Individual-Based Models for Ecosystem Simulations

Adam Aspinall
aspina1@uwindsor.ca
University of Windsor

November 19, 2008

Abstract. The increased availability of high computing power has laid a foundation for a new modeling technique called individual-based (or agent-based) models (IBMs or ABMs). As an alternative approach to classical ecological modeling, IBMs focus on individual variability and allow ecologists to replicate the behaviour of individual organisms while observing the effect they have on an overall system. There has been a great deal of discussion on the effects of individual-based modeling and ecology. Literature that presents applications of individual-based models is becoming more prevalent in recent years. The following is a survey of the research that has been conducted in this field, including milestone papers that analyze the potential, the effects, the uses, and the implications of this new modeling approach.

Keywords. Individual-based, Agent-Based, Simulation models, Theoretical ecology

---

Contents

1 Introduction

1.1 An Overview

Individual-based modeling is a bottom-up approach to simulating ecosystems that allows for the consideration of the traits and behaviour of individual organisms.

Whereas classical approaches to modeling ecology often ignore individual behaviour and instead consider an entire ecosystem as a whole, individual-based models aim to "treat individuals as unique and discrete entities"[Grimm, 1999]. By modeling individuals with varying ages, social ranks, and adaptability, for example, the properties of the system that the individuals represent can begin to emerge. This has a distinct advantage over the classical approach, namely that the assumptions made regarding individual behaviour (such as the desire for fitness and shelter) provide for a more realistic simulation than using a state-variable model that may begin by calculating birth and death rates.

The lack of explicit criteria for differentiating between classical modeling approaches and individual-based models is frequently described as a reason why individual based models may not provide a new method for modeling ecology [Uchmanski and Grimm, 1996]. Those against this approach may feel that individual-based models are merely a tool for simulating very specific environments. Advocates who favour the use of individual-based models are driven by paradigmatic motivation [Grimm, 1999] where such models may be used to formulate general theories of ecology.

The generality of individual-based modeling is an important area of consideration. As beneficial as a specific model may be, it is often more worthwhile to formulate general theories. The authors of the book "Individual-based Modeling and Ecology" [Grimm and Railsback, 2005] reserve several sections to discuss the generality of individual-based models. They describe the difficulty of creating generic ecological models by comparing ecology to physics. "Individuals [of ecology] are not atoms but living organisms" and that because "individual organisms have properties an atom does not have", such as the variation between them and their adaptive behaviour, aiming for generality in ecological models is much more difficult. Despite these reservations, there continues to be a rise in the use of individual-based models [Judson, 1994].

2 Survey of Research

This survey is organized as follows: section 2.1 introduces the topic of ecological modeling and presents significant publications that discuss different modeling approaches, section 2.2 addresses the issue of generality in ecology and the potential for generic individual-based models, section 2.3 provides an insight into the large number of sample individual-based models that cover a broad spectrum of the areas in the field of ecology, and section 2.4 examines the future of individual-based models.

2.1 Modeling and Ecology

The goal of modeling is to solve problems or answer questions, according to Grimm and Railsback [2005], who describe three key points for ecological modeling. Identifying a problem or question that needs to be addressed or answered should be one of the very first steps executed during the modeling process. Merely aiming for "realism", according to Grimm, is not a strong enough guideline for modeling and should not be the reason why a modeler sets out to represent a system or environment. Modeling an ecological system requires constraints and rules that restrict our attention to the problem. [Starfield et al., 1990] provide a comprehensive description on what they believe to be an appropriate process for modeling. They suggest that a modeler begins by phrasing the problem to be solved. Grimm and Railsback agree by saying, "Good science requires good questions" [Grimm and Railsback, 2005]. Drawing a simple diagram of the system to be modeled is identified as the second phase. Starfield et al. suggest that imagining yourself inside the system should be the third step. "What is going on around me?" and "What affects me, and what do I affect?" are two questions that Grimm and Railsback suggest a modeler asks him or herself [Grimm and Railsback, 2005]. Identifying the essential variables, outlining any simplifying assumptions, and attacking the problem through the use of many small steps (versus addressing it head-on) are suggested as the three last high-level phases in the modeling process [Starfield et al., 1990].

2.1.1 Classical Modeling

Uchmanski and Grimm [1996] describe basic models of classical ecology as ones that focus on an "average individual." Uncomplicated life cycles are routinely simulated and the development, metabolism and the aging of individuals is scarcely considered in classical modeling. "Classical models cannot take into account discrete individuals, which create local population non-uniformity that can affect population dynamics and ecosystem function" according to DeAngelis and Mooij [2005] who describe characteristics of simulations in the context of both classical modeling approaches and individual-based models. Few system characteristics can be simulated in classical models, according to DeAngelis and Mooij, such as some form of implicit learning where, for example, "a predator population could increase its preference for certain prey relative to other prey types" [DeAngelis and Mooij, 2005]. However, phenotypic characteristics occur at the individual level and classical models cannot replicate this behaviour to the same degree that occurs in nature.

Traditional modeling techniques often use state variables, such as population density, to describe an environment. Recognizing this drawback, [Judson, 1994] alleges that models of this type "sometimes produce dynamics that are not realistic." Even as modelers began to age age, size, and organism classes to classical models, this traditional approach does not produce simulations that accurately portray real environments.

2.1.2 Pattern-oriented Modeling

It is the belief of Grimm et al. [1996] that "ecological modelling should take its orientation more from real patterns observed in nature." Pattern-oriented modeling forces a relationship between spatial and temporal scales, according to Grimm et al., and that a pattern-oriented model is a tool that assists modelers to create predictions that are more easily tested than the predictions formulated by other modeling techniques.

Pattern-oriented modeling is described as bottom-up by Grimm et al. [2005] because it begins by collecting relevant information about individuals, then proceeds to formulate theories regarding the individuals' behaviour, and finally tests the theories in a computer simulation that allows the modeler to observe the environmental properties that emerge. This technique forces a modeler to use real patterns observed in nature as an aid during the design of a model or simulation. Moreover, the pattern-oriented modeling process described in [Grimm et al., 2005] unifies the concepts of individual-based models with the idea of modeling based on patterns. This method creates a model structure that is optimal, rigorous, and realistic, while sculpting the model into one that has an ideal complexity.

Testing alternative theories about the behaviour of individuals is easier with pattern-oriented modeling. By comparing a model's output with the data retrieved from real patterns observed in nature, modelers are quickly and easily able to draw conclusions about the accuracy of the hypothesis that was tested.

DeAngelis and Mooij [2005] provide a small discussion on how individual-based models can be used to show the emergence of patterns such as the formation of swarms, flocks, schools, herds, and other groups.

For all of these reasons, pattern-oriented modeling has been found to be a large stepping stone in the direction from classical ecological modeling to an individual-based approach.

Table 1: Summary of Research on Pattern-Based Models

Author(s)	**Journal**	**Title**	**Contribution**
Volker Grimm, Karin Frank, Florian Jeltsch, Roland Brandl, Janusz Uchmanski, and Christian Wissel.	The Science of the Total Environment, 1996.	Pattern-oriented modelling in population ecology.	Uses three examples from population ecology to demonstrate the strategy and importance of pattern-oriented modeling.
Volker Grimm, Eloy Revilla, Uta Berger, Florian Jeltsch, Wolf M. Mooij, Steven F. Railsback, Hans-Hermann Thulke, Jacob Weiner, Thorsten Wiegand, and Donald L. DeAngelis.	Science, 2005.	Pattern-Oriented Modeling of Agent-Based Complex Systems: Lesson from Ecology.	Discusses pattern-oriented modeling as a unifying framework for agent-based models.

2.1.3 Individual-based Modeling

As one of the original milestone papers to discuss the arrival of a new modeling technique, [Huston et al., 1988] isolates two key reasons why classical models "violate" theoretical ecology. Firstly, classical models attempt to describe all individuals in an environment with one variable. This tactic assumes, for example, that individuals do not vary in their behaviour or physiology, which is a fundamental flaw. Secondly, Huston et al. [1988] criticize classical models for not spatially isolating organisms within a system. Individuals are simulated in a way that causes each of them to have an equal effect on each and every other individual. However, it is a generally accepted principle that interactions between individuals occur only between organisms that come into contact with one another.

Huston et al. [1988] elaborate on the benefits of an individual-based approach by describe the effect of the degree to which individuals initially vary. When trees, for example, are at relatively similar heights to begin with, they will grow naturally at the same rate as the competition for light is an equal fight. However, when the initial variance of height is high, the result will be very few large plants and many smaller strained individuals.

The rise of the individual-based model is discussed in [Judson, 1994] which provides a short analysis of the properties and problems of individual-based models. The degree to which an individual's life cycle will be simulated, whether or not resource dynamics are taken into account, how the size of the population is represented, and the extent of variability among individuals of the same age are described as several classification criteria for evaluating the effectiveness of an individual-based model [Uchmanski and Grimm, 1996].

Although it is predominantly accepted that individual-based models are providing a new outlook on ecological modeling, an examination of how significant the contributions are reveals that there is little common motivation behind the movement [Grimm, 1999]. Grimm describes the use of individual-based models simply as a tool as having "pragmatic motivation." On the contrary, individual-based models that are designed to support theoretical ecology are driven by "paradigmatic motivation" which he describes as the pathway to developing generic IBMs.

In more recent years, as a means of providing a basis for the development of individual-based models, many frameworks are being developed. [Railsback, 2001] draws the concepts from complex adaptive systems as guidelines that will help "make the design of IBMs less ad hoc." Identifying what behaviours should emerge from the model, outlining what adaptive behaviours are to be simulated, deciding on what measures will be used to test fitness, and determining to what extent individuals are able to predict the outcome of their behaviour are all steps that [Railsback, 2001] suggests should be executed during the individual-based modeling process.

Modeling tools such as ECOTALK by Baveco and Lindeman [1992] and Baveco and Smeulders [1994], HOBO by Lhotka [1994], ECOSIM by Lorek and Sonnenschein [1998] and MOAB by Carter and Finn [1999] are all examples of tools that were designed to help develop individual-based models. Mamedov and Udalov [2002] recognized the fact that these frameworks demand that ecologists encompass some set of programming skills, and consequently they developed the CENOCON system. Alleging that it is flexible and requires no programming skill at all, Mamedov and Udalov promote CENOCON as a framework that "generates a virtual space, creates and populates the space with individuals" and "manages these virtual entities to act as real components of real ecological communities."

