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Quantitative Population Ethology

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Abstract

Since the advent of theoretical population biology, there have been a number of attempts to simulate the dynamics of biological systems using any number of individual-based modeling techniques. In some cases such techniques have been successful, while in other applications the same approaches have failed miserably. We present some of the properties that an individual within a small population may exhibit and discuss general properties a modeling approach must possess to account for the dynamics of individuals within a population. We offer a possible modeling technique that is uniquely dependent on the information that the biologist observes.

1. Introduction

Knowledge about the dynamics of populations comes from two intrinsically different types of research. Ethology involves extensive examination of the physical and behavioral properties of an individual and its relationship to other members of its community. At the other end of the spectrum, theoretical population biology studies the general characteristics and dynamics of whole communities. Quantitative population ethology (QPE) combines these two perspectives to simulate the dynamics of a population by accounting for the behavior of each individual within that population. This approach is quantitative in two senses. It is primarily based on quantitative laboratory measurements and field sampling techniques and can summarize spatial-temporal information over time and over populations of individuals. In this paper we examine some model requirements for simulating the properties, dynamics and structure of populations through events that occur to individuals.

The description of individual behavior combines both quantitative and qualitative data into an intriguing but incomplete mosaic of information about both the individual and its relationship to other individuals. Each member of a community responds to its unique history, environment, health and social position, possibly affecting the potential success or failure of other segments of that community.

One problem inherent in using individuals to describe an entire biological system is that individuals respond uniquely to stimuli in ways not easily characterized by `density response' summaries or ‘rate functions’. In addition, simulating a population of individuals, unless done judiciously, ultimately leads to substantial dimensionality problems. The complex operational properties of an individual preclude elegant analytic solutions at the population level (Judson 1994). On the other hand, simulations that closely mimic individual behavior tend to be weak in mathematical structure and are usually computationally intractable. QPE develops a simulation paradigm that balances attention to biological details with sufficient mathematical structure to yield relevant results.

In the following sections we examine some of the constraints on any effort to simulate population dynamics by accounting for individual behavior. In section 2 we review the seminal work of Holling (1959a,b) and formally define the properties of an individual. From those properties we assert that there are only a few possible simulation approaches. Using those observations, Section 3 outlines the probabilistic nature of QPE, arguing that key population processes ultimately are played out among individuals. We suggest studying the dynamics and structure of a population of individuals using an event driven competing risk simulation (Ewing et al. 2002). In section 4, we describe how this perspective affects our perception of ‘models’. That is, the researchers understanding of a system being studied can be mimicked by a collection of interconnected simulations. In Section 5, we summarize the ideas discussed in this paper.

2. Individual-Based Population Dynamics

Holling’s (1959a,b) seminal papers on the functional response of the praying mantis (*Hierodula crossa*, Giglio-Tos.) to a population of houseflies (*Musca domestica*) set the stage for effective models of individual-based population dynamics. He found that the predator-prey process is inherently complex, and decomposed mantid predation into three basic components:

1. Rate of successful search, depending on reactive distance of predator to prey, proportion of prey successfully attacked and movement speed of predator and prey.
2. Time prey are exposed to predator, depending on prey feeding and other activities.
3. Time spent handling each prey, including pursuing, subduing, eating and digesting.

Holling's analysis suggests viewing predator-prey interactions as a sequence of events involving individuals. An event is defined as a significant biological change that can be marked and counted, resulting in an instantaneous state change. Events occur under conditions that depend on the morphological and ethological characteristics of both predator and prey. For instance, a predator-prey interaction event depends on a sequence of many conditional probabilities that, in turn, depend upon the states of a particular pair of predator and prey. Implicit in Holling’s study is the concept of localization: the process called predation is an event with one predator consuming one prey at a specific time and place. Individuals carry the dynamics.

Since the concept of an individual is paramount, what constitutes an individual? The following twelve properties define an individual as a higher level living system:

1. An organism is inexhaustibly complex.
2. Its state cannot be completely determined.
3. It has no natural state-space representation.
4. It is highly organized internally.
5. It is unique relative to all other organisms.
6. It is unique relative to its own entire past and future.
7. It is sharply differentiated from its environment.
8. It has memory of its past that modifies its present behavior.
9. It responds to its environment as a discrete integrated unit.
10. It changes continuously and irreversibly.
11. It exchanges mass, energy, and information with its environment.
12. Its perception of its environment is incomplete, abstract, and specialized.

