 43, 320–326
- 33 Knowlton, N. and Jackson, J.B.C. (1993) in *The Natural History of Inbreeding and Outbreeding* (Thornhill, N.W., ed.), pp. 200–249, University of Chicago Press
- 34 Jackson, J.B.C. (1986) *Bull. Mar. Sci.* 39, 588–606
- 35 Richmond, R.H. and Hunter, C.L. (1990) *Mar. Ecol. Prog. Ser.* 60, 185–203
- 36 Richmond, R.H. and Jokiel, P.L. (1984) *Bull. Mar. Sci.* 34, 280–287
- 37 Glynn, P.W. et al. (1991) *Mar. Biol.* 109, 355–368
- 38 Palumbi, S.R. (1992) *Trends Ecol. Evol.* 7, 114–117
- 39 West-Eberhard, M.J. (1989) *Annu. Rev. Ecol. Syst.* 20, 249–278
- 40 Sale, P.F. (1989) *Proc. 6th Int. Coral Reef Symp.* 1, 19–27
- 41 Jackson, J.B.C. (1991) *BioScience* 41, 475–482
- 42 Hurlbert, S.H. (1984) *Ecol. Monogr.* 54, 187–211
- 43 Hutchinson, G.E. (1975) in *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 492–521, Harvard University Press

# The rise of the individual-based model in ecology

Olivia P. Judson

We are witnessing a major shift in the way that modelling is done in ecology, away from models governed by general equations and towards those that 'create' each and every individual in an ecological system in order to generate the dynamics of that system as a whole. In broad terms, we can liken these two approaches in ecology to the ideal of theoretical physics on the one hand, and on the other to the procedures of much present-day econometric modelling. This shift reflects the slow recognition among some ecologists of the implications of May's discovery in 1974 that even the simplest nonlinear equations can have complex and – more importantly – chaotic dynamics<sup>1,2</sup>. The eventual consequence of his discovery that 'even if we have a simple model in which all the parameters are determined exactly, long-term prediction is nevertheless impossible'<sup>2</sup> may be the resolution of the ongoing debate about the possibility of general theoretical statements in ecology, and with it, the transformation of ecological

**Recent advances of three different kinds are driving a change in the way that modelling is being done in ecology. First, the theory of chaos tells us that short-term predictions of nonlinear systems will be difficult, and long-term predictions will be impossible. The grave implications this has for ecology are only just beginning to be understood. Second, ecologists have started to recognize the importance of local interactions between individuals in ecological systems. And third, improvements in computer power and software are making computers more inviting as a primary tool for modelling. The combination of these factors may have far-reaching consequences for ecological theory.**

Olivia Judson is at the Dept of Zoology, University of Oxford, South Parks Road, Oxford, UK OX1 3PS.

modelling. Here, I examine the current status of generality in ecology, and in light of that examination, assess the pros and cons of these new approaches in understanding broader problems in ecology.

First, I discuss the quest for generality in ecology and its implications for individual-based models; second, I look at the properties and problems of this new class of models. Because this review aims to look at one new trend in ecological modelling, I do not discuss every aspect of theoretical ecology. Rather, I limit myself to a few examples to illustrate my arguments. Similarly, although the ultimate test of any model must be how well it stands up against field and laboratory data, I do not discuss the

role of empirical work in ecology, except in passing\*.

\*I define 'ecology' as 'a branch of science concerned with the interrelationship of organisms and their environments'<sup>3</sup>, with 'environment' including both biotic and abiotic components. I define 'general principle' as 'a comprehensive and fundamental law'<sup>3</sup> that applies equally well to one species as to another<sup>4</sup>, and that allows predictions to be made.

## Background: a shift in modelling

In classical population genetics, the drive for general mathematical statements is implicit and continues; the call for the use of general formulas in ecology was made explicit at least as early as 1974 when Maynard Smith wrote<sup>4</sup>:

A theory of ecology must make statements about ecosystems as a whole, as well as about particular species at particular times, and it must make statements which are true for many species and not just for one. . . . For the discovery of general ideas in ecology, therefore, different kinds of mathematical description, which may be called models, are called for. Whereas a good simulation should include as much detail as possible, a good model should include as little as possible.

