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EFFECT OF DIMENSIONALITY ON LOTKA-VOLTERRA PREDATOR-PREY DYNAMICS: INDIVIDUAL BASED SIMULATION RESULTS

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The effect of varying habitat dimensionality on the dynamics of a model predator-prey system is examined using an individual-based simulation. The general results are that in one dimension fluctuations in abundance of prey and predators occur over a large range of spatial scales (extinctions occur over many spatial scales). In two dimensions (and low mobilities of prey and predators) the dynamics become more predictably periodic at local scales and constant at larger scales due to statistical stabilization. In three dimensions, the model can become “phase-locked” with prey and predators displaying oscillations in abundance over large spatial scales.

Introduction. Variation in habitat structure abounds in nature, including such geometrical features as the size of the habitat (MacArthur and Wilson, 1967), connectivity to neighboring habitats (Harrison, 1991), and the environmental variation within a habitat (Milne, 1992). An additional feature of habitat structure, which has been studied to a much lesser extent, is the dimensionality of the habitat for a given species or community (Briand and Cohen, 1987; Whitehead and Walde, 1992). Dimensional variation is widespread in ecological systems. In aquatic systems, small streams and rivers

could be considered one-dimensional for species (e.g. benthic insects) that can move on a daily basis across the breadth of the system, but can only visit a small portion of the length of the stream during a generation. For some species the habitat dimensionality may be irrelevant: a lake is small for a cruising non-territorial predator, such as a fish, which may span the entire system in short times. The benthic region of the same lake, however, might present a large two-dimensional system for some aquatic insects, while being three-dimensional for both phytoplankton and zooplankton. Terrestrial systems can also be one-dimensional, such as narrow valleys in the Rocky Mountains, where the width may be about 1–2 km but the length might be over 100–200 km, compared to two-dimensional forests in the foothills of the Rocky Mountains. Clearly the definition of habitat dimensionality depends on the spatial structure of the habitat and organismal characteristics, such as mobility, behavior, and life-history features, for a particular species.

Given that dimensional variability is present in ecological systems, it is relevant to ask how this dimensionality influences the dynamics of ecological interactions. While it is well known that dimensionality affects many features of physical systems consisting of very simplistic interacting “entities” (Wu, 1982; Stauffer, 1985), these effects have not been considered to a large extent in ecological systems. Is dimensionality an important feature affecting population fluctuations? In this paper, we begin to explore the effects of dimensionality on the dynamics of ecological interactions. Holding all features of the interacting predators and prey fixed and restricting both the predator and the prey to habitats of the same dimensionality, it will be shown here that the dimensionality of the habitat has profound effects on the population dynamics at both small and large spatial and temporal scales.

Basic Features of the Model System. We will use the individual-based model (IBM) (DeAngelis and Gross, 1992) formulation described by Wilson *et al.* (1993) of a Lotka–Volterra (LV) model for the examination of dimensionality effects. This is a simulation that explicitly models thousands of individuals, each potentially carrying its own age, feeding, and other life history variables (McCauley *et al.*, 1993) distributed over a uniform space approximated by a lattice. Such an approach in population dynamics should be thought of as the analog to the simulations of spin systems in condensed matter physics (Huang, 1987), or lattice gas simulations in hydrodynamics (Frisch *et al.*, 1986). These approaches allow interesting and easy solutions to problems that, cast as stochastic coupled partial differential equations with arbitrary boundary and initial conditions, are essentially intractable. Our philosophy in applying these techniques is twofold: first, find agreement between the simulation and the assumed differential equations in some limit, then, second, examine the IBM in

the limit that mathematical methods cannot easily take us. Clearly, an analytic solution is to be favored over simulation results, but such simulations can also be beneficial in “posing” the correct analytic problem for specific biological scenarios. In this section we will discuss the basic simulation rules, present a comparison with a discrete-time analytic formulation, and explore initial results with limited mobility of the individuals on a two-dimensional lattice.

