Abstract. Predator–prey and other nonlinear ecological interactions often lead to oscillatory dynamics in temporal systems and in spatial systems when the rates of movement are large, so that individuals are effectively well mixed and space becomes unimportant. When individuals are not well mixed, however, properties of fluctuations in population densities, and in particular their amplitudes, are known to vary with the spatial scale at which the system is observed. We investigate the relationship among dynamics at different spatial scales with an individual-based predator–prey model that is stochastic and nonlinear. Results elucidate the role of spatial pattern and individual variability in the dynamics of densities. We show that spatial patterns in this system reduce the per capita rates of predation and prey growth but preserve functional forms. The functional forms remain those one would expect in a well-mixed system in which individuals interact according to mean population densities, but with modified parameters. This similarity of the functional forms allows us to approximate accurately the long-term dynamics of the spatial system at large scales with a temporal predator–prey model with only two variables, a simple system of ordinary differential equations of the type ecologists have been using for a long time. This approximation provides an explanation for the stabilizing role of space, the decrease in the amplitude of fluctuations from the well-mixed to the limited-movement case.

We also provide an explanation for the previously described aperiodic dynamics of densities at intermediate spatial scales. These irregular cycles result from the interplay of demographic noise with decaying oscillations, where the decay of the cycles is due to the spatial patterns. It is indeed possible to capture essential properties of these cycles, including their apparent sensitivity to initial conditions, with a model that follows individuals but parameterizes their spatial interactions in a simple way, using again the similarity of functional forms and the modified parameters. Thus, demographic noise appears essential at a spatial scale previously chosen for the high degree of determinism in the dynamics.

Our results illustrate a semi-empirical approach to simplify and to scale spatial ecological systems that are oscillatory from individual or local-scale to large-scale dynamics.

Key words: demographic noise; individual-based models; model simplification; nonlinear ecological interactions; oscillatory dynamics; parameterization of variability; predator–prey cycles; quasi-cycles; spatial pattern, effect on interaction rates; spatial scaling; spatio-temporal dynamics.

INTRODUCTION

A critical issue in ecology involves the interplay of dynamics at diverse spatial scales. Many ecological questions, and in particular those related to global problems, require models capable of addressing dynamics at large spatial scales. A key challenge thus is how to parameterize the effects of spatial patterns at the small scales that are not explicitly represented—the unresolved spatial patterns—in the models (Steele et al. 1993). By contrast, the formulation of models and the sampling of ecological systems are often most acces-

sible at small spatial scales, in some cases as small as those of the individual (DeAngelis and Rose 1992, Judson 1994). Spatio-temporal models incorporating these small-scale interactions are typically high-dimensional, including large numbers of variables, distributed ecological interactions, and elements of noise. Here, a fundamental question is how to simplify the resulting models by aggregating their basic units, and in so doing achieve both a better understanding and more robust predictions (Levin 1992, Levin and Pacala 1997, Pascual 2001).

Simplification of spatio-temporal models and parameterization of unresolved spatial patterns are intimately connected: learning about the former informs us about the latter. A major challenge to both is found in the nonlinearity of ecological systems, which allows variability to interact across scales and rich spatio-tem-
poral patterns to form. Nonlinearity is a common feature of models for populations, communities, and ecosystems, as the result of density-dependent interactions within and between populations, and of local interactions among the states of neighboring sites in a landscape, metapopulation, or patch model.

Nonlinear ecological systems for antagonistic interactions, such as those between predators and their prey and hosts and their pathogens, have been studied extensively to investigate the role of distributed interactions in space (e.g., Levin and Segel 1976, Crowley 1981, Taylor 1990, Hassell et al. 1991, Comins et al. 1992, McCauley et al. 1993, Donalson and Nisbet 1999). It is well known that these interactions can generate oscillations and that properties of these cycles, such as their amplitudes, vary with the spatial scale at which population densities are sampled and/or with the size of the system. This variation has implications for the level of detail that needs to be incorporated in models to understand questions of persistence, coexistence, and dynamics in general.

Recently, a number of papers have addressed the relationship between dynamics and scale in predator-prey systems (de Roos et al. 1991, Rand and Wilson 1995, Keeling et al. 1997, Jansen and de Roos 1999, Pascual and Levin 1999). These papers have focused on descriptive aspects of dynamics and scale, such as the prevalence of determinism vs. noise and the choice of a window size at which to aggregate individuals into densities. An intermediate scale is identified above which the dynamics of densities appear highly deterministic, predictable at least in the short term, and therefore at which aggregating individuals into densities becomes sensible (Keeling et al. 1997, Pascual and Levin 1999). This intermediate scale is typically of the order of the correlation length of the spatial patterns in the system. The proposed methods apply more broadly beyond individual-based models to spatial stochastic systems that are oscillatory—systems whose dynamics would exhibit periodic cycles under well-mixed conditions but whose fluctuations vary in character with the spatial scale of sampling when interactions are local. Still open is the question of how to translate the dynamics of such systems across spatial scales (Jansen and de Roos 1999, Pascual and Levin 1999).