Properties 1-4 state that the internal system of an individual is operationally unresolved. While an organism can be partially described in terms of constituent parts, a ‘complete’ understanding of its internal dynamics involves a hopelessly nonlinear system with deep hierarchical structure. Properties 5-9 assert that an organism functions as a unique, complete individual, reacting in novel ways to stimuli based upon its present state and partial memory of past events. Properties

10-11 imply that an organism obeys entropy, traversing a sequence of non-equilibrium states until it dies. Property 12 says each organism has finite memory, cannot recall all sensed stimuli, and responds selectively to only a few available stimuli.

An individual with the above twelve properties is an 'emergent phenomenon' that is irreducible. Intricacies of a biological system tend to emerge at the individual level. Each individual has a biased view of its environment and operates with subjective, incomplete and at times erroneous information. Coping strategies that may ultimately evolve into species characteristics initially appear in individuals. Some 'primitive' entities exhibit reasonably constant strategies during their lifespan. Highly developed individuals experience periods of learning that tend to improve their ability to exploit the local environment.

Any attempt to simulate the structure and dynamics of a population at the individual level is potentially so complex to become operationally intractable. Such a simulation probably possesses the following properties:

1. The individual is an inexhaustibly complex entity that is unique and operates with an incomplete view of its local environment.
2. The behavior of an individual depends upon a complicated sequence of conditional probabilities relative to its history.
3. These conditional probabilities change as events occur through feedback loops.
4. An underlying historical structure over a large number of events gets exploited via suitable strategies by both individuals and the researcher.
5. The high dimensionality of the state space forces the description to be probabilistic.
6. Numerical and analytic analogs are either impractical or impossible.

The biological structure emerges over a large number of events. The high dimensionality of the biological description forces the researcher to sample only a small part of the available state space. Prediction of future events for an individual or groups of individuals involves a level of abstraction. It may be possible predict global properties of a particular ecosystem, but these probably cannot be directly measured, and hence cannot be experimentally validated. Our philosophical caveat is that a particular mathematical or numerical technique should mimic the biological process as much as possible rather than constrain it. We suggest simulations be driven by how the biologist perceives a system and collects data.

3. The Probabilistic Nature of Quantitative Population Ethology

Ewing et al. (2002) presented a mathematical structure for a QPE simulation to study a biological community based on probabilistic choices for events that affect individuals, either singly or through interaction with other individuals. The non-homogeneous Poisson process provides a mathematical vehicle to mimic the biological process based solely on input provided by biologists. Discrete events drive this process, making time a function of those events. This implies a time ordering of future events across individuals that may be rearranged depending on the outcome of any current event. Each individual schedules its next future event based on its own state description and its perception of other individuals. There is no need to track all possible events and interactions. Instead we process next future event and allow the simulation to evolve its own structure.

Thus a biological system is simulated as a collection of individuals, each realizing a sequence of events over time based on its life history and interactions with other individuals and with the environment. Each event prompts the scheduling of one of several possible future events, implicitly setting a future event time, and possibly rescheduling or eliminating other individuals in the case of an interaction. An example of interaction is predation, in which a predator finds and kills a prey at a particular location, canceling future events for that individual and possibly modifying the future event structure of the predator. The simulation proceeds from event to event, processing future events in time order across all individuals in the biological system.

We reduce model dimensionality in three ways. First, the simulation is event driven, with action only at future event times. Second, the state space is minimized by considering only events that are defined within a given span and resolution. Resolution is the smallest increment of time and space that contributes useful information, with events over smaller scales assumed to occur instantaneously. Span is the largest amount of time and space the simulation can encompass, with aspects occurring over longer intervals considered as essentially constant or slowly varying in a smooth fashion. Third, spatio-temporal interactions for individuals are scheduled using distance-based probabilities rather than by stepping across a spatial grid. For a more detailed presentation of these concepts, see Ewing et al. (2002) and simulation tools available at www.stat.wisc.edu/~yandell/ewing.

4. A Network of QPE Models

What properties should simulations possess to capture the structure and dynamics of a biological system comprised of interacting individuals? Simulating individual-based population dynamics requires defining properties of an individual at some arbitrary operational level. Biologists do this all the time, having in mind some understanding at various scales of resolution. Those perceptions are ultimately translated into a series of field and/or laboratory experiments resulting in collected data, which reflects the researcher's understanding of the system at a particular time.