We first describe the interactions that take place within a cell of the lattice. Each cell can have one of four occupancy states: empty, prey, predator, or prey and predator. Every time step a prey can produce an offspring with probability α . Searches are performed to place this offspring into a cell near its progenitor. This limited search fails when a large fraction of the cells are occupied, in which case the offspring is aborted. Predators suffer mortality independent of age, spatial location, and feeding history. This mortality is applied by independently removing each predator with a probability δ each time step. Whenever a prey and a predator occupy the same cell, the predator consumes the prey with an attack probability β . A successful predator produces an offspring immediately following the attack with a conversion efficiency γ , and the offspring is placed onto the lattice in a similar manner to the prey offspring. All the runs discussed below will implement these values for the rates: $\alpha=0.25$, $\beta=1.0$, $\gamma=0.5$ and $\delta=0.1$. A common time scale for these interactions is specified by the discrete time step used in the simulation, which in the work presented here is fixed at $\Delta t=1$. These interactions are incorporated in a concurrent manner, as discussed by McCauley *et al.* (1993), meaning, for example, that predators marked for death during a time step are allowed full opportunity to attack prey and subsequently reproduce offspring during that same time step.

These rules describe a discrete time version of the Lotka–Volterra model:

$$\begin{aligned} V(t + \Delta t) &= V(t) + \alpha V(t) \Delta t - \frac{\beta}{N} P(t) V(t) \Delta t \\ P(t + \Delta t) &= P(t) + \frac{\beta}{N} P(t) V(t) \Delta t - \delta P(t) \Delta t, \end{aligned} \quad (1)$$

where N is the number of lattice sites in the system, and the other parameters are the probabilities discussed in the above section reinterpreted as rate constants. This discrete-time model will be compared with the simulation model in the limit that all prey and predators are randomly mixed over the entire lattice (the homogeneously mixed mass-action limit). The primary difference between the equations in (1) and the simulation is the restriction of at most one prey and one predator at each lattice site. This restriction introduces a “hard ceiling” in the populations at the number of lattice sites, N , that adds a

form of density-dependence onto the prey growth terms and the numerical response which only arises as densities approach their upper limit on the lattice. Further, partitioning individuals into lattice sites for finite time periods serves to limit the predators' access to prey individuals, altering the functional response. Poland (1989) shows that a Lotka–Volterra model having two features: (i) with cells being either unoccupied, occupied with a prey, or occupied with a predator, but not both; and (ii) a clustering of prey that reduces predators' access to the prey in the clusters' centers changes the dynamics of the LV model to one possessing a limit cycle in the continuous time limit. Our hard ceilings and interaction cells operate in a similar manner.

What we will show presently is congruence between the simulation model with homogeneous mixing, and equations (1) with the appropriate implementation of a hard ceiling. In the simulation, the hard ceiling was incorporated such that prey and predator “offspring” (those individuals produced within the present time step) are placed onto the lattice before the “adults” (produced in earlier time steps) marked for death are removed, and thus the offspring cannot occupy the sites of deceased adults. Then, in the finite-difference solution, the number of predator offspring added to the population, for example, is capped by requiring $P(t-1) + B(t) < N$, where $B(t)$ represents the net number of predator offspring produced during time step t , and $P(t-1)$ is the number of predators present at the end of the previous time step. The offspring produced above this amount are aborted. The placement of prey offspring is treated in a similar manner. An alternative for enforcing these ceilings is to remove the deceased adults before placing the offspring onto the lattice. This produces a quantitative difference in the results, but does not change the qualitative behavior.

Figure 1a presents the finite-difference solution of equation (1) when $\Delta t = 1$ and the parameters take on the values discussed above. Without the hard ceiling at $N = 16,384$, the oscillations would grow until the populations turn negative due to the temporal discretization. The individual-based simulation run corresponding to Fig. 1a is shown in Fig. 1b. A 128^2 lattice (16,384 lattice sites) is used with homogeneous mixing of the prey and predator populations, meaning each time step the locations of individuals are randomized, before the interactions take place. Good qualitative agreement is observed between the two cases, although some difference between the period of oscillation is observable most likely due to the softer ceiling in the simulation. We accept the similarities between the two figures as evidence that the homogeneously mixed individual-based simulation model is well characterized by the discrete-time model shown in equation (1).

