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Integrating ecological insight derived from individual-based simulations and physiologically structured population models

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ABSTRACT

Two contrasting approaches are widely used to derive population dynamics as an emergent property deriving from the physiology and behavior of individual organisms. “Individual-based models” (IBMs) are computer simulations where the “state” (e.g., age, size) of each individual in a population is followed explicitly along with changes in its environment. Population properties (e.g., density, age- or size-structure) emerge from simple bookkeeping and descriptive statistics. Physiologically structured population models (PSPMs) have an identical philosophy, but assume a very large (formally infinite) population and that all individuals in a given state have an identical response to any given environment. These assumptions allow the bookkeeping to proceed through a series of mathematical steps that lead to partial differential or integral equations describing the population dynamics. There is software for both approaches that handles the bookkeeping, with the modeler specifying solely the individual model using stylized files, thereby eliminating the need for technical expertise in either complex computer simulations or advanced calculus. Each approach has its advantages and disadvantages. IBMs are easier to formulate and to explain to people with limited mathematical experience than PSPMs, but PSPMs allow for more extensive mapping of possible dynamic attractors. IBMs alone can reveal the population level effects of demographic stochasticity and of differences among individuals. Formal equilibrium analysis of PSPMs show possible stable states (size distributions) of the populations that include unstable steady states from which slightly perturbed populations may start cycling. The equilibrium size structure at these unstable states can serve as an initial condition for IBMs, thereby facilitating study of the cycles. We illustrated the interconnections and contrasting insights from the two approaches using a food-chain model for which the PSPM was previously studied by De Roos and Persson (Proc. Nat. Acad. Sci. USA: 99, 12907–12912, 2002). Future general population ecology theory requires work with model populations that are both physiologically structured and distributed in space. We describe concepts from spatially explicit IBMs with identical individuals that, in combination with the results in this paper, may point to a way forward.

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1. Introduction

A long-standing aim for theoretical ecologists is to formulate and analyze models that relate processes occurring at different levels of biological organization. Models that relate population dynamics to the physiology and behavior of individual organisms are especially relevant in view of the importance of understanding population responses to environmental change. The most obvious

way to make this connection is to use “individual-based models” (IBMs)—computer simulations where some characterization (e.g., size, weight, age, nutritional status, probability of death, location in space) of each individual in a population is followed explicitly along with changes in its biotic and abiotic environment (Grimm and Railsback, 2005). Implementation of IBMs is conceptually simple—define a set of rules specifying how the state of each individual changes over some time interval and apply the rules repeatedly. Population dynamics is an emergent property described by summing among sets of individuals in the population. The use of IBMs has become increasingly popular as high performance computing has become cheaper and more accessible along with user friendly software for simpler models (Wilensky, 1999). There is a well-defined protocol (ODD: overview, design, details)

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for rigorous, unambiguous, model description (Grimm et al., 2006, 2010).

A contrasting approach for deriving population dynamics from individual physiology and behavior uses physiologically structured population models (PSPMs). *These models start from the same principles as IBMs*: the dynamics of a population emerges from rules describing the physiology and behavior of individual organisms. PSPMs then make simplifying assumptions that open the way to elegant mathematical formulations amenable to analyses that take advantage of the large body of knowledge of properties of dynamical systems. Key assumptions for most PSPMs are a very large (formally infinite) population, and that all individuals in a given state have an identical response to any given environment. In most cases, conceptually simple bookkeeping, together with careful mathematical reasoning leads to partial differential or integral equations describing the population dynamics. In spite of the simplifying assumptions, PSPMs have proved to be remarkably powerful tools for basic and applied ecology (e.g., de Roos and Persson, 2013 and references therein). The mathematical sophistication of the PSPM formalism has impeded their wide use by ecologists; however, there is now software (de Roos, 2014) that handles the bookkeeping with the modeler specifying solely the individual model using stylized files, thereby eliminating the need for technical expertise in advanced calculus.

To date, more general qualitative ecological theory has been developed using PSPMs, primarily because of access to general recipes for calculating the effects of model parameters on equilibrium, stability, and population cycles. It is harder to achieve such generality with IBMs, but they have the unique strength of allowing ready inclusion of many forms of *stochasticity* in a model. More broadly, their representation of individuals can reasonably be regarded as more “realistic”, but while added realism may open the way to more readily testable models, this may come at the cost of reduced generality (Murdoch et al., 1992). The thesis of this paper is that synthesizing the findings from both IBMs and PSPMs offers a route for the development of new general ecological theory that can support a wide spectrum of applications. This message is particularly appropriate in a volume recognizing the contributions to ecology of Don de Angelis. His early work recognized the strengths and limitations of simple deterministic models that admit mathematical analyses (e.g., Deangelis et al., 1975) and analogous simple stochastic models (e.g., Deangelis, 1976). A pioneer in the use of IBMs in ecology (e.g., DeAngelis and Gross, 1992), he recently highlighted their potential for addressing theoretical issues in ecology (DeAngelis and Grimm, 2014), the theme of this paper.

