

REPORT

## Simple temporal models for ecological systems with complex spatial patterns

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### Abstract

Spatial patterns are ubiquitous in nature. Because these patterns modify the temporal dynamics and stability properties of population densities at a range of spatial scales, their effects must be incorporated in temporal ecological models that do not represent space explicitly. We demonstrate a connection between a simple parameterization of spatial effects and the geometry of clusters in an individual-based predator–prey model that is both nonlinear and stochastic. Specifically we show that clusters exhibit a power-law scaling of perimeter to area with an exponent close to unity. In systems with a high degree of patchiness, similar power-law scalings can provide a basis for applying simple temporal models that assume well-mixed conditions.

### Keywords

Individual-based predator–prey model, modified mean-field equation, power-law scaling, cluster geometry.

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### INTRODUCTION

Spatial patterns and aggregated population distributions are common in nature and in a variety of spatio-temporal models with local ecological interactions (e.g. Pickett & White 1985; de Roos *et al.* 1991; Hassell *et al.* 1991; Ives 1991; Davis *et al.* 1992; Levin *et al.* 1993; Tilman & Kareiva 1997). However, there exists a large number of simple temporal models, descendants of the well-known Lotka–Volterra equations, that completely ignore space and consider only mean population numbers. Are these ‘mean-field’ or ‘box’ models mostly heuristic tools that should be relegated to ecological textbooks and to experiments that can impose well-mixed conditions? Or are there conditions under which these models can approximate ecological dynamics in systems with complex spatial patterns? These questions underlie recent efforts to derive macroscopic descriptions for quantities such as population or patch type densities from microscopic descriptions of local interactions (e.g. Levin & Pacala 1997; Filipe & Gibson 1998; Dieckmann *et al.* 2000; Socolar *et al.* 2001). They also relate to earlier efforts to parameterize the effect of aggregated spatial distributions in simple temporal models (e.g. Hassell & May 1974; Hassell 1978, 2000). These questions continue to be relevant today for understanding increasingly complex systems whose interactions are both local and nonlinear, for addressing dynamics at increasingly large scales, and for formulating spatially

implicit models amenable to policy analysis (Roughgarden 1997).

Translating dynamics from microscopic processes, at the individual or patch level, to macroscopic rates, at the population or landscape level, is essentially a scaling problem in the spatial dimension (Levin 1992). In parallel to and separate from work on such dynamical scalings, ecologists have also been interested in descriptions of how patterns vary with the spatial scale of observation (e.g. Bradbury & Reichelt 1983; Krummel *et al.* 1986; Palmer 1988; Hastings & Sugihara 1993). Power-law scalings have attracted particular attention as signatures of scale invariance, revealing the existence of heterogeneity over a broad range of scales (Sugihara & May 1990). We demonstrate here a link between a descriptive and a dynamical scaling in an individual-based predator–prey model with complex spatial patterns. Specifically, we demonstrate a relationship between the geometry of the spatial patterns and a simple modification of the mean-field equations proposed earlier (Pascual *et al.* 2001) to approximate the long-term dynamics of population densities at large scales. This simple approximation preserves the functional forms and modifies only the parameters of the mean-field equations. The modified parameters are exponents that account implicitly for the effect of patchiness on the population rates. In this sense, our approach is similar to that used in disease models that incorporate exponents to modify the mass-action transmission term and empirically take into account heterogeneous

mixing (e.g. Gubbins & Gilligan 1997; Finkenstädt & Grenfell 2000). We propose that a key property allowing this simple approximation in the predator–prey system is a power-law scaling of the clusters, which we suggest will also occur in other spatial stochastic systems for antagonistic interactions in ecology, such as those for disturbance–recovery and host–parasite dynamics. We further demonstrate the robustness of our results, including the constancy of the modified exponents and the applicability of the simple model for different parameters of the individual-based simulation. Although the focus here is on local interactions in space, similar questions apply to models for complex biological systems whose local interactions are defined over a social, physiological, or ecological network.