The usefulness of any individual-based simulation paradigm depends on its ability to correctly interpret collected data. Conversely, simulating a biological system is intrinsically dependent on what is measured and how individuals are sampled. Sampling 'quantizes' a system, restricting what facets of an individual are studied, which leads to an incomplete description of the dynamics of each organism. Researchers observe certain individuals and assign them to a sequence of quantifiable states. Unobserved individuals have unknown states, leading to a probabilistic projection of the observed states onto the whole population. Thus the measurement process chosen by the researcher restricts the class of possible models for understanding system dynamics. Further, measurement and comprehension of any complex system is itself a dynamic process. Typically a field biologist collects data at various resolutions in order to learn about particular aspects of biological processes. Further, processes may have different implications at different spatial scales. For example, studies of the *Verticicladiella*—Ponderosa Pine interaction develops over several decades while the Western Pine Beetle—Ponderosa Pine interaction lasts days or weeks, yet these processes are interrelated (Wood et al. 1972; Stephan and Dahlsten 1976a, 1976b; Wood et al. 1977).

Since field biologists view a biological system at multiple spatial and temporal scales, it makes sense to consider a network of QPE simulations over different spans and resolutions. The scope of questions asked of a biological system through a particular QPE simulation is implicit in the span and resolution of collected data from corresponding field experiments. Changing the resolution and span profoundly affects what features of a biological system can be studied, and vice versa. In essence, the QPE approach uses a network of interrelated simulations to study a biological system over many scales (Figure 1).

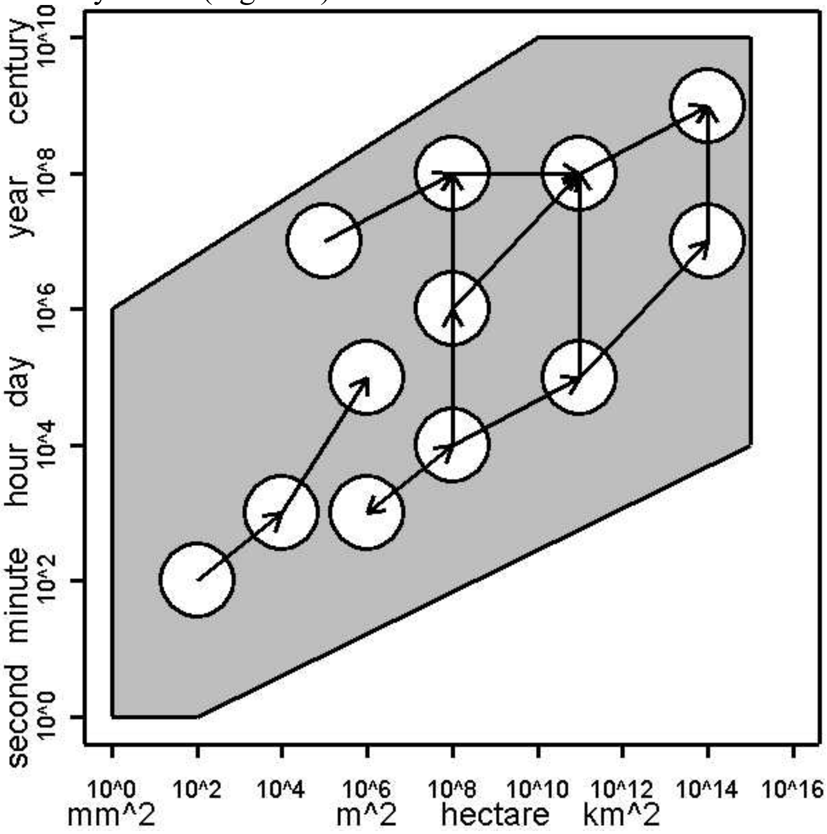

Figure 1. A network of simulations for a host-parasite system. Grey area contains range of biologically relevant scales. Each numbered circle is a simulation at a particular span and resolution. Connecting lines show information exchanges between different simulations.

The largest span may be at evolutionary and global scales, perhaps best studied by coalescent theory using individual DNA sequences across the host and parasite taxa. A much smaller scale models details of how a parasite probes a host to determine whether to attack it, at a resolution of fractions of a second and millimeters and a span of minutes and centimeters. For example, egg load studies might require a resolution of a few seconds and a span of a few days (Ives 1995; Rosenheim 1999; Casas et al. 2000; Rosenheim et al. 2000). Information gleaned from one simulation can feed into other simulations, either as constant aspects or instantaneous changes depending on the relationship of spans and resolutions across simulations.

