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Spatial Heterogeneity and Anomalous Kinetics: Emergent Patterns in Diffusion-limited Predatory–Prey Interaction

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The Lotka–Volterra model of predator–prey interaction is based on the assumption of mass action, a concept borrowed from the traditional theory of chemical kinetics in which reactants are assumed to be homogeneously mixed. In order to explore the effect of spatial heterogeneity on predator–prey dynamics, we constructed a lattice-based reaction–diffusion model corresponding to the Lotka–Volterra equations. Spatial heterogeneity was imposed on the system using percolation maps, gradient percolation maps, and fractional Brownian surfaces.

In all simulations where diffusion distances were short, anomalously low reaction orders and aggregated spatial patterns were observed, including traveling wave patterns. In general, the estimated reaction order decreased with increasing degrees of spatial heterogeneity. For simulations using percolation maps with p-values varying between 1.0 (all cells available) to 0.5 (50% available), order estimates varied from 1.27 to 0.47. Gradient percolation maps and fractional Brownian surfaces also resulted in anomalously low reaction orders. Increasing diffusion distances resulted in reaction order estimates approaching the expected value of 2.

Analysis of the qualitative dynamics of the model showed little difference between simulations where individuals diffused locally and those where individuals moved to random locations, suggesting that global density dependence is an important determinant of the overall model dynamics. However, localized interactions did introduce time dependence in the system attractor owing to emergent spatial patterns.

We conclude that individual-based spatially explicit models are important tools for modeling population dynamics as they allow one to incorporate fine-scale ecological data about localized interactions and then to observe emergent patterns through simulation. When heterogeneous patterns arise, it can lead to anomalies with respect to the predictions of traditional mathematical approaches using global state variables.

1. Introduction

In developing a quantitative theory for the interaction of predator and prey, Lotka (1956) and Volterra (1928) applied the logic of mass action to model the influence of predator and prey density on population dynamics. The assumption of mass action appears in the Lotka–Volterra model as a product of the respective populations:

$$dA/dt = rA - sAB \tag{1a}$$

$$dB/dt = tAB - uB \tag{1b}$$

where A and B are density of prey and predator, r and u are per capita change in the absence of each other, and s and t are rates of change due to interaction. The model treats populations rather like an ideal gas, i.e. the distribution of predators and prey are assumed to be uniformly mixed and homogeneous throughout. Thus the encounter rate between predator and prey can be approximated by the product of their respective biomasses. Dynamically, eqns (1a) and (1b) result in neutrally stable limit cycles. Mass action plays an important role in much of the physical sciences. It is particularly prevalent in the equilibrial theory of chemical kinetics where it may be referred to as a mean-field approximation

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(Snoeyink & Jenkins, 1980). A "mean-field" approach is commonly taken when modeling chemical reaction mechanisms and rates (Gardiner, 1972).

Whereas a mean-field approximation may be useful for modeling reactions in a chemostat, it is generally a poor assumption when considering population dynamics distributed spatially across a landscape. Space introduces lags in population responses to resource availability or predation because local increases in abundance do not immediately effect areas further away. Time is required for individuals to disperse. Spatial lags lead to a variety of complex spatial patterns ranging from traveling waves to chaos (Kareiva, 1990; Hassel *et al*., 1991; Dunning *et al*., 1992). Furthermore, habitat distributions can themselves be heterogeneous and exhibit scale-dependent fractal geometry (Milne, 1992). Individuals dispersing in patchy environments can exhibit both increased and decreased rates of diffusion depending not only on the geometry of the landscape, but also on the spatiotemporal scale over which one tracks individual movements (Johnson *et al*., 1992*a*). Patchy habitats can also stabilize competitive and predator–prey interactions which would otherwise be unstable (Huffaker, 1958; Godfray & Pacala, 1992; Palmer, 1992; however see Murdoch *et al*., 1992). Heterogeneous population distributions can arise both through the intrinsic dynamic of the "players" (i.e. organisms) and via a heterogeneous "playing field".

A number of approaches have been taken towards improving the mathematical treatment of predator–prey theory (for a review see Berryman, 1992). Prey density dependence may be added in the form of a logistic prey growth function, changing eqn (1a) to

$$\mathrm{d}A/\mathrm{d}t = rA(1 - A/K) - sAB, \tag{2}$$

where K is the equilibrium prey density. The second term on the right in eqn (2) (sAB) is known as the predator *functional response*. Prey density dependence results in a slanting prey zero-growth isocline and a stable focus equilibrium. The logistic approach may be extended to the predator equation as well (Leslie, 1948; Berryman, 1981) yielding

$$\mathrm{d}B/\mathrm{d}t = tB(1 - vB/A). \tag{3}$$

Equations such as (3) which include a predator–prey quotient are referred to as *ratio-dependent* models. Ratio dependence has also been applied to modeling predator functional responses (Aditi & Ginzburg, 1989).

Ratio-dependent models do not rely on mass action since ratios (e.g. predators per prey) approximate conditions experienced by each individual as opposed to the overall effect of one population on the other. Furthermore, these models overcome many of the limitations of the original Lotka–Volterra model, such as the "paradox of enrichment", in which traditional models predict that increased resource availability will lead to an increase in predator density, but not that of the prey (Berryman, 1992). Both experimental and empirical data support ratio-dependence as a model for trophic interactions (Arditi & Saïah, 1992; Ginzburg & Akçakaya, 1992; Gutierrez, 1992).

Although these approaches to modeling predator–prey dynamics rectify many of the weaknesses of the original Lotka–Volterra theory, they nonetheless rely on what Slobodkin (1992) refers to as "extensive" variables, i.e. global quantities. Individual organisms do not directly experience extensive quantities. The fate of individual interactions depends on "intensive" variables (i.e. local conditions) such as the number of prey neighboring a predator. Ratio- and per-capita based models (Berryman, 1992), although they approximate per-individual interactions, are derived as functions of extensive variables. Extensive variables are themselves transformations of intensive variables, generally a quantity summed over a given area. It is important to note that in general the transformation from local variables to global variables is not necessarily invertible, *unless the system is spatially homogeneous*. In the presence of significant spatial variation in abundance, knowing the total number of individuals distributed across a landscape provides little information about how many individuals one will find within a given local area.

