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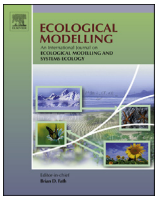

Integrating ecological insight derived from individual-based simulations and physiologically structured population models

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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 (PPSMs) 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.

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:

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

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

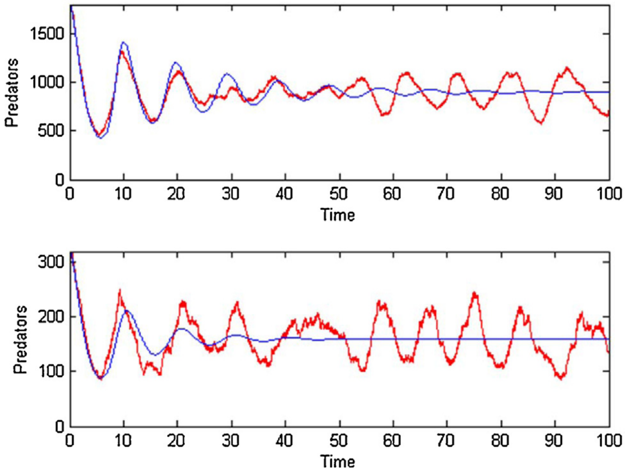

Fig. 1. Quasi-cycles for the simple damped Lotka–Volterra consumer resource model described in Section 2. Shown are plots of predator population against time for $r = 1.0$, $K = 5000$, $a = 0.001$ and $\delta = 0.5$, (top panel) and for $r = 1.0$, $K = 500$, $a = 0.005$ and $\delta = 0.5$, (bottom panel). Blue lines are solutions to the differential equations, red lines are stochastic simulations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Gurney, 1982). Stochastic models with discrete individuals can also exhibit quasi-cycles, even without explicit environmental variation. To illustrate this, we use a model whose deterministic counterpart is the damped Lotka–Volterra model where a prey population, N, and a predator, P, obeys the equations (Gurney and Nisbet, 1998, chapter 6)

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - aNP; \qquad \frac{dP}{dt} = aNP - \delta P \tag{2}$$

A minimal, individual-based, analog has transition probabilities per unit time (i.e., reciprocals of mean waiting times between events, sometimes called “propensities”) as follows:

Prey birth: rN; Prey natural death: $r\frac{N^2}{K}$

Meal (one prey death, one predator birth): aNP; Predator death: δP

Fig. 1 compares the dynamics of the deterministic model with the IBM for systems of two different “sizes”—determined by changing the (integer) value of the prey carrying capacity, K, and then scaling the parameter a (as $1/K$) so as to retain the same deterministic dynamics as before. Quasi-cycles are evident in both cases, but with the smaller population, the quasi-cycles have relatively larger amplitude.

2.2. *Multiple attractors, bistability, and hysteresis*

Many simple deterministic models admit more than one, locally stable equilibrium. A simple, single species, example is a model of spruce budworm (Ludwig et al., 1978) with the following equation:

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - \frac{\beta N^2}{\alpha^2 + N^2} \tag{3}$$

The population is assumed to grow logistically in the absence of predation, with (bird) predators, represented by the last term, switching to the location being modeled in response to population density. A minimal individual-based analog has transition probabilities per unit time (propensities):

Budworm birth: rN; Budworm natural death: $r\frac{N^2}{K}$

Bird predation: $\frac{\beta N^2}{\alpha^2+N^2}$

For certain parameter combinations, the deterministic model has two stable, non-zero equilibria. Fig. 2 shows sample realizations of the IBM for parameters that correspond to bistability for different initial conditions and system sizes. In the larger system, the IBM exhibits small amplitude fluctuations around the same steady state as would be predicted from the deterministic model, but in the smaller system there is *switching* between intervals of time spent close to each steady state. Not shown is the fact that with the smaller system the dynamical behavior is highly variable among replicates; Fig. 2 shows a pattern readily, if loosely, interpretable as switching between basins on attraction, but some other realizations with the same parameters exhibited less easily interpreted fluctuations.

Another much studied and important property of some bistable systems is *hysteresis*. If, for example, the system is at or near the lower steady state and environmental changed causes one of the model parameters (say r), to increase slowly, there is a critical value of r where there is an abrupt jump to upper steady state. If the change in r is now reversed, the transition down occurs at a lower value of r. This is illustrated in the bottom panels of Fig. 2.

Attractors in a deterministic dynamical system need not be stable equilibria and many PSPMs have combinations of parameter values for which two distinct periodic solutions are possible (de Roos and Persson, 2013), with at least one ecological context (*Daphnia* population dynamics), where the two types of cycle, and possible switching between attractors induced by stochastic factors, were observed in lab populations (McCauley et al., 2008; McCauley et al., 1999). Martin et al. (2013) demonstrated corresponding switching in an IBM.

Explicit incorporation of space within a model may also change the dynamics. For many situations, the introduction of diffusion destabilizes one of the steady states for any given parameter set. This is because any interface between spatially adjacent regions with population densities close to each steady state tends to advance (as a propagating “invasion wave”) in a direction determined by the model parameters (including diffusion coefficient) until the entire system is at one or other steady state (Murray, 1989). The implication is the possibility of sharp, reversible, discontinuities in equilibrium population in response to parameter changes rather than hysteresis. A further implication is the likelihood of sharp transitions in population along a *spatial* environmental gradient, an expectation verified by stochastic simulations with a lattice IBM (Wilson et al., 1996).

3. Integrating information from IBM and PSPM modeling: a case study

In this section, we describe work on an aquatic food chain model developed by De Roos and Persson (2002). The model recognizes three trophic levels: a resource, a size structured consumer population that feeds on the resource, and an unstructured predator population that feeds on the small consumers. Growth, reproduction, and mortality of individuals follow rules very similar to those in the bioenergetic model of Kooijman and Metz (1984). The model was parameterized to represent the life-histories of a freshwater zooplankton (resource), a planktivorous fish (consumer), and a piscivorous fish (predator), and makes strong predictions on conditions for persistence and invasion of the predator. We formulated an IBM *based on exactly the same core life history* in order to demonstrate how integrating findings from IBM and PSPM implementations of the model lead to a more nuanced understanding of predator dynamics than was previously known. A secondary aim is to describe how “dialog” between the two approaches led to this synthesis.