By those standards, Maynard Smith would have dismissed certain recent alternative approaches as not modelling in his sense at all; yet in the past several years they have been gaining notably in popularity and power. Thus, in 1990 Hamilton<sup>5</sup> asserted, 'The idea [that parasites drive sexual reproduction] is increasingly credible. This is not so much because favourable evidence is accumulating. . . . It is rather the model itself, its engineering and appropriateness for its task, that has improved'. Substantial evidence of the growth of the new approaches is provided by the range of topics addressed in *Individual-based Models and Approaches in Ecology*<sup>6</sup>. Authors in this collection deal principally with two types of individual-based models and the applications to which they are appropriate. Several authors mention, but do not emphasize, the crucial developments in computer software that are making such models easier to use and far more realistic in their results; nor do they place the rise of individual-based modelling against the modern backdrop of chaos theory and its derivatives. Opposition to individual-based modelling can be found in many biology and zoology departments; many ecologists continue to view it with extreme suspicion, in part because knowledge among biologists of the techniques available to produce substantial simulations may be limited, and in part because of a reluctance to admit that models of the old style may have failed to produce useful or realistic dynamics in ecology.

## The holy grail: generality in ecology

Underlying all considerations of the use of modelling in ecology are certain concurrent and related questions. The most fundamental is whether or not ecology can hope to derive rules or laws that have anything like the power and generality found in some other sciences. This has been debated (McIntosh provides a thorough review<sup>7</sup>) at least since the mid-1950s, with vigorous pronouncements made on both sides<sup>8,9</sup>. The attraction of a general and predictive theory of ecology is obvious, yet despite much effort little progress seems to have been made. While no one expects ecology to have laws analogous to those of thermodynamics, ecologists do expect to find principles rather than mere rules of thumb. However, one gets the impression from reading through basic ecological textbooks that the science only collects rough-and-ready rules, fortified with examples of organisms that fit them – see, for example, Wilson's discussion of keystone species<sup>10</sup>. But the problem with rules of thumb is that too often they turn out to be thumb-sucking. For example, until recently, theory of succession was based on the notion of *r*- and *K*-selection, a notion that now turns out to be fundamentally flawed<sup>11</sup>. Thus, the question of whether or not ecology itself has general rules is still open. We cannot

settle the question from first principles nor observation, nor even reach it except by considering approaches in ecological modelling. This article therefore sets out to scrutinize the newest and least-formalized methods, namely, individual-based modelling, both in the modern context provided by chaos theory and in their own right.

## The grail proves elusive: the trouble with traditional models

The complexity of ecological systems, such as tropical rain forests, arises not just from the multiplicity of details but in great part from the evolution of a system and its components. In 1964, in a treatise for mathematicians that still has much to say to biologists, Hammersley and Handscomb wrote that all complex systems present theoreticians with two alternatives. The first is to write a highly detailed mathematical description of a particular system. The second is to write a simple, abstract and general mathematical description that tries to elucidate the factors that cause systems to be different from each other<sup>12</sup>. These, of course, are the approaches that Maynard Smith, ten years later, designated simulation versus modelling, insisting that only the general descriptions provide the necessary basis of theoretical ecology<sup>4</sup>. In 1976, May demurred, perhaps because of his explorations of chaos, urging that both approaches may help to make sense of collected ecological data and experiments<sup>13</sup>.

Traditional general models in ecology have often used population densities as the state variable<sup>4</sup>. These models have shown certain limitations. For example, they sometimes produce dynamics that are not realistic, that is, they fail to predict dynamics of natural systems. In response, modellers have added complexity in the form of a breakdown of the population into, for example, age or size classes. Such aggregated models often give more realistic behaviours than their simpler counterparts<sup>14</sup>, although already they begin to lose generality. However, Huston and colleagues charge that even these more-complex models ignore two fundamental aspects of biology: that all individuals are different, whether by genetics or environment or both, and that interactions between individuals take place locally<sup>6,15</sup>.