## THE MODEL

Our predator–prey model follows individuals in space and time and is both stochastic and nonlinear (see Durrett & Levin 2000; or Pascual & Levin 1999). Space consists of a two-dimensional lattice in which each site is either occupied by a predator, occupied by a prey, or empty. The state of a site in the lattice changes in time according to the following processes. Predators hunt for prey by searching within a neighbourhood of prescribed size at rate 1. The parameter  $q$  specifies the number of sites in this neighbourhood. Only predators that find at least one prey can reproduce, and do so with a specified probability  $\beta_2 = 1/10$ . The offspring is placed in the original site of the predator which has moved to the site of its prey. This local growth of predators can correspond to two different biological scenarios: the production of real offspring by reproduction or the behavioural aggregation of predators near prey by immigration from outside the system. Predators that do not find prey are susceptible to starvation and die with probability  $\delta = 1/3$ . This loss can describe the actual mortality of starving predators, or their emigration from the system. The prey reproduce locally only if a neighbouring site is empty at rate  $\beta_1 = 1/3$ . There is movement through mixing: neighbouring sites exchange state at a constant rate  $\nu = 1$ . In the model, stochasticity is demographic, representing the uncertainty in the fate of an 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. Simulations have shown that the spatial patterns change continuously as clusters of prey form and disappear through local growth and predation (see figure 1 of Pascual & Levin 1999). Initially let us briefly summarize previous findings which show that a simple modification of the mean-field system accounts for the effects of spatial patterns on mean population densities (once transients have died out).

## THE MODIFIED MEAN-FIELD APPROXIMATION

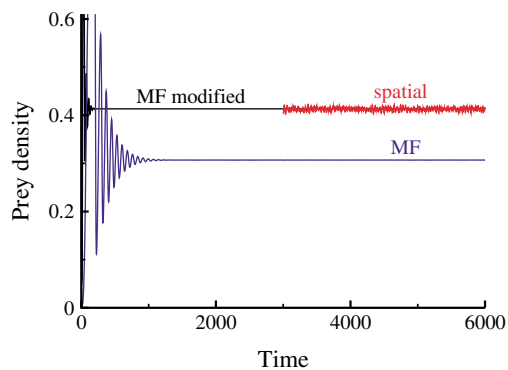
The dynamics of population densities vary with the spatial scale at which the system is observed, and in particular the amplitude of fluctuations decreases with scale. At the scale of the whole grid (e.g.  $700 \times 700$  sites), population densities show only small fluctuations around an apparent steady state. By contrast, the mean-field model that one would write if individuals were well mixed and space was unimportant displays pronounced limit cycles (Pascual & Levin 1999). These equations of the ‘Lotka–Volterra’ type are

$$\begin{aligned} \frac{dp}{dt} &= \beta_1 p [1 - (p + b)^k] - b [1 - (1 - p)^q] \\ \frac{db}{dt} &= \beta_2 b [1 - (1 - p)^q] - \delta b (1 - p)^q \end{aligned} \quad (1)$$

where  $b$  and  $p$  denote the predator and prey density, respectively, the exponent  $k$  equals one since the prey inspects a single site in its neighbourhood, and  $q$  equals eight, the number of sites in the hunting neighbourhood of the predator (Durrett & Levin 2000; Pascual *et al.* 2001).

A simple change to these ordinary differential equations permits one to approximate accurately the long-term dynamics of population densities in the spatial system (Pascual *et al.* 2001). We have shown that the spatial patterns in the original individual-based system reduce the per-capita rates of predation and prey growth but preserve their functional forms. The functional forms remain those of the mean-field model but with modified parameters. For example, in the per-capita predation rate  $[1 - (1 - p)^q]$  the exponent  $q$ , which specifies the size of the predator’s hunting neighbourhood, takes the value of 3.7 instead of 8. Similarly, the exponent  $k$  in the prey growth rate decreases, and only these two changes in parameters are needed to account for the effects of the spatial patterns on the dynamics of mean densities. Thus, the resulting system of ordinary differential equations takes a very specific form and one that is particularly simple to write: one can just borrow the expressions of the well-mixed model but modify the parameters to account for the role of space.