In this paper, we adopt a more direct approach to modeling predator–prey interaction based on intensive variables. We simulate individual predators and prey interacting on a lattice of cells. The outcome of individual encounters is determined by probabilistic interaction rules. We also introduce a novel approach to incorporating environmental heterogeneity into population models by simulating population dynamics on fragmented lattices. Several aspects of the model are considered and contrasted with traditional "extensive-variable" population models. Emergent spatial patterns on both homogeneous and fragmented lattices are explored. We then consider the effects of spatial heterogeneity on the instantaneous rates of population growth rates. Our analysis is based on the theory of anomalous chemical kinetics in heterogeneous media (Kuzovkov & Kotomin, 1988; Havlin, 1989; Kopelman, 1989). Finally, we examine qualitative aspects of the model in the phase plane comparing local versus global movement rules.

1.1. ANOMALOUS KINETICS

In order to quantify deviation in the behavior of the spatially explicit predator–prey model from the Lotka–Volterra model, we adopt an analogy to a chemical reaction system. Written as a set of reactions, the Lotka–Volterra equations correspond to

$$A \xrightarrow{k_1} 2A \tag{4a}$$

$$A + B \xrightarrow{k_2} 2B \tag{4b}$$

$$B \xrightarrow{k_3} 2C, \tag{4c}$$

where A represents "prey", B represents "predators", and k_i are reaction rate constants. The first reaction corresponds to prey reproduction. The second corresponds to predator reproduction due to consumption of prey and the last reaction represents predator mortality.

Following the basic analytical methods of chemical kinetics, we rewrite the reaction system as a set of differential equations

$$\mathrm{d}A/\mathrm{d}t = k_1 A^a - k_2 A^a B^b \tag{5a}$$

$$\mathrm{d}B/\mathrm{d}t = k_2 A^a B^b - k_3 B^b, \tag{5b}$$

which are equivalent to the Lotka–Volterra model. The exponents a and b represent, in the theory of chemical kinetics, the *order* of the reactions with respect to predator and prey density. In the well-mixed Lotka–Volterra model, these exponents are assumed to equal one and are therefore not given explicitly. It is important to note that in the theory of ordinary differential equations (ODEs), the term *order* is used in an entirely different sense and refers to the highest derivative appearing in a differential equation.

In ecological terms, reaction order can be thought of as the sensitivity of the growth, mortality, and encounter terms to changes in the density of predator or prey. Thus, for large reaction orders, increasing either predator or prey densities will have a proportionately large effect on the magnitudes of the terms in the equations.

Chemists use reaction orders to mathematically express the underlying mechanisms occurring in chemical reactions and their effect on overall reaction kinetics (Snoeyink & Jenkins, 1980). In classical kinetics, reaction orders are integer values determined by the molecular interactions that constitute the reaction. For instance we might have a simple decay reaction of a molecule into one or more products, such as in the decomposition of hydrogen peroxide to water and oxygen. The general form of the reaction and rate law are

$$A \rightarrow \text{products} \tag{6a}$$

$$\text{Rate} = K[A]^1, \tag{6b}$$

where in this case K would be a negative constant determining how fast the decomposition occurred. The reaction order is determined by summing the exponents of the concentrations. In this case, the reaction is first order. Bimolecular reactions are typically second order, but higher orders are possible and depend on the particular reaction mechanism of interest.

The classical theory of chemical kinetics is based on homogeneous distributions of reactants, much in the same manner as ecological theory based on the Lotka–Volterra model. Recently, the kinetics of diffusion limited reactions occurring in spatially heterogeneous environments has gained considerable attention (Kopelman, 1989; Havlin, 1989). Much of this work has focused on simulations of chemical reactions occurring on fractal structures. Fractals are geometric patterns that exhibit statistical self-similarity when viewed at different scales (Mandelbrot, 1982; Milne, 1992). Simulated chemical reactions on fractal surfaces show considerable deviations from the expectations of traditional kinetics, exhibiting both time dependence in the reaction rate coefficient and anomalous reaction orders (Kopelman, 1989).

Analytically, it has been shown that for homogeneous reactions in three dimensional systems, random diffusion of reactants is sufficient to maintain a mixed system and the reaction rate is linearly proportional to the diffusion coefficient (D) of the reacting molecules (Smoluchowski, 1971, as cited in Kopelman, 1989). However, in lower dimensional systems (i.e. surfaces and fractal-subsets of surfaces and volumes) diffusion is inhibited because particles are no longer free to move in all directions and are constrained to locally available sites. The result is what Kopelman (1989) has termed "fractal kinetics". A striking result from these investigations is the spontaneous emergence of spatial segregation of reactants in disordered, randomly diffusing reaction systems, a phenomenon referred to as self-organization (Nicolis & Prigogine, 1989).

Fractal patterns have proven to be important models of heterogeneous landscapes (Milne, 1992), and have important consequences for the movement of organisms (Johnson *et al*., 1992*a*) and co-existence of species (Palmer, 1992). Studies of Tenebrionid beetle movements in fractal landscapes have shown that spatial heterogeneity strongly affects diffusion rates of organisms and can cause both augmented (facilitated) diffusion rates as well as inhibited diffusion (Johnson *et al*., 1992*b*). This suggests that the anomalous kinetics observed in chemical systems may apply more generally to the movement of and interaction among organisms in heterogeneous landscapes.

2. Methods

2.1. MODEL IMPLEMENTATION

We used a model similar to a cellular automata, except that unlike a cellular automata, we did not focus on state changes within fixed neighborhoods. Rather the model consists of populations of finite automata (i.e. individual predator and prey) diffusing across the lattice. Encounters occurred when two individuals attempted to occupy the same lattice cell. Probabilities of movement, reproduction and mortality were stored in a rule table for each species. Updates to the lattice occurred in an asynchronous fashion, i.e. the outcome of each encounter was resolved before updating the next available cell. In order to avoid directional update biases, the model cycled through a randomized list of available lattice cells, thereby updating all cells during each iteration, but in random order.

Several movement rules were employed. In most simulations, a target cell was chosen from the four nearest neighbor cells. Individuals always moved to unoccupied target cells, whereas prey individuals could not move to a cell containing a predator. In other simulations, the target cell was chosen randomly some fixed distance away from an individual's current position. The final movement rule was to simply chose a random target cell from the entire lattice, thus removing any spatial effects.

Reproduction was simulated by a process analogous to cell division. When an individual moved to a new location, reproduction was accomplished by leaving a new individual at the old location. Prey reproduced by occupying empty cells, however if a prey moved to a cell occupied by another prey individual, then one of the two individuals were removed from the lattice imposing a strong density-dependent mortality. Prey reproduced at each time step effectively setting the generation time to one iteration. Predator reproduction and mortality occurred in the same fashion, except that predators only reproduced when moving to a cell occupied by a prey (simultaneously reproducing itself and "consuming" the prey). In addition, a 10% background rate of mortality was imposed on predators that did not encounter prey during a given iteration.