We investigate this question with a predator-prey model that is spatial, stochastic, and nonlinear, and is defined at the level of the individual (Durrett and Levin 2000). It has been previously shown that space in this model is important to the dynamics of densities at spatial scales that are large relative to that of the individual and relative to the typical correlation length of the spatial patterns (Pascual and Levin 1999); at these large scales, densities exhibit small fluctuations around an apparent steady state. If space is ignored, however, in a typical temporal model for well-mixed individuals, the resulting ordinary differential equations (ODEs) display limit cycles of pronounced amplitude. Thus, the effect of the spatial patterns in the individual-based simulations, which are clearly not represented in the ODEs, is nonnegligible and must be parameterized in order to model densities. We refer to this decrease in the amplitude of fluctuations in the spatial system relative to the well-mixed system as the “stabilizing effect of space.”

We develop here a semi-empirical approach to scale the system in space. In so doing we show that the effect of spatial pattern—that is, of the prey clusters that form and disappear continuously throughout space—is essentially to reduce the per capita rates of predation and prey growth. This reduction has been previously observed with other models (e.g., McCauley et al. [1993] for predation rates, Nisbet et al. [1998] for prey growth). However, we show here that this reduction in rates occurs in a remarkable way by preserving the functional forms while only modifying the parameters of the per capita rates of predation and prey growth. Furthermore, this similarity of the functional forms allows us to approximate accurately the long-term dynamics of densities at large scales with a temporal predator-prey model with only two variables, a simple system of ODEs. Because the functional forms are those one would write if individuals were well mixed, specifying the equations for population densities at large scales is greatly simplified. Furthermore, the accuracy of the approximation shows that the reduction in rates is sufficient to account for the stabilizing effect of space.

Perhaps more surprising is the result that such reduction in rates coupled to individual variability provides an explanation for the dynamics of densities at intermediate scales. These dynamics had been previously shown to be highly deterministic but aperiodic, with a strong temporal modulation of the amplitude of fluctuations. Results confirm our previous conjecture that the aperiodic nature of these cycles is due to the interplay of demographic noise with oscillatory transients. Spatial pattern is responsible for the decay of the cycles; noise interacts with these transient cycles to produce the modulation of the amplitude and the aperiodicity of the dynamics. We show that a model that takes these two factors into account approximates important properties of the dynamics, such as the dominant period and the shape of the power spectrum. More-detailed properties of the dynamics, such as sensitivity to initial conditions and the associated Lyapunov exponents, are also reproduced. These results demonstrate that at a window size chosen for the prevalence of determinism, it is nevertheless impossible to ignore the noise introduced at the individual scale. Individual variability plays an essential role in spite of the relatively large number of individuals.

We discuss these results in light of the recent proposal that intermediate spatial scales provide a characteristic size at which to simplify the system by ag-
ggregating individuals into densities. We also discuss the applicability of semi-empirical approaches, such as the one presented here, to scale the complex spatio-temporal models of specific ecological systems. Our results suggest that the parameterization of unresolved spatial patterns in other systems for antagonistic interactions may be achieved by simply changing the parameters of the typical temporal models that ecologists have been using for a long time. This result remains to be explored with a broader range of ecological models, especially those incorporating more-realistic types of transport and movement.

**The Predator–Prey Model**

We start by briefly presenting the model and summarizing some key features of its dynamics. (For further details see Pascual and Levin [1999] or Durrett and Levin [2000].)

The predator–prey model follows the fate of individual predators and their prey in continuous time and two-dimensional space. Space consists of a lattice in which each site is either occupied by a predator, occupied by a prey, or empty. The state of a site changes in time according to the following processes: Predators hunt for prey (at rate 1) by searching within a neighborhood of prescribed size, the eight adjacent neighboring sites in the lattice. Predators choose one prey at random within this neighborhood and occupy the site of the chosen prey. Only predators that find prey can reproduce, and do so with a specified probability \( \beta_2 \). The offspring occupies the original site of the parent predator. Predators that do not find prey are susceptible to starvation, and die with probability \( \delta \). Prey reproduce locally by giving birth onto an empty neighboring site at rate \( \beta_1 \). There is movement through mixing: each pair of neighboring sites exchange states at a constant rate \( \nu \).

In the model, nonlinearity results from rates of predation and prey growth that depend on local densities. Stochasticity is demographic, representing the uncertainty in the fate of any single individual, and is implemented through rates that specify probabilities for the associated events to happen in a given interval of time. Specifically, an event occurs at times of a Poisson process with the specified rate. Technically, the model is known as an “interacting particle system” (Durrett and Levin 1994), and is similar to a stochastic cellular automaton but differs in the continuous treatment of time.

