

SOME INEQUALITIES FOR THEORETICAL SPATIAL ECOLOGY

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Abstract

Inequalities for spatial competition verify the pair approximation of statistical mechanics introduced to theoretical ecology by Matsuda, Satō and Iwasa, among others. Spatially continuous moment equations were introduced by Bolker and Pacala and use a similar assumption in derivation. In the present article, I prove upper bounds for the k th central moment of occupied sites in the contact process of a single spatial dimension. This result shows why such moment closures are effective in spatial ecology.

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1. Introduction

Moment closure methods interest theoretical ecologists and mathematical scientists studying spatially mediated effects of adaptive dynamics in both continuous and discrete space [8]. Despite some effort aimed at defining formal properties of these techniques [18, 27], the approximations required to produce the resulting system of equations in continuous or discrete space often rely on heuristics. Nonetheless, there have been many successful achievements supported by computer simulation within these empirically validated frameworks [3, 14, 19, 20]. The analysis of spatial ecological models has consolidated in recent years throughout the literature of mathematical biology with some closures derived from variational principles. Similar modelling techniques with improved rigor were developed in metapopulation dynamics by Ovaskainen and Cornell [31], and in theoretical population genetics by Barton et al. [2]. The analysis by Ovaskainen and Cornell [31] is restricted to the equilibrium covariance structure of occupancy probabilities and studies stochastic perturbation dynamics about the deterministic, nonspatial mean-field theory. Barton et al. [2] use improved diffusion approximations for a stepping-stone model of

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migration, or structured coalescent process, that yield a set of stochastic partial differential equations from which are derived classical results of Malécot on probabilities of identity by descent. Raghieb et al. [34] justify a moment closure for a point process using constrained maximum entropy arguments.

Many of the pioneering applications of pair approximation to modelling adaptive dynamics in discrete space are reviewed by Rand [35]. Matsuda et al. [26] studied altruism as an evolutionary stable strategy with an individual-based statistical mechanics extension of the grouped (or nonindividual) dynamics in a Lotka–Volterra type model. Satō et al. [37] discovered that explicit space allows a pathogen-driven extinction region to appear in the phase diagram of the dynamics when nearest neighbour local interactions are included with the mean-field or global densities of a Lotka–Volterra type model. Harada and Iwasa [17] found that the dynamics of pair approximation correctly predicts that an optimal fraction of plant reproductive resource allocation between vegetative reproduction and seed production maximises the plant's equilibrium abundance, when compared with computer simulations of the full model. Those are pair-approximation results that the corresponding mean-field model fails to predict.

Analytically tractable spatial models of adaptive dynamics are often obtained by asymptotically approximating the entire model, which usually results in differential equations being formulated. By employing various asymptotic techniques, progress has been made in rigorous spatial modelling that is relevant to biological populations; see the review by Krone [23]. There is a loss of explicit spatial structure under these approximations that is still appealing, since it renders the problem more tractable in terms of either hydrodynamic equations or mean-field limit theorems. However, interacting particle system mathematics provides tools with which to formulate applied probabilistic ecological models where the effects of explicit spatial structure can be studied [10]. Adapting explicitly spatial probabilistic analysis, although more technically demanding and a domain of applied mathematicians, is useful for theoretical ecology [7, 29, 30].

The original spatial moment equations in ecological modelling that were proposed by Bolker and Pacala [4] are for a single species in a single spatial dimension. There is an established tradition of ecological modelling with spatial logistic equations [24], and this context also remains of interest to probabilistic analysts [12]. The results of the present article are obtained in this simple spatial arena and with simple rules of dispersal and mortality. This new approach justifies the main assumption of the moment closure technique. The proof developed in this article is of a technical level that requires some training in probability to follow, however the consequence of the result will be clear to mathematically inclined ecologists. This is an initial result that brings rigour to the moment closure and pair-approximation strategies for explicitly spatial ecological modelling.

The main assumption made in the derivation of the moment equations is that *the third central moments remain negligible* at the onset of spatial structure [5, 6, 33], where dispersal changes from infinite, or global, to finite. In lattice-based ecological

models, the local conditional probability of a site being occupied, given the state of two adjacent sites, is assumed to depend only on the state of one of the given sites. Whereas pair correlations are considered significant, correlations between three or more sites are assumed to be negligible, hence the name *pair approximation* [36]. Pair approximation is not obtained as a long-range limit, since both local and global site occupancy are connected by a feedback from local dispersal, which affects successful colonization due to cluster formation.