2.2. MODELING HETEROGENEOUS LANDSCAPES

Patchy or spatially heterogeneous environments are an important consideration in the dynamics of interacting populations (Kareiva, 1990). In order to examine the effect of spatial heterogeneity on the kinetics of predator–prey interaction, we ran simulations in which portions of the lattice were made unavailable according to a binary mask. Several methods were used to generate masks including percolation maps, gradient percolation maps, and segmented fractional Brownian surfaces (Peitgen & Saupe, 1988).

Percolation maps were constructed by generating a uniform random number between 0.0 and 1.0 at each lattice site. If the random number generated at a particular cell was less than an *a priori* probability or p-value, the cell was turned "on" (i.e. it is set to 1). Percolation maps are important models used in condensed matter physics (Kopelman, 1989), and have been used as models of heterogeneous landscapes in diffusion studies of animal movements and other ecological processes (Gardner *et al*., 1987, 1989; Turner *et al*., 1989; Johnson *et al*., 1992*a*). An interesting feature of percolation maps is the sudden appearance of a spanning cluster, a connected set of cells connecting opposite sides of the lattice, when the p-value is $\geqslant 0.5928$ (Kopelman, 1989).

Gradient percolation maps are constructed similarly, except that the probability of cells being turned on (p) is varied according to a linear gradient from left to right across the lattice (Fig. 1). As before, a random number between zero and one was generated at each lattice site and compared to the predetermined p-value for that site. Random numbers below a cell's p-value resulted in the cell being turned on.

For the purpose of comparing different gradient maps, we define a gradient parameter (γ) equal to the linear slope of the gradient times the width of the lattice. A gradient parameter of 1.0 produces a probability gradient varying from $p = 1$ at one edge to $p = 0$ at the other. Small values of γ produce shallow gradients, whereas large values of γ produce a sharp transition from "on" to "off". A γ-value of zero produces no gradient; the entire mask has a p-value of 0.5. Note that if a $\gamma = 0$ map is viewed at coarse resolution, it is homogeneous at the broad scale, but there is much heterogeneity at the fine scale, as any local neighborhood will have a random mixture of "on" and "off" cells. Conversely, as γ becomes large, the map exhibits broad-scale heterogeneity from large regions of totally "on" or "off" cells, but most local

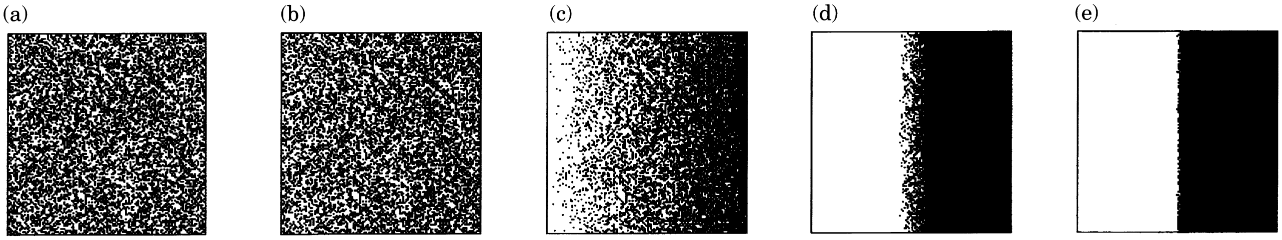

FIG. 1. Gradient percolation masks. Gradient parameters are (a) 0.01, (b) 0.02, (c) 0.05, (d) 0.14, (e) 0.37, (f) 1.00, (g) 2.72, (h) 7.39, (i) 20.09 and (j) 54.60. A gradient parameter approaching zero [Fig. 1(a)] produces a standard percolation map with $p = 0.5$. Available cells are shown in white.

neighborhoods are homogeneous (all "on" or all "off"), except in a narrow transition zone where "on" and "off" cells intermingle. Also note that the percolation gradient is symmetric and therefore the total area available to individual predator and prey is approximately equal across all γ-values.

Fractal landscapes were generated by segmenting fractional Brownian surfaces. This method provides a range of contagion or clumping in the resulting lattices and is a better approximation of real landscapes than are random maps (see Gardner *et al.*, 1987). The fractional Brownian surfaces were created using the algorithm described by Saupe (Peitgen & Saupe, 1988) and then "segmented" into a binary mask by setting all pixels less than the mean to zero and all greater than or equal to the mean to one. The resulting image contained approximately 50% on-cells. Fractional Brownian masks generated with a Hurst exponent of zero generated small clusters of "on" cells with relatively little contagion. Larger Hurst exponents result in increasing contagion and hence less fragmentation within clusters of on-cells (Fig. 2).

2.3. REACTION KINETICS

As discussed previously, the relationship between the concentration of a chemical reactant and reaction rate is termed the reaction order and corresponds to the exponents in a chemical rate equation [e.g. eqn (3)]. To estimate the "reaction order" of our ecological simulations we borrowed a technique commonly used in experimental chemistry. By alternately making prey and then predator populations non-limiting, the effect of each population density on reproduction rate can be measured empirically (Snoeyink & Jenkins, 1980). This was done by initializing the model with the predator population near zero and the prey population much larger. If predator densities can be considered negligible, the prey growth rate is determined by a pseudo-first-order equation:

$$\mathrm{d}A/\mathrm{d}t = K_1 A^a \quad B \ll A \ll N, \tag{7}$$

where A is the number of prey, N is the carrying capacity (number of on-cells in the lattice), and the rate constant $K_1 = k_1$. Moreover, if predators are present at low density in an environment where prey are essentially at their carrying capacity, prey densities can be regarded as constant and predator growth rates will follow pseudo-first-order kinetics:

$$\mathrm{d}B/\mathrm{d}t = K_2 B^b \quad B \ll A \approx N, \tag{8}$$

where B is the number of predators, N is the carrying capacity, and $K_2 = k_2 A^a - k_3$. Taking the logarithm of the equations, the system becomes

$$a = \frac{\log(\mathrm{d}A/\mathrm{d}t)}{\log(A)} + \log K_1 \tag{9a}$$

$$b = \frac{\log(\mathrm{d}B/\mathrm{d}t)}{\log(B)} + \log K_2 \tag{9b}$$

The reaction order is estimated by regression of the log–log plot of population growth rate versus density.