Simulations have shown that the spatio-temporal dynamics of the model change continuously as prey clusters form and disappear (Fig. 1, Pascual and Levin 1999). As a result, the dynamics of densities change character with the size of the sampling window (Fig. 1A and B). In particular, at small window sizes, demographic noise prevails and fluctuations are large. At intermediate window sizes \( (l^2 = 64 \times 64) \), cycles have a strong deterministic component but appear aperiodic.

**Fig. 1.** Temporal dynamics of prey densities at different scales of sampling; prey density = number of sites occupied by prey divided by the total number of sites in the sampling window: (A) the whole lattice \( l^2 = 700 \times 700 \); (B) the intermediate window size \( l^2 = 64 \times 64 \). (C) For comparison, the temporal dynamics of the mean-field equations, obtained by assuming that individuals are well mixed, are shown. The parameters in all simulations are chosen so that the dynamics of the mean-field equations are oscillatory converging to a limit cycle (the rate of giving birth onto an empty neighboring site, \( \beta_1 = 1/3 \); the probability that a predator reproduces, \( \beta_2 = 1/10 \); the probability that a predator dies of starvation, \( \delta = 1/3 \); and \( \nu = \) the mixing rate at which neighboring sites exchange state, = 1). The boundary conditions in the spatial simulations are periodic to eliminate boundary effects.

(Number 1B). At large window sizes \( (l^2 = 700 \times 700) \), the dynamics exhibit small fluctuations around an apparent steady state as local fluctuations that are out of phase average out (Fig. 1A).

These changes in the dynamics of densities with scale are found not only in this particular predator–prey model but in a class of spatial stochastic models whose corresponding mean-field equations display limit cycles (Durrett and Levin 2000). “Mean-field” refers here to the model one would write if individuals were well mixed and therefore space were negligible as individuals interact according to mean spatial densities. For our system, the dynamics of prey densities \( p \) and predator densities \( h \) would then be given by the following system of equations:

\[
\frac{dp}{dt} = \beta_1 p [1 - (p + h)^4] - h [1 - (1 - p)^4]
\]

\[
\frac{dh}{dt} = \beta_2 h [1 - (1 - p)^4] - \delta h (1 - p)^4 \quad (1)
\]

(Durrett and Levin, 2000). Although these equations only follow the temporal evolution of the populations, two terms still contain spatial information. The first one is the per capita predation rate, which is given by \( [1 - (1 - p)^4] \) and corresponding to the probability of
at least one site in the neighborhood of a predator being occupied by a prey. The exponent $q = 8$ is the number of sites a predator inspects when hunting for prey in its immediate neighborhood. The second term specifies the per capita rate of growth of the prey and is given by $b_1 [1 - (p + h)^k]$. In this, the expression within the brackets corresponds to the probability of an empty neighbor, and the exponent $k$ is 1 because the prey inspects a single neighbor.

Previous work (Pascual and Levin 1999) has shown that this temporal system of equations provides a poor approximation for the dynamics of densities, regardless of window size (Fig. 1C). Indeed, the long-term dynamics are periodic and converge to a limit cycle (Durrett and Levin 2000). The cycle fails to capture the dominant period, the shape of the spectrum, and the aperiodic character of the dynamics at intermediate scales (compare B and C in Fig. 1) (Pascual and Levin 1999). It also performs poorly in a comparison to the large scale dynamics (Fig. 1A and C), where even the temporal averages are off. We investigate next the source of these discrepancies.

**Functional Forms and Observational Scale**

The actual per capita rates of predation and prey population growth can be examined directly in the output of the spatial simulation. From this output, we can estimate the probability of a predator having at least one prey in its neighborhood (i.e., the probability of a predator being successful at finding a prey). To do this, we first choose a sampling scale, the size of the observational window, and then for each time unit we determine the frequency of predators with at least one prey in their hunting neighborhood. Fig. 2 (B and D)

---

**Fig. 2.** The estimated per capita rates of predation and prey growth at (A, B) large and (C, D) intermediate scales. The points correspond to estimates obtained from the spatial simulations at different times: in (B) and (D) the probability of at least one prey for a given prey density; in (A) and (C) the probability of an empty neighboring site for a given density of occupied sites. For comparison, the dotted lines show the functions expected under well-mixed conditions, that is, $f(p)$ and $g(p + h)$ for $q$ (the number of sites a predator visits when hunting for prey in its immediate neighborhood) = 8 and $k$ (the number of sites a prey inspects in its immediate neighborhood) = 1, respectively. The continuous lines show the same functions when these exponents are fitted to the points from the spatial simulations, by nonlinear least squares with a Gauss-Newton algorithm (in Matlab [MathWorks, Natick, Massachusetts, USA]). In (D) two such lines are shown for $f(p)$: one for the fitted exponent $q = 4.3$, and another above it, for the slightly higher value $q = 4.7$ (see Intermediate-scale dynamics).
Fig. 3. Phase-space trajectories for predator and prey densities in the mean-field equations: in (A), $q = 8$ and $k = 1$; in (B), $q = 3.7$ and $k = 0.62$; in (C), $q = 4.3$ and $k = 0.68$; and in (D), $q = 4.7$ and $k = 0.68$. The equations are integrated numerically with a 4th-order Runge-Kutta scheme with a fixed time step. For definitions of $q$ and $k$ see Fig. 2 legend.