The moment equations that have developed in the literature of mathematical ecology use a competition kernel to determine establishment probabilities [8], and thereby impose an implied spatial structure on the system. Establishment and mortality probabilities are modelled similarly as functions of local density in the methods of Bolker and Pacala [4, 5]. The interacting particle system here replaces the competition kernel with the actual spatial structure of the environment. It does this by suppressing births when the offspring is sent to a site that is already occupied, and thus density-dependent establishment results.

In this article, the ingredients of the adaptive dynamics are those of the *contact process*, namely individual birth and death rates, and density-dependent establishment, which are components of the ecological models described above. I show that the crucial assumption of moment closure (that spatial structure is weak but not negligible) can be expressed as a function of the birth rate and the offspring dispersal range. The main theorem in the next section is thus a basic measure for a Bolker–Pacala or Dieckmann–Law power-1 closure and is generalised for k -plets in the contact process.

2. A theorem for moment closure

2.1. The contact process and its dual The *contact process* with finite range is the interacting particle system on which the results here are introduced. This process lives on a rescaled integer lattice $(1/M)\mathbb{Z}$, where \mathbb{Z} is the set of all integers and M is an integer constant, although not necessarily a large constant. Each initially occupied site's offspring percolate throughout the lattice in continuous time. The complete set of occupied sites, or particles, at time t is denoted by ${}^M\xi_t^\mu$, where μ describes the distribution of the initial configuration throughout the lattice. The rules of percolation are as follows:

- (i) each particle dies at rate 1;
- (ii) a particle living at site $x \in (1/M)\mathbb{Z}$ attempts to give birth to another particle at rate β , sending the new particle to a new site chosen uniformly at random from sites located in $[x - 1, x + 1]$;
- (iii) the birth is suppressed if the chosen site is already occupied.

Note that ${}^M\xi_t^\mu$ is a subset of $(1/M)\mathbb{Z}$. The number of particles within an interval of the type described in (ii) is determined by M . Thus, the parameter M describes the *dispersal range* of the process over which parents can attempt to place their offspring.

Define $u_M(t, x) = P(x \in {}^M\xi_t^\mu)$; translation invariant initial conditions are assumed here by taking the initial configuration's distribution μ to be product measure.

A ‘graphical representation’ allows the evolution of the process to be traced forwards or backwards in time. The connection between the contact process, its reverse time dual and a branching random walk is well established [9, 38]. Rather than essentially reproducing those descriptions, only the necessary properties are mentioned here. The $M_{\xi_t}^{\mu}$ above is defined with respect to the measure μ , although my notation is adjusted slightly in parts of this article that are made clear from the context. A special property of the contact process is *self duality*, which states that for fixed sets (of sites) A, B ,

$$P(M_{\xi_t}^{A} \cap B \neq \emptyset) = P(M_{\xi_t}^{B} \cap A \neq \emptyset),$$

where $M_{\xi_t}^{B}$ is equal in distribution to $M_{\xi_t}^{A}$. It will be necessary later to start the dual from a single occupied site x , and this is denoted by $M_{\xi_t}^x$. Note that the time parameter used here is that of forward time, and dual time therefore runs from t down to 0.

Consider a copy of $M_{\xi_t}^x$ that counts only birth events by ignoring death events, and then denote this copy by $M_{\eta_t}^x$. The corresponding branching process is known as the *Yule process* [13]. The contact process has a further restriction in that birth events which attempt to place offspring onto an already occupied site are suppressed. The dual of this process can be contained in an *influence set* [9], which is a super-dual process, although the full construction details of the influence set are not necessary here. The dual process adds new particles at successful birth events and removes particles at deaths, whereas the influence set ignores deaths and only accumulates particles (at successful births). The use of influence sets simplifies the calculation of the probability of collisions between multiple dual processes, since the influence set can be coupled to a branching process. This coupling results from the fact that collisions within a single dual will occur with probability zero as the dispersal range tends to infinity [9, 28]. The influence sets constructed by only counting successful births, and the associated branching processes, will dominate the dual processes; especially so for a finite dispersal.