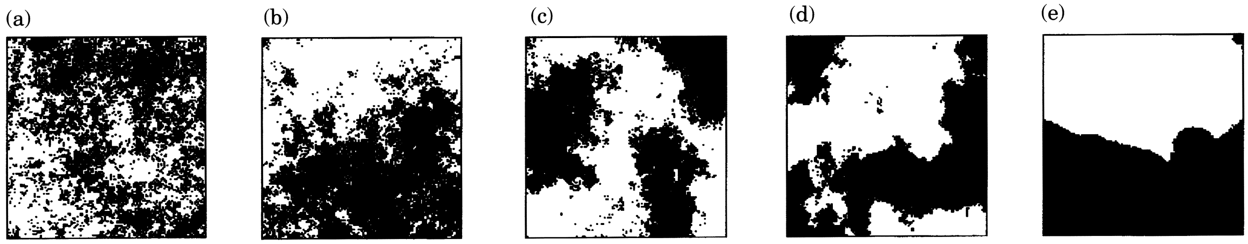

FIG. 2. Segmented fractional Brownian masks. Hurst exponents are (a) 0.0, (b) 0.25, (c) 0.50, (d) 0.75 and (e) 1.0. Available cells are shown in white.

2.4. SIMULATIONS

For each mask used, ten simulations were run for each of the cases (predator limiting, prey limiting) corresponding to eqns (4) and (5). Large lattices of 1000×1000 cells were used to reduce finite-size effects. For gradient percolation maps and fractional Brownian maps, where approximately 50% of the cells were available, there were approximately 5×10^{-5} cells available for colonization. On percolation maps, the number of cells varied according to the p-value with the expected number of on-cells being p times the total lattice size, i.e. $p \times 10^6$. Predator and prey growth rates were recorded over 20 iterations and the reaction order estimated from the log–log regression of growth rate versus density.

A second series of simulations was run to test the effect of increasing "jumping distance" of predator and prey individuals. Uniform lattices were used and the jump distance increased from one cell to ten cells, in effect increasing the diffusion rate. Reaction order was estimated as described previously.

2.5. PHASE PLANE ANALYSIS

A well known feature of the Lotka–Volterra system is that it exhibits neutrally stable limit-cycles in the phase plane, i.e. the eigenvalues of the Jacobian have zero real parts (Murray, 1989). Thus the Lotka–Volterra model has no dynamical attractor. Rather, the trajectory of the system is determined by the initial conditions. We qualitatively analyzed the dynamical behavior of our spatially explicit model by constructing phase portraits at 1, 10, 100 and 1000 time steps. Two simulations were run, the first with local (nearest neighbor) diffusion and the second with random placement on the lattice (complete mixing). The model runs were started from 10000 initial predator and prey population densities. Due to computational limitations 100×100 cell lattices were used. For each run the change in predator and prey density was recorded over a single time step. From these data, a "vector field" plot was drawn showing the direction and magnitude of the system trajectory in the predator–prey phase plane. The behavior was course grained by averaging nearby vectors into a 20×20 array.

3. Results and Discussion

3.1. EMERGENT SPATIAL PATTERN

Emergent traveling waves were observed in time series of the predator-prey simulation on homogeneous lattices (Fig. 3). For these simulations, the probability of prey reproduction on encountering an available cell was set to 1.0 [approximates k_1 in eqn (2)]; the probability of predator reproduction on encountering prey was set to 1.0 [approximates k_2 in eqn (2)]; and predator mortality was set to 0.05 per iteration [approximates k_3 in eqn (2)]. When predator and prey are given different colors, the structure of the waves becomes apparent. Prey form a thin, dense wave front, with a diffuse trailing edge of predators. Bulk movement of populations occurred even though the movement rule was local and directionally random. This movement resulted from differential mortality of individuals across the wavefront. Prey adjacent to predators experienced greater mortality due to predation, whereas predators along the trailing edge of the wave front experience a net decrease due to lack of resources (prey).

Emergent wave phenomena are common to a variety of biological and physical situations, including excitable media (Gerhart *et al*., 1990), certain chemical oscillators (Murray, 1989), aggregation of slime molds (Murray, 1989), as well as predator–prey systems as demonstrated here and elsewhere (see Karieva, 1990). A classic example is the Belousov–Zhabotinski reaction which can produce highly symmetric spiral waves (Murray, 1989; Nicolis & Prigogine, 1989). In terms of reaction kinetics (i.e. the encounter rate of predator and prey) we note that the wave patterns result in a relatively smooth, elongated boundary between predators and prey. This effectively reduces the encounter rate because the "reaction" occurs along a nearly linear boundary instead of in two dimensions as would occur in a randomly mixed system.

3.2. SPONTANEOUS SEGREGATION OF POPULATIONS

Simulations on gradients also produced emergent spatial patterns, with prey occurring more densely at intermediate levels of heterogeneity and predators tending to occupy more open parts of the lattice (Fig. 4). This apparently occurs because as fewer and fewer lattice sites are made available for colonization, it becomes increasingly unlikely that predators will encounter enough prey to offset their background rate of mortality. In more open areas, predators can rapidly increase and locally deplete the prey population, resulting in both lower prey density and prop agating waves as observed in homogeneous maps (Fig. 3).

We note that gradient percolation maps may be valuable models for studying ecotones (i.e. ecological transitions) and that these results suggest a number of hypotheses for field studies of population dynamics. Unfortunately, there has been little effort in the past to study spatial dynamics of populations in the field

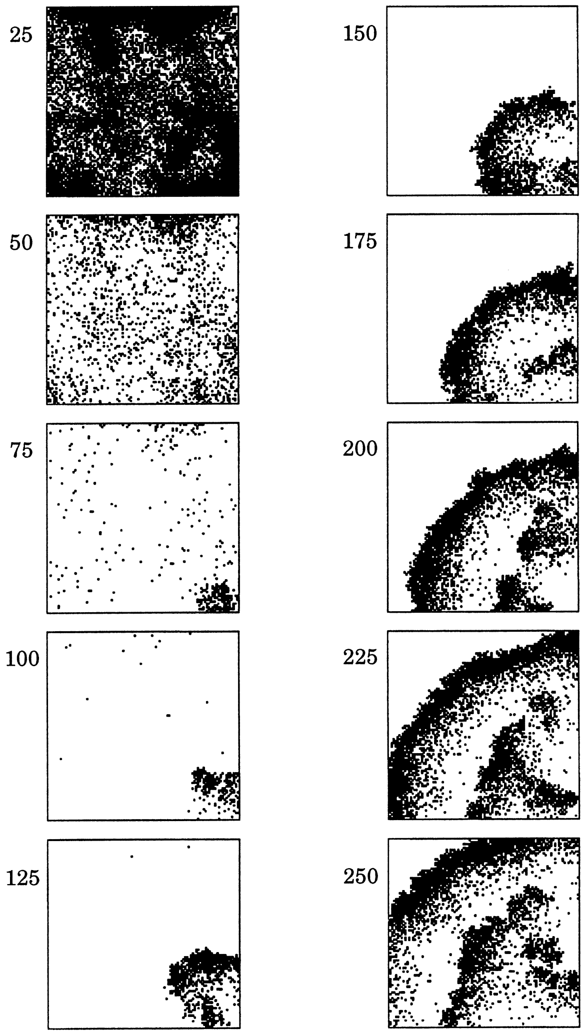

FIG. 3. Emergent wave patterns in the predator–prey model (shown on a 100 × 100 lattice). White cells are unoccupied, whereas black cells represent a single prey or predator individual. Each frame represents 25 time steps.