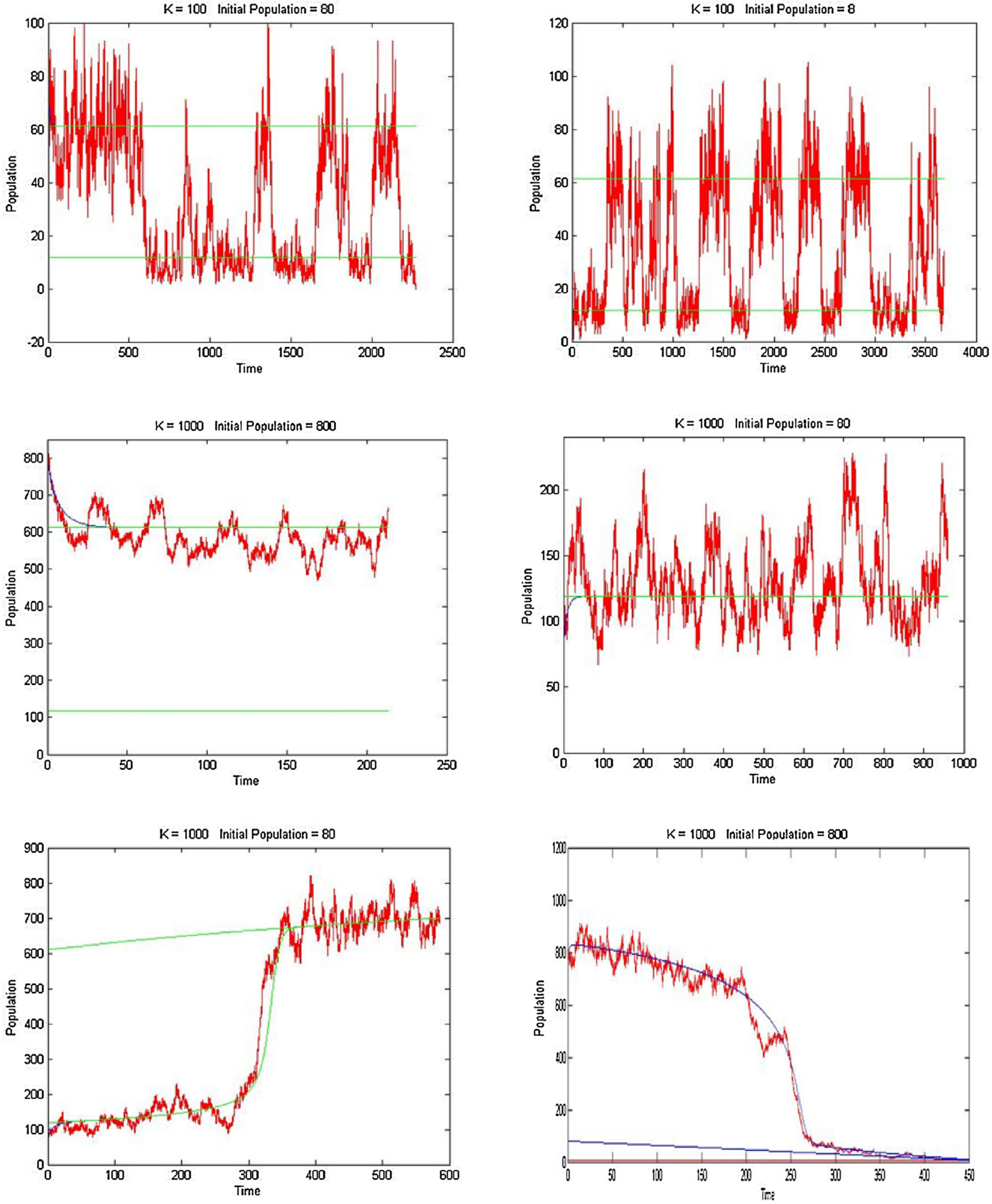

Fig. 2. Stochastic simulations of an IBM corresponding to the spruce budworm model of Ludwig et al. (1978). Red curves were generated using the Gillespie algorithm. The blue lines are the solutions to the deterministic differential equations. The green lines represent the equilibrium states in the top four panels and the nominal equilibrium state for the instantaneous parameter values in the bottom panels. Parameter values for the top panels are $r = 0.4$; $K = 100$; $\alpha = 14$ and $\beta = 10$ corresponding to a system with stable steady states (represented by green lines) at 61.2 and 11.9. The middle panels, representing a larger system increased carrying capacity, K, as well as the parameters α and β, by a factor 10 to yield a larger system with identical deterministic dynamics (other than the population scale). The bottom panels demonstrate hysteresis. The bottom left panel shows a realization of the large system with increasing r from 0.4 at a rate 10^{-4} per unit time with the values of all other parameters unchanged from the middle panels. The bottom right panel shows the response to decreasing values of r. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1. *Core life history model description*

Individual consumers are characterized by their length l. All individuals are born at length l_b and mature on reaching a length l_j. They feed on the resource, R, at a rate, I, proportional to their length squared, with a type II functional response:

$$I(R, l) = \frac{I_m R l^2}{R_h + R} \tag{4}$$

where, I_m is a proportionality constant and R_h is the half-saturation constant. Ingested food is assimilated with constant conversion efficiency and a fixed fraction κ of it is subsequently allocated to maintenance and somatic growth. Maintenance rate is assumed proportional to mass, which is taken proportional to their cubed length and takes precedence over growth. As a result, consumers grow in length following the von Bertalanffy equation, as long as the default allocation fraction of resource intake to growth and maintenance is sufficient to at least cover the latter. The growth rate (mass/time) of an *individual* is then

$$g(R,l) = \gamma\left(\frac{l_m R}{R_h + R} - l\right) \tag{5}$$

where, γ is the von Bertallanfy growth rate and l_m the maximum length when food density is not limiting. Consumers produce offspring after reaching maturity at length l_j at a rate proportional to their resource intake rate:

$$b(R,l) = r_m l^2 \frac{R}{(R_h + R)} \tag{6}$$

with the proportionality constant r_m relating the maximum reproduction rate at unlimited food density to consumer length.