Most interacting particle systems have intractable dual processes. For this reason, my probability calculations utilize influence sets rather than dual processes. The proof is thus made robust to model choice. Obtaining an accurate upper bound on the collision probability requires knowing how the size of the influence set grows, and distinguishing between the types of collisions that can occur. Sections 2.2 and 2.3 allow a more direct derivation that leads to better precision when calculating collision probabilities in Section 2.4. The proof sheds some light on the problem itself and is not merely of a technical nature.

2.2. Central moments of degree k A previous criterion conjectured to yield a nonzero value of the k th central moment of occupancy probabilities was that of having at least $k - 1$ collisions within a pair of duals [38], but this is shown here to be incorrect. A stronger criterion would require $k - 1$ collisions among the corresponding k dual processes, however this is still not strong enough for the conjecture to hold. To correct the previous conjecture I use much of the same notation and terminology. My approach is also similar in spirit, yet more precise, and a new generalization is

obtained. I prove a new theorem that sharpens the upper bound for the k th central moments, which yields a square root of the conjectured factor M^{-k} .

THEOREM 2.1. Define $\gamma_M^{x_i} \equiv M \xi_t^\mu(x_i) - u_M(t, x_i)$. There exist constants C_2, C_3, \dots, C_k (dependent on T) such that for all $t \in [0, T]$:

- (i)
$$\mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2}] \leq \frac{C_2}{M};$$
- (ii)
$$\mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \gamma_M^{x_3}] \leq \frac{C_3}{M^2};$$
- (iii)
$$\mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \gamma_M^{x_3} \gamma_M^{x_4}] \leq \frac{C_4}{M^2}.$$

Furthermore, the k th central moment is restricted as follows:

$$\mathbb{E}\left[\prod_{i=1}^k \gamma_M^{x_i}\right] \leq \begin{cases} \frac{C_k}{M^{(k+1)/2}} & \text{for } k \text{ odd,} \\ \frac{C_k}{M^{k/2}} & \text{for } k \text{ even.} \end{cases}$$

Note that distinct sites are considered here and $x_i \neq x_j$. The theorem is proven in Sections 2.3 and 2.4, where the constants of proportionality up to $k = 6$ are shown. I note that the order of magnitude in Theorem 2.1(i) and (ii) with respect to M are unchanged from Lemma 2.2 in the paper by Swindle [38], and his argument does roughly justify the finiteness of the constants of proportionality. Therefore, all subsequent results of that paper dependent on the order of magnitude of Theorem 2.1(ii) will remain valid, and the same applies for the results of Durrett and Neuhauser [28]. These works develop asymptotic results based on long-range (dispersal) limits of particle dynamics; see also a second paper of Durrett and Neuhauser [11] for fast-stirring (motion) limits. In fact, their rescaling argument involves fast stirring of particles between lattice sites that converges in a limiting process to a Brownian-like motion of the particles. This is comparable to taking a long-range limit such as in the first paper of Durrett and Neuhauser [28], in the sense that explicit spatial structure is lost. As was pointed out by Anderson and Neuhauser [1], ‘‘A consequence of [these limits] is that neighboring sites become independent, which greatly simplifies the analysis, but removes spatial effects that are due to spatial correlations.’’

The duality relation yields the following equation for development of the method of proof of the theorem:

$$P(x \notin \xi_t^\mu) = P(\xi_0^\mu \cap \tilde{\xi}_t^x = \emptyset) = \mathbb{E}\left[\prod_{z \in \tilde{\xi}_t^x} (1 - u_M(0, z))\right].$$

Thus, the probability of a site being unoccupied is equal to a product, taken over the dual of the site, of the probabilities of having been initially unoccupied. This

can be applied to show that the central moment of a collection of sites x_1, x_2, \dots, x_k can be expressed in terms of the probabilities of the duals of those k sites being initially unoccupied [38]. This approach yields a criterion for calculation of the central moments that can be phrased in terms of collisions between the duals.