shows these estimates for different times as a function of prey density, for both large ($l = 700$) and intermediate ($l = 64$) window sizes for a total of 8000 time steps after transients. For comparison the function specifying the per capita rate of predation with prey density in the well-mixed case, that is,

$$f(p) = 1 - (1 - p)^q$$  \hspace{1cm} (2)

with $q = 8$, is also plotted. Regardless of window size, the estimates from the spatial simulation fall below those expected for the well-mixed system. Thus, spatial pattern reduces per capita predation rates in the spatial system.

However, with modified exponent the functional form of the predation rate with prey density remains remarkably similar from the well-mixed system to the spatial simulation. This is most easily seen at the intermediate window size for which prey densities cover a wider range of values in the spatial simulation (Fig. 2D). The function $f(p)$ is shown for the least-square estimate $q = 4.3$ in Fig. 2D. The value of this exponent has decreased almost by half from its original value of 8. Thus, the predators behave as if, on average, they searched for prey in a much smaller neighborhood. Similarly at large window size, the fit of function $f(p)$ to the probability of at least one prey obtained from the spatial simulation gives a value of $q$ equal to 3.7 (Fig. 2B).

By following similar steps, we can examine the realized rate of prey growth (Fig. 2A and C). The probability of an empty neighbor as a function of the density of occupied sites, that is,

$$g(p + h) = 1 - (p + h)^g$$  \hspace{1cm} (3)

is estimated from the spatial simulation. In the mean-field equations, the exponent $k$ is 1 and $g(p + h)$ is a line plotted in Fig. 2A and C. As for predation, the prey growth rate is lower than that expected at mean densities but its functional form remains similar. Indeed, the function $g(p + h)$ provides a good fit to the estimated probability of an empty neighboring site. What changes is again the exponent. The least-square estimates of $k$ are 0.62 and 0.68 for large and intermediate window sizes, respectively. Thus, the prey in
FIG. 4. Comparison of the dynamics of densities at large scale in the spatial simulation and in the two-dimensional approximation. The dynamics of the spatial simulation are only shown after transients have died out starting at time 3000.

The spatial simulation grows as if it were able to sample, on average, less than one neighboring site. How important are these parameter changes to the dynamics of the system? Do they account for the changing character of the predator–prey cycles with observational window? These questions are explored next.

LARGE-SCALE DYNAMICS

System 1 exhibits a limit cycle when the exponents $q$ and $k$ take the original values of 8 and 1, respectively (Fig. 3A). At the scale of the whole lattice, however, these exponents decrease as the result of the spatial pattern in the system. The above results suggest that the large-scale system behaves as a well-mixed one in which the rates of predation and prey growth are effectively smaller. To further examine this possibility, we consider the dynamics of System 1 when $q = 3.7$ and $k = 0.62$.

Fig. 3B illustrates that for these parameters the predator and prey dynamics converge to an equilibrium, instead of a limit cycle, and do so with oscillatory transients. The amplitude of these transient cycles decays with time. Fig. 4 shows the transient and equilibrium dynamics as a function of time for both predator and prey. We superimpose on these time courses the dynamics of densities in the spatial system, sampled at a window size of $700 \times 700$ with transients removed.

The temporal system of predator–prey equations captures accurately the mean density of both populations, providing a remarkable approximation. The temporal system underestimates, however, the temporal variance of the spatial simulation. In the spatial model, fluctuations of small amplitude are still present at large scale. We return to this discrepancy below when addressing the intermediate-scale dynamics.

INTERMEDIATE-SCALE DYNAMICS

For an intermediate window size of $64 \times 64$, the estimated least-square exponents take the values of $q = 4.3$ and $k = 0.68$. For these values, System 1 exhibits an oscillatory approach to equilibrium (Fig. 3C). The oscillatory transients are longer and have larger amplitudes than those of the large-scale approximation (Fig. 3, compare C to B). Clearly, the two-dimensional system of differential equations is unable to capture the aperiodic behavior of the spatial simulation at intermediate scales (Fig. 1B), since such a deterministic system can only exhibit limit cycles and equilibria.

We had conjectured (Pascual and Levin 1999) that the aperiodic behavior of densities was produced by the interplay of the decaying oscillations with demographic noise. To examine this possibility, we simulate Eqs. 1 as a Monte Carlo simulation. This simulation incorporates demographic noise as it follows individuals (4096 of them for a lattice size of $64 \times 64$), but does not incorporate space. Individuals interact according to the terms of the well-mixed Eqs. 1. Fig. 5A illustrates the resulting irregular dynamics of prey density after transients have died out. We refer hereafter to these dynamics with the term “quasi-cycles,” which we borrow from Nisbet and Gurney (1976; see Discussion, below).