We consider here one additional set of parameters within this range, in which the neighbourhood for local growth and predation is given by 4 neighbouring sites instead of 8. In this case, the corresponding mean-field model exhibits decaying oscillations towards an equilibrium, instead of a limit cycle. As before, however, the mean-field model approximates poorly the dynamics of densities in the spatial system (Fig. 1). This is not surprising since spatial patterns develop as before, with prey clusters continuously forming and disappearing locally. By following the exact same steps as in Pascual *et al.* (2001), we can compute a modified exponent  $q = 2.75$ , for which the mean-field equations



**Figure 1** Comparison of the dynamics of prey densities at large scale in the spatial simulation (red,  $q = 4$ ), in the corresponding mean-field model (blue,  $q = 4$ ,  $k = 1$ ), and in the modified mean-field model (black,  $q = 2.75$ ,  $k = 0.81$ ). The dynamics of the spatial simulation are shown only after transients have died out, starting at time 3000. The modified mean-field model provides an accurate approximation of population densities in the spatial simulation only for the long-term dynamics after transients. Simulations of the spatial system use periodic boundary conditions and a grid size  $L^2 = 700^2$ .

approximate accurately the long-term dynamics of the spatial system (Fig. 1). It is important to note that the values of the modified exponents are not obtained by fitting these temporal trajectories but from an independent estimation of the associated rates. For example, the exponent  $q$  is obtained by fitting the per-capita predation rate  $[1 - (1 - p)^q]$  as a function of prey density  $p$  (Pascual *et al.* 2001).

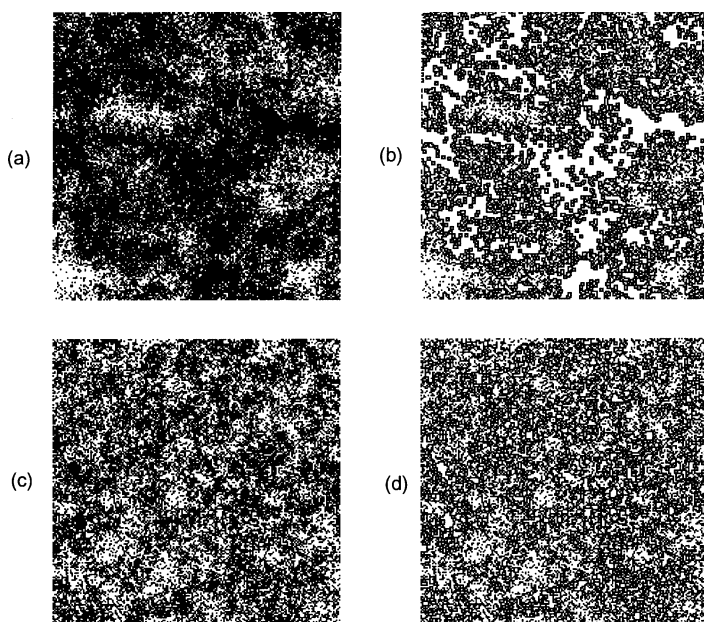
Thus, for the two spatial simulations considered (with  $q = 8$  and  $q = 4$ , respectively) the mean-field equations,

with modified parameters but identical functional forms, provide a simple model for the large-scale and long-term dynamics of population densities. This simple approximation begs the question of why it works at all, given the elaborate spatial patterns in the simulations. We focus next on the modified exponent  $q$  of the predation rate.

## CLUSTER GEOMETRY AND MODIFIED EXPONENT

We consider the clusters formed by the set of sites that are not occupied by prey, and are therefore either empty or occupied by predators. We refer to this set as the non-prey set  $B$ . This set is of relevance to explain  $q_m$ , the modified value of  $q$ , and more generally the per-capita predation rate,  $[1 - (1 - p)^{q_m}]$ , because in this rate, the term  $(1 - p)^{q_m}$  is the probability that a predator is isolated from prey and therefore, surrounded by non-prey sites. Recall that a predator eats only if it finds at least one prey in its neighbourhood. Thus, properties of the non-prey clusters, the environment where the predators live, are relevant to the isolation of predators and to the value of  $q_m$ . A non-prey cluster is defined as a group of non-prey sites connected to each other by neighbourhood distances, where the neighbourhood of a site is specified in the model.