Firstly, *modified duals* will be required that depend on an increasing number of the collection of duals being considered. *Collisions* between a pair of duals occur at particular spatial locations and times. To make this concrete, let

$$I_M[T, x, y] = \{(s, z) : 0 \leq s \leq T, \xi_s^x(z) = \xi_s^y(z),$$

and either

$$[\xi_{s-}^x(z) = 0, \xi_{s-}^y(z) = 1] \quad \text{or} \quad [\xi_{s-}^x(z) = 1, \xi_{s-}^y(z) = 0].$$

Define a *hierarchy* of modified dual processes that eliminate redundancies by forming a partition of the particles within the k dual processes under consideration:

- $\chi_t^{x_1}$ is an independent copy of $\xi_t^{x_1}$, and its own particles are unaffected by collisions;
- $\chi_t^{x_2}$ is an independent copy of $\xi_t^{x_2}$, and let $\zeta_t^{(x_1, x_2)}$ be a modified version of the copy such that its particles are annihilated by collisions with particles of $\chi_t^{x_1}$;
- $\chi_t^{x_3}$ is an independent copy of $\xi_t^{x_3}$, and let $\iota_t^{(x_1, x_2, x_3)}$ be a modified version of the copy such that its particles are annihilated by collisions with particles of $\chi_t^{x_1}$ and $\chi_t^{x_2}$.

Continuing as follows, $\chi_t^{x_k}$ is an independent copy of $\xi_t^{x_k}$, and let $\kappa_t^{x_k}$ be a modified version of the copy such that its particles are annihilated by collisions with particles of $\chi_t^{x_1}, \chi_t^{x_2}, \dots, \chi_t^{x_{k-1}}$.

It is convenient to define the following random variables:

$$\begin{aligned} f^x &\equiv \prod_{z \in \chi_t^x} (1 - u_M(0, z)), \\ g_y^x &\equiv \prod_{z \in \zeta_t^{x,y}} (1 - u_M(0, z)), \\ h_{y,y'}^x &\equiv \prod_{z \in \iota_t^{(x,y,y')}} (1 - u_M(0, z)), \\ i^x &\equiv \prod_{z \in \kappa_t^x} (1 - u_M(0, z)). \end{aligned}$$

Writing these out according to expressions obtained from the duality relation yields, for instance,

$$\begin{aligned} P(x_1 \notin \xi_t^{x_1}) &= \mathbb{E}[f^{x_1}], \\ P(x_1 \notin \xi_t^{x_1}, x_2 \notin \xi_t^{x_2}) &= \mathbb{E}[f^{x_1} g_{x_1}^{x_2}], \\ P(x_1 \notin \xi_t^{x_1}, x_2 \notin \xi_t^{x_2}, x_3 \notin \xi_t^{x_3}) &= \mathbb{E}[f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3}]. \end{aligned}$$

Under generalization to a collection of duals, note that the f^{x_i} for $i = 1, \dots, k$ are independent. Other members of the hierarchy of duals are dependent due to the modification procedure. Now, armed with this representation, the relationship between the central moments and collisions between duals is made precise in the next subsection.

2.3. Precise resolution of central moments Intuitively, no dual can be independent of the others in the central moment since first central moments are identically zero, and in the product the expectation would then trivially collapse. Any dual whose percolation up to time T has avoided collision has therefore percolated in a mutually exclusive way from the other duals, even though it had the possibility of collision. Self collision that occurs within a dual causes the corresponding birth to be suppressed, but it does not cause a collision with another dual process. I show how, up to time T , nonzero central moments of degree k result when none of the k duals have avoided collision within the group of k duals.

Consider the third central moment. Then the hierarchy of duals consists of only three tiers; the function i^x is omitted and the subscripts in $h_{y,y'}$ can be dropped. The following equation is also arrived at by Swindle [38], except for the replacement of the correct signs in the sum:

$$\mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \gamma_M^{x_3}] = \mathbb{E}[-f^{x_1} g_{x_1}^{x_2} h^{x_3} + f^{x_1} g_{x_1}^{x_2} f^{x_3} + f^{x_1} g_{x_1}^{x_3} f^{x_1} + f^{x_2} g_{x_2}^{x_3} f^{x_1} - 2f^{x_1} f^{x_2} f^{x_3}].$$

When $|I[x, y, T]| = 0$ there is pairwise independence as no duals collide. Promotions in the hierarchy of duals result: $h^{x_3} \equiv f^{x_3}$ and $g_{x_j}^{x_i} \equiv f^{x_i}$; the expectation above cancels to a zero sum. When $|I[x, y, T]| = 1$, one pair collides once only. The promotions in this case depend on which particular pair collides. For instance, if it is x_2 and x_3 that collide then $h^{x_3} \equiv g_{x_2}^{x_3}$, $g_{x_1}^{x_3} \equiv f^{x_3}$ and $g_{x_1}^{x_2} \equiv f^{x_2}$. The expectation collapses to zero in any case, whichever pair it is that does collide.