The quasi-cycles (QCs) are smaller in amplitude than the fluctuations of the spatial system (Fig. 5, compare A and B). They approximate, however, key properties of the aperiodic dynamics of densities better than the limit cycle of the mean-field equations (MFs). Specifically, the QCs accurately capture the mean levels of predator and prey, and better approximate $P$, the dominant period of the dynamics ($P = 40.8$ vs. 35.7 for the QC vs. 59 for MF). Beyond the dominant period, the distribution of the variance as a function of frequency is also closely reproduced as shown by the power spectrum in Fig. 6 (compare A and B).

As for the large-scale dynamics, however, the approximation underestimates the variance (compare Fig. 5, A and B noticing the different range in the axes).
Fig. 5. Aperiodic dynamics of prey density: (A) in the Monte Carlo simulation with $q = 4.3$ and $k = 0.68$; (B) in the original spatial system at the intermediate sampling scale; and (C) in Monte Carlo simulation with $q = 4.7$ and $k = 0.68$. For definitions of $q$ and $k$, see Fig. 2 legend.

The coefficient of variation (standard deviation divided by the mean) is only 0.19 compared to an original value of 0.37. One source of discrepancy can be found in the spread of the points used to estimate the exponents of the functional forms (Fig. 2C and D). The spread indicates that the exponents are not constant but vary in time. The variance of the QCs shows high sensitivity to these changes. This sensitivity is seen by considering a value of $q = 4.7$, only slightly above the estimated one. In fact, the curves $f(p)$ for $q = 4.7$ and for $q = 4.3$ are close, and both go through the cloud of points used to fit the functional form (Fig. 2D).

We chose $q = 4.7$ because the oscillatory transients of the mean-field Eq. 1 show, for this parameter, larger amplitudes and a slower convergence to equilibrium than those for $q = 4.3$. Thus, these oscillatory transients provide a deterministic template for the noisy trajectories with larger excursions than those for 4.3. In fact, for $q = 4.7$ the dynamics of the Monte Carlo simulation are still aperiodic but display larger amplitudes than for $q = 4.3$. The coefficient of variation is now closer to that of the original simulation (0.31 vs. 0.35). The dominant period of the QC is also closer to that of the spatial system ($P = 37$ compared to $P = 40.8$), and so is the shape of the power spectrum (Fig. 6, compare B and C).

Fig. 6. The power spectrum for the temporal dynamics of prey density (100 000 time units after transients have died out): (A) in the Monte Carlo simulation with $q = 4.3$ and $k = 0.68$; (B) in the original spatial system at the intermediate sampling scale; and (C) in Monte Carlo simulation with $q = 4.7$ and $k = 0.68$. For definitions of $q$ and $k$, see Fig. 2 legend.
In short, the QCs capture important properties of the dynamics of densities at intermediate scales. The results provide an explanation for the aperiodic dynamics observed in the spatial system at these scales and support our conjecture on the role of demographic noise. It is indeed possible to probe further into properties of the QCs to show their deeper similarity to the dynamics of the spatial system. Invariants of the dynamics, such as the dominant Lyapunov exponent, are closely approximated.

A Closer Look at the Quasi-Cycles: Sensitivity to Initial Conditions

Previous analyses have shown that the aperiodic dynamics of densities at intermediate scales are consistent with those on a finite dimensional attractor whose trajectories display sensitivity to initial conditions (Pascual and Levin 1999). Here, we confirm these results with a more detailed analysis that forms the basis for comparison with the non-spatial approximations. Comparisons of quantities associated with the stability of the dynamics and the dimension of the underlying attractor reveal a deep dynamical similarity.

In the following analyses, the time series of prey density in the spatial system (sampled at \( t = 64 \)) is denoted by \( p(t) \) and the time series from the Monte Carlo simulations, by \( QC_4.7(t) \) and \( QC_4.3(t) \) for the quasi-cycles (QCs) with \( q = 4.7 \) and \( q = 4.3 \), respectively. All three time series are 100,000 long, sampled every time unit after transients have died out.

Although all three time series are derived from dynamics that include a stochastic component, we treat them here as data from a dynamical system. This treatment is justified because the level of noise in the time series is low in spite of the stochastic nature of the underlying models. The prevalence of determinism, as measured by a determinism test from nonlinear time-series analysis (Kaplan and Glass 1995), was indeed the basis for selecting the intermediate scale in the first place (Pascual and Levin 1999). Similar results (not shown here) are obtained with the same test applied to the QCs. Thus, if we ignored the origin of the prey data, we would treat the time series as generated by a dynamical system with low levels of (dynamical or measurement) noise. In this treatment, we would further consider that prey density is only one of the variables in a dynamical system whose phase-space trajectories we wish to investigate.