Figure 2(a) shows the non-prey set  $B$  for the spatial simulation with  $q = 8$ . In Fig. 2(b), only the sites of this set that make up its interior perimeter are kept. This perimeter is defined as the set of sites in  $B$  with at least one prey in their neighbourhood. Thus a predator in the perimeter is by definition in contact with a prey. Comparison of Fig 2(a) and (b) shows that the perimeter accounts for a large fraction of the non-prey set almost everywhere in the grid. A



**Figure 2** Non-prey clusters and their interior perimeter shown for  $200 \times 200$  sites of the grid: in (a) and (c), the clusters (black) are shown for the simulations with  $q = 8$  and  $q = 4$ , respectively; in (b) and (d), only the sites within these clusters that belong to their interior perimeter are shown in the same colour. Comparison of the surface occupied by the clusters to that occupied by their interior perimeter (black sites, a and b, c and d) reveals that the perimeter accounts for a large fraction of the clusters' area.

similar pattern is seen for the simulation with  $q = 4$  (Fig. 2, compare c and d). Because this property of the perimeter will be key to our argument later, we show next that it is made possible by a particular scaling of the clusters of  $B$ .

Predators in this perimeter, by definition, are not isolated. Thus, isolated predators find themselves in the complement of this set, in the interior of  $B$ , which we call  $B_I$ . We denote the respective measures (or densities) of these sets in the lattice by  $b$  and  $b_I$ , and the interior fraction of  $B$  by  $F$ , with

$$F = \frac{b_I}{b}.$$

A perimeter that accounts for a large fraction of the non-prey set implies a low interior fraction  $F$  (23% and 28% for  $q = 4$  and  $q = 8$ , respectively). For sufficiently large lattices and clusters of regular geometry, such as that of circles and squares, the presence of large non-prey clusters would unavoidably lead to a large interior fraction  $F$ . To understand why this is not the case here, we consider the size and the interior perimeter of individual clusters. The size  $s$  is given by the number of sites in a cluster and its perimeter  $t_s$ , by the subset of sites that are in contact with at least one prey. Figure 3(a,c) shows that the perimeter scales as a power law with the size of the clusters, and that it does so with an exponent close to unity (0.98 and 0.97 for  $q = 4$  and  $q = 8$ , respectively). Thus, the perimeter of individual clusters grows as fast as their size, and close to the fastest possible rate. In this way, the interior fraction  $f$  of individual clusters, given by

$$f = \frac{(s - t_s)}{s}, \quad (2)$$

becomes independent of cluster size. Most important to our argument,  $f$  does not grow with size, and is comparable for small and large clusters (Fig. 3,b,d). The geometry embodied in the scaling  $t_s \approx s$  is thus one possible way to achieve a low interior fraction of the whole set  $B$ .

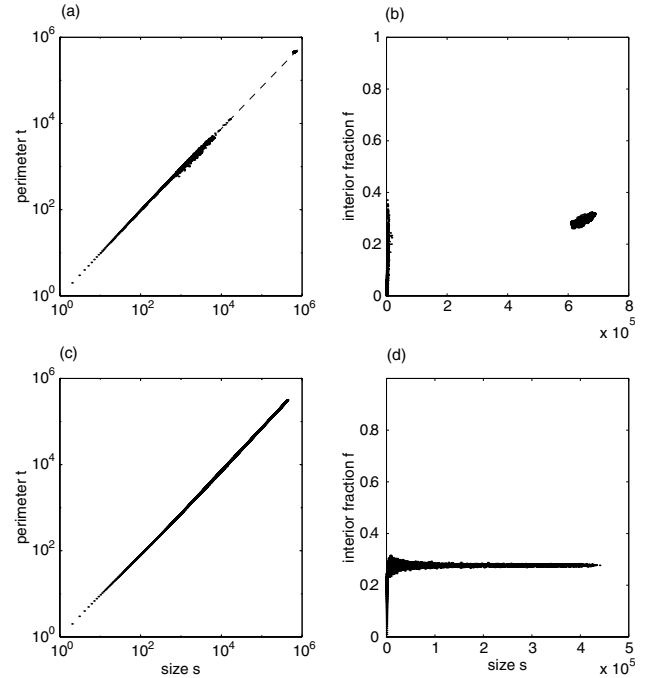
We return now to the value of the modified exponent  $q$  to establish its relationship to the geometry of the system. We start by assuming that predators are distributed at random in  $B$ , an assumption we later revisit. Then, the probability  $\pi$  that a predator is isolated can be computed as