Performing calculations that extend the approach taken above, the fourth central moment is written out by definition and, after taking complements, a similar equation is found. The next equation describes the fourth central moment and suggests the true criterion to ensure nonzero central moments:

$$\begin{aligned} \mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \gamma_M^{x_3} \gamma_M^{x_4}] &= \mathbb{E}[-f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3} i^{x_4} + f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3} f^{x_4} + f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_4} f^{x_2} \\ &\quad + f^{x_1} g_{x_1}^{x_3} h_{x_2, x_3}^{x_4} f^{x_2} + f^{x_2} g_{x_2}^{x_3} h_{x_2, x_3}^{x_4} f^{x_1} - f^{x_1} g_{x_1}^{x_2} f^{x_3} f^{x_4} - f^{x_1} g_{x_1}^{x_3} f^{x_2} f^{x_4} \\ &\quad - f^{x_1} g_{x_1}^{x_4} f^{x_2} f^{x_3} - f^{x_2} g_{x_2}^{x_3} f^{x_1} f^{x_4} - f^{x_2} g_{x_2}^{x_4} f^{x_1} f^{x_3} - f^{x_3} g_{x_3}^{x_4} f^{x_1} f^{x_2} \\ &\quad + 3f^{x_1} f^{x_2} f^{x_3} f^{x_4}]. \end{aligned}$$

The first two cases are identical to those in the preceding paragraph. When $|I[x, y, T]| = 0$ or $|I[x, y, T]| = 1$ the expectation collapses to zero. When $|I[x, y, T]| = 2$ there are two pairwise collisions. However, the particular duals involved determine whether the expectation collapses or not. For instance, assuming the collisions occur between x_1 and x_2 , and between x_1 and x_3 , the promotions are as follows: $i^{x_4} \equiv f^{x_4}$, $h_{x_1, x_2}^{x_3} \equiv g_{x_1}^{x_3}$, $h_{x_1, x_2}^{x_4} \equiv f^{x_4}$, $h_{x_1, x_3}^{x_4} \equiv f^{x_4}$, $g_{x_2}^{x_3} \equiv f^{x_3}$, $h_{x_2, x_3}^{x_4} \equiv f^{x_4}$, $g_{x_1}^{x_4} \equiv f^{x_4}$, $g_{x_2}^{x_3} \equiv f^{x_3}$, $g_{x_2}^{x_4} \equiv f^{x_4}$ and $g_{x_3}^{x_4} \equiv f^{x_4}$. In that case, the expectation does indeed collapse to zero. In contrast,

assuming the colliding pairs are x_1, x_2 and x_3, x_4 , the promotions are the same as above except for the following: $i^{x_4} \equiv g_{x_3}^{x_4}$, $h_{x_1, x_2}^{x_3} \equiv f^{x_3}$, $g_{x_1}^{x_3} \equiv f^{x_3}$, $h_{x_1, x_3}^{x_4} \equiv g_{x_3}^{x_4}$, $h_{x_2, x_3}^{x_4} \equiv g_{x_3}^{x_4}$ and $g_{x_3}^{x_4} = g_{x_3}^{x_4}$ (identical). In this case, the expectation above is

$$\mathbb{E}[-f^{x_1} g_{x_1}^{x_2} f^{x_3} g_{x_3}^{x_4} + f^{x_1} g_{x_1}^{x_2} f^{x_3} f^{x_4} + f^{x_1} f^{x_3} g_{x_3}^{x_4} f^{x_2} - f^{x_2} f^{x_4} f^{x_1} f^{x_3}] \neq 0$$

and the fourth central moment has not collapsed. Thus I have a counter-example to the criterion for the collapse of all central moments as being the number of collisions between a pair of duals. Replacing the pair with a collection of duals does not prevent the same failure.