5. Discussion

The need for and value of individual-based models for studying biological systems is demonstrated by the vast literature over the past decade (Judson 1994; Lambertson 2002). Faster and faster computers have driven efforts to model populations of interacting species using global population characteristics such as birth, death and migration rates. Stochastic dynamical systems have incorporated individual-based behavior (Mangel and Clark 1988; Wolff 1994; Ruxton 1996; Broom and Ruxton 1998; Gronenwold and Sonnenschein 1998; Ruxton and Saravia 1998; Wiegand etal. 1998; Wilson 1997; Hutchinson and McNamara 2000). Most individual-based simulations divide time and space into discrete `quanta' of equal size. Discrete time introduces probabilistic artifacts such as periodicity and synchronicity that persist as time steps get smaller. Similarly, discrete spatial patterns artificially constrict the type of interactions that can be modeled. Even recent successful simulations have been severely limited in population size and in temporal and spatial resolution relative to the span to compensate for the vast number of computations. Such models step through time, checking every individual at each point.

Donalson and Nisbet (1999) discussed some of the limitations of traditional modeling techniques when analyzing populations that exhibit spatial constraints. Analytical models of population dynamics have traditionally assumed that systems are spatially well mixed and large enough to be treated as continuous fluids. The Lotka-Volterra (Volterra, 1926) model is the classic example while the individual-based stochastic birth-death (SDB) model (Bartlett 1957) allows for demographic stochasticity (May 1973). Donalson and Nisbet (1999) compared SBD to their heuristic asynchronous discrete simulation (HADES) model, showing that predator-prey models become unstable if the system is not well mixed. Individual-based models are able to incorporate local behavior that reflects more realistic biological systems in a manner that is pragmatically impossible in global models. QPE extends the concept of HADES by providing an event driven simulation system that is tailored to the needs of biologists and their data.

An event-driven competing risk simulation steps from event to event (Donalson and Nisbet 1999; Ewing et al. 2002). It is only necessary to follow a few events per individual, hence computation is reduced dramatically. The computational complexity of an event-driven competing risk simulation is almost linear in the number of individuals and events, while time-driven models are exponential in the number of individuals. Partial memory can be added selectively to individuals or to types of events without dramatically increasing this number.

Another intriguing class of modeling techniques called ‘agent-based’ or SWARM models (www.swarm.org) take advantage of object oriented computing. Though many SWARM techniques are directly applicable to event driven competing risk simulations, we believe their philosophy would benefit from recognizing the inherent properties of ‘agents’ as unique individuals. It seems crucial that the researcher incorporate the properties of an individual into a simulation system to avoid spurious artifacts.

In this paper we have discussed the QPE paradigm as an addition or alternative to traditional population biology models. We suggest this as an alternative rather than a replacement to traditional techniques. Our focus on the uniqueness of individuals provides a philosophical alternative to standard techniques, giving field biologists a perceptual framework for analyzing the various processes and the structure of populations observed in the field using a network of QPE simulations. In addition, our approach has potential for analyzing self-organizing systems (Kauffman 1993, 1995; Paczuski and Bak 1999; Paczuski et al. 1995) in a potentially consistent manner.

Is this perspective capable of obtaining results one would expect under field conditions? The answer to that question depends on the fidelity of data and depth of understanding of the system by the field biologist. For example, if *Aphytis* uses a search algorithm for California red scale (see Forester et al. 1996; Forester et al. 1998) based on possible chemical queues (Vet

2001) but the simulation uses an ad-hoc search algorithm, then the simulation may be of limited use from the researcher's perspective. Perhaps this is the true value of the QPE paradigm. It provides a direct connection between how the researcher perceives the system under study and how event driven competing risk simulations are designed. QPE can provide tools to rapidly test various field scenarios, rather than for discerning global properties of a biological model. Quantitative population ethology should be applicable to a wide variety of problems including, for example, the Redscale/*Aphytis/Encarsia/Comperiella* system (Forester and Luck 1996; Forester et al. 1998; Luck and Nunney 1999; van Lenteren and DeBach 1981), the Western Pine Beetle, *Verticicladiella*, Ponderosa Pine interaction (Stephan and Dahlsten 1976a, 1976b; Wood et al. 1972, 1977), and wading bird nesting colony studies (Wolff 1994).

Perhaps most relevant is, what does QPE provide the researcher that is not already available? The approach suggested here is tied directly to data the biologist collects with a minimum of underlying mathematical requirements. QPE could allow a researcher to examine various scenarios in order to design an efficient sampling technique before actually performing a set of field experiments, serving as a virtual field study. Finally the direct relationship between simulation and data can highlight facets of the biology that are poorly understood, suggesting where and how to conduct future field observations.

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