$$\pi = F. \quad (3)$$

On the other hand, the probability of isolation can also be computed as

$$\pi = (1 - p)^{q_m} \quad (4)$$

where  $p$  is the density of the prey, and the exponent  $q_m$  corresponds to the effective number of sites in the neighbourhood of an isolated predator. If both prey and predators were well mixed,  $q_m$  would equal  $q$ , the original size of the neighbourhood in the spatial simulations.



**Figure 3** The perimeter of individual non-prey clusters scales linearly with their size in a log–log plot: in (a), for the spatial simulation with  $q = 8$ ; in (c), for that with  $q = 4$ . Notice that the size of clusters for the simulation with (a)  $q = 8$  displays a gap at intermediate sizes. Nevertheless, for all sizes, the points relating perimeter to size fall on the same line. As a result of the scaling of perimeter with size, the interior fraction  $f$  of the clusters remains constant with size. The resulting constancy of the interior fraction  $f$  with the size  $s$  of the clusters holds better for (d)  $q = 4$  than for (b)  $q = 8$ . For both, however, the largest clusters exhibit a small interior  $f$ , comparable to that of clusters orders of magnitude smaller.

However, the prey forms clusters and as a result, the space in which the predators live has a specific geometry, which modifies  $q$ . The resulting value  $q_m$  is obtained by equating eqns 3 and 4, which gives

$$q_m = \frac{\log(F)}{\log(1 - p)}. \quad (5)$$

Thus,  $q_m$  is a function of the interior fraction  $F$ , or equivalently, of its complement, the perimeter fraction of the non-prey set. Since  $b = (1 - p)$ , we can also write

$$q_m = \frac{\log(b_I)}{\log(b)} - 1, \quad (6)$$

which shows explicitly the dependence of  $q_m$  on the geometry of  $B$ . Table 1 gives the estimated value of  $q_m$  and compares it to the modified exponent  $q$  of the mean-field model for both simulations. Equation 6 provides a surprisingly good estimate of such exponent. This result

**Table 1** Comparison of the exponent in the per-capita predation rate  $[1 - (1 - p)^q]$ . The original value of  $q$  is that used in the spatial simulations and corresponds to the number of sites in the neighbourhood of the predator. The modified value of  $q$  is that for which the mean-field model approximates accurately population densities at large scale, once transients have died out. The value  $q_m$  is defined in the text and is determined from geometrical considerations

Original $q$	Modified $q$	Estimated $q_m$
8	3.70	3.20
4	2.75	2.75

confirms that the isolation of the predators itself, key to the formulation of the predation rate in the simplified model, can be estimated directly from the interior fraction  $F$  as postulated in eqn 3. The isolation of the predators created simply by the ratio of interior to total area of the space in which predators live, explains a reduction by almost one-half of the exponent from the well-mixed to the spatial case.

To close the argument we return to the assumption of the random distribution of predators in the non-prey set and relate it to the described geometry of this set, specifically to the perimeter scaling. From the local rules and parameters of the individual-based simulations, we do not expect the predators to be randomly distributed in  $B$ : predators must find prey to survive and reproduce with probability  $\beta_2$ , and they do so only if they are in the perimeter of  $B$ ; the resulting offspring are initially located at most one site away from this boundary; predators that deplete local clusters of prey find themselves isolated and die with probability  $\delta$ . Only for high  $\beta_2$  and low  $\delta$ , we expect the resulting distribution of isolated predators to be close to random, with a large fraction of predators in the interior of the non-prey set. For our simulations, however, most of the predators are in contact with the prey, lying in the perimeter of  $B$ , and most of the isolated predators are a single site away from their meal.