In more recent years, there has some focus on how the environment in an IBM is represented [Bian, 2003]. How the environment is represented in a model, says

Bian, “is a critical part of individual-based models.” Two traditional approaches for simulating the environment are prevalent - the grid model and the patch model. Bian [2003] analyses the implications of using both of these techniques and concludes that how the environment is represented in an individual-based model will have an effect on the data that is produced. Similarly, different scheduling methods for individual-based models will produce varying results [Caron-Lormier et al., 2008].

One of the most significant contributions to the study of individual-based modeling and ecology is [Grimm and Railsback, 2005]. Many compositions on the subject cite *Individual-based Modeling and Ecology* by Grimm and Railsback as a book that covers a broad spectrum of topics: a generic modeling process, pattern-oriented modeling, and individual-based modeling. Moreover, it discusses what the goals are of IBMs, what makes a model an IBM, and many examples of individual-based models. It presents a framework for the design and development of individual-based models and it reserves chapters for the examination of how individual-based models should be analyzed and how the model and the data produced by the model should be communicated and presented.

2.2 Generality and Ecology

It is suggested in [Grimm, 1999] that in order to extract general ecological theories from individual-based modeling, paradigmatic motivation must be the driving force. Only with unambiguous reference to theories of ecology and a solid, unifying foundation for building individual-based models will the new modeling approach begin to formulate ecological theories.

Whether or not ecology can benefit from structured rules and laws like those witnessed in other sciences is a discussion that has been had since the mid-1950s [Judson, 1994]. “The attraction of a general and predictive theory of ecology is obvious”, says Judson, “yet despite much effort little progress has been made.”

According to Grimm [1999], we must not confuse generality in ecology with generic individual-based models. The latter, such as [Hraber et al., 1997], are tools, or frameworks, for the development of (just about) any individual-based models. They are generic in the sense that they allow ecologists and modelers to adjust features and parameters to suit the simulation that they are after. The former, generality in ecology, is much more difficult to achieve. Organisms behave differently, according to Grimm [1999], and the thought of designing an individual-based model that produces theories capable of governing the behaviour of one or more species is almost incomprehensible. A survey of the work completed in the field of individual-based modeling clearly reveals this fact simply by examining the countless examples of individual-based models that have narrow scopes - they focus on a single species, or even more narrowly, a single type of organism. [Abbott et al., 1995] and [Juanes et al., 2000] are two examples, the first being a Master's thesis that presents SIMPDEL, a Spatially-Explicit Individual-Based Simulation Model of Florida Panther and White-Tailed Deer in the Everglades and Big Cypress Landscapes.

2.3 A Sample of Individual-based Models

Listing and describing all existing individual-based models is not possible in a relatively short survey such as this. Nevertheless, a short summary of several IBMs is presented here with the goal of demonstrating the wide range of applications of this modeling technique.

Fahse et al. [1998] demonstrate their protocol for extracting population parameters from individual-based models with the use of an IBM that simulates "nomadic birds in a heterogeneous landscape", similar to some living in parts of South Africa. Habitat selection by stream salmonids is simulated in an individual-based model in [Railsback and Harvey, 2002] and Bian [2003] uses an IBM that simulates salmon growth to support her theory that how the environment is represented in an IBM will affect the model's results.

Individual-based models of vegetation are also available. An individual-based model is used in [Breckling et al., 2006] to conduct a risk-analysis of genetically modified plants.

Upwards of 27 individual-based models are given as examples in [Grimm and Railsback, 2005]. They cover an extensive array of topics such as simulating the grouping behaviour of birds and fish, the population dynamics of social animals, the movement and dispersal of trout, the dynamics of plant populations, and the evolving traits of marine fish.

Table 2: Summary of Research on Individual-Based Models

Author(s)	**Journal**	**Title**	**Contribution**
Michael Huston, Donald DeAngelis, and Wilfred Post.	BioScience, 1988.	New Computer Models Unify Ecological Theory.	One of the first milestone papers to discuss the emerging technique of individual-based models.
H. H. Shugart, T. M. Smith, and W. M. Post.	Annu. Rev. Ecol. Syst., 1992.	The Potential For Application of Individual-Based Simulation Models for Assessing the Effects of Global Change.	Presents a computer model to predict ecological response to global changes.
Olivia P. Judson.	Trends in Ecology and Evolution, 1994.	The rise of the individual-based model in ecology.	Presents an analysis of generality in ecology and its implications for individual-based models.
Janusz Uchmanski and Volker Grimm.	Trends in Ecology and Evolution, 1996.	Individual-based modelling in ecology: what makes the difference.	Presents four criteria for classifying different modeling techniques.
Peter T. Hraber, Terry Jones, and Stephanie Forrest.	Artificial Life, 1997.	The Ecology of Echo.	Presents a generic individual-based simulation model.

IBMs for Ecosystem Simulations

Author(s)	**Journal**	**Title**	**Contribution**
Andre M. C. Campos and David R. C. Hill.	Transactions on Simulation, 1998.	An Agent Based Framework for Visual-Interactive Ecosystem Simulations.	Present a flexible and customizable framework for developing IBMs.
Lorenz Fahse, Christian Wissel, and Volker Grimm.	The American Naturalist, 1998.	Reconciling Classical and Individual-Based Approachs in Theoretical Population Ecology: A Protocol for Extracting Population Parameters from Individual-Based Models.	Presents a method for reconciling two different modeling approaches.
Volker Grimm.	Ecological Modelling, 1999.	Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future?	Describes the types of motivation behind IBMs.
Volker Grimm, Tomasz Wyszomirski, David Aikman, and Janusz Uchmanski.	Ecological Modelling, 1999.	Individual-based modelling and ecological theory: synthesis of a workshop.	Present a review of twelve papers to analyse the status of IBMs.
Adam Lomnicki.	Ecological Modelling, 1999.	Individual-based models and the individual-based approach to population ecology.	Presents four factors for describing relations between individuals.
Steven F. Railsback.	Ecological Modelling, 2001.	Concepts from complex adaptive systems as a framework for individual-based modelling.	Describes six concepts as a basis for IBMs.
Alexandre Mamedov and Sergey Udalov.	Ecological Modelling, 2002.	A computer tool to develop individual-based models for simulation of population interactions.	Present a flexible and customizable framework for IBMs.

Author(s)	Journal	Title	Contribution
Steven F. Railsback and Bret C. Harvey.	Ecology, 2002.	Analysis of habitat-selection rules using an individual-based model.	Presents and analyses an IBM of stream salmonids.
Ling Bian.	Ecological Modelling, 2003.	The representation of the environment in the context of individual-based modeling.	Analyses two approaches to representing the environment in IBMs.
Donald L. DeAngelis and Wolf M. Mooij.	Annu. Rev. Ecol. Evol. Syst., 2005.	Individual-Based Modeling of Ecological and Evolutionary Processes.	Present a basis for IBMs to determine the range of applications benefitting from IBMs.
Broder Breckling, Ulrike Middelhoff, and Hauke Reuter.	Ecological Modelling, 2006.	Individual-based models as tools for ecological theory and application: Understanding the emergence of organisational properties in ecological systems.	Analyses the potential of IBMs and presents a generic framework for IBMs.
Geoffrey Caron-Lormier, Roger W. Humphry, David A. Bohan, Cathy Hawes, and Pernille Thorbek.	Ecological Modelling, 2008.	Asynchronous and synchronous updating in individual-based models.	Investigates two approaches for scheduling and updating IBMs.

2.4 Comments and The Future of IBMs

In 1988, Michael Huston, Donald DeAnglis, and Wilfred Post determined that the use of classical modeling approaches in ecology failed for several reasons, among them is the fact that they rely on unrealistic assumptions about individuals such as using an "average individual" to represent the typical behaviour of an organism [Huston et al., 1988]. "The potential value of the individual-based modeling approach in extending ecological theory has only begun to be explored." This appears to remain true today.

Since then, there is evidence showing that the use of individual-based models in ecology has continued to grow. DeAngelis and Mooij [2005] claim that a search of articles in 1990 that contained the keywords "individual-based", or "individual-oriented", along with "model", yielded just a single result. In 2004, they say, the same search produced 150 results, with their belief that the number of papers on individual-based model is considerably higher if you factor in the articles on IBM that do not use these keywords.

This review survey demonstrated that although there has been an enormous increase in the research conducted on the individual-based modeling approach, it would appear that an end has not yet been reached. Further discussions on the potential for generality and ecological theory, extrapolated from individual-based models, continue. [Judson, 1994], [Uchmanski and Grimm, 1996], [Fahse et al., 1998], [Grimm, 1999], [Bian, 2003], and [DeAngelis and Mooij, 2005] are just a few examples of publications that address how theoretical ecology could potentially benefit from the individual-based modeling approach.

3 Acknowledgements

I very much appreciate the guidance that my supervisor, Dr. Robin Gras, has provided, especially for supplying me literature such as [Hraber et al., 1997] and [Grimm and Railsback, 2005] as they were some of the first publications I had read on the subject. Furthermore, I am grateful for the direction provided to me by Dr. Richard A. Frost.

4 References

Abbott, C. A., Berry, M. W., Comiskey, E. J., Gross, L. J. and Luh, H. K. [1995], Computational models of white-tailed deer in the florida everglades, Master's thesis, University of Tennessee, Knoxville TN.

Ackley, D. H. and Littman, M. L. [1992], 'Interactions between learning and evolution', *Artificial Life* **2**, 487 – 507.

Bart, J. [1995], 'Acceptance criteria for using individual-based models to make management decisions', *Ecol. Appl.* **5**, 411 – 420.

Baveco, J. M. and Lindeman, R. [1992], 'An object-oriented tool for individual oriented simulation: host-parasitoid system applciation', *Ecol. Model.* **61**, 267 – 286.

Baveco, J. M. and Smeulders, A. M. W. [1994], 'Objects for simulation: smaltalk and ecology', *Simulation* **62**, 42 – 57.

Beyer, J. E. and Laurence, G. C. [1980], 'A stochastic model of larval fish growth', *Ecol. Model.* **8**, 109 – 132.