and they remain largely a property of ecological models (Kareiva, 1990; however, see Johnson *et al.*, 1992*b*).

3.3. ANOMALOUS REACTION KINETICS

In order to place our qualitative observations in a more formal framework, we applied the theory of chemical kinetics in heterogeneous systems to the reaction–diffusion model presented here. This approach allows us to quantify the extent of the deviation the spatially explicit model exhibits relative to the assumptions of the ODE Lotka–Volterra model. As described previously, we estimated the reaction order, which expresses the sensitivity of the growth parameter to the population density, for simulations with different degrees of introduced spatial heterogeneity. For a homogeneously mixed system, the expected reaction order is 1.0 for both predator and prey (second order overall).

As spatial heterogeneity is increased (from $p = 1.0$ to $p = 0.5$), reaction order becomes increasingly anomalous, i.e. < 1.0 (Fig. 5). Even on a homogeneous lattice ($p = 1.0$), reaction order estimates are considerably less than the expected value of 1.0. For increasingly fragmented lattices, the reaction order drops considerably, falling below 0.4 for prey and below 0.2 for predators. Estimates for predators were consistently lower than for prey on heterogeneous lattices, which supports our observations that randomly diffusing predators are unable to exploit prey resources effectively in highly heterogeneous environments.

The variance of our reaction order estimates across ten simulations was, in nearly all cases, extremely small, perhaps due to the large (1000 × 1000) lattices used. The exception was for percolation lattices with $p \leqslant 0.5$, where variances suddenly increased (Fig. 5). For p-values less than 0.3, our method actually

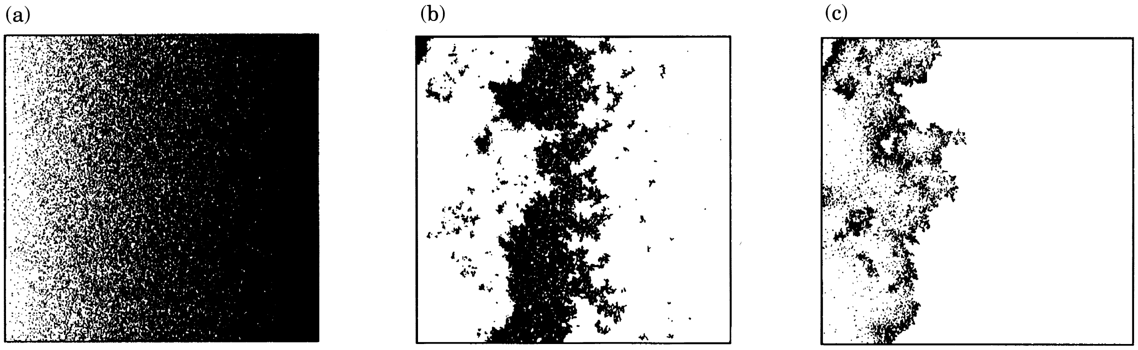

FIG. 4. Segregation of predator and prey populations on a 400 × 400 gradient percolation map: (a) gradient mask with available cells shown in white; (b) distribution of prey (shown in black); (c) distribution of predators (shown in black).

gave negative reaction order estimates. This was due to the fact that despite our use of small initial populations, populations decreased from the initial value on percolation maps with a low p-value. This suggests that our analytical framework breaks down when available sites are sparse and highly fragmented, and that a probabilistic or stochastic description of the population dynamics may be more appropriate.

The same general trend of anomalous reaction orders was observed with increasingly heterogeneous environments using gradient percolation maps and for segmented fractional Brownian surfaces (Figs 6 and 7). The difference between prey and predators is particularly striking for small gradient percolation parameters, with predator reaction order estimates approaching zero. The slight increase in the predator order estimate for $\gamma = 0.031$ is due to the fact that fragmented clusters at slightly higher γ-values can become joined as the on-cells become more evenly distributed across the lattice (see Fig. 1).

The results from the landscapes generated with fractional Brownian surfaces are less clear, but do show a general decrease with greater heterogeneity (smaller Hurst exponent). Whereas Hurst exponents approaching zero did produce complex, heterogeneous fractal patterns, they were clearly more contagious than random lattices. Nevertheless, the general trend holds, although we can suggest no explanation for the sudden drops in the reaction order estimate, such as for predators at $H = 0.5$.

The anomalous model behavior observed so far (Figs 5–7) was due to the diffusion-limited nature of the individual interactions. Because individual movements were constrained both topologically to a two dimensional surface, as well as by fragmentation of the lattices, random diffusion is not sufficient to completely mix the system and spatial pattern results. However, we can test the importance of diffusion-limited dispersal and the robustness of our analytical framework by augmenting the dispersal of simulated prey and predator. When the jump distance of individual predator and prey is increased, in effect decreasing the spatial correlation of individuals through time, increased mixing occurs and the kinetics are less anomalous (Fig. 8). The model converges on the expected reaction order of 1.0 for a well-mixed system (or 2.0 if summing across species).