But are these observations really inconsistent with the assumption of a random distribution of predators in  $B$ ? We claim that they are not, and that this is the case in these simulations because the interior fraction  $F$  is low. For low  $F$ , the perimeter is a large fraction of the non-prey set. Thus, if predators were distributed at random in this set, they would find themselves largely in its perimeter, and those that do not, the isolated predators, would be for the most part in contact with this boundary. As shown earlier, the low value of  $F$  is itself related to the power-law scaling of the perimeter with size for individual clusters, which leads to clusters whose interior fraction  $f$  is independent of size. The constancy of  $f$  further implies that predators live in environments with the same geometry, with regard to their proportion of perimeter to interior, whether in small “ponds”, “lakes”, or “oceans”.

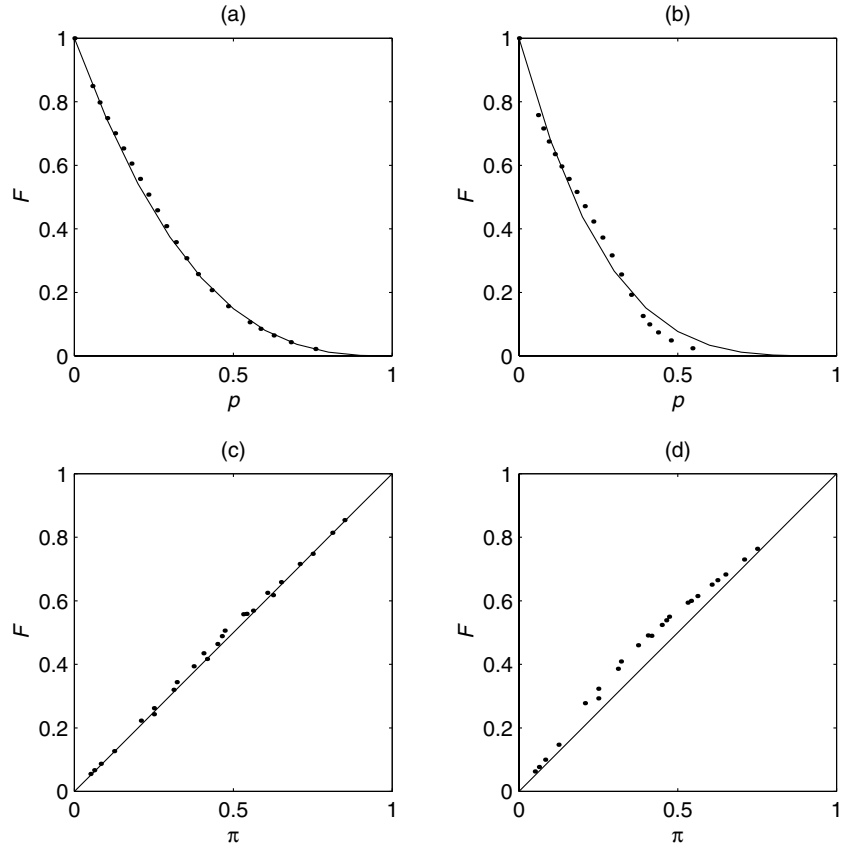
The proportion of perimeter to interior is also independent of the size of the lattice itself. To show this, we first observe that both the total size and the total perimeter of  $B$  scale as a power law with the size of the lattice and with the same exponent of two (results not shown). From these scalings, it follows by definition that  $F$  is constant with the size of the lattice. Then, for all clusters, their interior fraction  $f$  also takes this constant value since the scaling  $t_s \approx s$  implies that  $f = F$ .