Bian, L. [2003], 'The representation of the environment in the context of individual-based modeling', *Ecological Modelling* **159**, 279 – 296.

Breckling, B., Middelhoff, U. and Reuter, H. [2006], 'Individual-based models as tools for ecological theory and application: Understanding the emergence of organisational properties in ecological systems', *Ecological Modelling* **194**, 102 – 113.

Campos, A. M. and Hill, D. R. [1998], 'An agent based framework for visual-interactive ecosystem simulation', *Transactions on Simulation* **15**(4), 139–152.

Caron-Lormier, G., Humphry, R. W., Bohan, D. A., Hawes, C. and Thorbek, P. [2008], 'Asynchronous and synchronous updating in individual-based models', *Ecological Modelling* **212**, 522 – 527.

Carter, J. and Finn, J. T. [1999], 'Moab: a spatially explicit, individual-based system for creating animal foraging models', *Ecol. Model.* **119**, 29 – 41.

Caswell, H. [1989], *Matrix population models: Construction, analysis, and interpretation*, Sunderland, MA: Sinauer Associates.

Cornforth, D., Green, D. G., Newth, D. and Kirley, M. [2002], 'Do artificial ants march in step? ordered asynchronous processes and modularity in biological systems', *Artificial Life* **8**, 1 – 5.

Couclelis, H. [1992], *People manipulate objects (but cultivate fields): beyond the raster-vector debate in GIS*, Springer, Berlin, 65 – 77.

Dawkins, R. [1982], *The Extended Phenotype: The gene as the Unit of Selecetion*, Freeman, Oxford.

DeAngelis, D., Godbout, L. and Shutter, B. J. [1991], 'An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations', *Ecological Modelling* **57**, 91 – 115.

DeAngelis, D. and Gross, L. [1992], *Individual-based models and approaches in ecology: populations, communities and ecosystems*, Chapman and Hall.

DeAngelis, D. and Mooij, W. M. [2005], 'Individual-based modeling of ecological and evolutionary processes', *Annu. Rev. Ecol. Evol. Syst.* **36**, 147–168.

DeAngelis, D., Rose, K. and Huston, M. [1994], 'Individual-oriented approaches to modeling ecological populations and communities', *Lecture Notes in Biomathematics* **100**, 390–410.

Dieckmann, U. and Doebeli, M. [1999], 'On the origin of species by sympatric speciation', *Nature* **400**, 354 – 357.

Downing, K. and Reed, M. [1996], 'Object-oriented migration modeling for biological impact assessment', *Ecol. Model.* **93**, 203 – 219.

Durrett, R. and Levin, S. A. [1994], 'Stochastic spatial models: A user's guide to ecological applications', *Philos. Trans. R. Soc. London Ser. B* **343**, 329 – 350.

Epstein, J. M. and Axtell, R. L. [1994], Growing artificial societies: Social science from the bottom up, Technical report, Brookings Institution.

Eschenbach, C. [2000], 'The effect of light acclimation of single leaves on whole tree growth and competition - an application of the tree growth model almis', *Ann. Forest Sci.* **57**, 599 – 609.

Fahse, L., Wissel, C. and Grimm, V. [1998], 'Reconciling classical and individual-based approaches in theoretical population ecology: A protocol for extracting population parameters from individual-based models', *The American Naturalist* **152**, 838 – 852.

Gasser, L. and Briot, J. P. [1992], *Object-Based Concurrent Programming and DAI*, Kluwer Academic Press, Dordrecht, 81 – 108.

Goodchild, M. F. [1992], 'Geographical data modeling', *Comput. Geosci.* **18**, 401 – 408.

Grimm, V. [1994], 'Mathematical models and understanding in ecology', *Ecol. Model.* **75/76**, 641 – 651.

Grimm, V. [1999], 'Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future?', *Ecological Modelling* **115**, 129–148.

Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J. and Wissel, C. [1996], 'Pattern-oriented modelling in population ecology', *the Science of the Total Environment* **186**, 151–166.

Grimm, V. and Railsback, S. F. [2005], *Individual-based Modeling and Ecology*, Princeton University Press.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegant, T. and DeAngelis, D. [2005], 'Pattern-oriented modeling of agent-based complex systems: Lessons from ecology', *Science* **310**, 987–991.

Grimm, V., Wyszomirski, T., Aikman, D. and Uchmanski, J. [1999], 'Individual-based modelling and ecological theory: synthesis of a workshop', *Ecological Modelling* **115**, 275 – 282.

Grist, E. and des Clers, S. [1999], 'Seasonal and genotypic incfluences on life cycle synchronisation: further insights from annual squid', *Ecol. Model.* **115**, 149 – 163.

Hartviggsen, G. and Starmer, W. T. [1995], 'Plant-herbivore coevolution in a sptially and genetically explicit model', *Artificial Life* **2**, 239 – 259.

Hogeweg, P. and Hesper, B. [1990], 'Individual-oriented modeling in ecology', *Math. Comput. Model.* **13**, 83 – 90.

Hraber, P. T., Jones, T. and Forrest, S. [1997], 'The ecology of echo', *Artificial Life* **3**, 165–190.

Huberman, B. A. and Glance, N. S. [1993], 'Evolutionary games and computer simulations', *Proc. Natl. Acad. Sci. U.S.A.* **16**, 7716 – 7718.

Hurrion, R. D. [1976], The Design, Use and Required Facilities of an Interactive Visual Computer Simulation Lanaguage to Explore Production Planning Problem, *PhD thesis*, University of London.

Huston, M. and DeAngelis, D. [1987], 'Size bimodality in monospecific plant populations: a critical review of potential mechanisms', *Am. Nat* **129**, 678 – 707.

Huston, M., DeAngelis, D. and Post, W. [1988], 'New computer models unify ecological theory', *BioScience* **38**(10), 682–691.

Juanes, F., Letcher, B. H. and Gries, G. [2000], 'Ecology of stream fish: insights gained from an individual-based approach to juvenile atlantic salmon', *Ecology of Freshwater Fish* **9**, 65 – 73.

Judson, O. P. [1994], 'The rise of the individual-based model in ecology', *Trends in Ecology and Evolution* **9**(1), 9–14.

Kaiser, H. [1976], 'Quantitative description and simulation of stochastic behaviour in dragonflies', *Acta Biotheor.* **25**, 163 – 210.

Kemp, K. K. [1997], 'Fields as a framework for integrating gis and environmental process models. part 1: representing sptial continuity', *Trans. GIS* **1**, 219 – 234.

Levin, S. [1994], 'Patchiness in marine and terestrial systems: from individuals to populations', *Philos. Trans. R. Soc. London Ser. B* **343**, 99–103.

Lhotka, L. [1991], *Technology of Objeect Oriented Languages and Systems*, Prentice Hall, Hemel Hempstead, UK, 309 – 317.

Lhotka, L. [1994], 'Implementation of individual-oriented models in aquatic ecology', *Ecol. Model.* **74**, 47 – 62.

Lomnicki, A. [1988], *Population Ecology of Individuals*, Princeton University Press.

Lomnicki, A. [1999], 'Individual-based models and the individual-based approach to population ecology', *Ecol. Model.* **115**, 191 – 198.

Lorek, H. and Sonnenschein, M. [1998], 'Object oriented support for modeling and simulation of individual-oriented ecological models', *Ecol. Model.* **108**, 77 – 96.

Lorek, H. and Sonnenschein, M. [1999], 'Modelling and simulation software to support individual-based ecological modelling', *Ecol. Model.* **115**, 199 – 216.

Mamedov, A. and Udalov, S. [2002], 'A computer tool to develop individual-based models for simulation of population interactions', *Ecological Modelling* **147**, 53 – 68.

Metz, J. A. J. and Diekmann, O. [1986], 'The dynamics of physiologically structured populations', *Lecture Notes in Biomathematics* **68**, 46–77.

Middelhoff, U. [2000], Simulationsgestutzte Analyse der raum-zeitlichen Verteilung der Biomasse in einem Erlenwalk unter besonderer Berucksichtigung der Feinwurzeldynamik, *PhD thesis*, University of Kiel.

Mollison, D. [1986], 'Modelling biological invasions: chance, explanation, prediction', *Philos. Trans. R. Soc. London Ser. B* **314**, 675 – 693.

Murdoch, W. W., McCauley, E., Nisbet, R. M., Gurney, W. S. C. and de Roos, A. M. [1992], *Individual-based models: combining testability and generality*, Chapman and Hall, New York, 18 – 35.

Myers, J. H. [1976], 'Distribution and dispersal in populations capable of resource depletion: a simulation model', *Oecologia* **23**, 255 – 269.

Neuert, C., Rademacher, C., Grundmann, V., Wissel, C. and Grimm, V. [2001], 'Struktur und dynamik von buchenurwäldern: Ergebnisse des regelbasierten modells', *Natursch. Landschaftspl.* **33**, 173 – 183.

Oboshi, T., Kato, S., Mutoh, A. and Itoh, H. [2002], 'Collective or scattering: Evolving schooling behaviors to escape from predator', *Artificial Life* **8**, 386–389.

Oreskes, N., Shrader-Frechette, K. and Belitz, K. [1994], 'Verification, validation, and confirmation of numerical models in the earth sciences', *Science* **236**, 641 – 646.

Pimm, S. L. [1991], *The Balance of Nature?*, University of Chicago Press, Chicago.

Rademacher, C., Neuert, C., Grundmann, V. and Grimm, V. [2004], 'Reconstructing spatiotemporal dynamics of central european natural beech forests: the rule-based model', *Forest Ecology and Management* **194**, 349 – 368.

Railsback, S. F. [2001], 'Concepts from complex adaptive systems as a framework for individual-based modelling', *Ecological Modelling* **139**, 47 – 62.

Railsback, S. F. and Harvey, B. C. [2002], 'Analysis of habitat-selection rules using an invidual-based model', *Ecology* **83**(7), 1817–1830.

Railsback, S. F., Lamberson, R. H., Harvey, B. C. and Duffy, W. E. [1999], 'Movement rules for spatially explicit individual-based models of stream fish', *Ecological Modelling* **123**, 73 – 89.

Raper, J. and Livingstone, D. [1995], 'Development of a geomorphological spatial model using object-oriented design', *Intern. J. Geog. Info. Syst.* **9**, 359 – 383.