When food density is so low that a default fraction κ of the consumer intake allocated to growth and maintenance is not sufficient to cover the latter, individuals are assumed to stop growing, so that:

$$g(R,l) = 0 \quad \text{if} \quad l > l_s = l_m R/(R_h + R) \tag{7}$$

with individuals allocating all energy that remains after covering their maintenance costs to reproduction:

$$b(R,l) = r_m(l^2 R/(R_h + R) - \kappa l^3/l_m)/(1-\kappa) \quad \text{if} \, l > l_s = l_m R/(R_h + R) \tag{8}$$

Consumers have a background, per capita mortality rate μ_b and die instantaneously if their resource intake is insufficient to cover their maintenance costs. When approaching the starvation threshold, l_s, consumers experience increased mortality:

$$\mu(l) = \mu_b + \mu_s(l - (1-\phi) l_s - \phi l_\infty) \quad \text{if} \quad l > (1-\phi) l_s - \phi l_\infty \tag{9}$$

with μ_s a proportionality constant, and the parameter ϕ representing the fraction of the length interval between l_∞ and l_s in which consumers experience increased mortality due to starvation.

Small consumers, with a length between l_b and l_v (vulnerable length) are attacked by the predator population with a type II functional response. The additional morality risk for the young, vulnerable consumers is:

$$\mathrm{d}(P) = \frac{aP}{1 + aT_h B} \tag{10}$$

where, P is the predator population density, a is the attack rate of the predator, B is the biomass of vulnerable fraction of the consumer population (which is just the sum of their individuals masses), and T_h is the handling time required by the predator per unit mass of prey consumed. Predators are assumed to assimilate a fixed faction, ε, of ingested food and to have a background per capita mortality rate, δ, so that:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \left(\frac{\varepsilon a B}{1 + aT_h B} - \delta\right) P \tag{11}$$

The resource follows semi-chemostat dynamics (de Roos et al., 1990); thus

$$\frac{\mathrm{d}R}{\mathrm{d}t} = \rho(K - R) - \text{total rate of consumption by consumers} \tag{12}$$

3.2. IBM model implementation

The IBM differs from the PSPM model in only two ways: individual consumers are discrete, thus birth and death events can only occur as discrete events involving integer changes in consumer population, and individual death events are stochastic. Modeling discrete individuals implies that we must also be explicit about the size of the environment (the volume of water being considered). In the (deterministic) PSPM, the dynamics of the system involve *densities* (biomas/volume), with the absolute biomasses obtained by simply multiplying densities by the system volume. In the IBM, the size of the system may affect the population dynamics as shown with the toy models in Section 2.

We implemented the IBM model in NetLogo (Wilensky, 1999) and worked with discrete time steps. The state variables of the resource and predator populations and of individual consumers which obey ordinary differential equations were updated using the Euler method. If the time step Δt is large the order of operations can affect the dynamics; however, if a small enough Δt is used, the probability of two discrete events occurring at the same time to the same individual becomes negligibly small, at the cost of computation time. With parameters used in the work reported here, we chose a time step of 0.1 day, as further reductions in time step or different orders of events (e.g., reproduction before mortality) did not result in detectable differences in output. The resulting update rules are in the Appendix.

3.3. PSPM model implementation and analysis

The PSPM is based on the same life history as the IBM. Formulation of the partial differential equation that mathematically describes the population model does not require further assumptions (de Roos, 1997). Furthermore, specification of this partial differential equation is, not necessary for computing the equilibrium states of the PSPM, as an approach for these computations has been developed, which only relies on providing the functions of the core life history model as input (De Roos, 2008; de Roos et al., 2010; Diekmann et al., 2003). This technique has recently been implemented in a dedicated software package PSPManalysis (de Roos, 2014) that can compute the equilibrium states of a PSPM over a particular range of values of any arbitrary model parameter. The package furthermore allows for the detection of special equilibrium points, so-called bifurcation points, representing for example, the threshold value of maximum resource density K in our core life history model, above which the size-selective predator can invade a consumer–resource equilibrium. The location of these special, bifurcation points can also be computed as a function of any two parameters of choice.

Using the PSPManalysis package to analyze our size-structured food chain model requires the implementation of the life history functions for consumer growth, reproduction, and mortality plus the functions describing resource turn-over and predator foraging, discussed in the previous section in a stylized template of program code. The manual of the software package (see de Roos (2014)) uses our core life history model as an example to discuss step-by-step how to implement a life history model and how to subsequently use the package for complete analysis of the equilibrium states of the model as a function of the maximum resource density K and the predator mortality rate δ. We hence refer to Sections 7 and 8 in the software manual (available for download, see de Roos (2014)) for further details.

The equilibrium resource, consumer and predator densities we calculated with the PSPManalysis package are presented in Fig. 3 and discussed below. Although both stable and unstable equilibrium states of PSPMs can be computed, the package is not equipped to study oscillations or more complex dynamics. We therefore used the calculated equilibrium states from PSPManalysis as starting point for numerical simulations of the food chain model dynamics using the “Escalator Boxcar Train” method (EBT), which is a numerical technique specifically developed for studying the dynamics of PSPMs (Deroos et al., 1992). The use of the EBT method is