Understanding of the interconnections between models that recognize discrete individuals and their deterministic, continuous counterparts is facilitated by understanding dynamical patterns in simple “toy” models of populations with identical individuals. Similar patterns are commonly found in more complex PSPMs and IBMs. Thus, in Section 2, we describe features that can be understood by comparison of representations of populations that do, and do not, contain discrete individuals. In Section 3, we compare/contrast the properties of a three-trophic-level model (resource–consumer–predator) for which previous analysis of a PSPM demonstrated the possibility of bistability, hysteresis and population cycles (De Roos and Persson, 2002) with an analogous IBM that demonstrates how different forms of stochasticity influence qualitative outcome including invasion, persistence or extinction of the predator. The case study also demonstrates the value of “dialog” between the two approaches. The paper ends with a discussion of the contrasting strengths and limitations of IBMs and PSPMs and advocacy of using them in parallel to develop new theory in population ecology that takes account of spatially localized interactions.

2. Toy IBMs: an aid to understanding complex stochastic dynamics

Much ecological theory, including that based on PSPMs, is based on deterministic models that assume the future state of a population can be predicted from its present state. By contrast, stochastic models, including most IBMs, predict the *probability* of future states, given knowledge of the present state. Although some element of randomness is present in all ecological systems, deterministic models based on assumptions that parallel those in a stochastic model can give powerful insight on the likely stochastic dynamics (chapter 1 of Gurney and Nisbet, 1998). The connections rely on some general “rules of thumb” for characterizing qualitative differences between predictions from the two types of model. In this section, we describe these using simple, individual-based, representations of unstructured populations.

The conventional starting point for population models is a balance equation. In any population with discrete individuals, the change (ΔN) in the size of a population over a specified time interval (Δt) is always given by:

$$\Delta N = (B - D + I - E) \Delta t \quad (1)$$

where, $B\Delta t$, $D\Delta t$, $I\Delta t$, and $E\Delta t$ represent respectively the number of births, deaths, immigrants and emigrants during the time interval. In the simplest possible individual-based population models, sometimes called “birth and death models”, all individuals are assumed identical, each individual has a specified probability per unit time of giving birth or dying, the system is assumed to be spatially homogeneous, and there is no immigration or emigration. These stochastic models have continuous time, deterministic, analogs that treat population size (or density) as a *continuous* variable with dynamics described by an ordinary differential equation. This is justified as an approximation for large populations where the proportional population change due to a single birth and death can reasonably be regarded as infinitesimally small.

For such “unstructured” populations, there is a large body of theory that describes the relationship between the stochastic model and its deterministic counterpart. For a recent overview, see Black and McKane (2012) who note the ease of simulating sample populations using the Gillespie algorithm (Gillespie, 1992). Nisbet and Gurney (1982) and Renshaw (1991) gave detailed introductions to the dynamics of birth and death models. Real populations of course are not unstructured. Even the simplest unicellular organisms have a life cycle with distinct life stages responding differently to their environment. Nevertheless, many dynamic patterns exhibited by very simple unstructured models recur in more complicated or “realistic” IBMs and PSPMs. We now highlight two such patterns using maximally simple models.

2.1. Resonant quasi-cycles

Many texts describe near-equilibrium dynamics of deterministic systems described by ordinary differential equations (Gurney and Nisbet, 1998; Hastings, 1997; Kot, 2001; Murray, 1989). Commonly, a primary objective of such studies is to determine parameter combinations for which an equilibrium population is stable or for which there are sustained (limit) cycles. Model predictions can then be compared with data on real populations that apparently cycle (Kendall et al., 1999).

Deterministic models that can give rise to sustained population cycles inevitably also have a range of parameter values for which the approach to equilibrium involves a series of *damped oscillations*. With random variation in parameter values, realizations of the corresponding stochastic model exhibit sustained resonant “quasi-cycles”, i.e., bursts of near-cyclic fluctuations interspersed with periods of incoherent noise (Nisbet and Gurney, 1976; Nisbet

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