Ray, T. S. [1992], 'An approach to the synthesis of life', *Artificial Life* **2**, 371 – 408.

Reiss, M. J. [1989], *The allometry of growth and reproduction*, Cambridge University Press, Cambridge, 182.

Reuter, H. [2001], *Individual and Environment: Interaction and Feedback Processes in Individual Based Faunistic Ecological Models*, P. Lang, Frankfurt.

Ribbens, E., Silander, J. and Pacala, S. [1994], 'Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion', *Ecology* **75**, 794 – 806.

Rice, J., Miller, T., Rose, K., Crowder, L. and Marschall, E. [1993], 'Growth-rate variation and larval survival: inferences from an individual-based size-dependent predation model', *Can. J. Fish. Aquat. Sci.* **50**, 133–142.

Ruxton, G. D. [1998], 'Effects of the spatial and temporal ordering of events on the behaviour of a simple cullar automaton', *Ecol. Model.* **84**, 311 – 314.

Shoham, Y. [1993], 'Agent-oriented programming', *Artificial Intelligence* **60**, 51 – 92.

Shugart, H. H. [1984], *A theory of forest dynamics: The ecological implications of forest succession models*, Springer-Verlag.

Shugart, H. H., Smith, T. M. and Post, W. M. [1992], 'The potential for application of individual-based simulation models for assessing the effects of global change', *Annu. Rev. Ecol. Evol. Syst.* **23**, 15–38.

Sibly, R. M. and Calow, P. [1986], *Physiological ecology of animals*, Blackwell Scientific, Oxford.

Smith, M. [1974], 'Models in ecology', *Cambridge University Press* .

Starfield, A. and Bleloch, A. L. [1991], *Building Models for Conservation and Wildlife Management, 2nd edn.*, Burgess, Edina MN.

Starfield, A. M. [1997], 'A pragmatic approach to modeling for wildlfe management', *Journal of Wildlife Management* **61**, 261 – 270.

Starfield, A., Smith, K. A. and Bleloch, A. L. [1990], *How to Model It: Problem Solving for the Computer Age*, McGraw-Hill.

Stephan, T. and Wissel, C. [1999], 'The extinction risk of a population exploiting a resource', *Ecol. Model.* **115**, 217 – 225.

Tanemura, M. and Hasegawa, M. [1980], 'Geometric models of territory. 1. models for synchronous and asynchronous settlement of territories', *J. Theor. Biol.* **82**, 477 – 496.

Thompson, W. A., Vertinsky, I. and Krebs, J. R. [1974], 'The survival value of flocking in birds: a simulation model', *J. Anim. Ecol.* **43**, 785 – 820.

Tischendorf, L. [1997], 'Modeling individual movements in heterogeneous landscapes: potential of a new approach', *Ecol. Model.* **103**, 33 – 42.

Uchmanski, J. [1999], 'What promotes persistence of a single population: an individual-based model', *Ecol. Model.* **115**, 227 – 241.

Uchmanski, J. and Grimm, V. [1996], 'Individual-based modelling in ecology: what makes the difference?', *Trends in Ecology and Evolution* **11**(10), 437–441.

Uhrmacher, A. M. [1997], 'Concepts of object- and agent-oriented simulation', *SCS Transactions* **14**, 59 – 67.

Wiegand, T., Jeltsch, F., Hanski, I. and Grimm, V. [2003], 'Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application', *Oikos* **100**, 209 – 222.

Wissel, C. [1989], *Theoretische Ökologie*, Springer, Berlin.

Wissel, C. [1992*a*], 'Aims and limits of ecological modelling exemplified by island theory', *Ecol. Model.* **63**, 1 – 12.

Wissel, C. [1992*b*], 'Modelling the mosaic cycle of a middle european beech forest', *Ecol. Model.* **63**, 29 – 43.

Wu, J. and Marceau, D. [2002], 'Modeling complex ecological systems: an introduction', *Ecological Modelling* **153**, 1–6.

Zaika, V. E. [1975], *Balansovoye uravnenye rosts*, Nauka, Moscow, 25 – 33.

Zaika, V. E. and Makarova, N. P. [1971], 'Biologichesky smysl parametroc vkhodyashchykh v uravnenye rosta bertalanfi', *Dokl. Akad. Nauk* **199**, 242 – 244.

Ziv, Y. [1998], 'The effect of habitat heterogeneity on species diversity patterns: a community-level approach using object-oriented landscape simulation model', *Ecol. Model.* **111**, 135 – 170.

5 Annotations

5.1 Huston et al., 1988

Citation: [Huston et al., 1988]

The authors Michael Huston, Donald DeAngelis, and Wilfred Post criticize most mathematical models in ecology by suggesting that they are “based on assumptions that violate two of the basic tenets of biology.” First they say that models often use a single variable to describe an assortment of different individual organisms, despite the fact that individuals vary in their behaviour and physiology. Their second critique is that “most models do not distinguish among organisms locations.” This, they say, does not agree with the biological principle that interactions among individuals are local and instead assumes that every individual is able to have the same impact on any other individual.

Although Huston, DeAngelis, and Post agree that although there has been useful work completed within the limitations of state-variable models, these kinds of models ”can only approximate the individual behaviors of thousands or tens of thousands of individual organisms.”

Within the paper, the authors argue that individual organisms are the principal building block for modeling ecology. This, they say, is because simplifying equations and forcing assumptions are steps that are not needed to build individual-based models. They continue to emphasize the usefulness of individual-based models by stating that within this framework, properties of individual organisms and their behaviour within their environment can be measured.

To strengthen their position, authors Huston, DeAngelis, and Post refer to other work by Huston and DeAngelis [see review in Huston and DeAngelis, 1987]. It is within this reference that Huston and DeAngelis demonstrate the effect of slight differences in the initial conditions of individuals. By varying the initial heights among plants, the authors show that one tall individual among many shorter versions is able to capture the majority of the sunlight. These conditions leave to one or very few large plants and many small suppressed individuals. They extend this concept to state that when the initial variance of height is low and all individuals are relatively the same size, no one individual plant is able to gain a significant height advantage.

The authors continue to demonstrate the significance of modeling individuals by referring to [Tanemura and Hasegawa, 1980] and [Thompson et al., 1974]. The latter paper discusses a simulation of the flocking behaviour of birds. By modeling the birds individually within a forest canopy represented as a three-dimensional grid of cells, Thompson et. al. were able to produce similar bird behaviour observed in nature.

Huston, DeAngelis, and Post continue to cite papers by [Beyer and Laurence, 1980] that demonstrates the use of individual-based models of feeding and predation in fish species and [Myers, 1976] which used an individual-based model to ”investigate the stability of a plant-herbivore system.”

Although the authors spend a great deal of time discussing what they believe are the many benefits of individual-based modeling, they save a small paragraph near the end of their paper to remind the reader that they are not advocating for the dismissal of higher level approaches to modeling. In fact, they agree that ”there are many situations where aggregation studies indicate that models using population-level state variables are perfectly adequate for the questions being asked.”

Authors Michael Huston, Donald DeAnglis, and Wilfred Post believe that because individual organisms directly or indirectly effect other organisms, most ecological models that rely on state-variables are not suitable for detailing the kind of behaviour that is observed in nature. They argue that state-variable models rely on the assumption that all individuals are relatively similar and that each effect other individuals to the same degree. In this paper, the authors argue that the use of individual-based modeling is vast by referring to work previously done in the area of tree populations, fish species, insects and ecosystems.

5.2 Judson, 1994

Citation: [Judson, 1994]

The author Olivia P. Judson presents a review of individual-based modeling in ecology. She says that, among other things, it is because ecologists are recognizing the importance of interactions among individuals in an environment that there has been a shift in the way modeling is done in ecology. The purpose of this paper, she says, is to examine the current status of ecological generality and with it, determine the pros and cons of using individual-based modeling.

Judson begins the paper by referring to [Smith, 1974] in which author Maynard Smith said, “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...” Judson uses this quote as support for her belief that there needs to be generality in ecology. The desire for general theory in ecology is obvious, she says, but that very little progress has been made in that direction. She explains that although ecologists understand that it isn't suitable to expect laws similar to those of thermodynamics or some of the other sciences, they do "expect to find principles rather than mere rules of thumb."

She proceeds to discuss reasons why traditional modeling approaches fail. It is here that Judson refers to work by M. Huston and D. DeAngelis [see DeAngelis and Gross, 1992] who said that traditional state-variable models ignore two principles of ecology: all individuals are different and interactions among individuals are local. Although Judson appears to be in agreement with Huston and DeAngelis, she does not miss mentioning that others, such as Lomnicki, have questioned whether or not individual-based models are useful. It in her opinion that generality in ecology is what will determine the significant of individual-based models.

Within this paper, Judson provides an examination of the "current status of generality in ecology" and with this, "assess[es] the pros and cons of these new approaches in understanding broader problems in ecology." In order to do this, she begins by discussing the relevance of generality for individual-based modeling and then summarizes her paper by addressing problems that she believes exist with generality and ecology.

She captures a lot of the work that has already been done with regards to generality and individual-based models, including an analysis on when individual-based modeling should and should not be used, practical problems with individual-based modeling, and how individual-based models should be tested.

Judson aims at discussing a well-balanced view of individual-based modeling by first providing the user with an analysis of the shift in ecological modeling and then following this up with a look at generality in ecology and generality of individual-based models. Finally, Judson concludes the paper with a review of the problems associated with this modeling approach and how models of these types are tested.

5.3 Lhotka, 1994

Citation: [Lhotka, 1994]

The author Ladislav Lhotka describes an object-oriented library tool which he calls Hobo - a term to represent the idea of an independent individual pursuing its own interests. Identifying the need for a set of tools that make the development and simulation of individual-based models "a relatively easy task", Lhotka offers a set of Smalltalk classes that are designed to handle the "generic tasks of model specification, user interaction and information output."

The author exercises a focus on aquatic ecology and alleges that models in this field must be able to handle large numbers of species. This, he says, makes it difficult to identify individuals separately and as a result, some aggregation of individuals is necessary. He refers to the work of [DeAngelis et al., 1991] which grouped upwards of a few thousand individual bass that demonstrated similar characteristics such as age, size, and location. "A direct simulation of encounters" between individuals in a model that uses some form of aggregation "is not possible", he says. Despite this, he claims to be able to derive from a simulation a description of the encounters experienced by an individual.