To obtain phase-space trajectories from data on a single variable, we resort then to the well-known idea of attractor “reconstruction” (Packard et al. 1980, Takens 1981) which uses time-delay coordinates as surrogates for the unobserved variables of a dynamical system. Attractor reconstruction preserves the qualitative type of asymptotic dynamics, and invariants such as dimension and Lyapunov exponents that characterize stability. From the time series of prey density \( p(t) \), we construct the \( d_E \)-dimensional time series:

\[
P(t) = [p(t), p(t - \tau), p(t - 2\tau), \ldots, p(t - (d_E - 1)\tau)]
\]

where \( \tau \) is a selected lag and \( d_E \) is known as the “embedding dimension.” Critical to the reconstruction of the original attractor is the choice of \( d_E \), which needs to be sufficiently large but not larger than \( 2n + 1 \), where \( n \) is the unknown dimension of the space harboring the original attractor. Both the lag \( \tau \) and the value of \( d_E \) can be estimated, however, from the time series itself.

The choice of the delay \( \tau \) aims at defining statistically independent coordinates for reconstruction. A well-known rule of thumb is to select the value of the lag for which the autocorrelation function has decreased to a prescribed value such as zero. For shorter lags, when \( p(t) \) and \( p(t - \tau) \) are highly correlated, the reconstructed trajectory is not sufficiently unfolded. Here, the selected values are \( \tau = 10 \) for \( p(t) \) and \( \tau = 9 \) for \( QC_{4.7} \) and \( QC_{4.3} \). An alternative approach, based on the averaged mutual-information function (involving the joint probability density derived from the data; Fraser and Swinney 1986), confirms these values.

One particular approach for choosing \( d_E \), which we apply here, relies on the concept of false neighbors: if \( d_E \) is chosen too small, points that are far apart in phase space can appear close because of a projection effect. As soon as \( d_E \) is high enough, the reconstructed attractor is completely unfolded so that neighbors in this phase space truly result from the dynamics returning to similar states. The estimation of the percentage of false neighbors for increasing trial values of \( d_E \) forms the basis of an algorithm to select \( d_E \) (Kennel et al. 1992). Fig. 7 shows that for \( d_E = 6 \) the percentage of false neighbors has declined to a small value and remains low. The value of \( d_E = 6 \) is thus selected as the embedding dimension for all three time series.

Armed with the parameters to reconstruct a trajectory in phase space, we can now proceed to estimate the global Lyapunov exponents characterizing the stability of the dynamics. Each global exponent measures the average rate of contraction or expansion of a perturbation in specific directions along the orbit. A negative value indicates a contraction of the orbit perturbation while a positive value indicates an expansion. When the largest exponent is positive, the time evolution of the system is sensitive to initial conditions as any small perturbation grows exponentially with time along the corresponding direction. The global exponents measure the average expansion over the whole attractor but are estimated in practice from a given orbit. When data set length is not limiting, as is the case here, it is possible to examine the convergence of the estimates with the length of the orbit. The number of exponents is determined by the local (integer) dimension of the attractor, \( d_E \), which must be smaller than or equal to \( d_E \).
Locally, the directions of expansion or contraction along the orbit correspond to the eigenvectors of the linearization of the flow (the Jacobian matrix of the system), and the respective rates, to its eigenvalues. Thus, to estimate the Lyapunov exponents, we use a parametric method that fits local linear maps along the orbit. From their parametric representation we obtain the required partial derivatives in phase space and therefore the Jacobian matrices; these matrices are then composed along the orbit to compute the average exponents as the eigenvalues of the resulting matrix (Briggs 1990, Brown et al. 1991).

Table 1 shows the Lyapunov spectrum \( \lambda_i; i = 1, \ldots, 6 \) computed for time flowing forward, as well as the spectrum \( \lambda_i; i = 1, \ldots, 6 \) obtained with time flowing backwards (with a change of sign for comparison). Any local direction which is expanding for forward time, will become contracting when time is inverses, and vice versa, with the corresponding change in sign but not magnitude of its Lyapunov exponent. False exponents resulting from noise contamination or too high a local dimension (recall that 6 is an upper bound for \( d_L \) and therefore for the number of exponents) can often be detected by their sign remaining unchanged with a time reversal (Abarbanel 1996). Such a situation does not occur here, and both spectra are consistent for each of the three time series. We also verified that the sum of the exponents for each time series is negative, in accordance with the dissipative nature of the underlying systems. More importantly, all three time series exhibit a positive dominant Lyapunov exponent indicative of sensitivity to initial conditions, with comparable values across data sets. The three time series further share two positive exponents, three negative ones, and one that is not distinguishable from zero.