These criticisms have stimulated development of a new class, known as 'individual-based models'. Caswell and John point out that this heading includes two groups of models: those mentioned above that lump individuals together according to some common characteristic, known as 'individual-based distribution' models, and those models that, with a computer, track all the individuals in a population, known as 'individual-based configuration' models<sup>16</sup>. By tracking all individuals in a population, individual-based configuration models make individuals appropriately unique and their interactions local. The use of these models in ecology is increasing, but a debate has broken out over their utility. While Huston and colleagues have suggested that such models unify ecological theory<sup>15</sup>, Łomnicki and others have questioned whether they are sufficiently general to be useful<sup>14,17</sup>, or whether their results are anything more than an artefact of their construction<sup>18</sup>. To address these criticisms, we must return again to the question of generality. For brevity, I shall refer to 'individual-based configuration' models as simply 'individual-based' models.

## The grail vanishes: the lessons of non-linearity and chaos

One way to get at the question of generality is to consider the recent lessons of chaos theory. If even the simplest

nonlinear equations can often give rise to chaotic and therefore intrinsically unpredictable behaviours<sup>1</sup>, then the hope of deriving simple, general laws for systems in which nonlinearity is the norm must be illusory. And as May later pointed out, 'such nonlinear systems are surely the rule, not the exception, outside the physical sciences'<sup>2</sup>. For ecology, then, this may mean that simple generalities will be rare.

Another feature of systems that exhibit chaotic behaviour is that the outcome depends on the start – even vanishingly small differences in starting points can lead to highly divergent trajectories. This means that the history of a system has a critical effect on its future. The cause of a particular behaviour may be nothing more than an accident of history.

Further, the complexity of ecological systems far exceeds that of the simplest interacting systems capable of self-organization, the cellular automata. Even for these simple deterministic systems sometimes the only way to predict their behaviour is direct simulation<sup>19</sup>. However, for cellular automata, simulations from different starting points will give a general sense of the sorts of behaviours likely and of the limits on those behaviours (see Box 1). Direct simulation should allow us to identify statistically repeatable phenomena.

Thus, the lessons of chaos are that simple principles will be the exception, incidents of history are important, and that, because predictions are impossible, the only way to find out what is going on in some dynamic systems is to simulate them exactly. Individual-based simulations, then, may be the only way to find the 'texture' of a system, namely, the limits on and ranges of behaviours likely to appear in a given ecological system. Specifying the limits for each system in turn may be as precise as we can be. In this context, complaints about lack of generality may be meaningless – generality may not exist.

### **The generality of individual-based models: when to use them**

Another way to address the question of generality is to consider individual-based models themselves, and in particular, when they should be used.

Some recent textbooks in ecology begin with a section about individual organisms before they move on to more-complex areas such as species interactions, ecosystems and communities. This is an obviously sensible ordering – individual organisms underpin all other aspects of ecology. Further, an individual is easier to define than a species or an ecosystem, while the boundary between an organism and its environment is usually clearer as well<sup>22</sup>. Most important for evolution, individuals are the units of selection<sup>22</sup>. While models that explicitly use individuals as variables have appeared sporadically in ecology for at least 40 years<sup>23</sup>, their use has burgeoned in the past decade. This is due, in part, to an increase in computer power, which has made models that track large numbers of individuals more feasible, but also to the already-noted growing perception among some ecologists that traditional models are often inadequate to explain the dynamics of many of the systems seen in nature<sup>15,24</sup>. Even though these models are the simulations that Maynard Smith warned against<sup>4</sup>, models that follow individuals should be able, with fewer unrealistic simplifying assumptions, to generate complex behaviours of ecosystems, and to yield a greater understanding of some of the dynamics of ecological hierarchies beyond interactions among individuals<sup>15,25</sup>.

### **Box 1. Complexity theory and cellular automata**

The theory of complexity is closely related to the theory of chaos; complexity is often referred to as the 'edge of chaos' – the boundary between order and chaos. On this boundary, creative things are thought to happen<sup>20,21</sup>. Kauffman believes that living systems tend towards the edge of chaos, and that this edge is a sort of equilibrium<sup>20</sup>.

Even simple systems capable of self-ordering, the cellular automata, can show chaotic – and more than that – complex behaviours. A one-dimensional cellular automaton is a line of sites, with each site carrying a numerical value. At each time step, the value of each site is changed according to an identical deterministic rule that depends on its neighbouring sites. Changing the initial conditions will change the details of the patterns, but the patterns will have the same general form and statistical properties; changing the rule will change the pattern greatly. Cellular automata rules can yield the following four general classes of pattern: (1) a homogeneous form, (2) stable or periodic structures, (3) chaotic aperiodic behaviour, (4) complicated localized structures. The last two classes cannot be predicted except by direct simulation of all possibilities; the last two classes correspond to states of chaos and complexity, respectively<sup>19</sup>. If this is what happens in the simplest systems, what can we expect of ecological systems where none of the components is identical nor interacts with identical rules?