A previous discussion of his, [Lhotka, 1991], was the "starting point for the implementation of the Hobo simulation package." The author maintains the middle portion of the paper to describe Hobo. He goes into detail about how the simulation system is scheduled, how space is represented, and how the hierarchy of classes is structured.

In order to demonstrate the use of his Hobo system, Lhotka developed a "simple model of grazing behaviour." One of its purposes, he says, is to illustrate the potential of the individual-based approach. He describes the setup as follows: "a number of grazing individuals move around the space and eat the food they find. Food is distributed over the space and its growth or regrowth depends on local conditions of each patch. Inhomogeneities in the food distribution are flattened out relatively slow (by diffusion), hence no complete mixing is assumed." He created two organism classes, both representing species of starfish. They differ, he says, only in the way they determine the direction of movement. While one of the classes of starfish moves independently of each other, the second class uses the location of neighbouring starfish to determine its movement and ultimately create a herding effect. Providing a discussion on the model's output, Lhotka concludes that his simulation, built using his Hobo system, provides very similar results to those depicted in [Hogeweg and Hesper, 1990].

Lhotka concludes by reiterating the purpose of developing his library of Smalltalk classes. The main contribution of Hobo, he says, is to provide modelers with a toolset for the creation of spatial units and methods of handling dynamic entities. Although it is early in the development process, the future of Hobo, Lhotka says, will include a "more efficiently implemented event queue, inclusion of subsystems based on classical cellular automata, and extensions of the output tools and user interface."

5.4 Grimm et al., 1996

Citation: [Grimm et al., 1996]

It is the opinion of Volker Grimm, Karin Frank, Florian Jeltsch, Roland Grandl, Janusz Uchmanski, and Christian Wissel that ecological modeling should be a process built upon a foundation of patterns - real patterns that have been observed in nature. The authors present a discussion and analysis of three examples from population ecology as a means to support their belief that pattern-oriented modeling (POM) comes bundled with benefits.

The objective of pattern-oriented modeling, says Grimm et al., “is to understand the mechanisms that lie behind a pattern.” As a strategy for developing models, the authors allege that POM overcomes the barriers of current modeling techniques: producing a model based on a pattern forces a relationship between spatial and temporal scales, patterns give modelers an opportunity to approach a system from the top-down, and patterns act as a tool that, “together with the human mind”, will help to create predictions that are more easily tested.

The authors’ search for a more effective modeling strategy stems from the works of [Oreskes et al., 1994] which suggests that “models can only be evaluated in relative terms” and that ”because natural systems are never closed and because model results are always nonunique, verification and validation of numerical models of natural systems is impossible.” Moreover, Grimm et al. suggest that there is an urgent need to move models from population ecology to community and ecosystem ecology (without losing their “lucidity and manageability”). This, they allude, is discussed in [Pimm, 1991]. The authors description of pattern-oriented modeling is built upon the discussion in [Grimm, 1994].

To stress the importance of pattern-oriented modeling, the authors present three examples: the first on individual variability and the regulation of populations, the second on metapopulations in a correlated environment, and a third on the spread of rabies and spatial barriers. The authors analyze each of their three fictitious examples and claim to demonstrate how pattern-oriented modeling is suitable for each. For the first example, the authors conclude that modeling by patterns will remove “part of the arbitrariness” that would otherwise be used in population modeling. Although using patterns to model in the second example “has limited the generality of the resulting predictions”, Grimm et al. believe that they have demonstrated how POM can produce models that are more easily tested. They use the third example to illustrate how “a pattern provided guidelines for when and to what extent to aggregate biological information.” Moreover, POM allowed them to use a top-down approach which lead to a model with significantly few details. This, they say, makes the model more manageable.

The authors reserve their concluding remarks to discuss and analyze some of the problems associated with pattern-oriented modeling. Included in this analysis is their belief that “models should not only reproduce the pattern itself, but also independent testable predictions.” Simply because a mechanism is able to reproduce a pattern, they say, does not allow for a definite conclusion that it is the mechanism alone that is responsible for the formation of the pattern itself. “Patterns have to be tested against a null hypothesis before they can be made into points of departure for theoretical investigation”, says Grimm et al.. The authors propose that ecological modeling wavers between two extremes: on one end, a model may be too heavily concentrated on detail and thus provide an overwhelming amount of information and on the other end, a model may be too loose and “lose its contact with reality.” Pattern-oriented modeling, says Grimm et al., helps to prevail defeat this conflict.

5.5 Uchmanski and Grimm, 1996

Citation: [Uchmanski and Grimm, 1996]

The authors Janusz Uchmanski and Volker Grimm immediately start the paper with a question: “Is individual-based modeling really a new approach in ecology?” They proceed to suggest that because of an insufficient definition of individual-based models and a lack of explicit boundaries between classical approaches to modeling and IBMs, it is uncertain whether or not individual-based modeling is a new approach.

Uchmanski and Grimm are in agreement with the previous work of [Huston et al., 1988] and state that “[they] believe that individual-based modeling really makes a basic difference compared to the classical way of modeling.” In addition, the authors suggest that the popular classification of IBMs into *i*-state and *i*-distribution models [see Metz and Diekmann, 1986] do not completely cover the modeling technique. As a result, although this description has had much use in statistical physics, it does little to provide important information from a biological viewpoint.

The authors address this problem by suggesting the following four criteria for classifying different modeling techniques:

- *“The degree to which the complexity of the individual’s life cycle is reflected in the model”* Uchmanski and Grimm explain that basic models used in classical ecology define properties for an *average* individual that is born, produces offspring, and dies almost immediately. With this assumption about individuals' life cycles, "development, metabolism and aging of individuals, their behaviour or the amount of resources used during their lifetime are not explicitly taken into account."

- *"Whether or not the dynamics of the resources is explicitly taken into account"* The authors make reference to [DeAngelis et al., 1994] and agree that implicit representation of environmental resources - typically using a carrying capacity - is not in line with individual-based modeling. Although they encourage "explicit modeling of resource dynamics", Uchmanski and Grimm avoid discussing to what degree resources should be modeled *explicitly*.
- *"The use of real or natural numbers in representing the size of a population"* The authors criticize how classical models represent population size. They explain that for large population sizes, the classical methodology argues that the distinctness of individuals can be ignored. For this reason, classical models often use a real number, N, to represent population density. Because "individuals interact with other individuals only within a limited time horizon and spatial domain" and because "interactions between individuals take place on a short timescale" are two of the authors' reasons why population size should be represented as the number of individuals, forcing N to be a real number.
- *"The extent to which variability of individuals of the same age is considered"* How alike two individuals of the same age - or of the same generation - is the authors' forth and "most important" criteria. They state that subtle variation between individuals of the age, such as having all individuals of the same generation have an identical probability of reproducing, is rarely seen in individual-based models. Instead, they suggest that individuals of the same age be differentiated based on "random factors", such as competition, which can then lead to additional differences in the amount of resources the individuals use, their weight, rank, and behaviour. Uchmanski and Grimm conclude this remark by stating that this method of varying individuals of the same age will produce "more complex life cycles" and variation among the life cycles as well.

Uchmanski and Grimm believe so strongly in this method of classification that they state, "Most models of theoretical ecology describing dynamics of ecological systems may be classified according to these criteria." They proceed to suggest a new term, *individual-oriented models*, as a way to describe models that, although deal with individuals in some manner, do not adhere to all four criteria listed above. In addition, the authors describe models that do meet all four criteria as "genuine individual-based models" (or "narrowly defined" individual-based models).

The authors reserve the remainder of the paper to discuss whether or not individual-based models provide a better method for understanding and predicting ecology. Although they do not explicitly choose one modeling technique over another, they make reference to [Lomnicki, 1988] and some forest models that have produced results that support the use of individual-based models. They state that complexity and limited generality are usually described as the core shortcomings of individual-based modeling but that, "In our opinion, these shortcomings may be overcome by taking our orientation from real patterns observed in nature."

5.6 Hraber et al., 1997

Citation: [Hraber et al., 1997]

Peter Hraber, Terry Jones, and Stephanie Forrest identified the difficulty with modeling "complex adaptive systems (CAS)" - a term they use to refer to a system that is made up of a collection of agents with interactions among the agents and between agents and their environment. Global effects and agents that adjust to their environment is also possible, all of which causes the complex adaptive system to evolve over time. "Nonlinearities, discreteness, spatial inhomogeneities, and the changing behaviour of the primitive elements of the systems" are the reasons why they believe useful mathematical models are difficult to formulate.

Although they recognize simulation as the alternative modeling technique, the authors are still weary of this method. "Detailed simulations are also problematic", they say, "because it is often impossible to get all the details correct." For this reason, Hraber, Jones, and Forest analyse Echo, a model developed with the focus of reducing as much detail as possible and reserving only the most necessary interactions.

Previous CAS models are referred to, including [Caswell, 1989], [DeAngelis and Gross, 1992], and [Durrett and Levin, 1994], but these, they claim, do take into account "both ecological interactions and evolutionary dynamics." A model discussed in [Hartviggsen and Starmer, 1995], Sugarscape in [Epstein and Axtell, 1994], Tierra in [Ray, 1992], and ERL in [Ackley and Littman, 1992] are models that, they say, Echo resembles.

Hraber, Jones, and Forest include a description of the Echo system, including how individuals replicate, interact, combat, trade, and mate. Furthermore, the authors discuss an overview of the sequential events that occur in Echo, such as agent collecting resources, agents being killed at random, and agents moving to neighbouring sites.

As a means to test whether or not Echo closely reflects real ecosystem behaviour, the authors performed simulations and compared the output data on species diversity and abundance patterns with real data observed in nature. Their comparisons reveal that that data produce by Echo does not match "exactly with quantitative predictions."

5.7 Campos and Hill, 1998

Citation: [Campos and Hill, 1998]

Recognizing that "customizing ecosystem simulation applications is a complex operation", Andre Campos and David Hill developed a framework for agent-based simulations that they allege is customizable and capable of supporting both 2D and 3D interactive user interfaces. They denote their framework as Multi-Agent Visual Interactive Simulation (MAVIS).

