

R.S. Cantrell · C. Cosner

Deriving reaction–diffusion models in ecology from interacting particle systems

Received: 2 July 2001 / Revised version: 20 May 2003 /
Published online: 20 August 2003 – © Springer-Verlag 2003

Abstract. We use a scaling procedure based on averaging Poisson distributed random variables to derive population level models from local models of interactions between individuals. The procedure is suggested by using the idea of hydrodynamic limits to derive reaction-diffusion models for population interactions from interacting particle systems. The scaling procedure is formal in the sense that we do not address the issue of proving that it converges; instead we focus on methods for computing the results of the scaling or deriving properties of rescaled systems. To that end we treat the scaling procedure as a transform, in analogy with the Laplace or Fourier transform, and derive operational formulas to aid in the computation of rescaled systems or the derivation of their properties. Since the limiting procedure is adapted from work by Durrett and Levin, we refer to the transform as the Durrett-Levin transform. We examine the effects of rescaling in various standard models, including Lotka-Volterra models, Holling type predator-prey models, and ratio-dependent models. The effects of scaling are mostly quantitative in models with smooth interaction terms, but ratio-dependent models are profoundly affected by the scaling. The scaling transforms ratio-dependent terms that are singular at the origin into smooth terms. Removing the singularity at the origin eliminates some of the unique dynamics that can arise in ratio-dependent models.

1. Introduction

Ecological processes are distributed in space and time and occur on a wide range of spatio-temporal scales (O'Neill 1989). Interactions between individuals are inherently local, but the spatial scale of what is local may vary greatly from one organism to another. Local interactions summed over space combine to produce effects at the level of populations, but the dynamics of large distributed populations may be quite different from those of local subpopulations. This dichotomy was observed in the famous experiments of Gause (1935) which showed that species which typically coexist in nature may not be able to do so in a small, homogeneous environment. The entire metapopulation approach to spatial modeling is based on the idea that local populations can be expected to go extinct but at a larger scale recolonizations

R.S. Cantrell, C. Cosner: Department of Mathematics, University of Miami, Coral Gables, FL, 33124, USA. e-mail: {rsc;gcc}@math.miami.edu

Research partially supported by NSF grants DMS 99-73017 and DMS 02-11367

Key words or phrases: Reaction-diffusion – Interacting particle systems – Hydrodynamic limits – Population dynamics – Spatial models – Scaling – Lotka-Volterra – Ratio-dependence – Competition – Predator-prey – Hawk-Dove game

can allow a spatially distributed population to persist (Hanski 1996). In principle it might be desirable to formulate an ecosystem theory based on the behaviors of individual organisms and the consequences of those behaviors, but in practice, such a theory would necessarily be so complex as to be useless. Thus, it is highly desirable to find ways of rescaling systems from smaller to larger scales which preserve some important features of local interactions but allow enough simplification for tractability (Levin and Pacala 1997, Levin 2003). One approach to rescaling spatially distributed interactions at discrete sites up to a model for the dynamics of the overall population on a larger spatial scale is to take spatial averages of densities and vital rates in a way that yields a model for the dynamics of the average densities. In general the average of a function depending on population density may not be the same as the value of that function evaluated at the average density, so some care must be taken in this process. There are many possible ways of averaging population dynamics across space; see (Levin and Pacala 1997, Chesson 2000, Kshatriya and Cosner 2002) for some examples and discussion. In this paper we will study a method of averaging based on computing the expectations of functions of Poisson distributed random variables. This method is used in computing hydrodynamic limits of interacting particle systems to obtain reaction-diffusion models (Durrett and Levin 1994), but the method can also be used in other modeling approaches (Chesson 2000). In some cases spatial averaging of models can change their predictions. This phenomenon is noted in the context of hydrodynamic limits by Durrett and Levin (1994), but also occurs in other contexts (Pacala and Roughgarden 1982, Chesson 2000, Kshatriya and Cosner 2002). Chesson (1997) has introduced the term *scale transition* to describe such effects. The main goals of this paper are to develop methods and results that give some insight into the effects of the sort of averaging that arises in taking hydrodynamic limits of interacting particle systems and to use those methods and results to explore the extent to which this type of averaging can result in scale transition in some common types of models. The notion of averaging which arises in the process of taking hydrodynamic limits involves computing the means of functions of Poisson distributed random variables. This averaging process also can be used in some models that are not based on interacting particle systems, for example the types of models discussed by Chesson (2000). In this paper we will first describe effects that occur in all modeling contexts, and then we will address those that are specific to interacting particle systems. To clarify those aspects relating to interacting particle systems we give a brief review of how those systems work.

There are many issues related to connecting individual based models or models which explicitly count the number of individuals at each location with continuum models such as reaction-diffusion systems or models based on dispersal as described by integral kernels. (See (Tilman and Kareiva 1997) for a survey of spatial models in ecology and related areas.) There are also a number of issues which arise in rescaling models across different spatial and temporal scales. We will not attempt to review these topics systematically, but we will cite a few references to indicate where this paper is focused relative to the broader issues of connecting models of different types and understanding the effects of scaling. Transferring information from one scale to another or accounting for the presence of multiple spatial and tem-

poral scales is an issue even within the context of continuum models operating at the mesoscale or macroscale. Predator-prey models which incorporate multiple spatial scales by using reaction-diffusion models for the prey and spatially discrete immigration/emigration models for the predators are treated analytically in (Cantrell and Cosner 1996). Although the title of their paper indicates otherwise, Gao et al. (2001) treat scaling problems arising from changing the grid size in numerical solutions of reaction-diffusion models. Specifically, they assume that landscape dynamics can be described by a reaction-diffusion system (Gao et al. 2001, equation (1)) and ask how the numerical scheme for solving the reaction-diffusion model by discretization should be modified when the resolution, i.e. the mesh size of the grid, is changed. That problem of going from continuous to discrete modeling is in a sense the inverse of the type of problem we shall consider, where the goal is to start with a discrete model and rescale it into a continuum model. As noted previously, that is the same issue that is addressed from the viewpoint of more or less rigorous mathematics by Durrett and Levin (1994). Even more rigorous treatments of the underlying mathematics are given in (DeMasi and Presutti 1991, Spohn 1991, and Perrut 2000). In contrast, Wilson (1998) takes a phenomenological approach to constructing reaction-dispersal models which display some of the same types of behavior as individual based simulations. A very clear discussion of these two contrasting approaches is given by Wilson (1998). It would be of interest to put some rigor and mechanism behind Wilson's phenomenological models, perhaps by extending the mathematical and mechanistic approach of Durrett and Levin, but that appears to be beyond the reach of existing ideas and methods. The present paper is a modest step in that direction but much more remains to be done.

Variability in abiotic environmental factors and variations in the dispersal rates of organisms and the ways that they utilize space can have important effects on population dynamics in many ways on many scales; see for example (Cantrell and Cosner 1989, 1991, 1998, Tilman and Kareiva 1997, Cuddington and Yodzis 2000, Dockery et al. 1998) among many others. The mechanisms we shall study here, like those studied in (Chesson 2000) do not depend on abiotic variability or any particular assumptions about dispersal rates, although they may interact with those factors. Instead, they depend on the presence of variation in the number of individuals, and hence in vital rates if those are density-dependent, across a set of discrete sites. It turns out that rescaling a discrete model to a continuum model by averaging local populations and rates can modify the form of density dependence in some cases. In the context of interacting particle systems, averaging via hydrodynamic limits determines the diffusion rate independently from the reaction terms. In other words, assumptions about fast or slow diffusion in the original interacting particle system do not influence the form of the reaction terms in the rescaled model but do appear in the diffusion rate of that model. Thus, effects of slow diffusion such as those discussed by Cuddington and Yodzis (2000) cannot be understood by studying how the averaging process affects reaction terms, but if a slow rate of diffusion is imposed as an extra condition on the underlying interacting particle system then that feature is retained in the rescaled model. Thus, it may be possible to gain some insight into the effects of slow dispersal rates by using reaction-diffusion systems derived as limits of interacting particle systems, but that would be a problem in

reaction-diffusion theory rather than a problem directly related to rescaling vital rates via Poisson averaging. Some discussion of the effects of slow diffusion from the viewpoint of reaction-diffusion theory are given in (Cantrell and Cosner 1989, 1998) and (Dockery et al. 1998).

The present paper was inspired largely by a paper of Durrett and Levin (1994). In that paper Durrett and Levin compare and contrast the predictions of various types of spatial models. They observe that simple mean field models, or models obtained by simply adding a diffusion term to those mean field models, may give quite different predictions than computational simulations of interacting particle systems. They also propose that using hydrodynamic limits to rescale interacting particle systems into reaction-diffusion systems should lead to models which more accurately reflect the observed behavior of the original system, and they work out an example which supports that view. In the present paper we adopt the viewpoint and methods of (Durrett and Levin 1994), develop some mathematical machinery to facilitate the application of those methods, and apply them to a number of standard models for population dynamics and species interactions. The mathematical methods we develop provide information about the averages of Poisson distributed random variables that may be useful in other modeling contexts, for example in the approach used by Chesson (2000). We found it useful to think of the process by which reaction terms are computed from local interaction rates as a transform, in the sense of Laplace or Fourier transforms. We refer to the transform as the Durrett-Levin transform because it is based on the computations in (Durrett and Levin 1994). We derive a number of properties and operational formulas for the transform and use those to study the effects of rescaling in specific models. It turns out that in many cases the transforms of relatively simple functions cannot be computed explicitly in closed form, but it is usually possible to obtain enough information about them to draw some conclusions about the predictions of rescaled models.

One significant feature of averaging functions of Poisson random variables is that it smooths out interaction rates; that is, applying the Durrett-Levin transform to bounded functions yields functions that are infinitely differentiable. This is significant in the context of the Hawk-Dove game studied in (Durrett and Levin 1994) and also in the context of ratio-dependent predator-prey models (see (Cosner et al. 1999) and the references therein; also (Kuang and Beretta 1998, Jost et al. 1999)). It may be significant in other types of models such as epidemic models with proportional mixing. Those types of models involve interaction rates which are not differentiable at the origin, and those in turn admit dynamics which do not occur in similar models with smooth interaction terms. Hence, scaling via Poisson averaging can have profound effects on the predictions of such models, as noted in (Durrett and Levin 1994), and that is due largely to the smoothing property of the averaging procedure.

The paper is organized as follows: in section 2 we review background material, mostly from (Durrett and Levin 1994); in section 3 we define the Durrett-Levin transform and deduce some of its properties; in section 4 we apply the results of section 3 to a number of common models, and in section 5 we give a nonmathematical discussion of the implications of the calculations in section 4. Some mathematical details are treated in the Appendix.