### **Box 2. Complex deterministic models**

Intermediate between general models and individual-based models are the complex deterministic. These are deterministic models where equations could, in principle, be written, but would be so cumbersome, besides being impossible to solve analytically, that the exercise is not worthwhile. Although in many of these cases, modellers turn to individual-based modelling, the complex deterministic is an alternative. Like the systems analysis models of the late 1960s<sup>26</sup>, in these cases simulation is done in terms of component categories, processes and so on. These processes may be, in contrast to the individual approach, completely deterministic. Ecology is set out as a system of boxes all affecting one another, and filling and emptying. In essence, it is a system of complex differential equations that one has no hope of solving explicitly. Although older models of this sort tried to model all of the aspects of the system, leading to enormously complicated structures, one way to make this sort of model more feasible and meaningful is to use boxes filled in accordance with the rules of population genetics<sup>27</sup>. For many of their properties and problems, however, these models are similar to individual-based models. For example, complex deterministic models will also produce chaotic dynamics and be unpredictable; they will generate large amounts of data that may have no clear statistical meaning.

Huston and colleagues appear to believe that individual-based models should be used virtually everywhere, asserting that classical models are always inadequate<sup>15</sup>; this is too sweeping to be correct. Classical models can often be modified to account for variation among individuals<sup>22</sup>. However, Caswell and John have suggested a way to evaluate when these new models should be used<sup>16</sup>. They mention three situations. First, if individuals have many parameters of interest or importance, such as age, size or more than two loci, an individual-based distribution model may be too unwieldy to be tractable<sup>16</sup> (but see Box 2). Second, if the size of populations is small, deterministic models will produce sampling errors<sup>16</sup>. In principle, both difficulties can be overcome. In practice, highly complicated deterministic models may require too much computer memory. The third case is when interactions between individuals are local and the assumption of mixing fails: then Caswell and John say that individual-based models are a necessity<sup>16</sup>. DeAngelis and others have proposed three additional situations where individual-based modelling should be used: when the 'zoogeographics' have a large random element, when biological or environmental

discontinuities are frequent, and when rare events are important<sup>24</sup>.

All of these restricted usages at first seem to be situations where general assumptions cannot be made, forcing one to resort to individual-based modelling. Yet, some of the situations mentioned above may be more general than they first appear. For example, rare events such as forest fires reset forest growth. Also, local interactions between individuals may well govern most ecological systems. But the relative importance of rare events, or the nature of the local interactions, will still, in most cases, vary from system to system, rendering comparison between systems difficult or impossible. If this is the case, individual-based models may be as general as any models can be: the main generality may be that systems differ.

## Practical problems with individual-based modelling

Even if we decide that the lessons of chaos and of the models themselves are sound – that general principles in ecology cannot exist in any formal or traditional sense – and that to understand any particular system we need a detailed simulation of it, there are still reasons why one should resort to individual-based modelling with caution. Any new form of modelling will have teething pains, even in establishing a common basis of understanding that would make it easier to present and discuss the models. Fortunately, in the case of individual-based modelling, this is beginning to change. Software developments, such as object-oriented programming (see Box 3), make individual-based modelling conceptually simpler and more structured<sup>28,29</sup>. However, the establishment of object-oriented programming as a tool will probably not improve the ease with which models using completely different 'objects' can be compared.

### Box 3. Object-oriented programming

One recent software development that may help biologists without a grounding in computer science to write individual-based models is the object-oriented approach. This approach lends itself well to modelling of anything that has component parts, whether a population made up of individuals, or a plant made up of leaves and branches, for example.