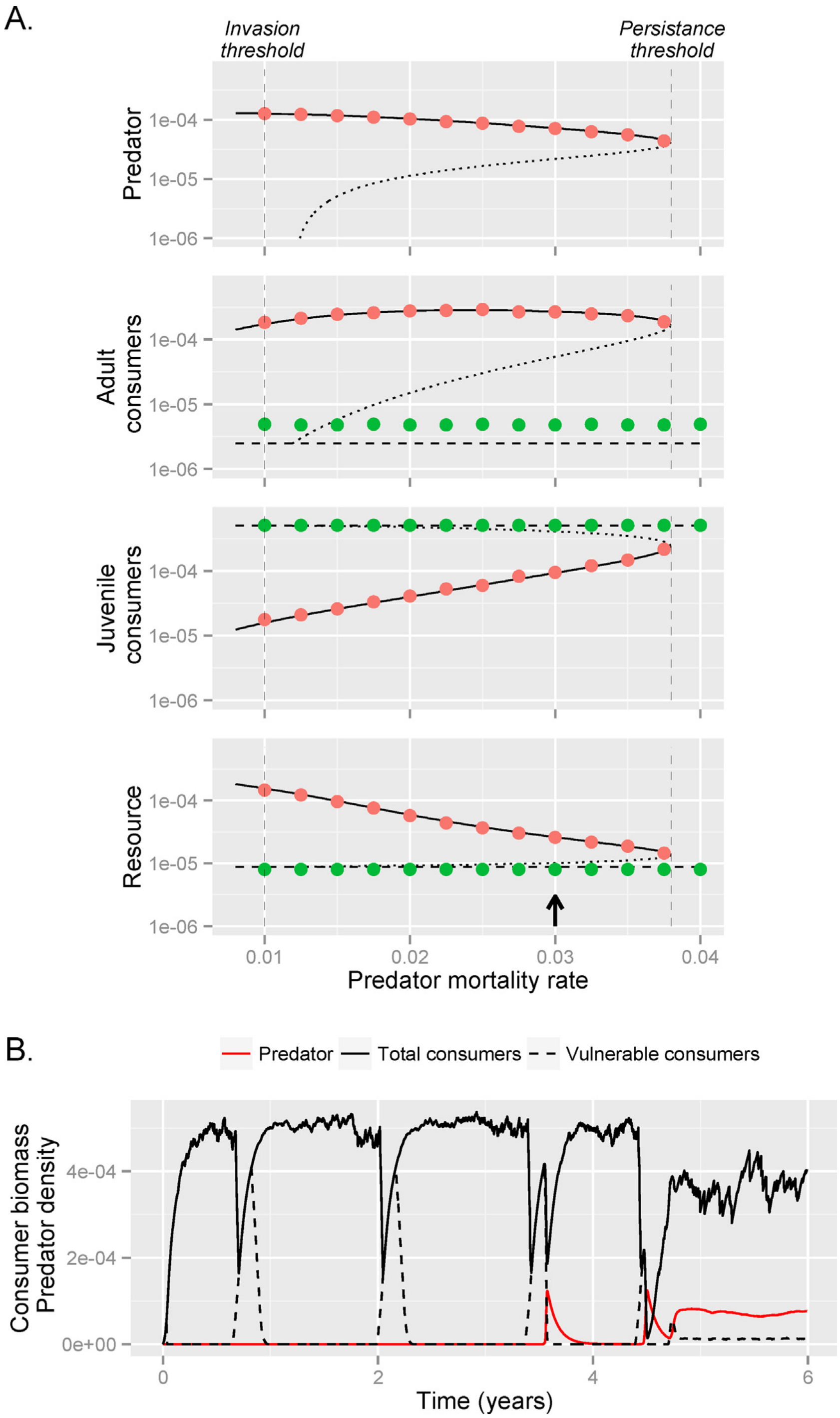

Fig. 3. (A). Comparison of IBM (points) and PSPM (lines) predictions for predator density (top panel; individual/L), adult and juvenile consumer biomass (2nd and 3rd panels; g/L), and resource biomass (4th panel g/L) in response to predator mortality (day^{-1}). Dashed lines and green circles represent the equilibria without predators. Solid lines (PSPM) and red circles (IBM) represent the equilibria with all three trophic levels. Shown also are the predicted range of bistability from the PSPM that occurs between the invasion and persistence threshold (vertical dashed lines). (B). Time series of total consumer biomass (solid black line), vulnerable consumer biomass (dashed line), and predator density (red line) during a successful predator invasion above the invasion threshold predicted by De Roos and Persson, 2002 (indicated by the black arrow in 3A; predator mortality rate = 0.03). The predator was introduced at year 3 at a density of 1e-9. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

facilitated by the software package EBTtool (https://staff.fnwi.uva.nl/a.m.deroos/EBT/), but the implementation of a particular PSPM in this package is not as straightforward as for the PSPManalysis package.

Using the EBT method, numerical integrations of the food chain model equations were carried out over long time periods with the total time of a single integration subdivided into intervals during which the value of all parameters are constant, while from one interval to the next the value of one particular parameter, the so-called bifurcation parameter, is increased or decreased by a small amount. A range of values of the bifurcation parameter is in this way scanned either from low to high or vice versa. The stepwise

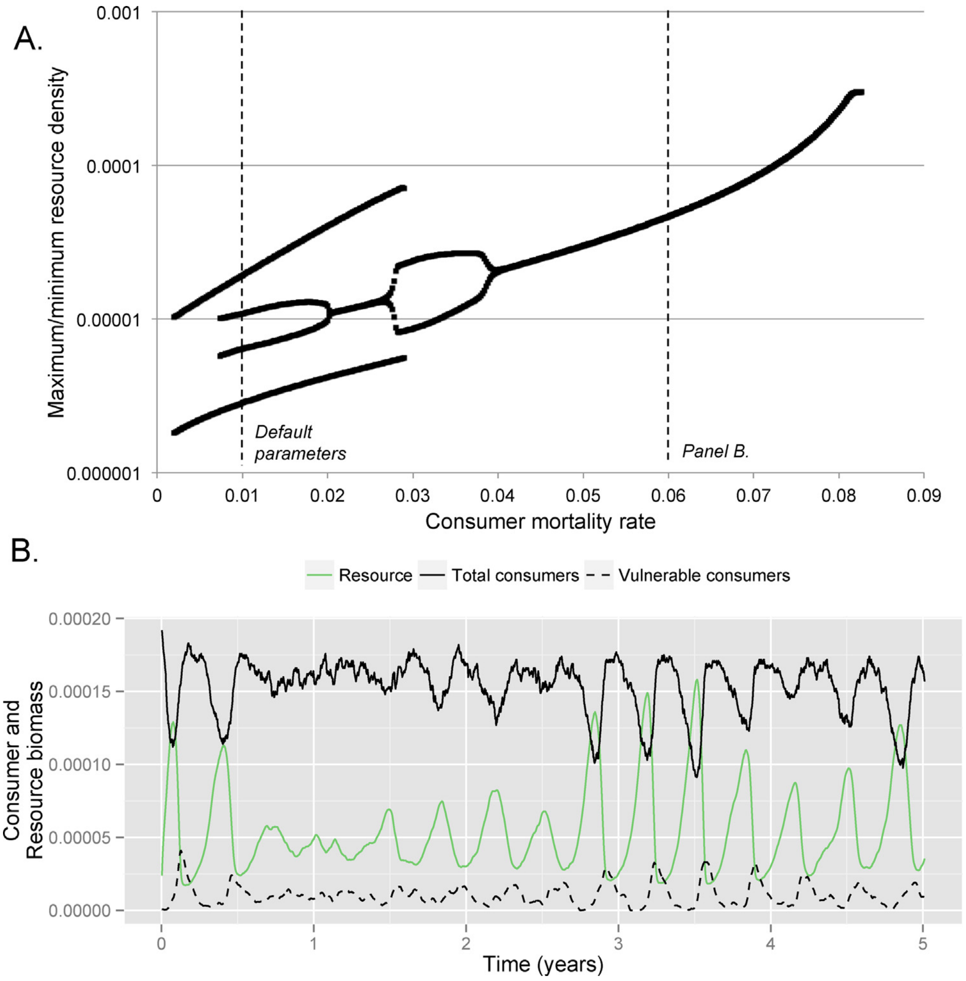

Fig. 4. (A). Bifurcation diagram generated from the PSPM model showing the dynamical attractors for consumer resource systems in the absence of predators as a function of consumer background mortality (day^{-1}). The leftmost vertical dashed lines show the value of consumer background mortality that was used in our analysis. (B). Time series of the resource and consumer population dynamics in an IBM simulation run with an alternate level of consumer background mortality (0.06) where the deterministic model predicted a stable equilibrium.