From the spectrum of exponents, an upper bound to the dimension of the attractor can be obtained by computing the Lyapunov dimension (Kaplan and Yorke 1979) given by

\[
D_L = \sum_{i=1}^{n} \lambda_i
\]

Table 1. Lyapunov exponents, \( \lambda_i \), and the Lyapunov dimension, \( D_L \), estimated from the time series of prey density from the spatial system \( p(t) \) and from the Monte Carlo simulations with \( q = 4.7 \) and \( q = 4.3 \), respectively \( [QC_{4.7}(t) \text{ and } QC_{4.3}(t)] \). The embedding dimensions \( d_L \) = 6.

<table>
<thead>
<tr>
<th>Exponent or dimension</th>
<th>QC_{4.7}(t)</th>
<th>p(t)</th>
<th>QC_{4.3}(t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \lambda_1 )</td>
<td>0.1254</td>
<td>0.1175</td>
<td>0.2051</td>
</tr>
<tr>
<td>( \lambda_2 )</td>
<td>0.0579</td>
<td>0.0627</td>
<td>0.1179</td>
</tr>
<tr>
<td>( \lambda_3 )</td>
<td>-0.0004</td>
<td>0.0094</td>
<td>0.0468</td>
</tr>
<tr>
<td>( \lambda_4 )</td>
<td>-0.0595</td>
<td>-0.0544</td>
<td>-0.0529</td>
</tr>
<tr>
<td>( \lambda_5 )</td>
<td>-0.1633</td>
<td>-0.1636</td>
<td>-0.2233</td>
</tr>
<tr>
<td>( \lambda_6 )</td>
<td>-0.4229</td>
<td>-0.4016</td>
<td>-0.5847</td>
</tr>
<tr>
<td>( D_{1397} )</td>
<td>6.76</td>
<td>4.83</td>
<td>5.16</td>
</tr>
</tbody>
</table>

Notes: QC = quasi-cycle; \( q \) = parameter in per capita predation rate.
value for the long-term dynamics of the spatial system at large. Resource (here space) needed for growth.

ephemeral refuge from predation, while limiting the reduction in rates would follow from the prey clusters to mean population densities but with lower rates. The mixed system in which individuals interact according to additional forms remain those one would expect in a well-mixed prey growth but not their functional forms. The functional forms between the spatial and the well-mixed system is key. Observed at large scales, population densities essentially behave as a well-mixed system whose predator-prey encounters and available space for prey growth have been reduced. Thus only the parameters but not the functional forms of the well-mixed model need to be modified.

The mean-field equations exhibit limit cycles for the original parameters of the individual-based model, but for the modified parameters of the approximation they exhibit instead an oscillatory approach to equilibrium. This change in behavior provides an explanation for the stabilizing effect of space in the individual-based model, that is, for the decrease in the amplitude of the predator-prey oscillations from the large limit cycles to the small fluctuations around an apparent steady state. Spatial patterns reduce the rate of predation and prey growth and this is sufficient to account for the change in the amplitude of the cycles.

Many earlier papers have addressed the role of space in stabilizing or destabilizing predator-prey and other antagonistic interactions, where “stability” (as in this paper) refers to the change in the amplitude of cycles and to the related question of population persistence (e.g., McCauley et al. 1993, Donalson and Nisbet 1999). In those papers, the comparison of different types of models, from simple ODEs to individual-based systems, has been a basic tool to understand the role of spatial patterns in the dynamics. We specifically refer here to two papers whose conclusions raise questions on the generality of the approximation we propose for the dynamics at large scales. McCauley et al. (1993), working with an individual-based predator-prey model not unsimilar to ours, conclude that the small decrease (15–20%) in the predator attack rate does not account for the large reduction in the amplitude of the cycles, between the spatial system with limited movement and that with well-mixed prey. They find that similar decreases in the predator attack rate in the ODEs lead to cycles of reduced amplitude but still too large relative to that of the spatial system with limited movement. There are two possible explanations for this apparent discrepancy with our results. First, spatial patterns should also reduce the prey growth rate, which was not taken into account. Second, the way in
which the reduction in predation rates are incorporated in the ODEs may be critical, and, in particular, an overall reduction in such rates may not work. In fact, if we compute an overall reduction of the rates from our simulations (22% and 27% for the rates of per capita predation and prey growth, respectively, in Fig. 2A and B) and use these values as a reduction factor to modify the corresponding per capita rates of the mean-field equations, we obtain limit cycles, instead of a steady state, whose amplitude is reduced but not sufficiently small. Furthermore, the mean of these cycles differs significantly from that of the spatial system. These observations underscore that the stabilizing effect of space in our model—and we believe more generally—depends not only on the magnitude of the reduction in rates but also on its shape, so that preserving the functional forms matters.