Maley and Caswell have laid out clearly and explicitly the differences between object-oriented programming and traditional programming, as well as some of the properties of object-oriented programmes that are particularly useful to biologists<sup>28</sup>. In brief:

Traditional programmes have data structures and control structures to manipulate them; object-oriented programmes have objects – which contain both the data and their controls. The objects are thus self-contained, and can be moved from programme to programme. However, they have other properties too. One of the most useful for individual-based models is inheritance<sup>28,29</sup>. For inheritance, a new object can take on the properties of another, previously defined object, and then add properties of its own. For example, a general object could be 'animal', with descendants of 'bird', 'lizard', etc. This leads to a hierarchy of objects from general to specific, but also to a biologically realistic conception of the way different objects can relate and interact. Unlike traditional programmes, where separate procedures are required to manipulate different data structures, a descendant's data can be manipulated in the same way as its ancestor's. This leads to more efficient programmes.

Individual-based models, then, can have individuals (the most specific objects) with their interactions defined by their ancestor objects. They can have the environment defined by a different type of object. And the interactions between all of the objects can be governed by an overall control structure<sup>28</sup>. However, the greatest advantage of object-oriented models in ecology is that ecological and individual-based concepts are easier to translate directly into a programme; the programme itself is simpler to create and understand<sup>29</sup>.

The process of constructing an individual-based model may be similar to that of constructing any other model<sup>24</sup>. Nonetheless, because individual-based models tend not to be mathematically rigorous, but 'fuzzy'<sup>24</sup>, and because, unlike mathematical analyses, computer code is rarely published in an appendix at the end of a paper, the construction of the program is difficult to question. This factor increases the suspicion with which the results of an individual-based model may be viewed<sup>18</sup>, a suspicion that is aggravated by loose terminology in model descriptions (see Box 4). Many descriptions of individual-based models fail to state their assumptions in depth, making comparison of models even more difficult<sup>35</sup>. One solution to these problems, i.e. the use of formal logic in model description, has been proposed<sup>35</sup> but does not seem to have been taken up by ecologists. If assumptions are not properly understood or stated, the results of a model may be misinterpreted. We must ask that a verbal description of a model should be sufficiently detailed about the design and assumptions that a similar program could be written from the methods section of a paper alone. Yet this is not often possible – at the very least, then, authors should offer, and say where to obtain, a copy of their programme.

Another problem that has only been touched on by the literature, is how to analyse and present the results from models that produce prodigious quantities of data<sup>16,24</sup>. While no doubt this will have to be dealt with separately for each model, the meaning of statistics done on such results is often philosophically moot, and is therefore something to be considered before embarking on an individual-based model. (However, bear in mind that once deterministic models are complex enough to have chaotic dynamics, their results may be equally difficult to understand.)

## Testing individual-based models

The handling of vast amounts of data leads into another area of concern, but one that has been well discussed<sup>14,17</sup>. Complicated models of any sort will be difficult to test; individual-based models are no exception. Even if an individual can be identified, its genetics, its parasite load, its energy intake and output, and so on, are all difficult to quantify. However, an individual-based model can be constructed to examine the local interactions between individuals, while having easily measurable parameters, such as size, for each separate individual. For example, DeAngelis and colleagues have modelled the distribution of fish in a pond, and managed to predict the final size distributions of fish on the basis of the initial size distributions<sup>36,37</sup>. Here, the individual-based models gave more accurate predictions than an analytical model<sup>38</sup>.

For empiricists, individual-based models are intuitive in a way that matrices and differential equations are not. Models based on general equations will not fit well to specific situations<sup>12</sup>; individual-based models may be able to point the way to any simpler principles<sup>14,39</sup>, although this is likely to be a lengthy process, beginning with a complex model and successively simplifying it until it fails to produce realistic dynamics<sup>14,39</sup>. However, the final test of any model must be how well it can account for data from natural systems.

## Individual-based models and population genetics

Traditional population genetics has been dominated by the use of one- or two-locus models because models of genetical complexity soon become intractable as the number of loci involved becomes large<sup>27</sup>. The usual solution has been to try and get mathematical tractability by

introducing unrealistic assumptions that are demonstrably false<sup>40</sup>. And yet we obviously need to be able to make some statements, even if they are vague, about population genetics under multiple varying loci, strong epistatic interactions and so on. Individual-based models provide a simple way to avoid unrealistic assumptions while still achieving genetical complexity. They have already started to be used in this manner<sup>41,42</sup>, and as their possibilities become clearer, will no doubt become crucial to population genetics as well as ecology.