increase or decrease of the bifurcation parameter implies that the final values of the model variables obtained for a particular parameter value are used as initial values of the model variables for the subsequent, slightly changed parameter value. The advantage of this approach can best be explained in the context of stable model equilibria. The final values of the model variables will in this case be close to their equilibrium values for the new value of the bifurcation parameter as long as the particular equilibrium exists for this new value. Only when the equilibrium becomes unstable or does not occur at all any more for the new value of the bifurcation parameter, will the model variables approach an entirely different equilibrium or a different type of dynamics, such as a limit cycle. Scanning a particular interval of the bifurcation parameter with increasing as well as decreasing parameter values in most cases also reveals the co-occurrence of alternative stable equilibria or alternative types of stable dynamics, such as the co-occurrence of different types of limit cycles, for the same value of the bifurcation parameter—though considerable care and very precise computations are required to elucidate behavior very close to bifurcation points. We used this approach to determine the different types of dynamics exhibited by the size-structured food chain model for a range of consumer background mortality rates, monitoring the average (biomass) densities in case of stable equilibrium dynamics and minimum and maximum values of these densities in case of oscillatory or other types of non-equilibrium dynamics (see Fig. 4).

3.4. *Equilibrium states and predator persistence thresholds*

A major result of De Roos and Persson (2002) was that the combination of resource dependent growth of the consumer population and size-selective predation (a general feature of many resource–consumer–predator systems) can lead to an *increase* in the equilibrium biomass of small consumers vulnerable to predation when predation mortality increased. As a consequence of this positive feedback, predators experience a so-called emergent Allee effect, such that for certain ranges of parameters both an equilibrium with predators and an equilibrium without predators are deterministically stable. This bistability can inhibit predator invasion, and lead to catastrophic collapses of the predator population when conditions change.

We were interested in whether novel or complimentary insights on predator invasion could be gained by using an IBM approach. Are the results of IBM and PSPM "normally" similar? Do differences between the approaches, specifically the inclusion of demographic stochasticity and individual variability (not attributed to size), in the IBM lead to qualitatively or quantitatively different results from the PSPM? And can the simultaneous use of both approaches (each with their own strengths and limitations) lead to deeper insights than would be gained by use of either approach in isolation?

Reassuringly, initial simulations with the IBM confirmed many of the results from the PSPM analysis (see Fig. 3). The long-term average biomasses of resource, adult consumers, juvenile consumers, and resource in IBM simulations match the explicitly derived equilibrium conditions predicted by the PSM over a wide range of parameter space (changes in predator mortality rate and resource productivity) for systems with all three species (resource, consumer, predator) present (red dots in Fig. 3A). Furthermore, by either slowly increasing predator mortality, or by slowly decreasing resource productivity, we found that predator population collapsed exactly, or very close to, the point called the *persistence threshold* by De Roos and Persson (2002) predicted by the PSPM model. Consumer and resource long time averages deviate slightly from the PSPM equilibria, but were close, when predators were excluded (Fig. 3A, green dots). The deviation is possibly because the populations were exhibiting either limit cycles or quasi-cycles, discussed later.

3.5. *Predator invasion and population cycles*

We ran simulations to determine the extent to which the demographic stochasticity in the IBM affected the ability of the predator to invade or re-establish itself from low densities. For a range of predator mortality rates and resource productivity, simulations were initiated with only consumers and their resource present; after a transient period (3 years), we introduced a predator at a low density (1e-9/L). Previously published PSPM results predicted a large difference between the persistence threshold and an *invasion threshold* characterizing the parameter values at which invasion by an infinitesimally small predator population becomes possible. By contrast, our initial simulations suggest that the predator population could successfully invade over its entire persistence range.

Analysis of the dynamics over time revealed that the loss of bistability is due to large fluctuations in size structure of consumers. In the IBM simulations, in the absence of predators, the consumer population exhibits single-cohort cycles, with all reproduction occurring over a short period, followed by a long resource-limited maturation period, during which background mortality thinned out population density allowing the resource density to recover. Upon reaching maturity, consumers initiate the next cycle with a large reproduction pulse. This large pulse of consumers within the vulnerable size window provides an opportunity for the predator population to invade, even in conditions right up to the persistence threshold (Fig. 3B). We call this pattern *large amplitude (LA) cycles*.

The analysis of the PSPM in De Roos and Persson (2002) only evaluated equilibrium conditions, and thus did not explicitly consider population dynamics. However, Persson et al. (2007) later reported the occurrence of stable population cycles in the consumer population in the absence of predation. These consumer–resource cycles are robust against predator invasion unless consumer dynamics are significantly perturbed by imposing harvesting mortality. However, they have much smaller amplitude and involve much smaller pulses of reproduction than were observed in our IMB simulations. We call them *small amplitude (SA) cycles*.

de Roos and Persson (2013; Fig. 9.13) subsequently reported on the occurrence of both small-amplitude (SA) and large-amplitude (LA) cycles in this model as stable dynamic attractors for the same parameter values. This latter work was not known to two of the authors (RMN and BTM) at the time the IBM simulations were performed, but learning that the LA cycles do occur in the PSPM immediately informed us that they were not solely a consequence of either having discrete individuals or a small system in the IBM simulations. Conversely, by initializing the IBM with the consumer size-structure matching the predicted equilibrium size-structure from the PSPM analysis we were also able to demonstrate small amplitude cycles in the IBM.

The question remains, under which conditions should we expect LA versus SA cycles and (more important) what are the consequences for predator invasibility? This requires sweeping some portion of parameter space to find the range of conditions where one, the other, or both will be found, and then exploring how characteristics of real ecological systems (stochasticity, individual variability) alter the domains of attraction. Fortunately, each of the tools at our disposal is particularly well suited to one of the two tasks: with PSPMs we can easily map out the attractors (though not their domains of attraction) with bifurcation analysis, and with the IBM we can at various points along this map check which parts of the map are robust to the realities of ecological systems.