The authors contribute the Visual Interactive Simulation (VIS) concept to [Hurrion, 1976] who, they say, was the first to introduce the idea. They also give credit to [Gasser and Briot, 1992], [Shoham, 1993], and, in particular, [Uhrmacher, 1997] for discussing agent-oriented programming techniques.

Campos and Hill spend the majority of the paper outlining the many details that comprise their framework. On the highest level, their software structure is broken down to three UML packages. They call the first component the simulator and allege that it is responsible for scheduling the events that occur within the simulation. The second component, the user-interface package, handles the "user input and visual outputs." The world package is the third component of MAVIS which they claim models the simulated environment such as the system's structure.

The authors provide class diagrams, entity relationship diagrams, and sequence diagrams as aids for describing their visual interactive framework. They follow their explanation of MAVIS with an analysis of the implementation issues that go along with the system. The authors are explicitly concerned with thread scheduling as they say "the number of threads to handle can be too large" and furthermore, "ecosystem models do sometimes have simultaneous processes competing for space." To address this issue, they offer a three phase approach to allow for "true parallel competition for spatial resources." They claim that when handling agents that are able to move to the same position in the environment, for example, a "true stochastic choice" will simulate parallelism.

To test their visual-interactive framework for agent-based simulations, Campos and Hill developed three different applications: one that simulates a predatory-prey environment, another imitating the memory of grazing sheep, and finally a third to mimic cattle and horses. Each of the three applications are described and shots of the interactive user interface are displayed. With these demonstrations, and the description of MAVIS, the authors claim to have presented a "reusable object-oriented application framework" designed to guide the "development of individual-based ecosystem simulations" asserting that their framework is reusable, customizable, and flexible.

5.8 Grimm, 1999

Citation: [Grimm, 1999]

Volker Grimm states that there is an issue regarding the use of individual-based models in ecology, namely, that because there is "no common motivation behind individual-based models" (IBMs), it is difficult to identify what exactly has been learned about ecology through the use of IBMs. Grimm describes two distinct types of motivation - paradigmatic, the motivation to use IBMs for "theoretical ecology", and pragmatic, which ignores the use of IBMs to develop theories and instead uses them simply as a modeling tool.

To illustrate his position, Grimm examined 50 individual-based animal population models and concluded that the majority of such papers demonstrate pragmatic motication.

Grimm suggests that in order to apply IBMs to general theoretical issues, two topics need to be addressed. The first is to more definitively describe the relationship between individual-based models and classical state-variable approaches. Grimm reminds us that IBMs are models at their forefront and for this reason, "creative, sophisticated mental activity" is necessary for the construction of models whether they are IBMs or state-variable models. He refers to the work of [Starfield et al., 1990] and says that models are "purposeful presentations", tools for problem-solving, and that one of the key differences between IBMs and classical modeling approaches is in the assumptions that the models make. "Strategies of formulating" and "analyzing more or less complex simulation models" is the second topic that Grimm suggests needs to be addressed. In order to suggest a solution to this problem, Grimm describes a list of heuristic rules throughout the latter half of the paper, including items such as, "Keep models as simple as possible", "Start modeling (if possible) with a pattern which can be observed in nature", and, "Individual-based modeling must refer to the framework of classical theoretical ecology."

Grimm reserves a page to address reasons why his suggestions may be criticized. Firstly, he recognizes that by examining only the last 10 years of individual-based modeling, he may have selected a window of time that is merely too short to completely examine the use of IBMs in ecology. Secondly, his selection of the 50 individual-based animal population models to review was "biased towards fish population models." Thirdly, because Grimm is claiming that too few IBMs are being used for theoretical ecology, his definition of theoretical ecology may be disputed.

Grimm summarizes this paper by answer the question in the title: "what could we learn in the future?" He claims that "much more" could be learned bout ecology if individual-based models are applied more directly to theoretical issues. However, Grimm fails elaborate on this subject. Instead of describing the areas of ecology that he believes could benefit from the use of IBMs (not as a tool, but applied to theoretical ecology), the author remains very general.

5.9 Grimm et al., 1999

Citation: [Grimm et al., 1999]

The authors Volker Grimm, Tomasz Wyszomirski, David Aikman, and Janusz Uchmanski present a review of twelve papers having to do with individual-based modeling in an attempt to address the issue of "whether and how individual-based modelling is changing ecological theory." They state that because there has been little common motivation behind individual-based modeling in the past decade, answering the question of whether or not individual-based modeling is simply a new tool or if it provides a method of obtaining a different perspective on ecology is difficult. This paper by Grimm, Wyszomirski, Aikman, and Uchmanski is an effort to show how the twelve selected papers demonstrate common issues regarding individual-based models and how it may be possible to deduce ecological theory out of this modeling technique in the future.

Of the twelve papers reviewed, nine of them present unique individual-based models, including [Grist and des Clers, 1999], [Stephan and Wissel, 1999], and [Uchmanski, 1999], while the remaining three are a review [Grimm, 1999], an essay [Lomnicki, 1999], and a paper by [Lorek and Sonnenschein, 1999] that discusses problems with implementing individual-based models.

The authors reserve a section of the paper to discuss problems associated with the complexity of individual-based models. They make reference to work by [Mollison, 1986], [Starfield and Bleloch, 1991], and [Wissel, 1992*a*] who have all criticized complex simulation models for three central reasons: "complex models are hard to develop, hard to communicate, and hard to understand."

The authors' analysis of the twelve selected papers reveals that there are common themes among them. These include a focus on individual variability (IV), population persistence, and comparing real data with data computed from simulated worlds. Grimm, Wyszomirsky, Aikman, and Uchmanski recognize that they have selected a very small sample of papers to represent the big picture of ecological modeling. Nevertheless, they believe that they have demonstrated how common motivations exist between these twelve papers and by extrapolating this result, the authors feel that "it should not be too difficult to extract even more theory out of IBMs in the future."

5.10 Lomnicki, 1999

Citation: [Lomnicki, 1999]

Adam Lomnicki discusses the basic theoretical and technical difficulties of applying the individual-based modeling technique to ecology. He identifies "the need for clear distinctions between individual variation, skewness, asymmetric competition and monopolization of resources."

Lomnicki begins the paper by mentioning reasons why population ecology is not as big a focal point for research as other areas of biology. However, it is his opinion that limited funding and the fact that ecological theory is presently flawed are barriers that can be overcome by the individual-based modeling approach.

The author cites the previous work of [Judson, 1994] which already gives three reasons why individual-based models are on the rise in ecology. Moreover, Lomnicki believes that the advancement of evolutionary ecology has lead the way for individual-based models and he gives credit to [Dawkins, 1982] for having "stressed the importance of the individual."

Lomnicki lists four factors for describing the relations between individuals: variation, skewness of distribution, asymmetric competition, and monopolization of resources. Combinations of these four factors, he says, may help to develop worthwhile individual-based models. For example, "the stability and persistence of a single population depend on whether competition among individuals is a scramble or a contest" and "variation, monopolization of resources, and distribution patterns can be used to predict population dynamics."

The author concludes the paper with a quick mention of general ecological theory. Because it is difficult to demonstrate individual differences and local interactions within mathematical models, he suspects that a "general theory of individual-based ecology is impossible" but recognizes that some general connections between individuals and population dynamics is within reach.

5.11 Uchmanski, 1999

Citation: [Uchmanski, 1999]

Population stability, or population persistence, has been a topic of discussion for many years. Having identified a need to determine what promotes the persistence of a population, author Janusz Uchmanski presents an analysis of the results produced by three different models: “a model with all individuals being identical, the same model but with a constant and resource-dependent mortality, and a model with individual variation due to competition for resources.”

His first model, which he calls the null model, is built upon [Zaika and Makarova, 1971], [Zaika, 1975], [Sibly and Calow, 1986], and [Reiss, 1989] which describe a balance equation for the weight of an individual. In this null model, all individuals are identical, says Uchmanski, with specific emphasis on their same initial body weight, their ability to obtain the same amount of resources, and their progression to the same final body weight.

In his second model, although individuals are still considered to be identical, Uchmanski introduces random mortality of two types. The first is a “constant mortality” - some randomly selected individuals in the model are subject to death before they are able to reproduce. Moreover, he assumes in this model that the individual that is selected to die does so immediately at the beginning of its life cycle. As a result, it does not consume any amount of resources. The second type of mortality is described as “resource-dependent mortality.” In this variation, Uchmanski creates conditions under which the mortality rate of the system declines when there is a plentiful amount of resources.

Individuals are not identical in the third model. Instead, Uchmanski ensures that they “differ in the initial body weight and in the amount of resources they can get as a result of competition.” The amount of resources that is obtained by an individual is a function of the total available resources and the individual’s body weight. All individuals die at the end of the generation, he says, and only some of them reproduce being doing so. Selective reproduction is used in this model where individuals with weights that are higher than some threshold are the ones able to reproduce.

Uchmanski provides an analysis of the three models and the results they produce throughout the paper. He alleges that the first model, the null model with identical individuals, produces a high growth rate at the beginning of the simulation when resources are abundant. As the resources are consumed throughout generations, however, the population approached a plateau period of stability. Uchmanski explains that this phenomena lasted just a few generations and as the resource amounts continued to decline, the population soon underwent a declining period until eventually the population became extinct. Uchmanski witnessed extinction of the population in this model at around the seventeenth generation.

Similar results were obtained in the second model incorporating random, but constant, mortality. Although "it is clear that for a wide spectrum of mortality values, the mean population extinction time is longer than in the model without random mortality", says Uchmanski, extinction of the population was the ultimate conclusion somewhere around the twenty second generation. Depending on the initial parameters, Uchmanski determined that the model incorporating a mortality rate that is resource-dependent produced results that varied between the null model and the model that used a random, constant mortality.

Although extinction was the result of the model incorporating individual variability, Uchmanski describes the population as going through oscillations - periods of high and low growth as the amount of resources experienced its own highs and lows. "It is possible to obtain very long extinction times of the population" in this third model, he says, with some of his results showing simulation runs that produced more than one hundred generations.

The author does not provide much in the way of a conclusion. From the culmination of his work, Uchmanski concludes that a population of identical individuals "cannot be regulated." Individual variation is needed, he says, in order to regulate a population of individuals.