2. Models and scaling: a brief review

The micro scale: interacting particle systems

The models that originally motivated us to study Poisson averaging are interacting particle systems of the type discussed by Durrett and Levin (1994). We shall use some of the notation from (Durrett and Levin 1994), and since the treatment in that paper is fairly comprehensive we shall only give a brief discussion of how the models are formulated. Our main goal here is to describe how to set up models that capture the local interactions of individuals. A key feature of these models is that they describe “density dependent” vital rates in terms of interactions between individuals, as opposed to casting them in terms of average densities. The underlying spatial framework for the interacting particle systems we consider is \mathbb{Z}^2 , the lattice of points in the plane with integer coordinates. For purposes of illustration we consider the case of two species, but the approach extends to arbitrarily many. Let $\eta_{1t}(x)$ and $\eta_{2t}(x)$ denote the numbers of individuals of types 1 and 2 respectively at location x and time t . We will assume that individuals disperse by moving at random to an adjacent grid point, but we want to allow more flexibility in our description of the local neighborhood where interactions can take place. For example, we may want to think of the “location” of an individual as the location of its nest, and think of the local neighborhood as the area over which the individual can search for prey. We can describe the neighborhood of a point x as the set $\{x + z : z \in \mathcal{N}\}$ where \mathcal{N} is a local neighborhood of $(0, 0)$. Typical choices would be $\mathcal{N} = \{z \in \mathbb{Z}^2 : |z_1| + |z_2| \leq 1\}$, which consists of $(0, 0)$ and its nearest neighbors, or perhaps $\mathcal{N} = \{(0, 0)\}$ so that the neighborhood is simply the site itself, or the neighborhood could be the larger diamond shape or square given by $\mathcal{N} = \{z \in \mathbb{Z}^2 : |z_1| + |z_2| \leq m\}$ or $\mathcal{N} = \{z \in \mathbb{Z}^2 : |z_1| \leq m, |z_2| \leq m\}$. We shall see that the only feature of \mathcal{N} which is still relevant after the models have been rescaled to the “macro” scale is the number of sites (i.e. grid points) in \mathcal{N} , which we denote as $|\mathcal{N}|$. In systems with more than two species there could be different local interaction neighborhoods for interactions between different pairs of species.

An important feature of the types of neighborhoods we consider is that they are defined in terms of the distance between grid points in some metric or distance function. If we let $d_1(x, y) = |x_1 - y_1| + |x_2 - y_2|$ then the neighborhood $\mathcal{N} = \{z \in \mathbb{Z}^2 : |z_1| + |z_2| \leq m\}$ could be defined as $\mathcal{N} = \{z \in \mathbb{Z}^2 : d_1(z, 0) \leq m\}$ which means that the neighborhood of x could be characterized as $\{y : d_1(x, y) \leq m\}$. We could also use $d_2(x, y) = \max\{|x_1 - x_2|, |y_1 - y_2|\}$, and obtain $\mathcal{N} = \{z \in \mathbb{Z}^2 : |z_1| \leq m, |z_2| \leq m\} = \{z \in \mathbb{Z}^2 : d_2(z, 0) \leq m\}$. A key feature of neighborhoods defined in terms of distances is that distance is symmetric, that is, $d(x, y) = d(y, x)$. It follows that for any given grid point x the number of grid points y for which $d(x, y) \leq m$ is the same as the number of grid points for which $d(y, x) \leq m$. In words, the number of grid points in the local neighborhood of x is equal to the number of grid points y to whose local neighborhoods x belongs. This is relevant in the formulation of predator-prey models because it means that the number of grid points within the search radius of a predator located at any given point is equal to the number of grid points from which a prey individual at point y is potentially subject to attack.

Following Durrett and Levin (1994) we specify the dynamics of the interacting particle system in terms of dispersal, local interactions, and neighborhood interactions:

1. **Dispersal:** Each individual of type i changes its location at rate μ_i . An individual changes its location by randomly selecting one of the nearest neighbors to its current position and moving to it, with each nearest neighbor site having equal probability of being selected.
2. **Local interactions:** Individuals of each type may reproduce and/or die at rates that depend on the number of individuals of either or both types present at the same site. These interactions would typically include crowding effects due to the presence of conspecifics.
3. **Neighborhood interactions:** Individuals may reproduce and/or die at rates depending on the numbers of individuals of either or both types present in the local neighborhood of the site. These interactions would typically include interference competition between different species or predator-prey interactions.

For purposes of describing local neighborhood interactions we will find it useful to define

$$\hat{\eta}_{it}(x) = \sum_{z \in \mathcal{N}} \eta_{it}(x+z) \quad (2.1)$$

as the number of individuals of type i in the neighborhood of x . In formulating interaction terms we shall assume that individuals do not crowd themselves or interact with themselves. This is one of the formulations given by Durrett and Levin (1994, p. 389). We have chosen to make that assumption because it seems more realistic and seems to lead to simpler scaling relations in some cases than other possible assumptions.

With the assumptions and notations described above, we can readily formulate models for population interactions at the “micro” scale. In a later section we shall examine a number of scenarios in detail, but for the present we shall only give a simple example and describe the general form that the interaction terms will take. Suppose that individuals of type 1 reproduce logistically with a *per capita* birth rate which decreases linearly with the number of other conspecifics at the same site (local interaction) and experience Lotka-Volterra predation from those individuals of type 2 in the neighborhood of the site (neighborhood interaction.) Since we assume individuals do not interact with themselves the logistic birth rate for type 1 at location x should have the form $a - b(\eta_{1t}(x) - 1)$ and the effect of predation should be to induce a death rate $-c\hat{\eta}_{2t}(x)$. (Recall that $\hat{\eta}_{2t}(x)$ represents the number of individuals of type 2 in the interaction neighborhood of x .) If we interpreted these rates as terms in a nonspatial model for population dynamics, the model would take the form

$$\frac{d}{dt}\eta_{1t}(x) = [a - b(\eta_{1t}(x) - 1) - c\hat{\eta}_{2t}(x)]\eta_{1t}(x) \quad (2.2)$$

However, this formulation makes sense only by analogy because η_1 and $\hat{\eta}_2$ are actually discrete random variables; hence the quotation marks. The reason why we have

presented equation (2.2) is to show how the rates occurring in the interacting particle system are related to the terms in a nonspatial deterministic model for local and neighborhood interactions. Since many types of interactions (e.g. predation with a functional response) are typically modeled as terms in ordinary differential equations for population densities, it seems worthwhile to illustrate the analogy between such terms and the rates in the interacting particle system. To get a logically sound formulation of the expected rate of change in the total population of type 1 at the point x we would calculate the expectation $E([a - b(\eta_{1t}(x) - 1) - c\hat{\eta}_{2t}(x)]\eta_{1t}(x))$. The main goal of this paper is to gain a better understanding of how such expectations behave if the interacting particle system is rescaled to a diffusion limit. The general form of interaction terms is $f(\eta_{1t}(x), \eta_{2t}(x), \hat{\eta}_{1t}(x), \hat{\eta}_{2t}(x))$, so the general forms of expectations we will want to compute will be the limiting cases of

$$E(f(\eta_{1t}(x), \eta_{2t}(x), \hat{\eta}_{1t}(x), \hat{\eta}_{2t}(x))\eta_{it}(x)). \quad (2.3)$$

We next turn to the issue of how to compute the large scale limits of interacting particle systems or other sorts of explicitly or implicitly spatial models.

The macro scale: spatial averaging and hydrodynamic limits

If a population is distributed over a collection of sites, with different numbers of individuals occupying different sites, and if additionally the rates at which individuals die or reproduce depend on the number of other individuals occupying the same site, then to obtain a population level model we must somehow average those rates across all sites. Unfortunately, if $\eta(x)$ is a random variable, $f(\eta)$ is a nonlinear function, and E denotes expectation, then in general $E(f(\eta)) \neq f(E(\eta))$. Thus, to correctly rescale individual based spatial models, interacting particle systems, etc. up to simple population level models we must take into account the way that the distribution of η interacts with the nonlinearity of f . A general approach to that issue is described by Chesson (2000), but the specific results depend in part on assumptions about the distribution of η . In this paper we will examine in detail the case where η has a Poisson distribution. That choice is motivated partly by the theory of hydrodynamic limits of interacting particle systems. That theory provides a mathematically rigorous way of rescaling interacting particle systems to reaction-diffusion systems. Rigorous treatments are given by DeMasi and Presutti (1991) and Spohn (1991). A rigorous derivation of some of the results stated by Durrett and Levin (1994) is given by Perrut (2000).

There are two key ideas underlying the formulation of hydrodynamic limits. First, if particles perform independent random walks on a grid then under appropriate assumptions on the initial state of the system, the large time limit of the joint distribution of the numbers of particles at the points belonging to any finite subset of the grid is a set of independent Poisson distributed random variables, each with the same mean. Second, in the models we envision, dispersal occurs on a faster timescale than population dynamics. As is standard in taking diffusion limits we scale the grid as ϵ and time as ϵ^2 and let $\epsilon \rightarrow 0$. This leads to a standard diffusion equation for dispersal. In this framework as we pass to the “macro” scale of time

and space by letting $\epsilon \rightarrow 0$, the variables $\eta_{it}(x)$ giving the numbers of individuals at site x should have limits that are independent and Poisson distributed on the set of sites in the interaction neighborhood of any given site. The means of the variables should be the population densities of the two types at the site in question. If the rate at which individuals of type i reproduce or die at site x is given by $f_i(\eta_{1t}(x), \eta_{2t}(x), \hat{\eta}_{1t}(x), \hat{\eta}_{2t}(x))$ then the reaction term in the limiting equation should be given by taking a limit of (2.3) as

$$E(f(U_1, U_2, \hat{U}_1, \hat{U}_2)U_i), \quad (2.4)$$

where U_i, \hat{U}_i are independent Poisson distributed random variables with means $u_i(x), |\mathcal{N}|u_i(x)$ respectively.

Formula (2.4) is the starting point for our investigations. Recall that if U is a Poisson distributed random variable with mean λ then U takes values $0, 1, 2, \dots$ with $P(U = k) = e^{-\lambda}\lambda^k/k!$. Thus, for any function $g(U_1, U_2, \hat{U}_1, \hat{U}_2)$ we have

$$\begin{aligned} E(g(U_1, U_2, \hat{U}_1, \hat{U}_2)) &= \sum_{j,k,\ell,m=0}^{\infty} g(j, k, \ell, m) P((U_1, U_2, \hat{U}_1, \hat{U}_2) = (j, k, \ell, m)) \\ &= \sum_{j,k,\ell,m=0}^{\infty} g(j, k, \ell, m) (e^{-u_1} u_1^j / j!) (e^{-u_2} u_2^k / k!) \\ &\quad \times (e^{-|\mathcal{N}|u_1} (|\mathcal{N}|u_1)^\ell / \ell!) (e^{-|\mathcal{N}|u_2} (|\mathcal{N}|u_2)^m / m!) \\ &= [e^{-(|\mathcal{N}|+1)u_1 - (|\mathcal{N}|+1)u_2}] \\ &\quad \times \sum_{j,k,\ell,m=0}^{\infty} g(j, k, \ell, m) |\mathcal{N}|^{\ell+m} u_1^{j+\ell} u_2^{k+m} / j! k! \ell! m!. \end{aligned} \quad (2.5)$$

Equation (2.5) shows how the term $g(U_1, U_2, \hat{U}_1, \hat{U}_2)$ arising from local and neighborhood interactions at the “micro” scale should be scaled up to the “macro” scale. The expression on the right in (2.5) shows how to compute the reaction term in the reaction-diffusion system arising as the “macro” scale limit of the original interacting particle system.

In analyzing expressions such as those occurring in (2.5) it can be useful to exploit the independence of the random variables. Suppose that $g = g(U_1, U_2)$ for simplicity. We have

$$\begin{aligned} E(g(U_1, U_2)) &= \sum_{j=0}^{\infty} \sum_{k=0}^{\infty} g(j, k) P((U_1, U_2) = (j, k)) \\ &= \sum_{j=0}^{\infty} \left[\sum_{k=0}^{\infty} g(j, k) P(U_2 = k) \right] P(U_1 = j). \end{aligned} \quad (2.6)$$

The point is that we can compute the rescaled form of $g(U_1, U_2)$ one variable at a time.