Proceeding similarly to the central moment of degree k , it can be shown that

$$\begin{aligned} \mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \cdots \gamma_M^{x_k}] &= \mathbb{E}[-f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3} i_{x_1, x_2, x_3}^{x_4} \cdots \omega^{x_k} \\ &\quad + f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3} \cdots \phi_{x_1, x_2, \dots, x_{k-2}}^{x_{k-1}} f^{x_k} + f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3} \cdots \phi_{x_1, x_2, \dots, x_{k-2}}^{x_k} f^{x_{k-1}} \\ &\quad + \cdots - f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3} \cdots \psi_{x_1, x_2, \dots, x_{k-3}}^{x_{k-2}} f^{x_{k-1}} f^{x_k} \\ &\quad - f^{x_1} g_{x_1}^{x_2} h_{x_1, x_2}^{x_3} \cdots \psi_{x_1, x_2, \dots, x_{k-3}}^{x_{k-1}} f^{x_{k-2}} f^{x_k} - \cdots \\ &\quad + \cdots + (-1)^k f^{x_1} f^{x_2} \cdots f^{x_k}]. \end{aligned} \quad (2.1)$$

Observe that identical terms arise and can be collected with coefficients of alternating sign according to the binomial theorem. That is, the expectation has the following form: there is a unique term of the first type shown above; k distinct terms of the second type in which each term contains two members at the top tier of the hierarchy of modified duals; $\binom{k}{2}$ distinct terms of the third type in which each term contains three members at the top tier; and so on, where the final term consists only of members at the top tier of the hierarchy. Note that the final term just described and the terms of the penultimate type will be the same, and so the final term cancels one of them out. Thus, $(-1)^{k-1} (k-1) f^{x_1} f^{x_2} \cdots f^{x_k}$ is the sum of the final term and penultimate terms, and is the actual final term of the expectation.

Promotions in the hierarchy of modified duals result from nominating certain duals to have avoided all collisions, up to a fixed time T . It can be shown by examining the consequences of an increasing number of particular duals that have avoided collision that a symmetry arises in the right-hand side of (2.1). There is a symmetric precipitation of terms that are promoted and that subsequently cancel out of the right-hand side of (2.1). These cancellations leave no remaining terms and the expectation collapses to zero without exception whenever promotions arise. Once each of the k duals are involved in at least one collision with some other dual there are no promotions. In this case, the first term on the right-hand side of (2.1) is unique and therefore the central moment cannot be zero.

2.4. The constants of proportionality in the theorem In Section 2.3, it was shown how promotions that result from collisions among the hierarchy of modified duals determine whether or not the k th central moment is negligible. More specifically, to avoid the collapse of the central moment, a certain number of *targeted collisions*

must be accumulated. These targeted collisions involve pairs of newly colliding duals, or colliding pairs in which only one of the duals had so far avoided any collisions. The minimum number of targeted collisions that leaves no dual having avoided a collision is $k/2$ when k is even, and $(k + 1)/2$ when k is odd. This is equivalent to the minimum number of targeted collisions that would yield a nonzero value of the k th central moment. A threshold results over which the central moments are rendered nonzero. That is, using an indicator function \mathbb{I} ,

$$\mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \cdots \gamma_M^{x_k}] = \begin{cases} \mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \cdots \gamma_M^{x_k} \mathbb{I}\{\geq k/2 \text{ targeted collisions}\}] & \text{for } k \text{ even,} \\ \mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \cdots \gamma_M^{x_k} \mathbb{I}\{\geq (k + 1)/2 \text{ targeted collisions}\}] & \text{for } k \text{ odd.} \end{cases}$$

In both cases, $|\mathbb{E}[\gamma_M^{x_1} \gamma_M^{x_2} \cdots \gamma_M^{x_k}]| \leq 1$ by definition, for all k . Therefore, the expectations on the right-hand side above cannot be greater than $P(\geq k/2 \text{ targeted collisions})$, and $P(\geq (k + 1)/2 \text{ targeted collisions})$, respectively.

As discussed in Section 2.1, each dual corresponds to a single particle initially, and the number of particles present in the dual after some time T is dominated by a Yule process. In the Yule process, starting from a single particle, the number of particles present after a fixed time T has a negative binomial distribution with parameters $(1, e^{-\beta T})$ [13]. Note that the probability of a collision between a pair of duals is highest when they both start from adjacent locations on the lattice, since they then share the highest number of potential sites for each other's offspring. By assuming that all offspring of an original particle remain within its own dispersal range, after m births the proportion of sites occupied by the dual is at most $(m + 1)/(2M)$ [38]. Therefore, the conditional probability of a collision between a pair of duals, given that m births have occurred, is at most $E(m(m + 1)/2M)$, in which m has the negative binomial distribution mentioned above. It is convenient to have omitted multiplication of the probability of the noncolliding birth events from this upper bound, since a decrease in the probabilistic bound and a more complicated expression would result. This bound is calculated under the assumption that collisions are rare, as is the case when M is fairly large. This is a reasonable way of characterizing the build up of collisions, which yield nonnegligible higher-order correlations, when dispersal is substantial but not (asymptotically) long range. Evaluating this expectation yields $e^{2\beta T}/M$. Collisions with particles of other duals do not count for this calculation and can be ignored without loss of generality of the upper bound.