5.12 Railsback, 2001

Citation: [Railsback, 2001]

It is Steven F. Railsback's belief that individual-based modeling has not provided as much contribution to ecological theory as what was initially expected from the modeling technique. Railsback cites work by [Murdoch et al., 1992] and [Bart, 1995] which provide a discussion on the potential problems associated with individual-based models. In addition, [Grimm, 1999], he says, "conclude[d] that IBMs have not yet fulfilled the promise identified by Huston et. al, in large part because many models have been built without sufficient attention to the appropriateness of the assumptions used."

The author identifies two substantial problems that prohibit the influence of individual-based models. The first, he says, is a lack of focus on the "toolmaking" aspect of individual-based models. Models of these types are often written in languages or executed in software that restraints the modeler from being able to properly observe and test the simulation. Secondly, Railsback contributes the unproductiveness of individual-based models to "inappropriate assumptions [that are] abound in IBMs."

Railsback proposes in the paper that concepts from complex adaptive systems (CAS) will help "make the design of IBMs less ad hoc" and as a result, aid in producing models of more value. Specifically, the author separates six concepts from CAS that he believes are relevant to individual-based modeling. They are:

- *"Emergence"*, such as considering what system behaviours should emerge from the model versus imposing the system behaviours on the model to begin with.
- *"Adaptation"*, including identifying what adaptive behaviours of the individuals should be modeled and pinpointing how the individuals adapt to changes in the environment.
- *"Fitness and strategy"*, comprising of questions such as what measures of fitness will be implemented in the model.
- *"State-based responses"*, taking into account what decisions individuals make will be based on the agent's current state.
- *"Prediction"*, which may involve identifying how an individual can anticipate and evaluate different alternative choices.
- *"Computer simulation"*, such as determining how the model execution will be observed, whether through "animated windows."

Railsback provides detailed discussions on each of the six concepts summarized above. He believes that "consistently addressing these concepts should help make the design of IBMs less ad hoc and reduce the formulation and implementation problems that have limited the success of this important technology."

The author concludes the paper by referring back to the problem he originally stated: not until modelers learn how to build realistic individual-based models, he says, will the advantages of this modeling approach become prevalent. He alleges that his analysis of complex adaptive systems and the concepts he extracted from them will help pave the way for the development of individual-based models that more accurately describe "the individual- and system-level responses of natural populations" and ultimately "lead to established approaches for individual-based ecological modeling."

5.13 Railsback and Harvey, 2002

Citation: [Railsback and Harvey, 2002]

Steven F. Railsback and Bret C. Harvey demonstrate the usefulness of individual-based modeling and patterns by developing an IBM to simulate stream salmonids. Alternative theories about habitat selection were tested by analyzing their IBM's ability to reproduce real patterns observed in nature. This they say, is a step in the direction of using individual-based models for ecological theory.

Alluding to [Huston et al., 1988], Railsback and Harvey suggest that, although individual-based models demonstrate a promising theoretical use, "this promise remains largely unfulfilled, in part because of the ability of IBMs to produce realistic behaviour has rarely been tested." They contribute this thought to [Grimm, 1999] and present their simulation experiments as a way to test the validity of an IBM of salmonids. Citing [Grimm, 1999] again and [Railsback et al., 1999], the authors describe two barriers for validating IBMs: a lack of software to allow for the visualization of individuals, and "the difficulty of quantifying the major factors driving habitat selection."

The authors' IBM of salmonids was tested to see how well it was able to reproduce six real patterns of habitat selection. Three theories of habitat selection were compared: selecting a habitat with the goal of maximizing growth rate, selecting a habitat to maximize survival probability, and selecting a habitat based on "expected maturity" (EM) which they describe as a product of the probability of surviving starvation and a fraction of reproductive size.

Detailed discussions of all three simulations are given. The authors allege that the goal of maximizing EM reproduced all six patterns of habitat selection by salmonids that are routinely observed in nature. Maximizing growth reproduced three of the sax patterns, they say, and maximizing survival was able to reproduce just two. Analyzing the results, Railsback and Harvey conclude that their IBM "appears successful because it avoids restrictive assumptions, incorporates competition for food, assumes salmonids make good habitat-selecteion decisions at a daily time step, and uses a habitat objective (EM) that provides reasonable trade-offs between growth and mortality risks."

5.14 Mamedov and Udalov, 2002

Citation: [Mamedov and Udalov, 2002]

Alexandre Mamedov and Sergey Udalov present a discussion on their CENOCON system which they claim is a tool to allow ecologists to run simulation models with a focus primarily on population dynamics. The authors perceived a need to develop a tool that allows for the execution of "conceptual ecological models" with the concept that such a tool should be flexible and require no programming at all.

Mamedov and Udalov acknowledge existing modeling tools such as ECOTALK by [Baveco and Lindeman, 1992] and [Baveco and Smeulders, 1994] and HOBO by [Lhotka, 1994]. In addition, ECOSIM, by [Lorek and Sonnenschein, 1998] and MOAB by [Carter and Finn, 1999] are also given as examples of modeling tools that support individual-based modeling. These systems, they say, demand that ecologists encompass some set of programming skills.

With these existing models in mind, Mamedov and Udalov designed the CENOCON software to accept as input a text file with descriptions of the organisms and with it, "generates a virtual space, creates and populates the space with the individuals" and "manages these virtual entities to act as real components of real ecological communities." With any ASCII-editor, the authors claim that a modeler is able to execute simulations in different areas of ecology: population dynamics, intra and inter-population competition, prey-predator relationships and complex food chains.

The authors follow their introduction with an explanation of the CENOCON system itself, including a discussion on the source files, an explanation on how the models are constructed, and example simulation executions such as a flowchart of cell activity. In addition to this flowchart, Mamedov and Udalov present more detailed examples of simulations run with their modeling tool: the first simulating interactions between protozoa species and the second dealing with arthropod populations.

Mamedov and Udalov do not provide much in the way of an analysis. The expected run time or complexity of a model carried out using their CENOCON system is not discussed nor is the necessary computer requirements. The authors provide an abrupt conclusion with minor insight into the future of their modeling tool: "the software is under ongoing improvements" and "the possibility to involve parasitic organisms is being worked out."

5.15 Bian, 2003

Citation: [Bian, 2003]

Ling Bian emphasized the importance of properly representing the environment, or ecosystem, in an individual-based model. How the environment is represented, she says, is a critical part of individual-based models and yet, it is her belief that the most "convenient or conceptual" methods are often used. Bian suspects that an evaluation of the two traditional approaches to modeling the environment - the grid model and the patch model, "and, in particular, the object-oriented version of the two approaches" - may provide ecologists with an insight into a more effective way of representing the environment in an individual-based model.

The paper begins with a discussion on the benefits of using an object-orientation approach. Subsequent to this section, Bian considers both the grid model and the patch model and finally, the paper is concluded with two examples - one relating to fish growth and movement and the other other to the movement of calving elk. Bian provides these two examples, she says, as support for her analysis of the two methods for representing the environment.

Bian refers to a number of papers that provide much discussion on the use of an object-oriented approach for representing the individuals and the interactions between individuals in an individual-based model. These include [Judson, 1994], [Downing and Reed, 1996], [Tischendorf, 1997], and [Ziv, 1998]. She goes on to say, however, that an "object-oriented approach has not been considered to be as effective" when it comes to representing the environment. In her discussion on space, an analogous term she uses to refer to the environment, Bian provides several sources of literature that discuss the representation of space, such as [Couclelis, 1992], [Goodchild, 1992], [Raper and Livingstone, 1995], and [Kemp, 1997].

Ling Bian proceeds to compare the grid data model with the patch data model approach. She provides descriptions of both techniques, including their benefits and detriments. "The regular grid data model is advantageous for modeling the environment that is heterogeneous and dynamics", she says as she emphasizes this technique's support for supporting localized interactions that require probing areas adjacent to a central cell. In contrast, she believes that the patch data model is beneficial for simulations that necessitate "landscape features, spatial relationships between them, and a rich set of attributes associated with the features." She alleges that individual landscape features that can be described separately and that are stable are particular benefits of this latter method. Bian lists the fact that the cell size in a grid data model much be set ahead of time as a disadvantage of this approach. Moreover, "arbitrary moving directions and distances typical of the grid model may cause simulation results to be unrealistic" and as a result, validating a model's data with real data observed in nature may prove to be difficult. The author refers to [Tischendorf, 1997] who suggests that the patch data model is less frequently used because of its intense software demand and the extensive learning curve associated with this technique.

The author follows her comparison with a discussion on the object-orientation forms of both of these modeling techniques. She then proceeds to describe two examples. The first is a model of Salmon growth and movement in an environment represented as a grid. The second example demonstrates the use of the patch model approach by simulating Elk movement in a short-grass prairie. Bian provides the reader with an insight into how the environment is represented in each of the simulations which she hopes supports her analysis of the two different techniques.

Bian concludes her paper by suggesting two approaches. The first, which she calls a hybrid approach, combines both the traditional grid model to represent the environment and an object-oriented approach to simulate the individuals. She denotes her second approach as an "all-object approach that combines the object-oriented patches of the environment and the object-oriented individual organisms." It is in her opinion that both of these techniques can result in successful individual-based models.

5.16 DeAngelis and Mooij, 2005

Citation: [DeAngelis and Mooij, 2005]

The authors Donald L. DeAngelis and Wolf M. Mooij state that the use of individual-based models in ecology has grown exponentially in the last fifteen or so years. Even with that in mind, however, they present in this paper a review to determine whether or not the increase in the number of articles that discuss individual-based models is correlated to progress in ecological theory. In order to assess scientific progress, DeAngelis and Mooij present a basis for individual-based models and as a method of determining the range of applications benefitting from individual-based models (IBMs), the authors create seven groups of "biological process for which IBMs have been developed."

DeAngelis and Mooij refer to papers such as [Hogeweg and Hesper, 1990], [Uchmanski and Grimm, 1996], and [Lomnicki, 1999] which all review the field of individual-based models. In addition, although they are aware of [Grimm and Railsback, 2005] which provided a set of guidelines for building, testing, and analyzing individual-based models, the authors are determined to provide a classification system for IBMs that will allow them to assess the current state of individual-based modeling.