### The nature of the grail: the problem of generality in ecology

Ecology, and indeed most of biology, is different from the other natural sciences in at least two fundamental ways. First, ecology cannot be derived from first principles in the same way as, for example, physics. Second, ecology has a unifying principle that other sciences do not have: evolution. Darwin put history into biology, which is to say that he introduced the stochastic and the contingent. The theory of evolution is predictive only inasmuch as it predicts that organisms will evolve; it does not predict in detail how they will evolve. The combination of these two differences makes ecology fascinating and frustrating. A common tendency among ecological modellers is to use physical models as justification for their approach, and to search for phenomena analogous to temperature or pressure<sup>4</sup>, or to invoke situations such as plasma physics<sup>15</sup> where local interactions are crucial. However, invoking physics misses the essence of biology. Biological rules and constants do exist; perhaps they should be used instead. Perhaps mendelian genetics could be incorporated into more individual-based ecological models. After all, genetics is one of the reasons all individuals are different. Another is the environment. Some predictions can be made based on the physical environment such as average temperature and variance of temperature. For example, if a habitat is cold, with little variance, resident animals will have adaptations to prevent heat loss, such as fur or fat. If a habitat is cold with a high variance in temperature, animals will tend to be adapted to one extreme, and to avoid the other, by migration or hibernation.

Haldane pointed out long ago that physical constraints on structure will determine the size of an animal<sup>43</sup> (see Box 5). These rules, while general, are rarely mentioned in ecological textbooks, and deserve more attention. However, ecology does have more precise rules: for example, individuals come only from other individuals, and the number of individuals in a closed region will decrease as a result of deaths of some of them<sup>18</sup>. Like Darwin's assumptions, such rules are trivial at first sight and yet can be surprisingly rich in subtle consequences. Among other such rules that could be mentioned are the ubiquity of parasitism<sup>47</sup> and kin selection<sup>48</sup>. But these rules are fundamentally different from laws of physics; and on reflection, we would not want or need to incorporate them into all models.

If evolution is primarily historical, then ecology is unlikely to give rise to many general principles; attempts to determine laws of history have always failed – 'That men do not learn very much from the lessons of history is the most important of all the lessons that history has to teach'<sup>49</sup>. The shift towards individual-based modelling represents the realization by ecologists that the time has come both to include the essence of biology in models and to recognize and accept the nonlinear nature of ecological systems. Single general models are being replaced by clusters of more-specific models that give better predic-

### Box 4. Definitions of 'Monte Carlo'

Equations, unlike words, leave little room for different interpretations. As the descriptions of most individual-based models are verbal, one way to combat the confusion and suspicion that words may cause is to be careful to define terms that may mean different things to different people. 'Monte Carlo' is one term often used when describing individual-based models. It is rarely defined in papers that say they have used it, and yet it has a host of definitions associated with it. For example:

- (1) 'Monte Carlo methods comprise that branch of experimental mathematics which is concerned with experiments on random numbers'<sup>12</sup>.
- (2) Monte Carlo is 'of, relating to, or involving the use of random sampling techniques and often the use of computer simulation to obtain approximate solutions to mathematical or physical problems esp. [sic] in terms of a range of values each of which has a calculated probability of being the solution'<sup>3</sup>.
- (3) '... "Monte Carlo method", a general term used to describe any algorithm that employs random numbers'<sup>30</sup>.
- (4) 'There are names for these different kinds of probabilistic algorithms. Those that are always fast and probably correct are dubbed *Monte Carlo*, and those that are always correct and probably fast are termed *Las Vegas*'<sup>31</sup>.
- (5) '... hard to treat analytically. The model has therefore been simulated by "Monte Carlo" methods; that is, by simulation in which each individual is separately represented in the computer'<sup>32</sup>.

However, 'Monte Carlo' is not usually synonymous with individual-based modelling. With reference to individual-based models, 'Monte Carlo simulation' means, perhaps, 'we used a random number generator and a probability distribution'<sup>33</sup>. But Monte Carlo methods can be used in other areas of biology – for example, in trying to analyse field data, 'Monte Carlo methods can also be used to calculate confidence limits for population parameters. Essentially the idea is to use computer-generated data to determine the amount of variation to be expected in sample statistics'<sup>34</sup>; therefore, it is probably a term that should be avoided or defined before using it to describe an individual-based model.