Exact collision probabilities depend on the history of the process. Collisions occur sequentially and can be treated independently by taking the probability of each collision as the maximal value calculated in the preceding paragraph. Other nontargeted collisions can also be ignored without loss of generality in this way. At a collision event the probability of it being a targeted collision is found combinatorially, with a uniform distribution over the particular pairs involved. Namely, calculate a quotient in which the denominator is the number of ways of forming j collisions in total, $\binom{k}{2}^j$, when j targeted collisions have occurred.

The k th central moment remains zero until each of the k modified duals is involved in at least one collision with another dual in the group. The very first collision is always a pairwise targeted collision, and therefore this first targeted collision occurs with probability $e^{2\beta T}/M$. This is an upper bound for the second central moment, and $C_2 = e^{2\beta T}$ in Theorem 2.1. There are two cases in general. Let i denote the number of single targeted collisions, and recall that these are targeted collisions where one newly colliding dual is involved. When k is odd, $i = 1, 3, 5, \dots, k - 2$, and when k is even, $i = 0, 2, 4, \dots, k - 2$. Let d_i denote the conditional probability of the total number of targeted collisions $(k + i)/2$. When $k \geq 3$ is odd,

$$P(\geq(k + 1)/2 \text{ targeted collisions}) \leq \frac{e^{(k+1)\beta T}}{M^{(k+1)/2}} \left[\frac{(k + 1)(k - 1)!}{2[k(k - 1)]^{(k-1)/2}} + d_3 \frac{e^{2\beta T}}{M} + d_5 \frac{e^{4\beta T}}{M^2} + \dots + \frac{(k - 1)!(k - 2)!}{\binom{k}{2}^{k-2}} \frac{e^{(k-3)\beta T}}{M^{(k-3)/2}} \right], \tag{2.2}$$

in which there are $(k - 1)/2$ coefficients and d_1, d_{k-2} are shown. Note that when $k = 3$, only the first term in the sum on the right-hand side above is required. When $k \geq 4$ is even,

$$P(\geq k/2 \text{ targeted collisions}) \leq \frac{e^{k\beta T}}{M^{k/2}} \left[\frac{(k - 2)!}{[k(k - 1)]^{k/2-1}} + \frac{(k - 1)!k^2(k^2 - 4)}{8[k(k - 1)]^{k/2}} \frac{e^{2\beta T}}{M} + d_4 \frac{e^{4\beta T}}{M^2} + \dots + \frac{(k - 1)!(k - 2)!}{\binom{k}{2}^{k-2}} \frac{e^{(k-2)\beta T}}{M^{k/2-1}} \right], \tag{2.3}$$

in which there are $k/2$ coefficients and d_0, d_2, d_{k-2} are shown. I have shown the coefficients up to and including that of the sixth central moment. Calculating higher-order coefficients is, in principle, straightforward using the combinatorial approach as above.

Essentially, the exponential quantity described above needs to be calibrated as the average number of offspring surviving an individual after T units of time, where offspring can be displaced M units away from a parent. This yields values of $e^{2\beta T}/M \ll 1$ in many situations. At the onset of spatial structure, when M is still quite large but $e^{2\beta T}/M$ remains significant, it is now clear that the bound on the third central moment $2e^{4\beta T}/(3M^2)$ will indeed often be negligible.

3. Polynomial density dependence

Allowing for nonlinear competitive interaction is another piece of the ecological puzzle, and is likely to allow new spatio-temporal mechanisms to be found [7]. Consider a polynomial density-dependent fecundity or establishment. In the current model, define fecundity as $C(x, y; \eta) = \beta\eta(x)[1 - \eta(y)]$, where $\beta > 0$ is a constant birth rate. This is a translation invariant fecundity. Clearly, $\eta(x) = 1$ when only occupied sites can give birth, and $\eta(y) = 0$ for offspring placement to succeed. This is abstracted

to a process with generalized rate functions as follows. Consider f as a polynomial function of some collection of sites in the neighborhood about x . This collection is $\{x_1, x_2, \dots, x_n\} \in \mathcal{N}_x$ such that

$$C(x, x_1, x_2, \dots, x_n, y; \eta) = \beta\eta(x)f(x_1, x_2, \dots, x_n)[1 - \eta(y)].$$