3.4. QUALITATIVE BEHAVIOR IN THE PHASE PLANE

So far we have been mainly concerned with the effects of spatial heterogeneity on the kinetics of the model. An alternative is to consider the global dynamics of the system in the phase plane (Figs 9 and 10). Although we have demonstrated anomalous behavior due to both emergent spatial patterns and fragmented lattice, the qualitative dynamics show only slight differences when compared to traditional ODE models (see for example, Berryman, 1992). Unlike the Lotke–Volterra model [eqns [(1a–b)], the lattice-based model exhibits strong density dependence resulting in a stable limit cycle with noise (owing to the stochastic nature of the interactions;

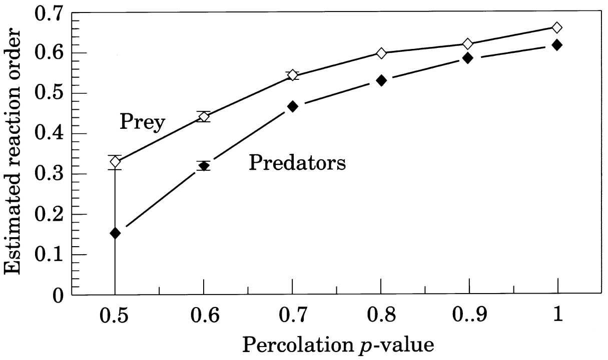

FIG. 5. Estimated reaction order of simulated predator–prey system using uniform percolation masks. Percolation p-value refers to the density of randomly placed available sites on the lattice. Error bars are ±1 SD.

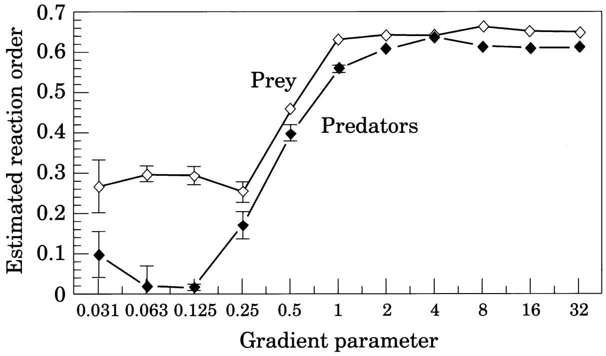

FIG. 6. Estimated reaction order of simulated predator–prey system using gradient percolation masks. Error bars are ±1 SD.

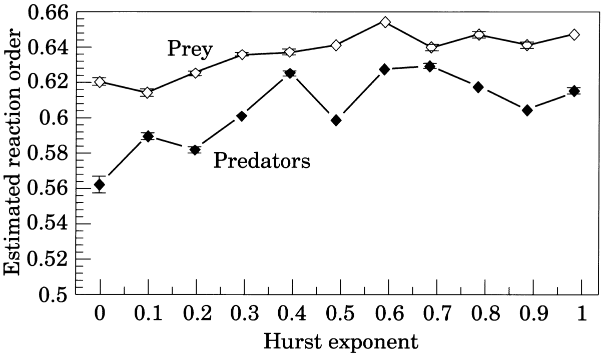

FIG. 8. Estimated reaction order of simulated predator–prey system with increasing jump distance (diffusion rate). Simulations occurred on homogeneous lattices. Error bars are ±1 SD.

Fig. 9). The density dependence arises not because of the implementation of the interaction rules, but rather due to the lattice itself. Because the number of individuals is strictly limited to the number of available cells, the phase space is compressed into a triangular region at or below the line where the sum of the populations equals the lattice size. Whereas the predator zero-growth isocline is roughly vertical [Fig. 9(a)] in accordance with the Lotka–Volterra predator equation [eqn (1b)], the prey isocline slopes downward toward the lower right corner indicating a logistic (i.e. density dependent) prey growth function as shown in eqn (2) with the lattice size setting the carrying capacity. (Note that this does not effect our analysis in Section 3.3 because $A/K \approx 0$ when $A \ll K$).

Simulations where a global movement rule was used showed essentially the same qualitative dynamics as did simulation where movement was local (Fig. 10). Again the trajectories indicate logistic prey growth [Fig. 10(a)] with the system eventually collapsing down to a noisy limit cycle [Fig. 10(b–d)]. The lack of a qualitative difference between the spatial and non-spatial versions of the model is intriguing. Local diffusive instability resulting in emergent spatial patterns such as those in Fig. 3 are often cited as a possible mechanism for maintaining global stability and coexistence of populations (Karieva, 1990; Wilson *et al.*, 1993). However, this idea is rarely tested by examining the behavior of equivalent models with and without local interactions. Our results suggest that emergent spatial patterns do not necessarily increase global stability.

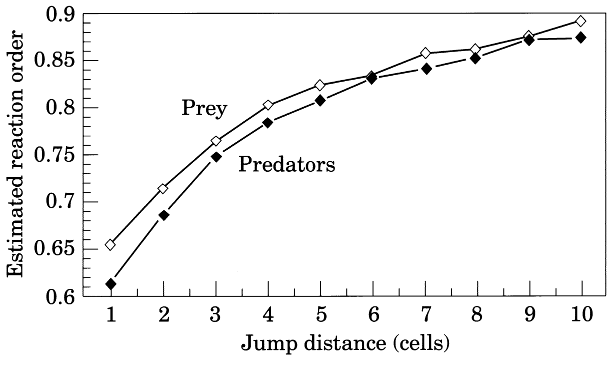

FIG. 7. Estimated reaction order of simulated predator–prey system using segmented fractional Brownian surfaces. The fractal dimension of the simulated landscapes is approximately $2.0 - H$ where H is the Hurst exponent. Smaller Hurst exponents represent increasing heterogeneity. Error bars are ±1 SD.

Although the local and global movement rules resulted in the same overall, qualitative dynamics (i.e. a noisy limit cycle), an important difference between the two systems does emerge. Initially, at $t = 1$ [Figs 9(a) and 10(a)], the phase plots are nearly identical. This is because the simulations were initialized with randomly placed individuals, hence early in the time series, both systems are well mixed. Later in the time series, localized movement results in emergent spatial patterns, whereas simulations with global movement remain homogeneous. In the phase plane, the difference is manifested as a change in the position of the center of the attractor, i.e. the point where $A \neq 0$, $B \neq 0$, and $\mathrm{d}A/\mathrm{d}t \approx \mathrm{d}B/\mathrm{d}t \approx 0$. In the spatially homogeneous system, the center remains fixed in phase space [Fig. 10(a–d)], however localized interactions result in a shift of the center as the system evolves [Fig. 9(a–d)]. Generally, the shift is toward slightly higher prey density and considerably lower predator density. As noted previously, local movement results in segregation of predator and prey populations, reducing the predation rate, thus supporting larger prey populations and fewer predators. In the ODE approach, phase portraits can be constructed analytically by writing the autonomous system $\mathrm{d}A/\mathrm{d}B = f(A, B, \ldots)$. Time no longer enters into the equation and therefor the dynamics are, by definition, time-independent. Yet we have just shown that localized interactions can lead to a shift in the dynamics as spatial patterns emerge. Thus a time-dependence in the attractor of the system, along with time dependence of rate constants and non-analytic reaction orders (Kopelman, 1989), may be added as another "anomalous" property of spatially heterogeneous reaction systems.