### Box 5. Physical and environmental constraints

Organisms are constrained by their structures; as evolution is gradual, and radical alterations in structure are improbable, we can predict limits on their evolution. For example, birds and mammals are constrained by their oxygen transport system – they will never be able to be as small as the smallest insects<sup>44</sup>. Humans are constrained by what their bones can support – we will never be truly gigantic<sup>43</sup>.

The environment imposes physical and biological constraints. For example, if we have a set of dry, windswept islands without any mammals, the trees that can grow there must be able to resist wind and desiccation. And, they must not depend on mammals for seed transport or burial. When we look at such a set of islands, this is what we find<sup>45</sup>.

Although these sorts of predictions may seem absurd or obvious, as Fisher pointed out, we cannot understand why most sexual species have only two genders until we have considered what might happen if there were three<sup>46</sup>. Perhaps before we can understand what is possible in evolution, we must first consider what is not possible – then we can find the limits of evolutionary potential.

tions of the limits on the behaviour of particular systems<sup>50</sup>. As the problems with individual-based models are overcome and as computers continue to improve, these sorts of models will become essential to ecology.

### Acknowledgements

I would like to thank Bill Hamilton, Bob May, Richard Ladle, Laurence Hurst, Allen Herre, Carlo Maley, Ron Ritter, Mark Suzman and two referees for many helpful comments, criticisms and suggestions. This work was supported by a grant from the Fulbright Commission and by a grant from the National Science Foundation.