3. The Durrett-Levin transform

Definition and basic properties

A crucial element in our approach to understanding the effects of Poisson averaging is to interpret the calculation of the expectation of a function $f(U)$ of a Poisson random variable U with mean u as a transform which yields a new function of u in analogy with the way that the Laplace and Fourier transforms act on functions to produce new ones. Once Poisson averaging is conceptualized as a transform we can attempt to understand it by deriving operational formulas analogous to those possessed by Laplace or Fourier transforms and using those to study its effects on various sorts of functions. Since we were inspired to study the topic of Poisson averaging by Durrett and Levin (1994) we have used the term “Durrett-Levin transform” to denote the transform arising from Poisson averaging.

Definition. *The Durrett-Levin transform of a function $f(U_1, U_2, \dots, U_n)$ whose domain is the set of n -tuples of nonnegative integers is defined as*

$$\mathcal{DL}\{f\}(u_1, \dots, u_n) = \sum_{j_1, \dots, j_n=0}^{\infty} f(j_1, \dots, j_n) \times e^{-(u_1+\dots+u_n)} u_1^{j_1} u_2^{j_2} \dots u_n^{j_n} / (j_1!)(j_2!) \dots (j_n!) \tag{3.1a}$$

or equivalently as the Poisson average

$$\left. \begin{aligned} \mathcal{DL}\{f\}(u_1, \dots, u_n) &= E(f(U_1, \dots, U_n)) \\ \text{where } U_1, \dots, U_n &\text{ are independent Poisson random} \\ \text{variables with means } E(U_i) &= u_i. \end{aligned} \right\} \tag{3.1b}$$

Using definition (3.1b) we may rewrite (2.6) as

$$E(g(U_1, U_2, \hat{U}_1, \hat{U}_2)) = \mathcal{DL}\{g\}(u_1, u_2, |\mathcal{N}|u_1, |\mathcal{N}|u_2) \tag{3.2}$$

where $u_i = E(U_i)$, so that $|\mathcal{N}|u_i = E(\hat{U}_i)$. Our goals are to understand how Poisson averaging changes the form of terms describing interactions and hence might change the predictions of models as in (Durrett and Levin 1994), and to derive properties and operational formulas for the Durrett-Levin transform which can inform our understanding of the effects of scaling or aid in computation and/or analysis of the transforms of specific functions. To that end we shall state some lemmas about the transform.

Lemma 3.1. *Suppose that $|f(j_1, \dots, j_n)| < M_0 \cdot M_1^{(j_1+\dots+j_n)}$ for some positive constants M_0, M_1 . Then $\mathcal{DL}\{f\}(u_1, \dots, u_n)$ is well defined and is a real analytic function of (u_1, \dots, u_n) on \mathbb{R}^n , so that in particular $\mathcal{DL}\{f\}(u_1, \dots, u_n)$ is C^∞ in (u_1, \dots, u_n) .*

Proof. The bound on f implies that the series defining $\mathcal{DL}\{f\}$ in (3.1a) is majorized by the series

$$\sum_{j_1, \dots, j_n=0}^{\infty} M_0 |M_1 u_1|^{j_1} \dots |M_1 u_n|^{j_n} \cdot e^{-(u_1 + \dots + u_n)} / (j_1)! (j_2)! \dots (j_n)!,$$

which converges to $M_0 (e^{|M_1 u_1| - u_1}) \dots (e^{|M_1 u_n| - u_n})$, so the power series for $\mathcal{DL}\{f\}$ converges for all $(u_1, \dots, u_n) \in \mathbb{R}^n$, with uniform convergence on any compact subset of \mathbb{R}^n . \square

A number of features of the Durrett-Levin transform are apparent from inspection of (3.1). We have

Lemma 3.2. *The Durrett-Levin transform is linear. If f is nonnegative then $\mathcal{DL}\{f\}(u_1, \dots, u_n)$ is nonnegative if $u_i \geq 0$, $i = 1 \dots n$. If in addition $f(j_1, \dots, j_n) > 0$ for some (j_1, \dots, j_n) then $\mathcal{DL}\{f\}(u_1, \dots, u_n)$ is strictly positive if $u_i > 0$, $i = 1 \dots n$.*

Various properties of the Durrett-Levin transform follow from (3.1b) and standard results about independent random variables. Some of those are given in the following:

Lemma 3.3. *i) $\mathcal{DL}\{1\} = 1$.*

ii) $\mathcal{DL}\{U_i\} = u_i$.

iii) If $f(U_1, \dots, U_n) = f(U_{i_1}, \dots, U_{i_k})$ for some combination of indices $\{i_1, \dots, i_k\} \subseteq \{1, \dots, n\}$ then $\mathcal{DL}\{f\}(u_1, \dots, u_n) = \mathcal{DL}\{f\}(u_{i_1}, \dots, u_{i_k})$.

iv) If $\{i_1, \dots, i_k\}$ and $\{j_1, \dots, j_\ell\}$ are disjoint subsets of $\{1, \dots, n\}$ and $f(U_1, \dots, U_n) = g(U_{i_1}, \dots, U_{i_k})h(U_{j_1}, \dots, U_{j_\ell})$, then $\mathcal{DL}\{f\}(u_1, \dots, u_n) = \mathcal{DL}\{g\}(u_{i_1}, \dots, u_{i_k}) \cdot \mathcal{DL}\{h\}(u_{j_1}, \dots, u_{j_\ell})$.

A sketch of the proof is given in the Appendix.

Explicit Computations

Ideally we would like to obtain explicit formulas for the reaction terms arising from rescaling. This approach is taken for the Hawk-Dove game in (Durrett and Levin 1994). Unfortunately, it turns out that such explicit computations can be difficult even for simple types of functions, so that a uniform approach based on explicit computation does not seem feasible. By definition (3.1a), the Durrett-Levin transform can always be evaluated numerically as a power series, but it is illuminating to consider some specific cases where it can be computed in a simple closed form. We shall focus primarily on simple expressions in one or two variables.

Example 1. *Let $n = 1$.*

i) If k is a positive integer,

$$\mathcal{DL}\{U(U-1)(U-2) \dots (U-k+1)\} = u^k$$

ii) $\mathcal{DL}\{e^{\alpha U}\} = e^{(e^\alpha - 1)u}$

$$\begin{aligned} \text{iii) } \mathcal{DL}\{U/(U+1)\} &= \begin{cases} 0 & u = 0 \\ [u - 1 + e^{-u}]/u & u \neq 0 \end{cases} \\ \text{iv) } \mathcal{DL}\{U/(U+2)\} &= \begin{cases} 0 & u = 0 \\ [u^2 - 2u + 2 - 2e^{-u}]/u^2 & u \neq 0. \end{cases} \end{aligned}$$

(See the Appendix for derivations).

Example 1 reveals some important features and limitations of the Durrett-Levin transform. Cases i) and ii) show that it maps polynomials of degree m to other polynomials of degree m and maps exponentials to exponentials, but it typically changes the coefficients in both cases. Cases iii) and iv) are more subtle. In those cases the algebraic forms of the functions are changed. However, it turns out that many of their qualitative features are preserved.

For example, in the case $f(U) = U/(U+1)$ we have

$$\begin{aligned} \lim_{U \rightarrow \infty} f(U) &= \lim_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) = 1; \\ [\mathcal{DL}\{f\}(u)]' &= \begin{cases} [1 - (1+u)e^{-u}]/u^2 & (u \neq 0) \\ 1/2 & (u = 0) \end{cases} \end{aligned}$$

so $[\mathcal{DL}\{f\}(u)]' > 0$ since $(1+u) < e^u$ for $u \neq 0$. It turns out that in general the Durrett-Levin transform preserves monotonicity and some aspects of asymptotic behavior. However, cases iii) and iv) of Example 1 show that it generally does not preserve the algebraic form of functions. An examination of the derivation of iii) and iv) shows that the same method would apply to $U/(U+k)$ if k is a positive integer but not otherwise. We do not know how to compute $\mathcal{DL}\{U/(U+k)\}$ in closed form for general k . In the case where k is a positive integer the algebraic form of $\mathcal{DL}\{U/(U+k)\}$ becomes more complicated as k increases. Similarly, it is unclear how to compute $\mathcal{DL}\{U^\gamma\}$ if γ is not an integer.

Example 2. (see also Durrett and Levin 1994). Let $n = 2$ and let $f(U_1, U_2) = U_1 U_2 / (U_1 + U_2 - 1)$ if $U_1, U_2 \geq 1$, $f(0, U_2) = f(U_1, 0) = 0$. We have

$$\mathcal{DL}\{f\} = \frac{u_1 u_2}{u_1 + u_2} (1 - e^{-(u_1 + u_2)}).$$

A derivation is given in the Appendix. The function $f(U_1, U_2)$ in this example arises in the analysis of the Hawk-Dove game if one assumes that individuals do not “play the game” against themselves; see (Durrett and Levin 1994). The derivation fails if we consider functions such as $U_1 U_2 / (U_1 + 2U_2 - 1)$ or $U_1 U_2 / (U_1 + U_2 + k)$ when k is not an integer. Rates depending on $U_1 U_2 / (U_1 + U_2)$ or $U_1 U_2 / (U_1 + U_2 - 1)$ occur naturally when individuals encounter each other with frequencies depending on the fraction of the local interacting population of each type. (The presence or absence of the -1 in the denominator depends on whether individuals interact with themselves.) Thus, it is good to be able to compute their Durrett-Levin transforms in closed form. However, forms like $U_1 U_2 / (AU_1 + BU_2 + C)$ with general coefficients A , B , and C also occur naturally in ratio-dependent and Beddington-DeAngelis forms of functional response terms, and in general those do not have Durrett-Levin transforms which can be expressed in closed form.

Conclusions. We can compute the Durrett-Levin transforms of certain functions, notably polynomials and exponentials, explicitly in closed form. However, for many other expressions which occur frequently as descriptions of interaction rates, explicit computations are difficult or impossible. Thus, we shall try to obtain enough information about the properties of the Durrett-Levin transform so that we can draw conclusions about the behavior of models involving them without having to compute them in closed form.

Operational formulas and additional properties

We shall derive some results which allow us to obtain fairly detailed information about the Durrett-Levin transforms of functions even if we cannot compute them explicitly. Some of the formulas may also be useful for explicit computations.

Lemma 3.4. *Suppose that $f_1(U_1, \dots, U_n) \geq f_2(U_1, \dots, U_n)$. Then $\mathcal{DL}\{f_1\} \geq \mathcal{DL}\{f_2\}$.*

Proof. This follows immediately from (3.1a) by comparing series term by term.

Remark. If $f(U_1, \dots, U_n) \geq f_2(U_1, \dots, U_n)$ for all (U_1, \dots, U_n) with strict inequality for some (U_1, \dots, U_n) then $\mathcal{DL}\{f_1\} > \mathcal{DL}\{f_2\}$ for $(u_1, \dots, u_n) \neq (0, \dots, 0)$.