4. Conclusions

Assumptions of spatial homogeneity are interwoven throughout ecological theory, particularly in models based on Lotka–Volterra dynamics. The study of ecological interaction in spatially complex environments is increasingly seen as an important area for both empirical (Kareiva, 1990, Johnson *et al*., 1992*b*) and theoretical research (Godfray & Pacala, 1992; Murdoch *et al*., 1992; Milne, 1992). However, despite obvious limitations in the Lotka–Volterra model (Slobodkin, 1992), it holds an important place in ecological theory. In certain respects, it can be viewed a "frictionless pendulum" for ecology. Much as friction introduces anomalous behavior to real physical pendulums when analyzed in the context of classical mechanics, investigation into the "anomalous" behavior of simulated and natural populations provides important insight into the underlying mechanisms and constraints determining ecological dynamics. This approach, we feel, will lead to a richer formalism for ecological theory.

A model similar to ours was investigated by Wilson *et al*. (1993). Although they concentrated

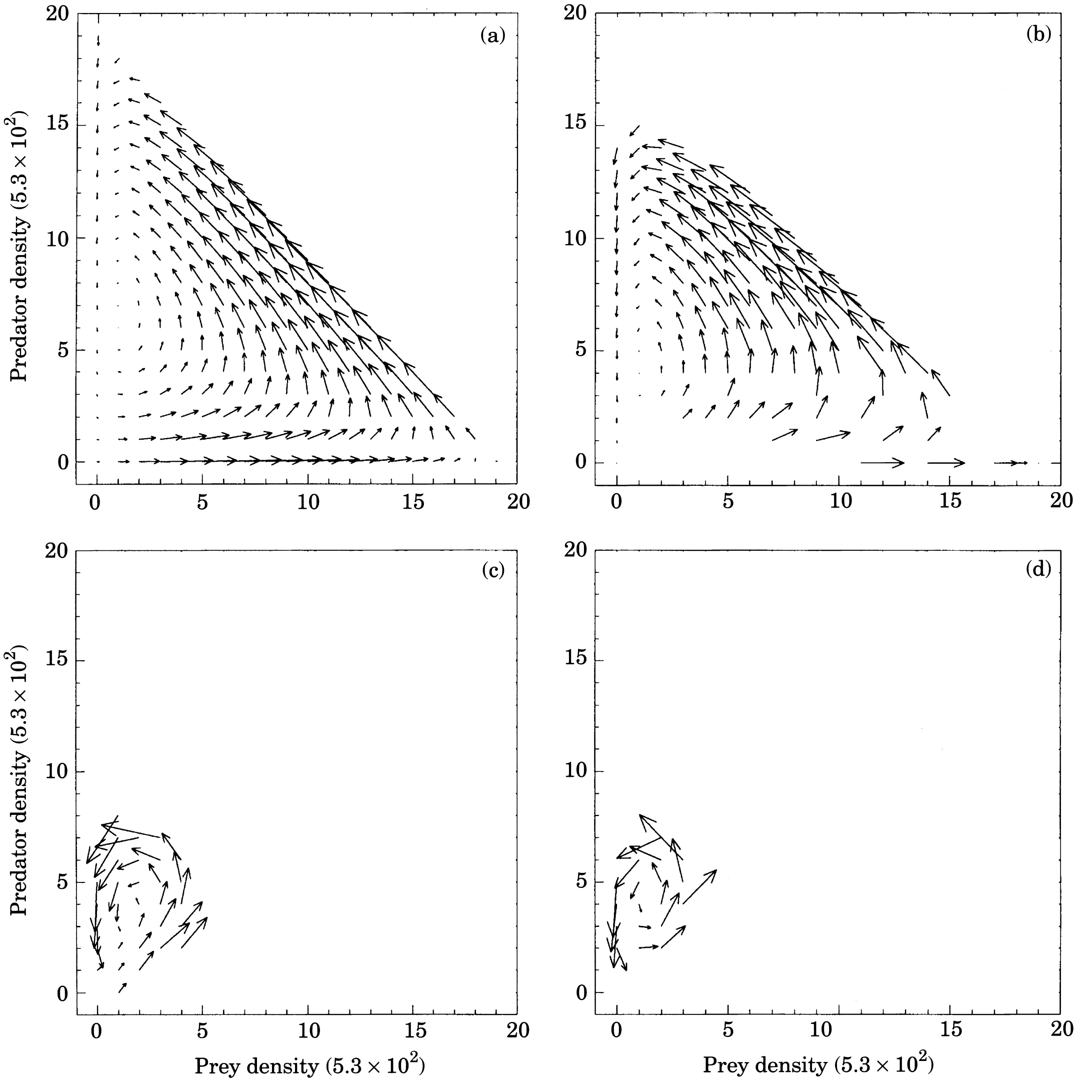

FIG. 9. Phase plane plot of predator–prey model at (a) $t = 1$, (b) $t = 10$, (c) $t = 100$ and (d) $t = 1000$ time steps. Vectors represent change in predator and prey density over a single time step.

exclusively on spatially homogeneous environments, their work makes an important contribution toward explicating the sources of deviations from standard Lotka–Volterra dynamics. In their analysis of an individual-based predator–prey model, they observed local diffusive instabilities leading to overall stability of the populations. Under most scenarios, the patterns observed were static with small-scale (relative to the lattice) emergent patchiness in the populations. Traveling wave fronts were observed by Wilson *et al.* (1993), but only when prey growth rate was varied in an oscillating checker-board fashion. We can think of no natural situation to support such an assumption.

In general, however, the conclusions of Wilson and co-workers are in agreement with our observations. They point out that the discrete nature of space and time in individual-based models leads to deviations from a continuous differential equation representation. In the limit as the time step and lattice cell size go to zero, their discrete model converged to Lotka–Volterra dynamics, much in the same manner as our results for increasing individual diffusivity (Fig. 8). Our analysis extends their conclusions to include the effects of a spatially heterogeneous environment, a situation, we argue is more general in nature.