Bifurcation analysis using PSPManal confirmed the co-existence of two types of cycle with our default parameters (Fig. 4a). We did identify one potentially important difference between the two representations, that could have been anticipated from the toy models of Section 2, is that in situations where the PSPM predicts a stable equilibrium, there may be bursts of apparently cyclic dynamics in the IBM (Fig. 4b). The central region of that figure shows small fluctuations around a stable equilibrium, whose magnitude is consistent with the Fig. 4a, but earlier and later there are bursts of apparently quasi-cyclic behavior. Exploring these dynamics is beyond the scope of this paper; they may be quasi-cycles caused by the simple resonance mechanism discussed in Section 2 or they may reflect nonlinear excitation of some (possibly unstable) oscillatory mode not previously identified. Either way, the take-home message is that understanding the dynamics is greatly facilitated by the parallel work with the two approaches.

We used IBM simulation experiments to determine how two characteristics of real ecological systems not included in PSPMs (demographic stochasticity and individual variation) affect the ability of the predator to invade. Fig. 5 shows the results of many IBM simulations of the consumer resource dynamics with three different environment sizes (1e7, 5e7, and 1e8 liters), and four levels of individual variation in the feeding rate. Individuals either had no variation in parameter values or had their feeding rate drawn from a normal distribution with a standard deviation of 2.5%, 5%, or 10% of the population mean feeding rate. For each combination of environment size and individual variation, we initiated simulations with initial conditions either close to SA or LA attractor. We then simulated consumer population dynamics in the absence of predators for 10 years and after 10 years introduced a predator at low density 1e-9/L and monitored the predator population dynamics for another 10 years.

In the absence of individual variation in parameter values, the ability of the predator to invade depended entirely on whether the resident consumer population exhibited LA or SA cycles; when consumer populations exhibited LA cycles the predator was able to invade when introduced at a low density. All simulations initiated with conditions corresponding to LA conditions continued to exhibit LA cycles, regardless of the environment size. Environment size, however, did affect the stability of the SA attractor. The propensity for populations exhibiting SA cycles to switch to LA cycles was greater in smaller environments. In the smallest environment investigated, SA cycles were maintained only for a few population cycles, and thus were successfully invaded by the predator regardless of initial conditions. By contrast, in larger environments populations initiated with SA conditions were more likely to remain in SA cycles throughout the 20-year simulated period, and were less frequently invaded by the predator.

SA cycles are maintained by the survival of large consumers (close to l_j in size) through the nadir of the resource that can reproduce quickly once resource conditions improve, which in turn keeps the resource from growing too high. These large consumers make up a small fraction of the total population, and thus, in small environments, the maintenance of SA cycles depends on the survival of a small number of discrete individuals. If, due to chance most of them die during a cycle, there are not enough individuals to quickly suppress resource growth as conditions improve. In larger

