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Review

Individual-based ecological models: Adjunctive tools or experimental systems?

Brian MacPherson[a,c,*], Robin Gras[a,b]

[a] Department of Biology, University of Windsor, Canada
[b] School of Computer Science, University of Windsor, Canada
[c] Department of Philosophy, University of Windsor, Canada

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ABSTRACT

The role that individual-based computer modeling (IBCM) should play in the field of integrative ecology needs to be clarified in light of the continuing concern with the empirical validation of individual-based computer models. Though perfectly legitimate and understandable, the requirement of empirical validation has been taken to extremes. The result of doing so is that potentially useful scientific investigations involving computer simulations risk being thwarted on the grounds that they are not empirically calibrated or perhaps not historically validated. We shall argue that the role that IBCM plays in integrative ecology depends on whether one is doing applied ecology with concerns such as species conservation or whether one is doing theoretical ecology. In the former case, computer modeling should incorporate real-world elements and actual experimental data if the goal is to model existing ecosystems and to make long-term predictions about these systems. In this case, IBCM functions more like an investigative tool for scientific inquiry. On the other hand, if one's concerns are more theoretical, then IBCM has value in its own right in terms of high generality and equally high predictive power. Although the modeling should be realistic in a broad sense that is consistent with species generally that evolve in a world with predation, pathogens and fluctuating resources, simulations for more theoretical investigations need not incorporate experimental data – especially in light of the fact that these are not always obtainable in the field. They are experimental systems in their own right and not merely adjunctive tools.

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* Corresponding author at: Department of Biology, University of Windsor, Canada.
Tel.: +1 519 253 3000x2317.
E-mail address: macphe4@uwindsor.ca (B. MacPherson).

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1. Introduction

1.1. A brief characterization of individual-based modeling in integrative ecology

Individual-based computer modeling involves the use of computer simulations of either real or artificial populations involving discrete interacting individuals with distinct life histories (DeAngelis and Mooij, 2005). Thus, individual-based modeling is said to involve a 'bottom-up' approach where interactions between discrete individuals give rise to emergent properties such as species distribution at the population and ecosystem levels (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). Grimm and Railsback (2005) argue that what distinguishes individual-based models from other kinds of models are four key characteristics, namely, degree of complexity of individual life-cycles, variation in resources used by individuals, quantities measured by discrete numbers vs. reals and variability between individuals of the same age. Further, individual-based modeling is distinguished from equation-based modeling (EBM) in that the latter involves a so-called 'top-down' approach in the sense that equation-based simulations (involving the evaluation of differential equations, for example) do not provide a high degree of resolution in terms of life histories of individuals, and instead impose conditions on populations (Parunak et al., 1998; DeAngelis and Mooij, 2005).

It could be objected that like empirical investigation, individual-based computer modeling involves inferring general truths from particular facts about individuals as opposed to starting with general truths like equation-based modeling. In that case, as with empirical investigation, IBCM is faced with the so-called problem of induction. However, besides inferential statistics as a tried and true method of inductive inference for empirical investigation, IBCM experiments can be repeated varying or not the experimental conditions and paired with machine learning (see below), which involves using such tools as decision trees to arrive at general rules that can be applied to other systems. Granted, there is a trade-off between higher resolution and lower levels of generality with IBCM, but this trade-off is in part overcome by machine learning.

Moreover, IBCM is part of an evolving and developing movement in ecology that Grimm and Railsback (2005) refer to as "individual-based ecology" (IBE) that investigates populations, communities and ecosystems as complex systems with emergent properties arising from the traits and interactions of individuals. They regard the IBE approach as a major departure from traditional ecology that effectively glossed over these interactions (Grimm and Railsback, 2005). Further, IBCM has itself been integrated with machine learning techniques for the purpose of rule extraction (hybrid modeling) as has been observed by Parrott (2011). For example, Mashayekhi et al. (2014b) employed an IBCM, EcoSim along with machine learning to extract a set of rules that can be used to predict extinction of a variety of species.

Individual-based computer modeling is increasingly becoming identified with agent-based computer modeling (ABCM), although the current convention is to refer to individual-based models in ecology and agent-based models in other areas such as economics or social science (DeAngelis and Mooij, 2005; Grimm and Railsback, 2005; Heckbert et al., 2010; DeAngelis and Grimm, 2014). Roughgarden (2012) proposes that ABCM be regarded as a subcategory of IBCM where the individuals in ABCM are goal-directed intelligent agents as for example in a simulation of humans interacting with their environment. Following the lead of Roughgarden (2012), for the remainder of this review, I shall employ the term IBCM as a generic category that includes ABCM.

1.2. Applied ecology vs. theoretical ecology and the question of empirical validation

There is a de facto distinction made in the literature between theoretical vs. applied ecology, primarily on the basis of what the aims of the research are (May and McLean, 2007). May and McLean (2007) observe that applied ecology involves the employment of ecological theory (e.g., the dynamics of predator–prey interactions, the species area relationship, etc.) to solve practical problems such as how to manage fisheries or how to conserve species. In such cases, theoretical and applied ecology go hand in hand, so that the use of IBCM that results in theoretical advances will also have applications to real ecosystems. However, is the distinction between applied and theoretical ecology merely de facto? Codling and Dumbrell (2012) argue that this distinction is a false dilemma on the grounds that collecting data and making observations without theory leads nowhere and at the same time, pure theorizing without some connection with real data is equally pointless. While they are right that theory and data collection go hand in hand, it important to note that whereas applied ecology is concerned with particular ecosystems, theoretical concerns in ecology such as the prevalence of sexual reproduction in animal and plant species are more general in scope. At the very least, the concerns of theoretical ecology have the potential to be highly general.

Although the use of IBCM is an integral part of both theoretical and applied ecology as acknowledged by Grimm and Railsback