One question that has received little attention, but is nonetheless important, is the relative importance of global density dependence (resulting from simulating on a finite lattice) versus localized diffusive instabilities in determining the overall model behavior. Kareiva (1990) for example, discusses the importance of localized patterns in altering the stability properties of predator–prey models. While we have

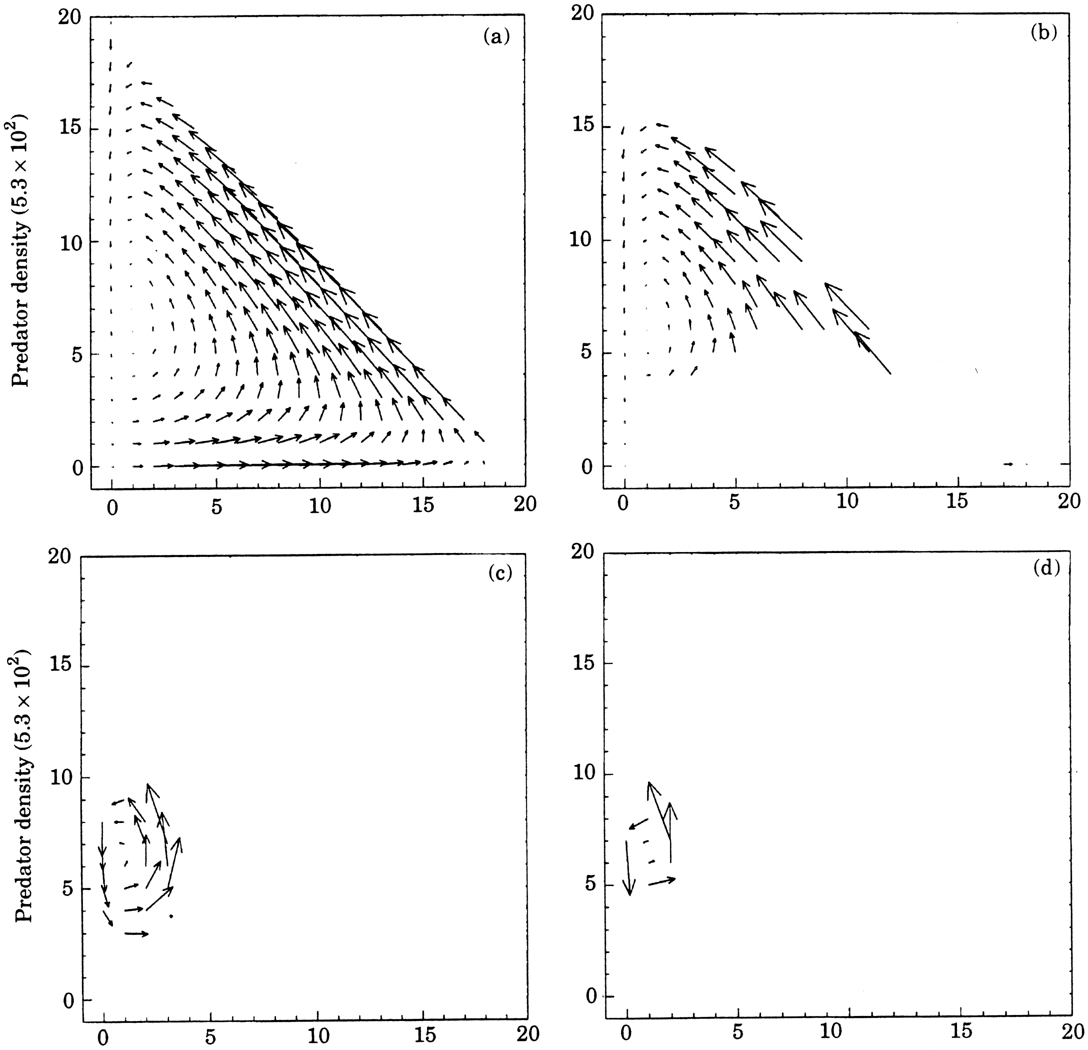

FIG. 10. Phase-plane plot of predator–prey model with random placement at (a) $t = 1$, (b) $t = 10$, (c) $t = 100$ and (d) $t = 1000$ time steps. Vectors represent change in predator and prey density over a single time step.

shown that emergent spatial patterns are important in determining rates of population growth and interaction (as evidenced by an anomalously low reaction order), qualitatively there appears to be little difference between the phase-plane trajectories of simulations where spatial patterns were observed and those with random mixing of the populations. We did however, observe time-dependence in the position of the attractor due to emergent spatial patterns. This suggests that when localized interactions are modeled, the attractor has a higher embedding dimension than the two-dimensional phase plane. A measure of the spatial distribution of the populations, such as a fractal dimension or a spatial cross-correlation, might be added as a third axis. It is possible that embedding the attractor in this higher-dimensional phase space would remove the time-dependent behavior.

Individual-based models, such as the one presented here, have a natural appeal for modeling ecological systems (Huston *et al*., 1988). Ecosystems are spatially structured and the movement and interaction among organisms takes place in a spatial context. The explicit representation of individuals and implementation of rules that define local interactions in individual based models allows a direct mechanism for including fine-scale ecological knowledge to be included in course-scale predictive models. One advantage of analytical approaches based on differential equations is the ability to manipulate the equations and deduce novel hypotheses. However, the mapping of local assumptions about individual behavior onto global state variables, as with differential equations, introduces a layer of abstraction between the model and its underlying assumptions. For instance, we might want to introduce a directional movement bias that varies depending on the location of the individual. This is a fairly straightforward process in an individual based model, but requires, in the case of differential-equation-based model, that the modeler extrapolate this local behavior onto a global parameter.

Our model clearly shows systematic deviations in terms of kinetics from the expectations of Lotka and Volterra's predator–prey model when diffusion is limited by local movements. The effect is enhanced in heterogeneous landscapes. However, the qualitative dynamics were not effected by localized interactions and could be derived from traditional ODE models with prey density dependent growth. Thus, although spatially explicit models may make different predictions than their ODE counterparts, both approaches are appropriate under different circumstances. For instance, when detailed information about individual dispersal and foraging behavior are lacking, but large-scale population and demographic data are available, ODE or extensive-variable approaches can be used to characterize the system dynamics (Berryman *et al*., 1987). On the other hand, when data are available to parameterize local dynamics, spatially explicit models can have distinct advantages, such as the ability to make predictions at specific locations in the landscape. In a management context, simulations can be run directly on top of digitized geographic information and the model used to assess the overall effect of localized alterations of the landscape. Such models could be used for instance in deciding the location, size and frequency of timber harvests or other actions which would change the spatial configuration of available habitat. In a theoretical context, spatial, individual-based models are complimentary to extensive-variable approaches such as ODE population models. Spatial models can be compared to their non-spatial analogs to explore the effect of localized interactions on the model dynamics. Another approach is to use a spatial model to parameterize or derive a mathematical description. We believe that these approaches, along with empirical validation of the models, will enhance the development of theoretical ecology.

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