The individual-based model is now examined with diffusive predator and prey populations. All individuals move via a random walk with D steps taken per time step. We interchangeably refer to D as the mobility or diffusivity. Each

(a)

(b)

Figure 1. A comparison of: (a) the discrete-time solution to equation (1), and (b) the results of the homogeneously-mixed simulation model using the temporal evolution of the prey and predator numbers. The starting densities in the two plots are similar, enabling comparisons between both transients and steady-state features. Good agreement is observed, although the periods are slightly different (evidenced by the differences at time step 500) due to the imprecise agreement between the hard ceiling in the discrete time equations set at $N=16,384$ and the “softer” ceiling in the simulation due to the finite lattice of 128^2 sites, the limitation of one individual per lattice site, and the localized search for offspring placement.

of the D steps are performed concurrently for all individuals according to the following process. Every individual chooses one nearest neighbor site to move to during the step. If that site is occupied (whether the present occupant will move or not) the individual forfeits this step and stays at its previous site. If two

individuals choose the same site, one of them is chosen at random to be the winner. If three or more individuals choose the same site, all of them are placed back at their previous sites. Once all such conflicts have been resolved, all individuals are updated, and the algorithm is repeated D times. This algorithm has been used successfully in diffusion problems (Wilson and Laidlaw, 1992).

This algorithm is made more difficult because of three dimensions. In the lower dimensional lattices, each site has four nearest neighbors. One of these nearest neighbour sites is chosen randomly by choosing two random bits (having values 0 or 1 with 50% probability each) with combinations 00, 01, 10 and 11. Associating each of these combinations with a unique direction presents an efficient way of choosing nearest neighbor sites since generating random bits is rather cheap (in CPU currency) (Kirkpatrick and Stoll, 1981) compared to floating point random number generators (for example `drand48()` in C). However, in three dimensions each site has six nearest neighbors. This requires either using floating point random number generators, or approximating the $1/6$ probability of choosing each direction with a $1/8$ probability (requiring three random bits) and throwing away two of the eight possible combinations. We have implemented the random bit alternative. Thus, the mobility of individuals in three dimensions is automatically reduced by three-quarters. To make equal comparisons with the mobilities in the lower dimensions, we have reduced the mobility of each individual in the lower dimensional systems by applying an additional movement probability of 0.75, meaning that only three-quarters of the population moves in any one diffusion step. All mobilities mentioned below will be in units of this $3/4$ stepping probability.

Figure 2 presents snapshots of the lattices at various times for equal predator and prey mobilities of (a) $D=1$ and (b) $D=5$ with the 0.75 movement probability. The spatial habitat is approximated by an 256×256 square lattice with periodic boundary conditions where, for example, an individual stepping off the top of the lattice enters at the bottom of the lattice. Each black dot in the picture represents an individual that travels, on average, only a few percent of this width during its entire lifetime in the high mobility case. The total populations are roughly 16,000 prey and 19,000 predators in the respective pictures. Dynamics operating at a local scale can be ascertained by comparing differences between successive frames, and are similar to the homogeneously mixed system shown above, since in a small quadrat similar in size to the diffusion length scale, say a 10×10 region, the populations within that region are relatively well mixed. Spatial structuring on larger scales is clear, with spatially distant regions being out of phase with one another. These features are enlarged in the higher mobility case, which in many ways looks similar to zooming in on a smaller quadrat of the low mobility system (Wilson *et al.*, 1993).

An alternative plot that presents temporal variation of the population densities, in addition to the spatial variation, can be generated. Figure 3 shows these “spatiotemporal” plots for: (a) $D=1$; and (b) $D=5$. In these plots a horizontal row shows the occupancy of a row of lattice sites at a specific time, with $t=0$ at the top row and $t=1000$ at the bottom row. Every other time step is displayed. A column in one of these figures shows the occupancy of a specific site throughout the simulation. Hence, these figures present most spatial and temporal correlations of interest between the population densities. The transient visible in the upper portion of each figure is present due to the initial condition of occupying only a $L/2 \times L/2$ square of the lattice at $t=0$, not including the row being displayed. At subsequent early times we see the invasion of the prey into the empty portion of the network, followed closely by an invasion of the predators. The results at unit mobility demonstrate a somewhat random variation in the predator and prey densities. Sustained, local oscillations of prey and predator populations are observed in time that last up to roughly five cycles and are then disrupted, with the cycles reappearing later. Neither case shows much lasting sensitivity to the initial conditions.