Put a restriction on the polynomial rate functions such that the state of each site examined contributes to the value of the function. Specifically, f must take the form

$$f(\eta(x_1), \eta(x_2), \dots) = \prod_{i=1}^n \eta(x_i).$$

For example, the contact process has $C(x, y; \eta) = \beta\eta(x)[1 - \eta(y)]$; the so-called sexual reproduction process [28] has $C(x, y; \eta) = \beta\eta(x)\eta(x + \epsilon)[1 - \eta(y)]$, where $\epsilon = 1/M$.

For polynomial density-dependent fecundity, an upper bound of the collision probability for a pair of adjacent duals can be found similarly to the previous section. Thus, the average size up to a fixed time T of the influence set, when each birth event adds n particles, cannot be greater than $e^{n\beta T}$. An upper bound on the probability of collisions under polynomial density-dependent fecundity can be found by adapting the approach of the previous subsection. However, this will become decreasingly accurate as n increases, since the effective birth rate in the resulting process is considerably lower than the rate given above due to the constraints on the occurrence of reproduction events.

Alternatively, density-dependent establishment may be incorporated in an identical way. Consider sites in \mathcal{N}_y , and redefine $f = \prod_{i=1}^n (1 - \eta(y_i))$. In this process, the proportion of successful births is less than or equal to that of the regular duals. In this case, the growth of the dual will be slower, and the upper bounds derived in the previous subsection will not be exceeded.

4. Discussion

The main assumption made in spatial moment equations and pair approximation is studied with an interacting particle system that captures the ingredients of the kinds of models in which moment closure strategies are applied. It is shown that collisions of duals of the contact process can be interpreted as corresponding to the value of central moments that describe spatial structure in ecological modelling. Inequalities are proven that describe the emergence of spatial structure in the contact process as dispersal range decreases below the asymptotic long-range limit. I have shown that nonnegligible central moments are more extensive than was previously thought, and the rate of decay of the higher-order moments is over-estimated by anticipating a zero expectation based only on the number of regular collisions among a collection of duals.

These results provide steps toward understanding how significant higher-order spatial correlations can build up due to a trade-off between dispersal range and

birth rate. The benefits of looking more carefully at how collisions contribute to the higher-order correlations is also recognized as useful in the literature of theoretical ecology [32].

The use of influence sets has the benefit of making my results robust to complicated dual processes that allow for deaths of particles, but in which direct calculation of similar bounds is complex and would require consideration of the criticality of the birth rate. I have shown that the ratio of the third to the second central moment is $2e^{2\beta T}/3M$, and that an upper bound on the fourth central moment is $e^{4\beta T}/3M^2(1/2 + e^{2\beta T}/M)$.

An ecological outcome that the moment closure and pair-approximation techniques currently fail to predict is competitive exclusion when inter-species competition is more intense than intra-species competition, which leads to a phalanx strategy (see the papers by Bolker et al. [7, p. 141] and Neuhauser [29, pp. 363–365] for discussion). Instead, founder control is seen which simply depends upon the initial densities, and as noted by Bolker et al. [7] this may be due to the effects of large scale spatial structure being underestimated [21]. This is one of many areas of theoretical ecology that suggest explicit, rather than implicit, spatial interaction and consideration of transient spatial structure.

Adaptive dynamics in spatial mathematical models ascertain patterns observable in biology; there are exceptions to this where such patterns are merely transient and fragile artifacts of the models themselves [1]. Identifying these causality relationships correctly equates to understanding more fully the role of spatial axes in ecological interactions [22].

As Bolker [3] points out in his review, “Spatial moment equations, and also pair approximations, eliminate the explicitly stochastic, discrete-individual nature of the population dynamics they are meant to represent,” and “moment equations are not technically stochastic since they represent average behavior over space or across ensembles of similar ecological arenas.” The statistics of clusters and their evolution under interface motion are crucial to the outcomes of competing species dynamics [15, 16]. Extensions of moment closure techniques have been developed to analyse detraction from spatial equilibrium in continuous space by Lewis and Pacala [25], and in discrete space by Thomson and Ellner [39].

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