## ROBUSTNESS OF THE RESULTS

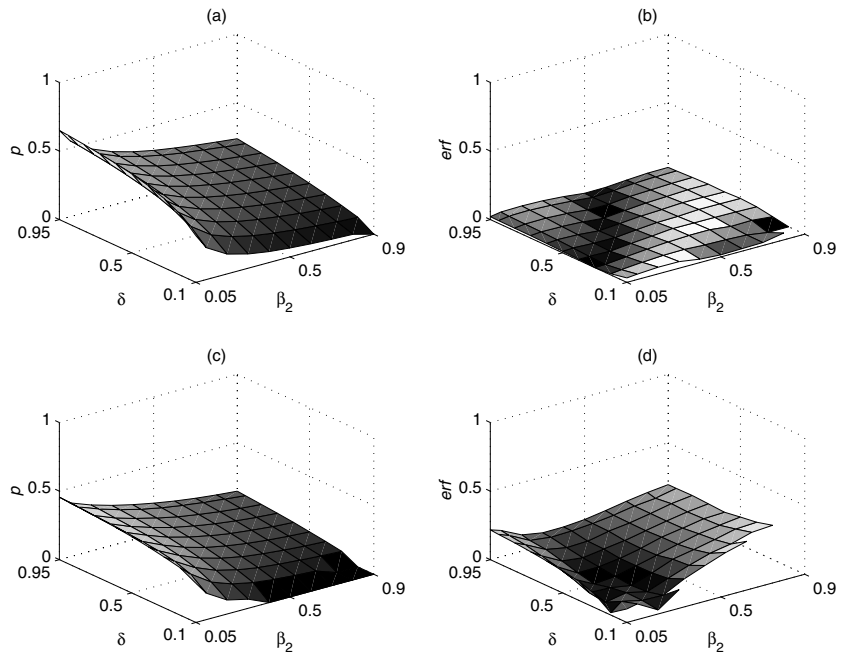
We end with evidence for the robustness of our results to variation in the parameters at the individual level. We focus first on the relationship key to our argument equating the isolation of the predators  $\pi$  to the interior fraction  $F$ . Figure 4(c,d) shows that for different values of the probabilities of starvation  $\delta$  and reproduction  $\beta_2$ , the numerical value of  $\pi$  in the simulations is close to that  $F$ . This similarity holds for different values of the prey's growth rate ( $\beta_1 = 0.1, 0.4$ , and  $0.7$ , results not shown). In these plots, high values of  $F > 0.5$  are obtained only for a combination of high  $\beta_2$  and low  $\delta$ . In this case, prey are sparse, forming small clusters. Predators deplete local clusters fast, giving rise to many offspring that survive a long time but become isolated and distributed randomly in the interior of the non-prey set. It is away from these extreme parameter values, when prey are not sparse and prey patchiness develops, that the equality of  $\pi$  and  $F$  becomes non trivial. The argument presented in this paper is relevant for this large region of parameter space.

Further evidence for robustness reveals the constancy of the modified exponent  $q_m$  across parameters of the individual-based model. Equation 5, which relates this exponent to  $F$ , holds regardless of parameter values (Fig. 4 a,b). These graphs demonstrate an even stronger constraint between dynamics and geometry the exponent remains constant as the density of the prey and the isolation of the predators vary. Figure 5 shows that the proposed modified mean-field model with the *same* modified exponents approximates well the long-term dynamics of population densities for different parameters values of the spatial simulations.

Finally, the power-law scaling relating perimeter to area of the non-prey clusters is also robust to parameter variations. This scaling holds with an exponent close to one across parameter space, breaking down progressively only for large  $\beta_2$  and low  $\delta$  when prey are sparse and finite non-prey clusters span too small a range. The exponent of the power law falls in  $[0.88, 0.99]$  and  $[0.86, 0.97]$  for  $q = 4$  and  $8$ , respectively, for  $0.1 \leq \beta_2 \leq 0.7$ ,  $0.1 \leq \delta \leq 0.9$ , with  $\beta_1$  set at  $0.1, 0.4$  or  $0.7$ .



**Figure 4** (a, b) The modified exponent  $q_m$  is constant across parameters at the individual level. The symbols (\*) plot the value of  $F$  as a function of mean prey density  $p$ , both computed from the spatial simulation, for different parameters  $\beta_2$  (in  $[0.05, 0.85]$ ) and  $\delta$  (in  $[0.15, 0.95]$ ). The curves plot the expected relationship between these variables (equation 5) for a fixed value of (a)  $q_m = 2.75$  and (b)  $q_m = 3.7$ . (c, d) The similarity of  $F$  and the probability of isolation of a predator  $\pi$  also holds across the same range of parameters. Similar results are obtained for different values of the prey's growth rate  $\beta_1$  (0.1, 0.4, and 0.7).