A considerable change occurs when the mobilities of the prey and predators are increased to $D=5$ in Fig. 3b, where, near the bottom, the plot looks more like a series of horizontal lines, nearly continuous across the entire width of the lattice. The bands have a slope near zero, which implies either one of two things: there is a permanent traveling wave moving in the y -direction (perpendicular to the displayed row), or the entire system oscillates in phase [phase locking (Murray, 1989)]. The pictures displayed in Fig. 2 show that the system is not of a traveling wave form. The two-dimensional system in Fig. 3a is not phase locked in the sense that the system is made up of spatially separated regions, each of which are oscillating at the same frequency but with a random phase: in some regions prey are on the upswing, while in other regions the prey are on the downswing. Phase-locking occurs when some mechanism causes these regions to oscillate in phase with one another, resulting in a global oscillation. In experimental systems this phase-locking mechanism can be as simple as mass exchange between two oscillating systems (Marek and Stuch, 1975). Figure 4 displays the temporal dynamics of the total population for the prey and predators for: (a) $D=1$; and (b) $D=5$. Although the oscillations in the high mobility case are not as extreme as in the homogeneously mixed system (Fig. 1b), there is a much more coherent oscillation than in the low mobility scenario. The effect is amplified even more with slightly higher mobility (McCauley *et al.*, 1993; Wilson *et al.*, 1993). Results of these runs show that the mobilities of the predators and prey can be a critical factor determining the stability of population numbers, and this effect, at least in this model, makes itself evident for just slightly increased mobilities (de Roos *et al.*, 1991).

Figure 2(a)

Figure 2. Snapshots of the predator and prey spatial distributions at various time steps for: (a) low mobility ($D=1$); and (b) high mobility ($D=5$) using a 256×256 lattice with periodic boundary conditions. Each black dot marks an individual prey or predator, with roughly 16,000 prey and 19,000 predators in the respective figures.

Figure 2(b)

At local scales the low mobility distributions follow the temporal dynamics of the homogeneous system observed in Fig. 1, but for much larger scales display overall stability due to statistical stabilization. In the high mobility case, the homogeneous oscillations extend over much larger spatial scales.

Figure 3. Spatiotemporal plots of the prey and predator distributions for low ($D=1$) and high ($D=5$) mobilities. These plots show the spatial distribution horizontally. The plots are built up vertically with time by appending the spatial distribution of a specific row to the bottom of the figure. Thus, the top represents $t=0$ and the bottom represents $t=1000$. The plots for high mobility show phase-locked oscillations over large spatial scales evidenced by the horizontal bands in both the prey and predator pictures.

Figure 4. Prey and predator population numbers for the low and high mobility simulations presented in Fig. 3 are plotted temporally to show the enhanced oscillatory behavior with high mobility.

Dimensionality Effects. The model described above is examined in this section on lattices of one, two and three dimensions to elicit the effects of habitat dimensionality on population-level dynamics. The sole feature that is changed involves the lattice structure itself. A one-dimensional system is approximated by a strip of length L and narrow width W . The one-dimensional systems implemented here have $L = 2048$ lattice sites. The width, however, will be treated as an independent variable, and increased from a minimum of four lattice sites. This variation in the width approximates a continuous change from a one-dimensional to a two-dimensional system. Roughly speaking, the one-dimensional system becomes two-dimensional when the width becomes larger than the correlation length (a measure of the spatial scale over which populations appear homogeneous) (de Roos *et al.*, 1991), which we have shown to be dependent on the life-history features of individuals and their mobility. Likewise, the crossover from two to three dimensions is studied by using a

system of constant length $L=512$ and constant width $W=512$, but with a “depth” H that is varied from two lattice sites to eight lattice sites. The largest three-dimensional lattice is indeed more like a pancake (CPU requirements for larger lattices are prohibitive), but the depth is sufficient to give some indication of three-dimensional behavior.