## References

- 1 May, R.M. (1974) *Science* 186, 645–647
- 2 May, R.M. (1976) *Nature* 261, 459–467
- 3 Mish, F.C., ed. (1991) *Webster's Ninth New Collegiate Dictionary*, Merriam-Webster
- 4 Maynard Smith, J. (1974) *Models in Ecology*, Cambridge University Press
- 5 Hamilton, W.D. (1990) *J. Genet.* 69, 17–32
- 6 DeAngelis, D.L. and Gross, L.J., eds (1992) *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems*, Chapman & Hall
- 7 McIntosh, R.P. (1985) *The Background of Ecology: Concept and Theory*, Cambridge University Press
- 8 Ruse, M. (1973) *The Philosophy of Biology*, Hutchinson
- 9 Mayr, E. (1988) *Toward a New Philosophy of Biology: Observations of an Evolutionist*, Harvard University Press
- 10 Wilson, E.O. (1992) *The Diversity of Life*, The Penguin Press
- 11 Stearns, S.C. (1992) *The Evolution of Life Histories*, Oxford University Press
- 12 Hammersley, J.M. and Handscomb, D.C. (1964) *Monte Carlo Methods*, Methuen & Co.
- 13 May, R.M., ed. (1976) *Theoretical Ecology: Principles and Applications*, Blackwell Scientific Publications
- 14 Murdoch, W.W., McCauley, E., Nisbet, R.M., Gurney, W.S.C. and de Roos, A.M. (1992) in *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems* (DeAngelis, D.L. and Gross, L.J., eds), pp. 18–35, Chapman & Hall
- 15 Huston, M., DeAngelis, D.L. and Post, W. (1988) *Bioscience* 38, 682–691
- 16 Caswell, H. and John, A.M. (1992) in *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems* (DeAngelis, D.L. and Gross, L.J., eds), pp. 36–61, Chapman & Hall
- 17 Lomnicki, A. (1992) in *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems* (DeAngelis, D.L. and Gross, L.J., eds), pp. 3–17, Chapman & Hall
- 18 Metz, J.A.J. and de Roos, A.M. (1992) in *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems* (DeAngelis, D.L. and Gross, L.J., eds), pp. 88–111, Chapman & Hall
- 19 Wolfram, S. (1984) *Nature* 311, 419–424
- 20 Ruthen, R. (1993) *Sci. Am.* January, 110–117
- 21 Kauffman, S. (1991) *Sci. Am.* August, 78–84
- 22 Lomnicki, A. (1988) *Population Ecology of Individuals*, Princeton University Press
- 23 Leslie, P.H. and Chitty, D. (1951) *Biometrika* 38, 269–292
- 24 DeAngelis, D.L. and Rose, K.A. (1992) in *Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems* (DeAngelis, D.L. and Gross, L.J., eds), pp. 67–87, Chapman & Hall
- 25 Barbault, R. (1991) *Acta Oecologica* 12, 139–163
- 26 Sharov, A.A. (1992) *Oikos* 63, 485–494
- 27 Hamilton, W.D. *J. Heredity* (in press)
- 28 Maley, C.C. and Caswell, H. (1993) *Ecol. Modell.* 68, 75–89
- 29 Sequeira, R.A., Sharpe, P.J.L., Stone, N.D., El-Zik, K.M. and Makela, M.E. (1991) *Ecol. Modell.* 58, 55–89
- 30 Knuth, D.E. (1981) *The Art of Computer Programming, Vol. 2: Seminumerical Algorithms*, 2nd edn, Addison-Wesley
- 31 Harel, D. (1992) *Algorithmics: The Spirit of Computing*, 2nd edn, Addison-Wesley
- 32 Maynard Smith, J. (1978) *The Evolution of Sex*, Cambridge University Press
- 33 Jacquard, A. (1974) *The Genetic Structure of Populations (Biomathematics, Vol. 5)*, Springer-Verlag
- 34 Manly, B.F.J. (1991) *Randomization and Monte Carlo Methods in Biology*, Chapman & Hall
- 35 Robertson, D., Bundy, A., Muetzelfeldt, R., Haggith, M. and Uschold, M. (1991) *Eco-logic: Logic-based Approaches to Ecological Modelling*, MIT Press
- 36 DeAngelis, D.L., Cox, D.K. and Coutant, C.C. (1979) *Ecol. Modell.* 8, 133–148
- 37 DeAngelis, D.L., Godbout, L. and Shuter, B.J. (1991) *Ecol. Modell.* 57, 91–115
- 38 DeAngelis, D.L., Svoboda, L.J., Christensen, S.W. and Vaughan, D.S. (1980) *Ecol. Modell.* 8, 149–163
- 39 Murdoch, W.W. (1993) in *Biotic Interactions and Global Change* (Kareiva, P.M., Kingsolver, J.G. and Huey, R.B., eds), pp. 147–162, Sinauer Associates
- 40 Beniwal, B.K., Hastings, I.M., Thompson, R. and Hill, W.G. (1992) *Heredity* 69, 352–360
- 41 Hamilton, W.D., Axelrod, R. and Tanese, R. (1990) *Proc. Natl Acad. Sci. USA* 87, 3566–3573
- 42 Ladle, R.J., Johnstone, R.A. and Judson, O.P. (1993) *Proc. R. Soc. London Ser. B* 253, 155–160
- 43 Haldane, J.B.S. (1985) *On Being the Right Size and Other Essays* (Maynard Smith, J., ed.), Oxford University Press
- 44 Schmidt-Nielsen, K. (1984) *Scaling: Why is Animal Size so Important?*, Cambridge University Press
- 45 Leigh, E.G., Jr, Wright, S.J., Herre, E.A. and Putz, F.E. (1993) *Evol. Ecol.* 7, 76–102
- 46 Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press
- 47 Price, P.W. (1980) *Evolutionary Biology of Parasites*, Princeton University Press
- 48 Hamilton, W.D. (1964) *J. Theor. Biol.* 7, 1–52
- 49 Huxley, A. (1959) *Collected Essays, 'Case of Voluntary Ignorance'*, Triad
- 50 Shugart, H.H., Smith, T.M. and Post, W.M. (1992) *Annu. Rev. Ecol. Syst.* 23, 15–38

## In the next issue of *TREE*:

- Patterns and processes in communities of helminth parasites, *W.P. Sousa*
- Mammalian eusociality: a family affair, *J.U.M. Jarvis et al.*
- Monoterpenes and the growth-differentiation balance hypothesis, *M. Lerdau et al.*
- *Mycobacterium tuberculosis*: just desserts for an ungrateful guest, *M.E. Halloran*
- Optimality and evolutionary genetics, *A.J. Moore and C.R.B. Boake*
- Arctic and alpine biodiversity, *F.S. Chapin III and Ch. Körner*