**Figure 5** The modified mean-field system with fixed exponents  $q$  and  $k$  approximates the dynamics of population densities for different values of the parameters  $\beta_2$  and  $\delta$ . In (b) and (d), the error of the approximation  $erf$  is computed as  $|p_s - p_{MMF}|/p_s$ , where  $p_s$  is the mean prey density in the spatial simulation and  $p_{MMF}$  the prey density in the modified mean-field model, both after transients have died out. In (a) and (c), the corresponding value of  $P$  is shown. (Top panels:  $q = 4$  and  $k = 1$  in spatial simulation,  $q = 2.75$  and  $k = 0.81$  in MMF; bottom panels:  $q = 8$  and  $k = 1$  in spatial simulation,  $q = 3.7$  and  $k = 0.62$  in MMF). Similar results are obtained for different values of the prey's growth rate  $\beta_1$  (0.1, 0.4, and 0.7).

## DISCUSSION

We have shown that an individual-based predator–prey model generates long-term spatial patterns characterized by a power-law scaling of the perimeter of the clusters with their size. This scaling was related to an implicit representation of space in a simple temporal model for the long-term dynamics of population densities. Numerous power laws have been described for spatial patterns in nature (Sugihara & May 1990; Hastings & Sugihara 1993). Power-law scalings similar to the one described here can provide a basis for applying mean-field or ‘box’ models with modified parameters, in systems for which well-mixed conditions do not hold and interactions and movement are local, resulting in patchy distributions. The empirical implication is that functional responses for well-mixed systems but with modified parameters, can yield reasonable approximations to per-capita population rates at large scales. Empirical fits of such functional responses would yield the modified parameters, in our case exponents, and not the values expected under well-mixed conditions. These modified exponents account for the effect on population rates of spatial patterns at smaller scales.

We conjecture that similar results will apply to other spatio-temporal models with local and antagonistic ecological interactions, specifically those whose corresponding well-mixed dynamics display either decaying or sustained cycles. Candidates include spatial models for host–parasite interactions and models for gap dynamics through physical disturbances. This conjecture is supported by recent findings showing that two other lattice models display similar cluster-size distributions to that of the prey in our predator–prey system (Pascual *et al.* in press). Although the systems differ in the details, they share local processes of growth and inhibition that can lead to decaying or persistent cycles under well-mixed conditions. Future work will address the applicability of our results to dynamics that treat space continuously and incorporate larger neighbourhoods of interaction and different movement patterns and distances. We expect the results to break down progressively with larger neighbourhoods. In the extreme limit of large  $q$ , the mean-field model itself with no modification of the exponents should hold. We have treated here the opposite case of local neighbourhoods composed of near neighbours. What happens in between remains to be examined. Ultimately, however, no single approach to treat space implicitly will hold universally. There is clearly a variety of spatial patterns and mechanisms generating these patterns in nature. But the results presented here suggest that a key issue is to identify properties of the spatial patterns that underlie the success of a given approach.

The modified mean-field model provides a semi-empirical method to scale the system from local (individual or patch) to large (population or landscape) levels. The method can be labelled as semi-empirical because the computation of modified exponents requires knowledge of the spatial distributions at the local level to fit the functional responses (Pascual *et al.* 2001). Semi-empirical approaches to scale spatio-temporal dynamics complement more formal (mathematical) ones such as the method of moments. Moment approximation methods (or pair approximation for discrete states) modify both the functional forms and the dimensionality of mean-field systems by adding variables for spatial variances and covariances (e.g. Bolker & Pacala 1999; Sato & Iwasa 2000; Keeling *et al.* 2001). By contrast, the number of variables and the expression of the functional forms are preserved in our simple model. Furthermore, formal methods are applicable only when the details at small scales are known and sufficiently simple to allow the derivation of equations for aggregated quantities and their spatial moments. The parameterization of spatial effects on temporal dynamics, however, may often be required for systems in which knowledge and measurements of small scale processes are unavailable. In such cases, more empirical approaches are needed which represent space implicitly by using properties of the spatial patterns (e.g. Hassell & May 1974; Hassell 1978, 2000). Modified mean-field models provide one possible avenue. We know how to write the equations and all spatial effects are captured in the modified parameters.

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