Lemma 3.5. *If $f = f(U_1, \dots, U_n)$ then*

$$\begin{aligned} \frac{\partial}{\partial u_k} \mathcal{DL}\{f(U_1, \dots, U_k, \dots, U_n)\} &= \mathcal{DL}\{f(U_1, \dots, U_k + 1, \dots, U_n)\} \\ &\quad - \mathcal{DL}\{f(U_1, \dots, U_k, \dots, U_n)\} \\ &= \mathcal{DL}\{f(U_1, \dots, U_k + 1, \dots, U_n) \\ &\quad - f(U_1, \dots, U_k, \dots, U_n)\}. \end{aligned} \quad (3.3)$$

Lemma 3.5 has a number of important implications. Some will only become apparent when we examine how scaling affects population dynamics, but others are immediate:

Corollary 3.6. *If f is increasing (resp. decreasing) in U_k then $\mathcal{DL}\{f\}$ is increasing (resp. decreasing) in u_k .*

Proof. If f is increasing in U_k then $\mathcal{DL}\{f(U_1, \dots, U_k + 1, \dots, U_n)\} \geq \mathcal{DL}\{f(U_1, \dots, U_k, \dots, U_n)\}$ with strict inequality if $(u_1, \dots, u_n) \neq (0, \dots, 0)$.

By (3.3), $\frac{\partial}{\partial u_k} \mathcal{DL}\{f\} \geq 0$ with strict inequality for $(u_1, \dots, u_n) \neq (0, \dots, 0)$. If f is decreasing in U_k then the inequalities are reversed.

Remark. If f is concave up with respect to U_k in the sense that

$$\begin{aligned} &\frac{f(U_1, \dots, U_k + 1, \dots, U_n) + f(U_1, \dots, U_k - 1, \dots, U_n)}{2} \\ &\geq f(U_1, \dots, U_k, \dots, U_n) \end{aligned} \quad (3.4)$$

then applying (3.3) twice and arguing as in Corollary 3.6 shows that $\partial^2 \mathcal{DL}\{f\}/\partial u_k^2 \geq 0$ so that $\mathcal{DL}\{f\}$ is concave upward. In general f need not be differentiable, or even defined for $(U_1, \dots, U_n) \notin \mathbb{N}^n$, but if $\partial^2 f/\partial U_k^2 \geq 0$ then (3.4) holds. Thus, the Durrett-Levin transform preserves the monotonicity and convexity properties of f if those properties are global. Some additional properties follow from the lemmas below. (Proofs or sketches are given in the Appendix.)

Lemma 3.7. *Suppose that $|f(U_1, \dots, U_n)| \leq f_0$. If $u_k \geq 0$ for $k = 1, \dots, n$, then $|\mathcal{DL}\{f\}| \leq f_0$.*

Lemma 3.8. *If $\lim_{U \rightarrow \infty} f(U) = \alpha$ then $\lim_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) = \alpha$.*

Lemma 3.9. $\mathcal{DL}\{U_k f(U_1, \dots, U_k, \dots, U_n)\} = u_k \mathcal{DL}\{f(U_1, \dots, U_k + 1, \dots, U_n)\}$.

Remark. To understand how Poisson averaging affects the predictions of some types of models it is of interest to know whether it decreases or increases the original function. In general it may increase the value of the original function on some intervals and decrease it on others. However, if $f(U)$ is concave then $f(U) \leq a + bU$ whenever $a + bU$ is a tangent line to $f(U)$, so $\mathcal{DL}\{f\}(u) \leq a + bu$. Since $f(U) \leq a + bU$ for the tangent line at $U = c$ given by $f(c) + f'(c)(U - c)$ it follows that $\mathcal{DL}\{f\}(u) \leq f(c) + f'(c)(u - c)$ so that $\mathcal{DL}\{f\}(c) \leq f(c)$. Thus, Poisson averaging decreases concave functions. Similarly, it increases convex functions. See also (Chesson 2000) for a related discussion of concavity and convexity vs. spatial averaging.

The examples and lemmas in this section show that the Durrett-Levin transform preserves a number of important qualitative features of functions, including monotonicity. However, it does not always preserve the algebraic form of the original function, and for many common functions it is not clear how to compute the transform, or even that the transform can be expressed in closed form. The transform is a smoothing operator which maps bounded functions to analytic functions. It turns out that in models with nonsmooth rate terms such as the hawk-dove game, epidemiological models with proportional mixing, or ratio-dependent predator-prey models, the smoothing property of the transform can have profound effects on model predictions.

We end this section with another lemma which will be used in one of the applications. It is based on the computations used in Example 2. The proof is in the Appendix.

Lemma 3.10. $\mathcal{DL}\{f(U_1 + U_2)\}(u_1, u_2) = \mathcal{DL}\{f(U)\}(u_1 + u_2)$.

(As long as f satisfies the bounds in the hypothesis of Lemma 3.1 all the series in the proof will converge uniformly on compact subsets of \mathbb{R}^2 .)

4. Applications and implications

In this section we apply the results of the preceding section to some specific situations. Our goals are to illustrate the effects of Poisson averaging and to explore how

it can be used in the specific context of hydrodynamic limits of interacting particle systems to obtain simple models that retain certain features of the spatial structure of the original model. Our treatment is not intended to be exhaustive, and we hope that other researchers will explore these topics further. The issue of determining what Poisson averaging does or does not do can be addressed directly by applying the results of section 3, and is relevant in modeling approaches such as those of Chesson (2000) which are not based on interacting particle systems. To correctly understand how to translate the modeling assumptions underlying an interacting particle system into interaction terms in a simple continuum model requires an examination of those assumptions as well as an application of the results of section 3. Thus, we shall first consider general issues related to Poisson averaging and then turn to the more specific issue of translating interacting particle systems into reaction-diffusion models, even though our main interest is modeling via reaction-diffusion systems.

Effects of Poisson averaging in simple models

The simplest sorts of models for which our methods are relevant are based on the idea that individuals at a given site x die or reproduce at rates that depend on the numbers $\eta_{it}(x)$ of individuals of type i in the same site. If we assume that individuals of type i interact only with others of type i , and that individuals do not crowd themselves but do experience logistic crowding effects from other conspecifics in the same location, the logistic birth rate at location x should be given by $[a - b(\eta_{it}(x) - 1)]$, so to compute the reaction term for the corresponding hydrodynamic limit we would calculate $\mathcal{DL}\{[a - b(U_i - 1)]U_i\}$. By the calculations of Example 1, Section 3,

$$\mathcal{DL}\{[a - b(U_i - 1)]U_i\} = au_i - bu_i^2. \quad (4.1)$$

Thus, the hydrodynamic limit model is given by

$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + (a - bu_i)u_i,$$

where Δ denotes the Laplacian $\partial^2/\partial x_1^2 + \partial^2/\partial x_2^2$. This is simply the standard logistic equation with diffusion. In this case the hydrodynamic limit has been derived with complete mathematical rigor; see (DeMasi and Presutti 1991). Poisson averaging has essentially no effect on this model. Suppose now that the species present at each site interact with each other according to the principle of mass action; that is, their interactions are described by a Lotka-Volterra model. If species i has a linear birth or death rate, logistic interactions with other conspecifics, and Lotka-Volterra interactions with other species, then the local population growth rate at a given site is

$$f_i = a\eta_i - b\eta_i(\eta_i - 1) + \sum_{\substack{j=1 \\ j \neq i}}^n c_{ij}\eta_i\eta_j.$$

Computing the Durrett-Levin transform (using part iv) of Lemma 3.3) yields

$$\mathcal{DL} \left\{ aU_i - bU_i(U_i - 1) + \sum_{\substack{j=1 \\ j \neq i}}^n c_{ij}U_iU_j \right\} = au_i - bu_i^2 + \sum_{\substack{j=1 \\ j \neq i}}^n c_{ij}u_iu_j.$$

Thus, Poisson averaging per se has no effect at all on Lotka-Volterra systems. Evidently a greater amount of nonlinearity must be present in the model if we are to see any effects from Poisson averaging.

Effects of Poisson averaging on nonlinear competition

To see how Poisson averaging might affect nonlinear interaction rates it is useful to recall how Poisson averaging affects various sorts of nonlinear functions. By the results of section 3, if $f(U)$ is globally monotone or concave or convex, then so is $\mathcal{DL}\{f\}(u)$. However, Poisson averaging decreases concave functions and increases convex functions. If f is smooth then

$$\frac{\partial}{\partial u} [\mathcal{DL}\{f(U)\}(u)]|_{u=u_0} = \mathcal{DL}\{f(U+1) - f(U)\}|_{u=u_0}. \quad (4.2)$$

If $u_0 = 0$ then the right side of (4.2) is simply $f(1) - f(0)$. In the case where f is strictly concave and smooth we have $f(U+1) - f(U) < f'(U)$ so in particular

$$\frac{\partial}{\partial u} [\mathcal{DL}\{f(U)\}(u)]|_{u=0} < \mathcal{DL}\{f'(U)\}|_{u=0} = f'(0). \quad (4.3)$$

Thus, for concave functions the Durrett-Levin transform decreases the derivative of f at low densities. Similarly, it increases the derivative of f at $u = 0$ if f is convex. In many cases the predictions of models with respect to coexistence or extinction depend on whether species can increase their density from an initial low density, i.e. on invasibility. The behavior of a model when one of the species is introduced at a low density while the others are at equilibrium is often determined by the linearization of the model at the equilibrium, but the linearization depends on derivatives of the functions describing interaction rates evaluated when one of the densities is zero. Thus, rescaling via Poisson averaging can have quantitative effects which should sometimes affect predictions of invasibility and hence of persistence, coexistence, competitive exclusion, etc. A connection between invasibility and coexistence can be made via the mathematical theory of permanence for dynamical systems; see for example (Hutson and Schmitt 1992). In some cases monotone methods can be used to obtain results on competitive exclusion by combining information about invasibility with conditions that rule out coexistence equilibria; this is done in (Cantrell et al. 1993), for example. Because of the connection between $\partial[\mathcal{DL}\{f\}(u)]/\partial u|_{u=0}$ and $f'(0)$ given by (4.3) it is easier to understand the effects of Poisson averaging on invasibility and hence persistence or extinction than it is to understand possible effects on dynamics at higher densities. We will return to issues of global dynamics, pattern formation, etc. later but first

we will explore some examples that illustrate how Poisson averaging can affect persistence in nonlinear models.

Suppose that two species compete in such a way that their *per capita* growth rates at a given site are given by $f_i(\eta_1 + \eta_2)$. If we simply use those growth rates applied to mean densities we obtain the model

$$\frac{du_i}{dt} = f_i(u_1 + u_2)u_i, \quad i = 1, 2. \quad (4.4)$$

On the other hand, if we use Lemmas 3.9 and 3.10 to compute $\mathcal{DL}\{f_i(U_1 + U_2)U_i\}$ we obtain

$$\begin{aligned} \mathcal{DL}\{f_i(U_1 + U_2)U_i\}(u_1, u_2) &= \mathcal{DL}\{f_i(1 + U_1 + U_2)\}(u_1, u_2)u_i \\ &= \mathcal{DL}\{f_i(1 + W)\}(w)|_{w=u_1+u_2}u_i. \end{aligned}$$

Thus, if we let $F_i(w) = \mathcal{DL}\{f_i(1 + W)\}(w)$ then the system analogous to (4.4) after Poisson averaging is

$$\frac{du_i}{dt} = F_i(u_1 + u_2)u_i, \quad i = 1, 2. \quad (4.5)$$

Generically, models such as (4.4) and (4.5) in which competition depends on a single factor (in this case $u_1 + u_2$) predict that one competitor excludes the other. Unless $f_1(w)$ and $f_2(w)$ happen to be zero for the same value of w , the system (4.4) cannot have an equilibrium. The situation in (4.5) is analogous. It then follows from the monotone property of two-species competition models that if the first competitor can invade the system when the second is at its single-species equilibrium then first competitor will exclude the second. Arguments of this type are given in (Cantrell et al. 1993) in the context of Lotka-Volterra systems with diffusion, but the same considerations apply to general models for two competitors in continuous time.) Thus, because the model (4.5) still involves only one competitive factor, Poisson averaging will generally not lead to coexistence in models such as (4.4). However, Poisson averaging can have quantitative effects on nonlinear functions, so in some situations Poisson averaging might lead to a reversal of the model's predictions relative to competitive dominance. The case considered here, where the competitive factor is simply $u_1 + u_2$, is special in that we can use Lemma 3.10 to analyze the effects of Poisson averaging. In general it is not clear what the effects would be if the competitive factor were $u_1 + cu_2$ with $c \neq 1$ or had some more complicated form, although the possible quantitative effects of Poisson averaging should still be able to reverse competitive dominance in some situations.