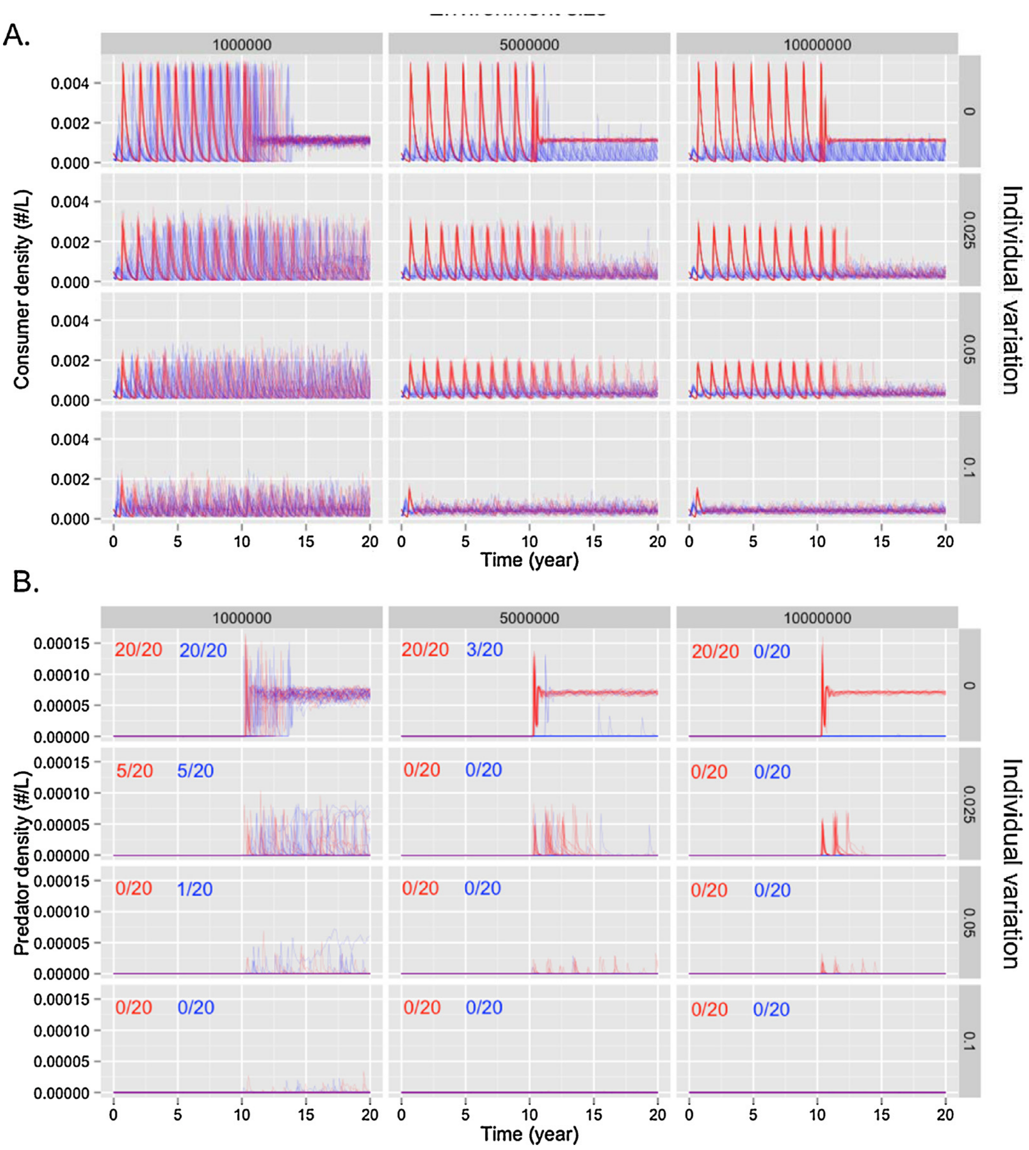

Fig. 5. Consumer (A) and predator (B) population dynamics before and during the introduction of the predator at a low density over a range of environment sizes, levels of individual variability, and initial conditions. Each panel shows 20 replicate simulations for a given environment size and level of individual variability that either started with initial conditions near the SA attractor (blue lines) or the LA attractor (red lines). The lines are partially transparent, thus the darkness of a lines represents the degree of overlap among replicates. Consumer population dynamics were simulated in the absence of predators for 10 years. On year 10 the predator population was introduced a low density 1e-9/L. The predator population density was not allowed to drop below the invasion density (if it fell below the initial invasion density it was set to 1e-9/L). The red and blue fractions in panel B indicate the fraction of simulations where the predator successfully invaded for simulations initiating with LA or SA initial conditions respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

systems, there is a much smaller likelihood of stochastic mortality reducing the large consumer population to below the critical level required to maintain SA cycles.

In general, individual variation in feeding abilities of consumers reduced the ability of the predator to invade; the predator successfully invaded only in a small fraction of the simulations at the lowest level of individual variability and smallest environment. Unlike in the scenarios with no individual variability, a successful predator invasion was not guaranteed by LA cycles in the consumer population. Although consumer populations initiating in LA cycles continued to exhibit LA cycles at the two intermediate levels of individual variability (2.5%, 5%), the amplitude of the cycles decreased with increasing individual variability, and they were rarely successfully invaded by the predator. In many cases, the predator once introduced to a consumer population exhibiting LA cycles, initially grew to a high density. However, at a high density, the predator's size-selective predation caused the consumer population to switch from the LA to SA attractor. Once the consumer population began to exhibit SA cycles, the predator population declined, and could not invade as long at the consumer population continued to exhibit SA cycles. At the highest level of individual variability, consumer populations exhibited quasi-stable dynamics regardless of initial conditions, thus the prohibiting the predator population from invading.

We conclude that three characteristics of real ecological systems (discrete, stochastic, individual variability), can strongly affect the ability of the predator to re-establish itself from a low density. For small populations, stability of the SA cycle is vulnerable to stochastic mortality of just a few large individuals, and when there is little or no individual variation in feeding rates, this allows the predator to invade more frequently. Individual variability on the other hand dampens some of the "extreme" dynamics predicted from the model, and reduces the ability of the predator population to invade.

4. Discussion

Many of the classic unifying concepts in population ecology derive from simple models—often deterministic. Examples include density-dependent population regulation, prey–predator cycles, paradox of enrichment, competitive exclusion, invasibility, Tilman's R^* rule and many more. Other well-established concepts such as bistability and hysteresis emerged from the *combination* of studies with ordinary differential equations and simple stochastic simulations.

Some more recent contributions to general theory have their origin in PSPMs, notably theory on the many types of population cycle that can occur with consumer–resource interactions in structured populations (Deroos et al., 1991; Murdoch et al., 2003; Murdoch et al., 2002). However, the sophistication of the mathematics used in many continuous-time, structured population models has restricted their use in modeling, and many ecologists develop models without consideration of this body of theory. The problem of mathematical sophistication is resolvable with user-friendly software such as the PSPManalysis package described here.

A more serious issue is the rareness of the studies that quantify the extent to which the properties of PSPMs rely on the assumptions of large populations and no individual variability. Thanks again to user-friendly software like Netlogo, minimal technical expertise is required to formulate IBMs analogous to any given PSPM with discrete individuals. In this paper, we demonstrated that general theory could be advanced by simultaneous work with an IBM and the analogous PSPM. Both approaches start by specifying the dynamics of individual organisms faced with some environment; population dynamics is an emergent property in both cases. Each has strengths and limitations:

- IBMs are easier to formulate and to explain to people than PSPMs, but PSPMs allow for more extensive mapping of possible attractors. For example, constructing a figure like Fig. 4a from IBM simulations would require huge computational effort, great sophistication in automating the interpretation of simulations, and in all likelihood, a lot of luck.
- Once a realization of an IBM has been simulated, additional metrics characterizing the dynamics (e.g., variances, co-variances, auto-correlations) can easily be derived in post processing. These may be directly compared with "time-series probes" previously proposed as tools for comparing population models to data (Kendall et al., 1999)
- Equilibrium analysis of PSPM shows possible stable states (size distributions) of the populations. The analysis also identifies unstable steady states, from which slightly perturbed populations may start cycling. The equilibrium size structure at the unstable state can serve as an initial condition for IBMs, thereby facilitating study of the cycles. Again, much luck would be required to arrive at the appropriate starting distribution for simulation without aid from the PSPM.
- More sophisticated computations with PSPMs can reveal stable limit cycles (see for example Fig. 4a).
- IBMs subsequently can beautifully reveal how demographic and individual stochasticity perturb and reshape the dynamics that can be more extensively revealed and mapped out by PSPMs (see for example Fig. 5).

From an ecological point of view, it is interesting to see that some of the extreme types of dynamics that our case study model predicts (in particular the large-amplitude single-cohort cycles) are in real systems probably destabilized by demographic stochasticity and transformed into smaller amplitude cycles that are also cohort-driven/cohort-based, but not of such an extreme character. Our work also suggests that variability in model parameters among individuals may stabilize the latter dynamics. This finding may have some generality: Ananthasubramaniam et al. (2011) introduced individual variability in individual growth rate into a different structured consumer resource model whose deterministic version (McCauley et al., 2008; Nelson et al., 2007) exhibits coexisting small and large amplitude cycles and found that growth rate variability increases the region of parameter space over which small-amplitude cycles or quasi-cycles occur.