In a more recent paper, Donalson and Nisbet (1999) propose that the concept of a functional form may not be applicable to individual-based systems in which space and demographic stochasticity are taken into account. It would follow that formulating ODEs of the Lotka-Volterra type to approximate and explain the role of space in these spatial systems is not viable. The direct comparison of their results to ours is difficult because they examine functional responses within single cycles. Averaging over a large number of oscillations was needed for us to extract the noisy functional responses. Perhaps more important to the discrepancy are the differences in the spatial population patterns generated by these two different individual-based models. In their simulations, small population clusters coexist with a large wave that propagates through the whole system and is of its size. Such a wave may result from the directional movement of individuals until they reach a boundary and/or from the lack of density dependence in prey growth in their model. It is absent from our simulations, where only clusters are observed and space is isotropic. In the presence of such a wave, our results may not apply. In fact, we conjecture that there is a strong connection between the geometry of the population patterns and the similarity of the functional forms described here. This connection, which is explored elsewhere (M. Pascual, A. Franc, and M. Roy, unpublished manuscript), can establish the generality of our findings by specifying the systems they would apply to based on the geometry of population clusters.

We have also shown here that oscillatory transients resulting from the stabilizing role of space can explain the aperiodic dynamics of densities observed in a number of predator–prey models at intermediate window sizes. When demographic noise interacts with these transients, an equilibrium is never reached but instead persistent cycles of modulated amplitude develop. We have called these dynamics “quasi-cycles” (QCs), borrowing a term first introduced by Nisbet and Gurney (1976) for the irregular cycles produced by environmental noise and oscillatory transients. We had shown before that the QCs in the predator–prey model exhibit a high degree of determinism, in the sense of being highly predictable in the short term (Pascual and Levin 1999). Paradoxically, the noise produced by the uncertainty at the individual level, that is by individual variation, plays an essential role in determining important properties of the dynamics, such as their dominant period, power spectra, and their apparent sensitivity to initial conditions.

Several recent papers have proposed that this intermediate scale provides an ideal window size at which to aggregate individuals and model densities. The role of noise we describe here casts some doubt on the viability of a fully deterministic approximation. The intermediate scale retains, however, a special significance. Above this observational window, the changes in the fitted exponents of predation and prey growth are small. Thus, the sampling of real systems at this scale would provide reasonable parameters for modeling densities at larger scales when sampling efforts at those scales are difficult or prohibitive. The sampling at intermediate scales would further provide information about the shape of the functional forms when these are unknown. The shape of the functional forms emerges most clearly at this system size, because the noise levels are reduced relative to those at smaller windows and the range covered by density fluctuations is wider than that of larger windows.

The method we have illustrated for scaling the system is semi-empirical in the sense of relying in part on the data produced by the simulation. Such a method presents both advantages and disadvantages relative to more formal (mathematical) methods such as moment closure and hydrodynamic limits (e.g., Bolker and Pacala 1997, Levin and Pacala 1997). Formal methods may be difficult if not impossible to apply to the complex models developed for specific ecological systems. Semi-empirical methods, by contrast, should be widely applicable. However, because they are tied to specific simulations, they can lack generality with respect to variation in parameters and environmental conditions. Thus, while they are useful to explain changes in dynamics with scale for specific simulations, they cannot completely replace the large numerical simulations of high-dimensional systems. To a large extent, their success in reducing numerical complexity will depend on a better understanding of why they work and what are the data requirements to obtain their parameters. For the specific approach we propose here a key question is why the mean-field model with modified parameters works at all to approximate the aggregated dynamics of a system with rich spatial patterns.

Studies on the scaling of heuristic ecological models, such as the one considered in this paper, can also provide insights into the parameterization of unresolved spatial scales in more realistic models. In particular, they can establish when it is possible to use “well-mixed” and other common “box” models that ignore
space a priori. Our results suggest that this is possible in oscillatory systems with random mixing. To establish the generality of these results, other oscillatory systems need to be considered, in particular those with more realistic patterns of movement and transport.

Aggregated distributions of prey, parasites, and parasites have been incorporated in previous temporal models using the negative binomial distribution, one of a family of clumped distributions useful to describe natural populations (e.g., Hassell and May 1974, Hassell 1978). Spatio-temporal models such as the one presented here provide the means to examine such parameterizations further as a function of scale, through specific comparisons between spatial and non-spatial models.

For systems in which the functional forms remain similar across scales, a key question becomes how, in practice, can we best obtain parameters for large-scale dynamics from field measurements? For most systems, parameterization of unresolved scales will not proceed from a detailed model including these scales. Questions on the feasibility of estimating parameters from time-series data, a common practice in ecology, should be addressed.

Acknowledgments

We thank Roger Nisbet, Manojit Roy, and an anonymous reviewer for valuable comments on the manuscript. M. Pascual is pleased to acknowledge the support of the James S. McDonnell Foundation through a Centennial Fellowship, and S. Levin, the support of the National Science Foundation grant DMS-9807755 and the Alfred P. Sloan Foundation grant 97-3-5.

Literature Cited