Smooth consumer-resource models

A common approach to resource competition is to construct consumer-resource models and then either treat them directly or scale out the resource in some way to obtain a competition model. Part of our purpose in this paper is to see how the specific method of scaling that arises from Poisson averaging affects models, so we will examine some consumer-resource models directly, with scaling only via

Poisson averaging. Consumer-resource models typically involve a nonlinear rate of resource consumption called the functional response. There are a number of forms which are used to at least some extent in ecological models. If U_1 represents the consumer and U_2 the resource, some standard smooth forms are

$$g(U_2) = aU_2/(1 + bU_2) \quad (\text{Holling II})$$

$$g(U_2) = aU_2^2/(1 + bU_2^2) \quad (\text{Holling III})$$

$$g(U_1, U_2) = aU_2/(1 + bU_2 + cU_1) \quad (\text{Beddington – DeAngelis}).$$

(There are other forms of functional response that are not smooth, including the ratio-dependent form which has engendered some controversy, but we will consider those separately.) A typical model for a single consumer (species 1) and a single resource (species 2) would postulate a consumer birth or death rate at any particular site given by $[eg(\eta_1, \eta_2) - d]\eta_1$ and a birth or death rate for the resource given by $a\eta_2 - b\eta_2(\eta_2 - 1) - g(\eta_1, \eta_2)\eta_1$, where η_i is the population of the i th species at the given site. (In the absence of the consumer the resource is assumed to grow logistically, but individuals are assumed not to crowd themselves.) A population level model simply using the rates from the model for individual interactions directly would take the form

$$\begin{aligned} \frac{du_1}{dt} &= (eg(u_1, u_2) - d)u_1 \\ \frac{du_2}{dt} &= au_2 - bu_2^2 - g(u_1, u_2)u_1. \end{aligned}$$

(The contribution to overall density by a single individual is typically negligible at densities high enough for deterministic models to be reasonable, so normally for a population P inhabiting an area A we would replace $(P/A)(P - 1)/A$ with $P^2/A^2 = u^2$ rather than $(P^2/A^2) - (1/A)(P/A) = u(u - 1)$.) As noted previously, if $g(U_1, U_2) = g_0U_2$ (the Lotka-Volterra case) then Poisson averaging has no effect at all on the model. If $g(U_1, U_2) = h(U_2)$ and $h(U)$ is monotonically increasing and concave, with $h(U) \rightarrow \alpha$ as $U \rightarrow \infty$, then those properties are inherited by $\mathcal{DL}\{h\}(u)$, but $\mathcal{DL}\{h\}(z) \leq h(z)$ for all z . Thus, if $h(U)$ is a Holling II functional response the averaged system

$$\begin{aligned} \frac{du_1}{dt} &= [e\mathcal{DL}\{h\}(u_2) - d]u_1 \\ \frac{du_2}{dt} &= au_2 - bu_2^2 - \mathcal{DL}\{h\}(u_2)u_1 \end{aligned}$$

will have a functional response with the same general properties as h but with a different algebraic form and a quantitatively smaller value at any given density u_2 . Thus, Poisson averaging does not change the qualitative structure of the model but could have quantitative effects on the model which would result in the same sorts of changes in predictions that might be induced by changing parameters in the original model. In particular, since Poisson averaging decreases h in the Holling II case, it could in principle shift the model’s prediction from coexistence to extinction of

the consumer. In the case of a Holling type III functional response the effects of Poisson averaging may be stronger. Specifically, if $h(U) = aU^2/(1 + bU^2)$ then $\mathcal{DL}\{h\}(u)$ will still be increasing in u and will have the same asymptotic limit as h when $u \rightarrow \infty$, but by formulas (4.2) and (4.3), $d\mathcal{DL}\{h\}(u)/du|_{u=0} > 0 = h'(0)$, and in some cases Poisson averaging may eliminate the sigmoid shape of the graph of $h(U)$. Thus, although the qualitative effects of Poisson averaging on models with a Holling III functional response are still relatively modest, they are strong enough to influence predictions that depend on the sigmoid shape of the functional response or on having $h'(0) = 0$. The effect of Poisson averaging on the Beddington-DeAngelis functional response is similar to its effect on the Holling II form. Again, concavity and monotonicity (in both variables for the terms $U_1 U_2/(1 + cU_1 + bU_2)$ appearing in the model) will be preserved, but the algebraic form will change and we will have $\mathcal{DL}\{g(U_1, U_2)U_1\}(u_1, u_2) \leq g(u_1, u_2)$ because of the concavity of $g(U_1, U_2)U_1$.

One approach to understanding resource competition is via consumer-resource models with more than one consumer. If species 1 and 2 are consumers and species 3 is a resource, a typical model for resource competition obtained by substituting u_1, u_2 , and u_3 into the local rates of interaction between discrete individuals would take the form

$$\begin{aligned}\frac{du_1}{dt} &= [e_1 g_1(u_1, u_3) - d_1]u_1 \\ \frac{du_2}{dt} &= [e_2 g_2(u_2, u_3) - d_2]u_2 \\ \frac{du_3}{dt} &= au_3 - bu_3^2 - g_1(u_1, u_3)u_1 - g_2(u_2, u_3)u_2.\end{aligned}\quad (4.6)$$

(Again, we have replaced the logistic term $U(U - 1)$ with u^2 in going to the macroscale model). In the case where g_1 and g_2 depend on U_1 and U_2 respectively, for example in the Beddington-DeAngelis case, the two consumers may coexist because of the effects of intraspecific feeding interference. In cases where g_1 and g_2 depend only on u_3 , coexistence in the sense of permanence is generally ruled out because permanence implies the existence of a positive equilibrium. In (4.6) the u_3 component of an equilibrium must satisfy both $e_1 g_1(u_3) = d_1$ and $e_2 g_2(u_3) = d_2$, which generically is not possible. Coexistence based on the Armstrong-McGehee mechanism of temporal periodicity (Armstrong and McGehee 1976, 1980, Abrams and Holt 2002) is possible in models such as (4.6). Applying Poisson averaging in the context of (4.6) with $g_1 = g_1(U_3)$, $g_2 = g_2(U_3)$ yields

$$\begin{aligned}\frac{du_1}{dt} &= [e_1 \mathcal{DL}\{g_1\}(u_3) - d_1]u_1 \\ \frac{du_2}{dt} &= [e_2 \mathcal{DL}\{g_2\}(u_3) - d_2]u_2 \\ \frac{du_3}{dt} &= au_3 - bu_3^2 - \mathcal{DL}\{g_1\}(u_3)u_1 - \mathcal{DL}\{g_2\}(u_3)u_2.\end{aligned}\quad (4.7)$$

Structurally (4.7) has the same features as (4.6), so again permanence is generically ruled out, but coexistence based on the Armstrong-McGehee mechanism is still possible in some cases. Thus, Poisson averaging does not induce stronger forms of persistence than those found in the original model, although it may have quantitative

effects that switch competitive dominance or influence the Armstrong-McGehee mechanism in the same sorts of ways as the parameters in the original model. If the Beddington-DeAngelis functional response is used in (4.6) then permanence is possible because of the intraspecific feeding interference that is built into that functional response (Cantrell et al. preprint). Poisson averaging of terms of the form $U_i U_j / (1 + bU_i + cU_j)$ yields terms which are still monotone and concave in each variable, and since $\mathcal{DL}\{f(U_i, U_j)U_i\}(u_i, u_j) = \mathcal{DL}\{f(U_i + 1, U_j)\}(u_i, u_j)u_i$, we also see that $\mathcal{DL}\{U_i U_j / (1 + bU_i + cU_j)\}(u_i, u_j)$ has the form $g(u_i, u_j)u_i u_j$ where g is decreasing in u_i and u_j and has limit zero as $u_i \rightarrow \infty$ or $u_j \rightarrow \infty$. Thus, the key qualitative features of the Beddington-DeAngelis functional response are preserved by Poisson averaging, although it may induce quantitative changes. Hence, the range of phenomena supported by the Beddington-DeAngelis response is not changed, although the quantitative changes created by Poisson averaging could perhaps affect which of the supported phenomena actually occurs in a specific model.

Dynamics and pattern formation in smooth models

So far we have concentrated on examining how Poisson averaging affects predictions of persistence or coexistence versus extinction. There are two reasons for doing that. First, we believe that the issue of persistence is fundamental and thus most of our research in recent years has been devoted to that topic. Second, because of the principle “invasibility implies coexistence” (which can be made rigorous via the notion of permanence) we are able to say things about model predictions relative to persistence by examining linearizations around equilibria where some components are zero, and we can use the relation $\partial \mathcal{DL}\{f(U)\}/\partial u|_{u=0} = f(1) - f(0)$ to study those. That approach does not tell us much about detailed dynamics or pattern formation, but we can get some information by observing the structural effects of Poisson averaging. The results of Section 3 show that it preserves the product structure of terms of the form $f_1(U_1)f_2(U_2)$ and that it preserves monotonicity and concavity. It has no effect on linear terms or products of the form $U_i U_j$. Thus, it has no effect on the dynamics of Lotka-Volterra models. (The formulation of hydrodynamic limits used by Durrett and Levin (1994) incorporates some extra spatial structure in the form of local interaction neighborhoods which is not present in simple Poisson averaging, and which has quantitative effects even in Lotka-Volterra models. We will return to that topic later.) For predator-prey models of the form

$$\begin{aligned}\frac{du_1}{dt} &= [eg(u_2) - d]u_1 \\ \frac{du_2}{dt} &= r[1 - (u_2/k)]u_2 - g(u_2)u_1\end{aligned}$$

applying Poisson averaging keeps the predator isocline as a vertical line, and if g has the geometric features of concavity, monotonicity, and saturation (e.g. if g is Holling II) then those features and hence the shape of the prey isocline will be preserved. Thus, the dynamic phenomena that the system might support are the same

with and without Poisson averaging, although the quantitative effects of averaging might shift the model predictions from one regime to another. In models involving terms that are sigmoid or have more complicated nonlinear behavior the situation is less clear. For example, if $g(U) \geq 0$ is concave, increasing, and saturating, with $g(0) = 0$, then the model $dU/dt = g(U) - aU$ can have at most one positive equilibrium. If $g(U)$ is sigmoid then multiple equilibria are possible. If Poisson averaging destroys the sigmoid property (which is possible) then it might eliminate the possibility of multiple equilibria.