Edge effects are generally minimized by applying periodic boundary conditions: the one-dimensional system is best visualized as a long soda straw with the two ends joined together. We have examined reflecting boundaries in one-, two- and three-dimensional systems but no qualitative differences result. Absorbing boundaries, on the other hand, where individuals and offspring can step off the edge of the lattice and be removed from the system, are strongly stabilizing. These boundaries all have their counterparts in the mathematical literature. Using periodic boundary conditions one is effectively tiling an infinite space with an identical square system (in two dimensions), conceptually similar to obtaining Fourier solutions to periodic systems where one assumes that a system of size R has the Dirichlet boundary condition $f(x)=f(x+R)$, where f represents the function of interest and x one of the spatial dimensions. In the simulation, however, this periodicity holds for all derivatives as well. Absorbing boundaries set the function to zero at the edges, implying a positive flux towards the boundaries (for non-negative functions) which is responsible for the loss of organisms. Reflecting boundaries, on the other hand, implement Neumann boundary conditions forcing the first derivative to be zero at the boundaries, meaning zero flux at the edges. In situations where the system’s edges advance or retreat in response to internal mechanisms (Wilson *et al.*, 1994) the appropriate choice of boundaries is of utmost importance, however in this system we find no important differences between reflecting and periodic boundaries.

Figure 5 shows the spatiotemporal plots for the prey distributions progressing from lattices of size: (a) 2048×4 , (b) 2048×8 , (c) 2048×16 , (d) 512×512 , (e) $512 \times 512 \times 2$, (f) $512 \times 512 \times 4$, and (g) $512 \times 512 \times 8$ sites. The base model parameters are used, $\alpha=0.25$, $\beta=1.0$, $\gamma=0.5$ and $\delta=0.1$, along with unit mobility. The spatiotemporal pictures are built up from the populations along a specific row in the lattice measured over 1000 time steps. Panels (a)–(c) show a small section (512 sites) of the long dimension (2048 sites) for ease of reproduction and comparison. In Fig. 5a the system is only four sites wide in the thin dimension, and the populations are essentially uniform in that dimension. The dynamics are effectively those of plane waves, as described by Zeigler (1977). This leads to the dramatic spatiotemporal dynamics observed in Fig. 5a, where the prey invade empty regions, predators invade prey regions and drive the prey to extinction, then the predators perish. This dynamic appears to occur over a large range of spatial and temporal scales. Both the predator and prey spatiotemporal plots exhibit these plane wave dynamics.

However, there is an element of stochasticity that is introduced by the possibility for prey to “leak through” the oncoming predator wave, as evidenced by, for example, leftward moving prey bands producing a rightward moving side branch.

Significant changes in the dynamics of the system result when the small dimension is increased slightly. In Fig. 5b the width of the system is expanded from four to eight sites. The change in the dynamics results directly from an increased likelihood that prey escape from the oncoming predator wave to appear on the other side. Fewer “large-scale” events are observed in the spatiotemporal plots due to the decreased probability of extinction over these scales. A further increase in the small dimension to 16 sites, as in Fig. 5c, considerably decreases the likelihood of large-scale extinction events.

The two-dimensional system is displayed in Fig. 5d, and is effectively indiscernible from the 16-site wide one-dimensional system, Fig. 5c. These systems display great stability (population constancy) over large spatial scales and temporal scales, as demonstrated by the population counts vs time plot shown in Fig. 4a. Figure 5e is the spatiotemporal prey plot from a system that lays two two-dimensional lattices one on top of the other, and should produce only the smallest change from the two-dimensional results. Figure 5f uses a thickness of four lattices, and Fig. 5g uses a thickness of eight lattices. Increasing the thickness of the system (changing to three dimensions) results in phase-locking into larger scale oscillations that have strong persistence in time, as observed previously in Fig. 3 for increased mobility. Thus, the effect of increasing habitat dimensionality to three dimensions is similar to that of increasing individual mobility within a two-dimensional habitat.

These effects are not limited to the parameter set chosen above. In the next three figures we present one-dimensional (Fig. 6), two-dimensional (Fig. 7) and three-dimensional (Fig. 8) results for increased and decreased prey growth and predator mortality rates. The panels in these figures use: (a) $\alpha=0.35$; (b) $\alpha=0.15$; (c) $\delta=0.15$; and (d) $\delta=0.05$ with the remaining parameters set to those of the base parameter set, and unit mobilities. Clear differences exist between the images at each dimension, but the overall effect remains the same: increasing habitat dimensionality increases the spatial scale over which oscillations are correlated.