This paper has focused on models that relate the interactions between individual organisms and their environment to population dynamics, emphasizing approaches that represent population dynamics as an emergent property caused by a large number of individual-environment interactions. However, the aim of population ecology is to understand not only the abundance of living organisms, but also their *distribution*. Thus future general population dynamic theory must focus on ways of simultaneously modeling organismal physiology and interactions that are localized in space. The challenge will be to achieve a level of generality comparable with that achieved in the synthesis of de Roos and Persson (2013). We suggest that progress will again rely on synthesizing insight from simple deterministic and stochastic "toy" models of identical individuals distributed across space, along with new work on spatial IBMs and PSPMs.

There is a large biomathematical literature on deterministic spatial models of populations of identical individuals, predominantly reaction–diffusion models. For an overview, see Cantrell and Cosner (2003). Reaction–diffusion models explicitly or implicitly assume a separation of time scales so that at a local spatial scale individuals interact with effectively an infinitely large population. This assumption is analogous to the "local equilibrium assumption" widely adopted in hydrodynamics and non-equilibrium thermodynamics. However, this time scale separation is likely to be inappropriate in many ecological applications and there is very little formal theory for situations without time scale separation. Current insight on situations where this assumption is invalid largely derives from a contrasting class of models, mostly encompassing spatial IBMs (Deroos et al., 1991; Donalson and Nisbet, 1999; Mccauley et al., 1993; Nisbet et al., 1998; Wilson et al., 1993, 1995) that explicitly considers the *individual mobility* that gives rise to *local interactions between individuals*, such as prey searching behavior by predators, and focus on how local movement of individuals shapes their interactions and hence population dynamics. General mathematical theory explaining how local individual mobility influences the rate with which individuals interact with conspecifics and other species members is under-developed, but a mix of IBM studies and some mathematical modeling has elucidated some key processes.

When individual mobility is low, intraspecific competition tends to be increased, because reproduction leads to locally high densities of individuals (Murrell, 2005), but encounter rates with competitors and predators tend to be low. Intuition on the effects of such local movement on average population densities follows from understanding these effects on interaction rates: for example, an increase in prey mobility may lead to an increase in encounters with predators and thus a decrease in prey density (Wilson et al., 1993; Murrell, 2005). Limited mobility may dampen population fluctuations by decoupling changes in local abundance in different parts of the habitat. For example, in predator–prey systems fluctuations in prey and predator densities within small neighborhoods may resemble in amplitude the coupled predator–prey oscillations known from well-mixed systems, but on larger scales, abundances in different parts of the habitat may oscillate out of phase with each other leading to global dynamics that resemble fluctuations around a stable equilibrium (Deroos et al., 1991; Mccauley et al., 1993). It has been argued that dynamics of prey and predator populations with limited mobility resemble the dynamics of comparable well-mixed system with lower attack rates (Hosseini, 2003; Pascual et al., 2001). Finally, changing the mobility of different species or even individuals of the same species in different life stages may have asymmetrical effects on the dynamics of interacting populations. For example, increasing the mobility of adult predators has been shown to destabilize dynamics in predator–prey systems, whereas increasing the mobility of juvenile predators stabilizes these dynamics through large-scale pattern formation in prey density (de Roos et al., 1998; McCauley et al., 1996).

These spatially explicit studies of physiologically *unstructured* population models together with our case study on a spatially homogeneous, physiologically structured system offers hints at the possible effects of local interactions on predator invasibility. Spatially localized interactions would introduce factors that may have both stabilizing and destabilizing effects on population cycles. We anticipate enhanced demographic stochasticity, as the size of the *local* population with which an individual interacts will be much smaller than the entire population, and thus more sensitive to demographic stochasticity. If the conjectures of Hosseini (2003) and Pascual et al. (2001) hold, we could also anticipate changes in mean average values of parameters characterizing interactions. Local interactions will also increase individual variability, through differences in feeding histories of individuals within a cohort. IBMs offer a way to determine how the destabilizing effects of demographic stochasticity and the stabilizing effect of individual variation play out, but such an investigation would be completely impractical without choice of simulation parameters and starting conditions being based on the dynamics of the (non-spatial) IBM and PSPM. In short, the tools are now in place for using a judicious mix of toy models, PSPMs and IBMs to test the robustness of existing theoretical concepts in population ecology and to guide the discovery of new paradigms.

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Appendix A. Update rules for individual-based resource–consumer–predator model

For the resource, the change, ΔR in a time step Δt is

$$\Delta R = \left[\rho(K - R) - \Sigma(I(R,l))/s\right]\Delta t \tag{A1}$$

where, $\Sigma(I(R,l))$ is the sum of the resource intake $I(R,l)$ (Eq. (2)) over all individual consumers, and s, is the size of the environment in liters.

The growth of individual consumers in a time step is calculated following Eq. (5) in the main text as:

$$\Delta l = [\gamma(l_m R/(R_h + R) - l)]\Delta t \quad \text{if } l < l_\infty = l_m R/(R_h + R) \tag{A2}$$

and

$$\Delta l = 0 \quad \text{otherwise}$$

For individuals with $l > l_j$ the change in the reproduction buffer is calculated following Eq. (6) as:

$$\Delta b = \Big[r_m l^2 R/(R_h + R)\Big)]\Delta t \quad \text{if } l < l_\infty = l_m R/(R_h + R) \tag{A3}$$

and

$$\Delta b = [r_m(l^2 R/(R_h + R) - kl^3/l_m)/(1-k)]\Delta t \quad \text{otherwise}$$

The growth of the predator population in a time step Δt depends on the number of stochastic encounters with consumers within the vulnerable range. To calculate this, each individual consumer in the vulnerable range is assigned a probability of dying through predation given by:

$$Pr(d) = 1 - \exp(-d(P)\Delta t) \tag{A4}$$

where, $d(P)$ is the per capita predation mortality rate from Eq. (10). Thus the predator growth rate in a time step becomes:

$$\Delta P = \varepsilon B_p - \delta\Delta t \tag{A5}$$

where, B_p is the sum of the biomass of vulnerable individuals that are consumed in a time step. Background mortality was calculated by drawing an age at death for each individual at birth from an exponential distribution with a mean $1/\mu(l)$ defined via Eq. (9). Individuals die in a time step during which their age exceeds their age at death.

Finally, mature individuals with enough energy to produce offspring, i.e., $b > 1$, produce as many discrete offspring as they have energy for, i.e., $[b]$, where $[.]$ denotes "largest integer less than.". Newborn individuals initialize in the next time step with $l = l_b$ and a randomly selected age-at-death. The order of events in our IBM simulations was: (i) calculate the changes in state variables, update state variables; (ii) remove dead consumers; (iii) reproduce.

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