The situation in the case of pattern formation is somewhat similar. For two-dimensional systems, pattern formation via diffusive instabilities (i.e. the Turing mechanism) typically cannot occur unless there is some type of activator/inhibitor mechanism present. Such mechanisms are present in predator-prey models but are ruled out by monotonicity in most models for two competitors or mutualists. Poisson averaging preserves monotonicity, so it generally will not give rise to pattern formation in models for two competitors or mutualists. However, if a predator-prey model predicts pattern formation for some parameter values then the quantitative effects of Poisson averaging might shift the model into or out of the regime where pattern formation occurs. For models involving three or more species the general issue of pattern formation becomes much more complicated. The same general considerations apply as far as Poisson averaging is concerned. In models where pattern formation is possible the quantitative effects of Poisson averaging might influence whether or not it occurs. (Whether the effect is more likely to favor or to inhibit pattern formation is not clear.) In simple models whose qualitative structure does not allow pattern formation Poisson averaging is unlikely to induce it. The effects on models with complicated nonlinearities can be more dramatic.

Nonsmooth models

The most profound effects of Poisson averaging occur in the context of nonsmooth models. The hawk-dove game studied by Durrett and Levin (1994) and described in Example 2 of Section 3 is an example of such models. In ecology the best-known nonsmooth models are ratio-dependent predator-prey models, which have been the source of some controversy. Nonsmooth models are also used in epidemiology. If a population is divided into a susceptible class S and an infected class I , then under the assumption that the total rate of contacts between individuals is fixed, the rate at which susceptibles become infected will be proportional to the fraction of infected individuals in the population, so that $dS/dt = a[I/(S + I)]S + \dots$. The term $SI/(S + I)$ occurring in such models has the same form as some of the terms in ratio-dependent models or the hawk-dove game. For a discussion of epidemic models see for example (Mena-Lorca and Hethcote 1992). In standard models for a single predator species and a single prey species the origin is typically a saddle point and either the predators and prey coexist or the predators become extinct while the prey persist. In ratio-dependent models there is also the possibility that for initial data in a certain sector of the phase plane both predators and prey become extinct; see (Jost et al. 1999) or (Kuang and Beretta 1998) for the case of predator-prey models or (Durrett and Levin 1994) for similar results in the

hawk-dove game. The reason why the origin need not be a standard node, saddle point, or spiral point in these models is because the function $xy/(x + y)$ is not smooth at $(0, 0)$. The effect of Poisson averaging is to remove the singular behavior by smoothing such nonlinear terms. In the case of the hawk-dove game this converts the origin to an ordinary saddle point (Durrett and Levin 1994). The case of ratio-dependent predator-prey models is similar. There does not seem to be as much discussion of singular behavior arising from ratio-dependence in the literature on epidemic models, although the same sorts of effects could be expected there. As shown by Example 2 and Lemma 3.10 in Section 3, the case of nonlinearities based on $U_1 + U_2$ (as opposed to $aU_1 + bU_2$ with $a \neq b$) is especially nice from the viewpoint of Poisson averaging because explicit calculation of the Durrett-Levin transform is often possible.

Spatial effects in interacting particle systems

In the model formulation used by Durrett and Levin (1994), individuals may interact with other individuals located at the same site, or they may interact with individuals in the local neighborhood. (See section 2 of this paper for a brief discussion.) A crucial feature of the interacting particle systems used by Durrett and Levin is that they describe rates of interaction with other individuals, as opposed to models that have already been rescaled so that populations interact with, say, resource densities. Thus, the correct interpretation of a local interaction neighborhood is that it describes an area through which an individual might search for prey, competitors, or conspecifics with which to interact. In the predator-prey context, a predator with a larger local neighborhood will search a larger area per unit time than one with a smaller local neighborhood. If the two predators are similar, the one that searches over a larger area may require more energy. In comparing different types of predators that may not always be the case. Avian predators such as raptors may be able to search larger areas per unit time at a given rate of energy expenditure than mustelids such as weasles. In this context it does not make any sense to let the local neighborhood size $|\mathcal{N}|$ increase indefinitely, because any individual can only visit some finite maximum number of sites per unit time. In the context of competition, the notion of a local interaction neighborhood seems difficult to interpret in the case of resource competition that does not involve direct interactions between competing individuals. For interference competition where individuals of different species may fight each other, the size of the local interaction neighborhood would reflect the area that an individual would search for competitors to fight per unit time.

As an example of how local neighborhood interactions can be incorporated into simple models, suppose that species 1 preys on species 2, with a simple mass-action law describing the rate of prey consumption. Suppose the prey species grows logistically in the absence of the predator, and the predator declines exponentially in the absence of prey. Finally, suppose that increasing the size of the local interaction neighborhood increases the predator death rate by increasing energy consumption and exposure to hazards. These assumptions will lead to a Lotka-Volterra predator-prey model that incorporates the size of the local neighborhood. Let η_i represent the population of species i at site x and time t for $i = 1, 2$. Let $\hat{\eta}_{it}(x)$ represent

the population of species i in the local neighborhood of x at time t . Predators at site x then consume prey at the rate $c\hat{\eta}_{2t}(x)$ and convert them to new predators at rate $ec\hat{\eta}_{2t}(x)$. Predators at site x also die at a rate $d + f|\mathcal{N}|$ where $|\mathcal{N}|$ represents the size of the local neighborhood. Thus, the overall growth or loss rate for the predator population at site x is $[ec\hat{\eta}_{2t}(x) - d - f|\mathcal{N}|]\eta_{1t}(x)$. Recall that the general machinery of hydrodynamic limits treats η_i and $\hat{\eta}_i$ as Poisson distributed random variables U_i, \hat{U}_i with means u_i and $|\mathcal{N}|u_i$ respectively. Thus, for a spatially rescaled model the interaction term for the predator should be given by $\mathcal{DL}\{ec\hat{U}_2U_1 - dU_1 - f|\mathcal{N}|U_1\} = ec|\mathcal{N}|u_1u_2 - du_1 - f|\mathcal{N}|u_1$. The situation is slightly different from the prey's perspective. A prey individual at location x may be preyed upon by any predator in the local neighborhood. The predators at each point $x + z$ in the local neighborhood of x consume prey at a rate $c\hat{\eta}_{2t}(x + z)\eta_{1t}(x + z)$. However, this predation is spread over the entire local neighborhood of $x + z$, but the fraction of prey (and hence the fraction of attacks) at x is given by $\eta_{2t}(x)/\hat{\eta}_{2t}(x + z)$, so the rate of attacks on prey at location x should be given by summing the attack rates from each location $x + z$ in the local neighborhood of x :

$$\begin{aligned} \sum_{z \in \mathcal{N}} [c\hat{\eta}_{2t}(x + z)\eta_{1t}(x + z)](\eta_{2t}(x)/\hat{\eta}_{2t}(x + z)) &= \sum_{z \in \mathcal{N}} c\eta_{1t}(x + z)\eta_{2t}(x) \\ &= c\hat{\eta}_{1t}(x)\eta_{2t}(x). \end{aligned}$$

Thus, the total growth rate for the prey is given by $a\eta_{2t}(x) - b\eta_{2t}(x)(\eta_{2t}(x) - 1) - c\hat{\eta}_{1t}(x)\eta_{2t}(x)$, so in the hydrodynamic limit the prey's reaction term should be $\mathcal{DL}\{aU_2 - bU_2(U_2 - 1) - c\hat{U}_1U_2\} = au_2 - bu_2^2 - c|\mathcal{N}|u_2u_1$.

The corresponding reaction-diffusion model is

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= D_1 \Delta u_1 + (ec|\mathcal{N}|u_2 - d - f|\mathcal{N}|)u_1 \\ \frac{\partial u_2}{\partial t} &= D_2 \Delta u_2 + (a - bu_2 - c|\mathcal{N}|u_1)u_2. \end{aligned} \quad (4.8)$$

The model corresponding to (4.8) but without diffusion is a Lotka-Volterra predator-prey model in which the prey is always predicted to persist. The predator is predicted to persist if it can invade the system when the prey is at its logistic equilibrium a/b ; that condition can be written as

$$[(eca/b) - f]|\mathcal{N}| - d > 0 \quad (4.9)$$

For predator persistence (4.9) requires that $(eca/b) - f > 0$, which can be interpreted as saying that if the prey were at equilibrium (a/b) the energy (and other benefits) gained by searching a given area would exceed the energy cost (and other risks) required to search it. Recall that f represents the cost of searching in this model.) If $(eca/b) - f > 0$ but $(eca/b) - f < d$ then we must have $|\mathcal{N}| > 1$ in (4.9) for predator persistence. This could be interpreted as a minimum foraging area that would be needed to sustain a predator population. Care must be taken with this approach, however, because the size of the local neighborhood cannot be increased arbitrarily. The size is strictly limited by the movement rate of the organisms being modeled, even if we do not consider energy costs.

5. Discussion

Conclusions about Poisson averaging

By interpreting Poisson averaging as a transform (which we have called the Durrett-Levin transform), studying its properties, and deriving operational formulas for it, we can make the following observations:

- 1.) Even simple forms of interaction terms generally have Durrett-Levin transforms which cannot be expressed in closed form, but only as power series. When the Durrett-Levin transform of an interaction term can be expressed in closed form, it usually has a different algebraic form than the original term. An important class of exceptions are mass action terms, such as those occurring in Lotka-Volterra models, whose form is unchanged by Poisson averaging, although their coefficients may change.
- 2.) The operational formulas for the Durrett-Levin transform show that many of the qualitative properties of interaction terms are preserved by Poisson averaging. In particular, the Poisson averaging preserves positivity, monotonicity, concavity or convexity, and boundedness. In the case of terms that only involve one variable, Poisson averaging preserves limits at infinity. Even if the Durrett-Levin transform of a term cannot be computed as closed form, it is usually possible to compute the derivative of the Durrett-Levin transform at zero. These properties sometimes make it possible to determine whether a system predicts persistence or extinction after Poisson averaging, even if the averaged system cannot be computed in closed form.
- 3.) The Durrett-Levin transform is a smoothing operator in the sense that it converts bounded functions, no matter how irregular, into real analytic functions. This is not important if the original interaction terms are smooth, but it can be of profound importance if the interaction terms are discontinuous or undifferentiable. In particular, Poisson averaging destroys the singularity at the origin in ratio-dependent models and models with proportional mixing which allows such models to display richer dynamics than similar sorts of models with smooth interaction terms.

Conclusions about models and scaling

The effects of Poisson averaging increase with the degree of nonlinearity in the model. Lotka-Volterra models are completely unaffected. This is not surprising since the underlying assumption of those models is that interaction rates follow a mass-action law, which in turn is based on the assumption that populations are homogeneously mixed. If things are already homogeneous locally then averaging will not have much of an effect. For simple models with smooth nonlinearities that are monotone and concave or convex, Poisson averaging typically changes the algebraic form of the nonlinearities and often leads to averaged terms that cannot be expressed in closed form, but it preserves the qualitative features of concavity or convexity and monotonicity. It reduces the values of concave functions and increases the values of convex functions. Thus, for many standard models such as

predator-prey models built from a Holling II functional response or simple nonlinear competition models, the effects of Poisson averaging are typically similar to those obtained by varying parameters in the original model. (A similar effect was observed to occur via the different mechanism of slow diffusion by Cuddington and Yodzis (2000).) In particular, we could not find any cases where Poisson averaging shifted the predictions of a class of competition or two-consumer one-resource models from competitive exclusion to coexistence, although it might reverse competitive dominance. Since Poisson averaging often converts simple algebraic expressions into functions that can be represented only as infinite series, it may be wiser to account for the effects of spatial averaging by suitably changing coefficients rather than by Poisson averaging provided all the nonlinearities are monotone and concave or convex. For models with more complicated smooth nonlinearities, for example predator-prey models with Holling III functional response, Poisson averaging can change the qualitative properties of the nonlinearity. In the Holling III case the sigmoid shape of the nonlinearity may or may not be preserved, and the averaged nonlinearity will have a nonzero derivative at zero density. In rescaling such models it is wise to see how Poisson averaging affects the nonlinearities. Since Poisson averaging can produce terms that cannot be expressed in closed form, it may be preferable to use it to deduce the general features of the rescaled nonlinearities and then replace them with simpler forms having the same features.