In order to categorize individual-based modeling, authors DeAngelis and Mooij suggest the following five types of variances among individuals:

- *"Special variability, local interactions, and movement"*
- *"Life cycles and ontogenetic develoopment"*
- *"Phenotypic variability, plasticity, and behaviour"*
- *"Differences in experience and learning"*
- *"Genetic variability and evolution"*

DeAngelis and Mooij examined 900 papers related to individual-based modeling and determined that, with respect to the main type of biological process each of them addressed, seven groups emerged:

- *"Movement through space"*
- *"Formation of patterns among individuals"*
- *"From foraging and bioenergetics to population dynamics"*
- *"Exploitative species interactions"*
- *"Local competition and community dynamics"*
- *"Evolutionary processes"*
- *"Management-related processes"*

Despite the wide range of subject areas that individual-based modeling has covered, the authors still question to significant of IBM to ecology. They state that for certain applied areas in ecology, such as forest gap-phase models, fish models, and population-variability analysis, IBMs have an obvious significance.

Theoretical ecology has also benefited from individual-based modeling. DeAngelis and Mooij refer to some spatially explicit individual-based models that have been used to investigate the impact of individual interactions on stability, persistence, and coexistence.

DeAngelis and Mooij reserve a large amount of the remainder of the paper to discuss six papers "as representatives of areas of high concentration of IBMs." Among them are [Rice et al., 1993] and [Ribbens et al., 1994], papers that focus on fish and forest IBMs, respectively, and [Dieckmann and Doebeli, 1999], a paper that addresses speciation. They use their selected papers as support for their categorization of individual-based modeling by demonstrating how each of them exhibit one or more of the types of variances listed above.

It is in the authors' opinions that the number of papers discussing the use of individual-based models in ecology will continue to increase and with this increase, new uses of IBMs will emerge. For now, however, they believe that two general views of IBMs exist - the first is that "IBMs are an extension of classical approaches" and the second is one that believes IBMs "constitute a new philosophical paradigm." DeAngelis and Mooij expect a theory to emerge that combines both of these views of individual-based modeling but until then, they say, this rivalry is likely to be a source of creativity in theoretical ecology.

5.17 Grimm and Railsback, 2005

Citation: [Grimm and Railsback, 2005]

The authors Volker Grimm and Steven F. Railsback wrote a book "to provide guidelines for making individual-based models more coherent and effective." With this generic primary objective, the authors offer strategies for optimizing model complexity and handling the complexity of individual-based models. Moreover, Grimm and Railsback propose a "general, theory-based research program for individual-based modeling." Calling their new approach "individual-based ecology (IBE)", Grimm and Railsback allege that individual-based models allow ecologists to experience an entirely new way of viewing ecology.

The book begins with an introduction to modeling. Citing work such as [Uchmanski and Grimm, 1996], the introduction discusses what individual-based modeling is, how modeling in ecology should be performed, and why and how patterns should be used for ecological modeling. Subsequent to the introduction, part two focuses on individual-based ecology. Building upon Grimm's previous work, [Grimm, 1999], the authors conclude that single individual-based models are not easily extrapolated to form a general understanding of ecosystems. "If different IBMs have different purposes and no common underlying theme, they cannot be coherent", says Grimm and Railsback. For this reason, the authors propose a theoretical framework that aims to "formulate theories of the adaptive behaviours of individuals and tests the theories by seeing how well they reproduce, in an IBM, patterns observed at the system level." The remaining sections of part two are reserved for a discussion of IBE, suggestions for developing individual-based models, and proposals for testing IBMs. To demonstrate their theories of individual-based ecology and individual-based models, Grimm and Railsback provide twenty seven examples of IBMs.

The latter half of the book focuses on software choices for developing individual-based models, how IBMs should be analyzed, and how the results produced by a model should be communicated to the scientific community.

Grimm and Railsback provide an amusing glance into the future of individual-based modeling. With witty and clever remarks, the authors describe a fictitious laboratory supervised by Dr. S, "at a university of the not-too-distance future." They hint at a well organized community of scientists and students all collectively working on individual-based ecology, using published data and real patterns observed in nature to develop and test individual-based models as a means of producing general ecological theories.

5.18 Grimm et al., 2005

Citation: [Grimm et al., 2005]

A need for general principles that solidify a foundation for agent-based complex systems is a problem identified by Volker Grimm, Eloy Revilla, Uta Berger, Florian Jeltsch, Wolf M. Mooij, Steven F. Railsback, Hans-Hermann Thulke, Jacob Weiner, Thorsten Wiegand, and Donald L. DeAngelis. This group of authors identify the lack of a generic framework for the "designing, testing, and analyzing" of "bottom-up models" but all agree that recent progress in ecological modeling has given way to a basic strategy called pattern-oriented modeling.

Subsequent to their discussion of the need for a modeling strategy that aids in the formation of agent-based models, the authors offer their analysis of pattern-oriented modeling, including its origin, its purpose, its benefits, and its future.

Grimm et. al associate with the previous work of [Wissel, 1989] which discusses the need to start ecological modeling with specific questions. "From these questions", they say, "we first formulate a conceptual model that helps us decide which elements and processes of the real system to include or ignore." They make reference to [Wiegand et al., 2003] when the authors advocate for models that are "structurally realistic" which, they say, is the result when the model is designed to produce multiple patterns. The authors also provide readers with references to [Wissel, 1992*b*], [Neuert et al., 2001], and [Rademacher et al., 2004] which used multiple patterns to model beech forests.

It is in the authors' opinions that real patterns observed in nature can be used to build a model structure that is optimal, rigorous, and realistic. They claim that using pattern-oriented modeling will also help to guide ecologists in finding "an optimal zone of model complexity." Furthermore, as a means to deduce how agents make behavioural decisions, Grimm et. al suggest testing alternative theories in a bottom-up model. Then it is simply a matter of comparing the model's output with the real patterns observed in nature: the better the model's data matches real data, the more accurate the theory is. They believe that this use of pattern-oriented modeling can be used to test any set of contrasting theories.

Grimm et. al continue with their analysis of pattern-oriented modeling with a discussion on how the technique is able to reduce the level of uncertainty in a model's set of parameters. First, they say, "it helps make models structurally realistic, which usually makes them less sensitive to parameter uncertainty." Secondly, "the realism of structure and mechanism of pattern-oriented models helps parameters interact in ways similar to interactions of real mechanisms."

Although they realize that patterns are already commonly used by modelers, the authors believe that pattern-oriented modeling "is the first attempt to explicitly formulate a rigorous and comprehensive strategy for modeling [agent-based complex systems]." Finally, because they theorize that patterns provide a way to ensure that a model is neither too simple nor too complex, Grimm et. al anticipate a quick increase in the use of this modeling technique.

5.19 Breckling et al., 2006

Citation: [Breckling et al., 2006]

Broder Breckling, Ulrike Middelhoff, and Hauke Reuter discuss the span of potential uses for individual-based models by identifying four issues. Using data that was collected from two projects in Northern Germany, the authors organize the paper into four sections: an explanation of a "generic model structure for individual-based models", a look into several areas of ecology that are benefiting from individual-based models, a demonstration of how the approach is being used in an active project concerning genetically modified plants, and finally a discussion on the effects of individual-based models on theoretical ecology.

Breckling, Middelhoff, and Reuter begin their introduction of individual-based models by citing the one of the first applications of IBMs [Kaiser, 1976] and proceed to reference [DeAngelis and Gross, 1992] and [Judson, 1994] as work that recognize the emergence of the new modeling technique.

The authors progress by introducing a generic model structure for individual-based models, one that they allege is "highly flexible" and allows for individuals to react to "external conditions." Moreover, they describe their model as one that is "suitable to specify predator-prey interactions, schooling, diapauses, behavioural shifts under varying conditions, the formation of colonies and the description of structural-functional development of modular organisms."

An overview of examples of individual-based models is presented in the next section. It is here that the authors describe phenomena such as how the behaviour of individual fish creates the schooling effect. Moreover, [Middelhoff, 2000] and [Eschenbach, 2000] are referenced for having used an object-oriented individual-based modeling approach to "analyse the growth of alder trees." Other models such as [Reuter, 2001], a model application "integrating a wider interaction network", are given as further examples of the use of individual-based modeling.

After presenting a discussion on the use of individual-based models to simulate the risk of genetically modified plants, Breckling, Middelhoff, and Reuter reserve a page for an analysis of the "epistemological implications of individual-based models." It is their belief that because of individual-based models, the idea of simulating environments at the population level ceases to exist. "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." Analogous to the "butterfly effect" in physics' chaos research, the authors say, individual-based models can be used to trace how the behaviour of a single individual can affect the properties of the overall system.

5.20 Caron-Lormier et al., 2008

Citation: [Caron-Lormier et al., 2008]

Geoffrey Caron-Lormier, Roger W. Humphry, David A. Bohan, Cathy Hawes, and Pernille Thorbek identified a need a to test the effects of different scheduling methods in individual-based models. Having identified with recent work in cellular automata simulation models, which demonstrated that the method used to update the model had significant effects on the model's output, the authors extended this concept to test it with individual-based models.

The authors begin the paper by identifying two methods for updating individual-based models: synchronous and asynchronous. The former updates individuals' parameters only at the end of a complete execution of a time cycle and the latter refers to an updating method that adjusts the objects' characteristics immediately and instantaneously makes the new values available for all other objects. It is their belief that the two methods of updating an individual-based model will produce different results.

Caron-Lormier, Humphry, Bohan, Hawes, and Thorbek refer to the work of [Grimm and Railsback, 2005] which contains a more thorough explanation of synchronous and asynchronous updating. In addition, the authors have used the work of [Huberman and Glance, 1993], [Ruxton, 1998], and [Cornforth et al., 2002] which demonstrate synchronous and asynchronous updating in cellular automata simulation models.

The authors test their suspicion by implementing both updating methods in simulations that are executed for the same initial parameters. They spend a large section of the paper discussing what they recognize to be a very simple individual-based model.

They immediately follow an explanation of their IBM with a description of their obtained results. It is their claim that the energy levels of producers and consumers varied as much as 22% between the two updating methods. They experienced an increasing disparity between synchronous and asynchronous updating as the "number of interactions increases." Based on these results, the authors conclude that the method of updating an individual-based model will have an effect on the model's output and for this reason, they suggest that "the updating model should be chosen carefully to best represent the (eco)system they are modelling."

This survey is completely my own work.

Adam Aspinall

Adam Aspinall