Discussion. We have examined a generic predator–prey model, based upon the Lotka–Volterra system, as habitat dimensionality is changed. The model displays a rather diverse range of population level behaviors as dimensionality is increased. In one dimension, the system displays a high degree of “instability” over a large range of spatial scales. Prey extinction and recolonization is a very common feature with bands of prey followed closely by bands of predators sweeping across the lattice. At a fixed spatial location population pulses are

(a)

(c)

(b)

(d)

Figure 5. Spatiotemporal figures of the prey spatiotemporal plots for simulations with increasing habitat dimensionality from one to three dimensions. Systems of size (a) 2048×4 , (b) 2048×8 , (c) 2048×16 , (d) 512×512 , (e) $512 \times 512 \times 2$, (f) $256 \times 256 \times 4$ and (g) $256 \times 256 \times 8$ sites. The base model parameters are used, $\alpha=0.25$, $\beta=1.0$, $\gamma=0.5$, and $\delta=0.1$, along with unit mobility. Only a 512-site section of (a)–(c) is displayed. The resultant dynamics depend highly on the habitat dimensionality, ranging from extinction/recolonization on a wide range of spatiotemporal scales in one dimension, to nearly phase-locked oscillations in three dimensions.

Figure 6. Comparison of the prey spatiotemporal plots for various parameter combinations using a one-dimensional habitat of size 2048×4 with only a 512 section displayed. The base model parameters, $\alpha=0.25$, $\beta=1.0$, $\gamma=0.5$ and $\delta=0.1$, along with unit mobility, are used, with the exceptions (a) $\alpha=0.35$, (b) $\alpha=0.15$, (c) $\delta=0.15$ and (d) $\delta=0.05$.

observed distributed randomly in time with large periods of extinction between "occupation" events. The temporal record of the simulations look very similar to the results of the neural model for shell pattern formation (Ermentrout *et al.*, 1986; Murray, 1989), with a shell pattern being the temporal record of the neural activity at the mollusc's mantle.

In two dimensions the model displays a high degree of "constancy" at large spatial scales due to statistical stabilization (de Roos *et al.*, 1991). The dynamics occurring in three dimensions results in phase-locked oscillations

Figure 7. The runs of Fig. 6 are performed using a two-dimensional habitat of size 512×512 .

over space, similar to the behavior observed in two dimensions due to increasing the mobilities of the individuals. It appears, then, that there are many considerations when predicting the “stability” of populations in space, not only biological features such as life-history and mobility, but habitat features such as dimensionality as well.

We suspect that this phase-locking in higher dimensions is the result of simple topology: an oscillating region is surrounded by a greater number of neighboring regions in three dimensions than in two dimensions. This strengthened coupling results in phase locking. The change in dimensionality is not equivalent to changing the type of lattice within the same dimension. For

Figure 8. The runs of Fig. 6 are performed using a three-dimensional habitat of size $512 \times 512 \times 8$.

example, a site in the cubic lattice (three dimensions) has six nearest neighbors (called the coordination number of the lattice), the same number as the triangular lattice in two dimensions. We would not expect that simply changing the coordination number by using a triangular lattice instead of a square lattice (with coordination number 4) would alter the dynamics in the way shown above. Correlated regions in two dimensions span many lattice spacings in radius, averaging out such small-scale features as the coordination number of the lattice. Phase-locking in our system is a phenomenon that occurs on spatial scales larger than the lattice spacing and should be independent of such details.

Our results may have important implications for the dynamics of metapopulation models (Comins *et al.*, 1992). In these formulations, habitats are spatially subdivided into patches that are linked via dispersal and/or migration. The influence of habitat dimensionality has not been investigated, and existing studies have focused solely on two-dimensional representations.

Implications for an empirical system are manifold, given the precondition that the biological system examined at a spatial scale just greater than the individual's lifetime range displays oscillatory dynamics. Fluctuations in population densities on all spatial and temporal scales should be observed in one-dimensional habitats (where the width of the habitat is on the same scale as the lifetime range of an individual). Increasing the habitat dimensionality enhances the connectivity of regions to one another, which tends to increase the correlations in the oscillations at distant locations. Hence, in two dimensions one may observe a constant population or oscillating population at large spatial scales. Without any changes in biological features of the model, population fluctuations at a given spatial scale in three dimensions should be greater than their two-dimensional counterparts.

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