The most profound effects of Poisson averaging occur in nonsmooth models. If a nonsmooth model has dynamic behavior that is not possible in the corresponding smooth model (as in the case for the hawk-dove game and for ratio-dependent predator-prey models), that form of dynamics will be eliminated by the smoothing effects of Poisson averaging. (Similar effects may be relevant in epidemic models with proportional mixing.) Thus, for rescaling nonsmooth models, it is probably necessary to use Poisson averaging if the rescaled model is to duplicate the behavior of the underlying discrete model. In the special case of nonlinearities involving terms of the form $uv/(u+v)$, which occur in the hawk-dove game and other models with proportional mixing, the operational properties of the Durrett-Levin transform typically allow explicit calculation of the averaged system in closed form. Thus, in those cases, the correct approach to rescaling is to use Poisson averaging. In the case of ratio-dependent models in general, explicit calculations may not be possible, so an alternative approach to rescaling might be to approximate Poisson averages by fitting simpler but qualitatively similar curves to them.

In the specific context of interacting particle systems, the additional spatial effect of allowing organisms to interact with other individuals in nearby sites can be incorporated into rescaled models via local interaction neighborhoods. This notion is well established and is discussed in some detail by Durrett and Levin (1994). In some cases it is possible to deduce potentially interesting effects on population interactions arising from the size of the local neighborhood, but the method is limited because the underlying discrete modeling must be based on interactions between individuals. Thus, local neighborhoods for interactions make sense for predator-prey models, or for the hawk-dove game, because those models envision direct interactions between individuals. It is not clear that it makes sense to talk about models for resource competition in terms of direct interactions between com-

petitors, so it is not clear how to properly formulate local interaction neighborhoods in that case. In the case of predator-prey models increasing the size of the local interaction neighborhood may increase the per capita rate of prey consumption. In that situation the maximum size of local neighborhood needed to sustain a predator can be interpreted as something like a minimal homerange size needed for persistence. Note that in the underlying interacting particle system individuals are envisioned as moving through the entire local neighborhood and interacting with the individuals found there in a single unit of time. Thus, there is a strict limit imposed on the possible size of the neighborhood by the movement rate of the organism. Additionally, increasing the size of the neighborhood may entail energy costs.

We have focused our attention on the effects of Poisson averaging (and local neighborhood interactions) on persistence. We consider that issue to be fundamental. Often it can be addressed by studying the linearizations of models at equilibria where at least one population is zero, and it turns out to be possible to say things about such linearizations of rescaled models even in cases where the rescaled nonlinearities cannot be expressed in closed form. Our general conclusions about the effects of Poisson averaging on persistence also apply to pattern formation and other aspects of dynamics. For simple smooth systems Poisson averaging preserves most structural features and also preserves monotonicity and concavity or convexity. Thus, it generally will not change the range of phenomena a model of that type will support, although it may shift model predictions within that range. For more highly nonlinear models, and especially nonsmooth models, Poisson averaging could in principle have much more dramatic effects on dynamics and perhaps pattern formation, as it does on persistence.

References

- Abrams, P.A., Holt, R.D.: The impact of consumer-resource cycles on the coexistence of competing predators. *Theor. Pop. Biol.* **62**, 281–295 (2002)
- Armstrong, R.A., McGehee, R.: Coexistence of two competitors on one resource. *Theor. Biol.* **56**, 499–502 (1976)
- Armstrong, R.A., McGehee, R.: Coexistence of species competing for shared resources. *Theor. Pop. Biol.* **9**, 317–328 (1980)
- Cantrell, R.S., Cosner, C.: Diffusive logistic equations with indefinite weights: population models in disrupted environments. *Proc. Royal Soc. Edinburgh* **112A**, 293–318 (1989)
- Cantrell, R.S., Cosner, C.: Diffusive logistic equations with indefinite weights: population models in disrupted environments II. *SIAM J. Math. Anal.* **22**, 1043–1064 (1991)
- Cantrell, R.S., Cosner, C.: Models for predator-prey systems at multiple scales. *SIAM Rev.* **38**, 256–286 (1996)
- Cantrell, R.S., Cosner, C.: On the effects of spatial heterogeneity on the persistence of interacting species. *J. Math. Biol.* **37**, 103–145 (1998)
- Cantrell, R.S., Cosner, C., Hutson, V.: Permanence in some diffusive Lotka-Volterra models for three interacting species. *Dynam. Syst. Appl.* **2**, 505–530 (1993)
- Cantrell, R.S., Cosner, C., Ruan, S.: Intraspecific interference and consumer-resource dynamics. Preprint

- Chesson, P.: Making sense of spatial models in ecology. In: *Modelling Spatiotemporal Dynamics in Ecology*, Bascompte, J., Solé, R. (eds) Landes Bioscience, 1997, pp. 151–156
- Chesson, P.: General theory of competitive coexistence in spatially-varying environments. *Theor. Pop. Biol.* **58**, 211–237 (2000)
- Cosner, C., DeAngelis, D.L., Ault, J.S., Olson, D.B.: Effects of spatial grouping on the functional response of predators. *Theor. Pop. Biol.* **56**, 65–75 (1999)
- Cuddington, K.M., Yodzis, P.: Diffusion-limited predator-prey dynamics in Euclidean environments: an allometric individual based model. *Theor. Pop. Biol.* **58**, 259–278 (2000)
- DeMasi, A., Presutti, E.: *Mathematical Methods for Hydrodynamic Limits*. Lecture Notes in Mathematics **1501**, Springer-Verlag, 1991
- Dockery, J., Hutson, V., Mischaikow, K., Pernarowski, M.: The evolution of slow dispersal rates: a reaction-diffusion model. *J. Math. Biol.* **37**, 61–83 (1998)
- Durrett, R., Levin, S.: The importance of being discrete (and spatial): *Theor. Pop. Biol.* **46**, 363–394 (1994)
- Gao, Q., Yu, M., Yang, X., Wu, J.: Scaling simulation models for spatially heterogeneous ecosystems with diffusive transportation. *Landscape Ecology* **16**, 289–300 (2001)
- Gause, G.F.: *The Struggle for Existence*. Williams and Wilkins, Baltimore, 1935
- Hanski, I.: Metapopulation ecology. In: *Population Dynamics in Space and Time*, Rhodes, O., Chesser, R., Smith, M., (eds) University of Chicago Press, Chicago, 1996, pp. 13–43
- Hutson, V., Schmitt, K.: Permanence in dynamical systems. *Math. Biosci.* **111**, 1–71 (1992)
- Jost, C., Arino, O., Arditi, R.: About deterministic extinction in ratio-dependent predator-prey models. *Bull. Math. Biol.* **61**, 19–32 (1999)
- Kshatriya, M., Cosner, C.: A continuum formulation of the ideal free distribution and its implications for population dynamics. *Theor. Pop. Biol.* **61**, 277–284 (2002)
- Kuang, Y., Beretta, E.: Global qualitative analysis of a ratio-dependent predator-prey system. *J. Math. Biol.* **36**, 389–406 (1998)
- Levin, S.A.: Complex adaptive systems: exploring the known, the unknown, and the unknowable. *Bull. Am. Math. Soc.* **40**, 3–21 (2003)
- Levin, S.A., Pacala, S.W.: Theories of simplification and scaling of spatially distributed processes. In: *Spatial Ecology*, Tilman D., Kareiva, P. (eds) Princeton University Press, Princeton, NJ, 1997, pp. 271–295
- Mena-Lorca, J., Hethcote, H.W.: Dynamic models of infectious diseases as regulators of population sizes. *J. Math. Biol.* **30**, 693–716 (1992)
- O'Neill, R.V.: Perspectives in hierarchy and scale. In: *Perspectives in Ecological Theory*, Roughgarden J., May R.M., Levin, S.A. (eds) Princeton University Press, Princeton, NJ, 1989, pp. 140–156
- Perrut, A.: Hydrodynamic limit for a two-species reaction-diffusion process. *Ann. Applied Probability* **10**, 163–191 (2000)
- Spohn, H.: *Large Scale Dynamics of Interacting Particles*. Springer Verlag, New York, 1991
- Tilman, D., Kareiva, P.: *Spatial Ecology*. Princeton University Press, Princeton, NJ, 1997
- Wilson, W.G.: Resolving discrepancies between deterministic population models and individual based simulations. *Am. Nat.* **151**, 116–134 (1998)

Appendix

Sketch of the proof of Lemma 3.3: Properties i) and ii) are true by definition. Properties iii) and iv) arise from the independence of the random variables $\{U_i\}$. We illustrate the proof for the case of (iv) with $n = 2$; the cases of general n in iii) and iv) use the same ideas but require a bit more notation. Suppose that

$f(U_1, U_2) = g(U_1)h(U_2)$. We have:

$$\begin{aligned}
 \mathcal{DL}\{f\} &= E(f(U_1, U_2)) = E(g(U_1)h(U_2)) \\
 &= \sum_{i,j=0}^{\infty} g(i)h(j)P(U_1 = i|U_2 = j)P(U_2 = j) \\
 &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} g(i)h(j)P(U_1 = i)P(U_2 = j) \\
 &= \left[\sum_{i=0}^{\infty} g(i)P(U_1 = i) \right] \left[\sum_{j=0}^{\infty} h(j)P(U_2 = j) \right] \\
 &= \mathcal{DL}\{g\}\mathcal{DL}\{h\}.
 \end{aligned}$$

It is clear from the calculation that $\mathcal{DL}\{g\}$ depends only on the distribution of U_1 , which in turn depends only on u_1 , and similarly $\mathcal{DL}\{h\}$ depends only on u_2 ; hence iii) follows from iv) and i).

Derivation of Example 1:

- i) For $f(U) = U(U-1)\cdots(U-k+1)$ the first k terms in the series defining $\mathcal{DL}\{f\}$ are zero, so

$$\mathcal{DL}\{U(U-1)\cdots(U-k+1)\} = u^k \sum_{j=k}^{\infty} e^{-u} u^{j-k} / (j-k)! = u^k.$$

(Note that this formula allows the computation of $\mathcal{DL}\{U^m\}$ for any positive integer m since we can write U^m in terms of $U, U(U-1), U(U-1)(U-2), \dots, U(U-1)\cdots(U-m+1)$.)

ii) $\mathcal{DL}\{e^{\alpha U}\} = \sum_{j=0}^{\infty} e^{\alpha j} e^{-u} u^j / j! = \sum_{j=0}^{\infty} e^{-u} (e^{\alpha} u)^j / j! = e^{(e^{\alpha}-1)u}.$

iii)

$$\begin{aligned}
 \mathcal{DL}\{U/(U+1)\} &= \sum_{j=0}^{\infty} [j/(j+1)] e^{-u} u^j / j! \\
 &= \sum_{j=0}^{\infty} \left(1 - \frac{1}{j+1}\right) e^{-u} u^j / j! \\
 &= e^{-u} \left(\sum_{j=0}^{\infty} u^j / j! - \sum_{j=0}^{\infty} u^j / (j+1)! \right).
 \end{aligned}$$

It is clear from the first line of the calculation that $\mathcal{DL}\{f\}(0) = 0$. For $u \neq 0$ we have

$$\begin{aligned}\mathcal{DL}\{U/(U+1)\}(u) &= e^{-u} \left(e^u - (1/u) \left[\sum_{j=0}^{\infty} u^{j+1}/(j+1)! \right] \right) \\ &= e^{-u} (e^u - (1/u)[e^u - 1]) \\ &= (u + e^{-u} - 1)/u = 1 - (1 - e^{-u})/u.\end{aligned}$$

$$\begin{aligned}\text{iv) } \mathcal{DL}\{U/(U+2)\} &= \sum_{j=0}^{\infty} j/(j+2) e^{-u} u^j / j! \\ &= \sum_{j=1}^{\infty} [j(j+1)] e^{-u} u^j / (j+2)!\end{aligned}$$

The calculation can be completed by writing $j(j+1)$ in terms of $(j+2)(j+1)$ and $(j+2)$. We have $j(j+1) = (j+2)(j+1) - 2(j+2) + 2$ so that

$$\mathcal{DL}\{U/(U+2)\} = \sum_{j=1}^{\infty} [(1/j!) - (2/(j+1)!) + (2/(j+2)!)] e^{-u} u^j.$$

After some shifting of indices and algebraic manipulations we obtain for $u \neq 0$

$$\mathcal{DL}\{U/(U+2)\} = [(u^2 - 2u + 2) - 2e^{-u}] / u^2.$$

A similar calculation can be used for $U/(U+k)$ if k is a positive integer but this method does not seem to apply to other values of k .

Derivation of Example 2:

Let $f(U_1, U_2) = U_1 U_2 / (U_1 + U_2 - 1)$ if $U_1, U_2 \geq 1$, $f(0, U_2) = f(U_1, 0) = 0$. We have

$$\mathcal{DL}\{f\} = \sum_{i=1}^{\infty} \sum_{j=1}^{\infty} [ij/(i+j-1)] e^{-u_1} e^{-u_2} u_1^i u_2^j / i! j!.$$

This sum can be viewed as being taken first in the “ j ” direction and then the “ i ” direction. It is also possible to sum first over the set $i+j=k$ for each fixed $k \geq 2$ and then sum over k , i.e. sum first in the “diagonal” direction then over k . Doing so yields

$$\mathcal{DL}\{f\} = \sum_{k=2}^{\infty} \sum_{j=1}^{k-1} \left[\frac{j(k-j)}{k-1} \right] \frac{e^{-u_1} e^{-u_2} u_1^j u_2^{k-j}}{(j!)(k-j)!}.$$

(j is summed from 1 to $k - 1$ since the $j = 0$, $j = k$ terms would be zero.) Some algebra yields

$$\mathcal{DL}\{f\} = \sum_{k=2}^{\infty} \frac{u_1 u_2 e^{-u_1} e^{-u_2}}{(k-1)!} \sum_{j=1}^{k-1} \frac{(k-2)! u_1^{j-1} u_2^{k-j-1}}{(j-1)!(k-j-1)!}.$$

We have (using the binomial expansion theorem)

$$\sum_{j=1}^{k-1} \frac{(k-2)!}{(j-1)!(k-j-1)!} u_1^{j-1} u_2^{k-j-1} = \sum_{\ell=0}^{k-2} \frac{(k-2)! u_1^{\ell} u_2^{k-2-\ell}}{\ell!(k-2-\ell)!} = (u_1 + u_2)^{k-2}$$

so that

$$\begin{aligned} \mathcal{DL}\{f\} &= \sum_{k=2}^{\infty} \frac{u_1 u_2 e^{-u_1} e^{-u_2} (u_1 + u_2)^{k-2}}{(k-1)!} \\ &= \left[u_1 u_2 e^{-(u_1+u_2)} / (u_1 + u_2) \right] \sum_{k=2}^{\infty} \left[(u_1 + u_2)^{k-1} / (k-1)! \right] \\ &= \left(\frac{u_1 u_2}{u_1 + u_2} \right) e^{-(u_1+u_2)} \left[e^{(u_1+u_2)} - 1 \right] \\ &= \frac{u_1 u_2}{u_1 + u_2} \left[1 - e^{-(u_1+u_2)} \right]. \end{aligned}$$

This type of calculation can also be done in more explicitly probabilistic terms by taking conditional expectations of $U_1 U_2 / (U_1 + U_2 - 1)$ conditioned on $U_1 + U_2 = k$ then summing appropriately over k (see (Durrett and Levin 1994)) but the key idea of summing over $U_1 + U_2 = k$ is the same.

Proof of Lemma 3.5 (for $n = 2$, $k = 1$; the general case is essentially the same.) By (3.1a),

$$e^{u_1} \mathcal{DL}\{f(U_1, U_2)\} = \sum_{j=0}^{\infty} \sum_{i=0}^{\infty} f(i, j) u_1^i u_2^j e^{-u_2} / i! j!.$$

Differentiating, we have

$$\begin{aligned} e^{u_1} \mathcal{DL}\{f(U_1, U_2)\} + e^{u_1} \frac{\partial}{\partial u_1} \mathcal{DL}\{f(U_1, U_2)\} \\ &= \sum_{j=0}^{\infty} \sum_{i=1}^{\infty} f(i, j) u_1^{i-1} u_2^j e^{-u_2} / (i-1)! j! \\ &= \sum_{j=0}^{\infty} \sum_{\ell=0}^{\infty} f(\ell+1, j) u_1^{\ell} u_2^j e^{-u_2} / \ell! j! \\ &= e^{u_1} \mathcal{DL}\{f(U_1 + 1, U_2)\}. \end{aligned}$$

Dividing by e^{u_1} and rearranging terms yields (3.3).

Proof of Lemma 3.7: For $u_k \geq 0$, $k = 1, \dots, n$, we have

$$\begin{aligned} |\mathcal{DL}\{f\}| &\leq \sum_{i_1, \dots, i_n=0}^{\infty} |f(i_1, \dots, i_n)| u_1^{i_1} u_2^{i_2} \dots u_n^{i_n} e^{-u_1} e^{-u_2} \dots e^{-u_n} / i_1! i_2! \dots i_n! \\ &\leq \sum_{i_1, \dots, i_n=0}^{\infty} f_0 u_1^{i_1} u_2^{i_2} \dots u_n^{i_n} e^{-u_1} \dots e^{-u_n} / i_1! \dots i_n! = f_0. \end{aligned}$$

Proof of Lemma 3.8: We shall prove that if $\limsup_{U \rightarrow \infty} f(U) \leq \alpha$ then $\limsup_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) \leq \alpha$. A similar analysis shows that if $\liminf_{U \rightarrow \infty} f(U) = \alpha$ then $\liminf_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) \geq \alpha$. From those observations it follows that if $\lim_{U \rightarrow \infty} f(U) = \alpha$ then $\alpha \geq \limsup_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) \geq \liminf_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) \geq \alpha$ so that $\lim_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) = \alpha$.

Suppose $\limsup_{U \rightarrow \infty} f(U) = \alpha$. For any $\epsilon > 0$ there exists N such that $f(U) \leq \alpha + \epsilon$ for $U > N$. We have

$$\begin{aligned} \mathcal{DL}\{f\}(u) &= e^{-u} \sum_{i=0}^N f(i) u^i / i! + e^{-u} \sum_{i=N+1}^{\infty} f(i) u^i / i! \\ &\leq e^{-u} \left(\sum_{i=0}^N f(i) u^i / i! \right) + e^{-u} \sum_{i=N+1}^{\infty} (\alpha + \epsilon) u^i / i! \\ &\leq e^{-u} \left(\sum_{i=1}^N f(i) u^i / i! \right) + e^{-u} (\alpha + \epsilon) \sum_{i=0}^{\infty} u^i / i! \\ &= e^{-u} \left(\sum_{i=1}^N f(i) u^i / i! \right) + \alpha + \epsilon. \end{aligned}$$

The term $e^{-u} \left(\sum_{i=1}^N f(i) u^i / i! \right)$ is in the form of e^{-u} times a polynomial in u , so

$\lim_{u \rightarrow \infty} e^{-u} \left(\sum_{i=1}^N f(i) u^i / i! \right) = 0$. Thus, there exists a value N_0 so that if $u > N_0$

then $e^{-u} \left(\sum_{i=1}^N f(i) u^i / i! \right) < \epsilon$. For $u > N_0$ we have $\mathcal{DL}\{f\}(u) \leq \epsilon + (\alpha + \epsilon) =$

$\alpha + 2\epsilon$. It follows that $\limsup_{U \rightarrow \infty} \mathcal{DL}\{f\}(u) \leq \alpha + 2\epsilon$. Since $\epsilon > 0$ was arbitrary,

$\limsup_{u \rightarrow \infty} \mathcal{DL}\{f\}(u) \leq \alpha$.

Sketch of the proof of Lemma 3.9:

Suppose $n = 2$ and $k = 1$. (The general case is similar.)

$$\begin{aligned}
\mathcal{DL}\{U_1 f(U_1, U_2)\} &= \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} i f(i, j) u_1^i u_2^j e^{-u_1} e^{-u_2} / i! j! \\
&= \sum_{i=1}^{\infty} \sum_{j=0}^{\infty} f(i, j) u_1^i u_2^j e^{-u_1} e^{-u_2} / (i-1)! j! \\
&= \sum_{\ell=0}^{\infty} \sum_{j=0}^{\infty} f(\ell+1, j) u_1^{\ell+1} u_2^j e^{-u_1} e^{-u_2} / \ell! j! \\
&= u_1 \mathcal{DL}\{f(U_1 + 1, U_2)\}.
\end{aligned}$$

Proof of Lemma 3.10: By (3.1a) we have

$$\mathcal{DL}\{f(U_1 + U_2)\}(u_1, u_2) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} e^{-(u_1+u_2)} f(i+j) u_1^i u_2^j / i! j!.$$

Rearranging the order of summation so that we sum first over all terms of the same degree yields

$$\begin{aligned}
\mathcal{DL}\{f(U_1 + U_2)\}(u_1, u_2) &= \sum_{k=0}^{\infty} \sum_{i=0}^k e^{-(u_1+u_2)} f(k) u_1^i u_2^{k-i} / i! (k-i)! \\
&= \sum_{k=0}^{\infty} \left[e^{-(u_1+u_2)} f(k) / k! \right] \sum_{i=0}^k k! u_1^i u_2^{k-i} / i! (k-i)!
\end{aligned}$$

so by the binomial expansion theorem,

$$\begin{aligned}
\mathcal{DL}\{f(U_1 + U_2)\}(u_1, u_2) &= \sum_{k=0}^{\infty} e^{-(u_1+u_2)} f(k) (u_1 + u_2)^k / k! \\
&= \mathcal{DL}\{f(U)\}(u_1 + u_2).
\end{aligned}$$