From Individuals to Populations: Spatial Structure, Size Structure, and the Challenge of Moment Closure

Michael Raghib Moreno

Department of Mathematics,
University of Glasgow, United Kingdom

Goal

To truncate the hierarchy of moment equations describing a population with spatial and size structure by (i) maximizing the entropy functional of the underlying point process or (ii) minimizing the L^2-norm of the hierarchy of moment equations. To construct numerical algorithms for computing the entropy of a realization of a (marked and unmarked) point process and for solving the truncated moment hierarchy.

Background and motivation

Models of endogenously generated pattern, derived from individual-level interactions and capable of making predictions at the population level, are at the cornerstone of much current research on population dynamics (Bolker and Pacala, 1997; Bolker, 2003; Dieckmann and Law, 2000; Flierl et al., 1999; Law et al., 2003; Levin, 2002; Moorcroft et al., 2001), the main objective being the development of theoretical tools that can be of use in understanding the scaling mechanisms by which biological processes occurring at the level of the individual lead to patterns at the level of the population. In this setting, by pattern we mean deviations from complete spatial randomness (i.e. spatial aggregation or segregation of individuals) and deviations from uniformity in the distribution of sizes. The more mathematically inclined among these models have focused exclusively on either spatial pattern (Bolker and Pacala, 1999; Dieckmann and Law, 2000; Law et al., 2003), or size structure (Hara, 1994), a notable exception being Moorcroft et al. (2001), who nevertheless assumed uniformly distributed dispersal. This separation between size and space is somewhat artificial, given the ubiquity of size hierarchies *and* spatial structure in the field literature (Condit et al., 2000; Pfister and Stevens 2002; Weiner, 1985). The next generation of models should take into account that life-history traits are likely to be affected by placement in both size hierarchy and spatial configuration. The concept of a 'plant's eye-view' of the community, on which previous models have been built, then requires to be extended to include dependences on the number and location of neighbors, as well as on their relative differences in size.

This project is based on preliminary attempts to construct a model extending current approaches in a manner that allows size hierarchies and spatial structure to arise naturally; the questions of interest being whether spatial effects vary in the presence of a size-driven competitive hierarchy and, from the opposite perspective, whether spatial pattern has a relevant role in shaping size variability. In order to address these questions, we developed a toolkit of theoretical and computational tools namely, (a) an individual-based model (IBM), defined by updating rules that depend on both differences in size and location. These rules were inspired by experimental work by Purves and Law (2002) on

Arabidopsis Thaliana; (b) a marked spatio-temporal point process (MSTPP), constructed from the rules of the IBM, mainly for the purpose of providing a theoretical basis for analytically approximating the dynamics of the IBM; and (c) a method for obtaining expected values and their rate of change from the MSTPP, in particular the conditional first- and second-order intensities of the process. We stopped at second order since most of the statistics of biological interest (i.e. total population numbers, subpopulations classified by size, total biomass, aggregation/segregation indices, coefficients of variation, size distributions, and mark correlation functions) are obtained from the first two moments.

Research questions

The approach discussed in the previous section posits significant challenges. As a consequence of the nonlinear and non-local nature of the interaction terms in the rules of the IBM, the equation for the rate of change of the expected density of individuals (e.g. first-order conditional intensity), depends on the density of *pairs* of individuals. This in turn requires a second expression for the density of pairs of individuals which, once obtained, turns out to depend on the density of triplets of individuals, i.e. on the third-order moment. This trend continues up to the order that matches total population size. The occurrence of such moment hierarchies is unfortunate, and a major obstacle in deriving population-level models from individual behavior with realistic interaction terms. Clearly, some method for closing the hierarchy must be obtained. The main focus of this project will be to obtain such closure by means of entropy maximization methods. Given that we already have at our disposal the IBM, the MSTPP, and its deterministic approximation, what remains to be done in order to have a functioning model, is a method for truncating the hierarchy of moment equations.

Methods and work plan

Given that a satisfactory analytical tool for dealing with the problem of closure is lacking to date, much work on the moment-closure problem has relied on a combination of heuristic reasoning and goodness of fit with numerical simulations. For example, Bolker and Pacala (1997) assumed that central third-order moments vanish, an assumption that seriously undermined the applicability of their model, particularly for clustered populations. Law et al. (2003) chose an asymmetric power-2 closure for the third moment, justified by additional arguments, such as positivity, (a)symmetry, and limiting behavior under complete spatial randomness. Their method, however, required the coefficients of the terms of the closure to be chosen on the basis of agreement with numerical simulations. This strategy has recently been taken a step forward by Murrell et al. (2004), who discussed the additional requirement of invariance under relabelling, which ensures that a closure predicts the same third moment independently of whether it is applied to a population as a whole or separately to arbitrary partitions of the population.

It is therefore desirable to strengthen the rationale for obtaining a closure, particularly by the application of some variational principle that can be justified by both the observed biology and the properties of the process. It seems plausible that such a principle can take the form of entropy maximization, justified by the assumption that the preferred state towards which the population settles is that of `maximum ignorance'. We envision two alternative ways of accomplishing this, either by maximizing the entropy functional of the process (Daley and Vere-Jones, 2003: 286), or by minimizing an L^2-norm in the hierarchy of PDEs, both under the constraint of fixed lower-order moments. The former has an important history on processes on the real line (McFadden, 1965), and an extension to spatial-temporal processes will be required. The L^2-norm approach has recently been proven to be successful in a similar setting (i.e. transport equations for velocity jump processes) by Hillen (2004).

The project will involve the following: (a) development of Matlab code for the computation of the entropy of a realization of a point process, in order to provide a `test bed' for theoretical procedures, (b) extending the concept of entropy to realizations of marked spatio-temporal point processes, (c) construction of an L^2-norm satisfying an H-theorem for the hierarchy of PDEs, and (d) maximization of either measure of entropy to yield a closure.

Relevance and link to ADN's research plan

This project falls within ADN's research focus on *Simplifying Spatial Complexity* and builds on previous ADN work by extending the results of Dieckmann and Law (2000) to size structure. Additionally we expect to obtain a justification of a moment closure via a variational principle (entropy maximization). Both have the potential of opening new lines of research and will make available for exploration a class of dynamical systems of direct relevance to population dynamics, derived consistently from individual-based models.

Expected output and publications

The results of my project will form part of a chapter of my PhD thesis and will result in a co-authored journal article.

References

Benjamin Bolker and Stephen W. Pacala (1997). Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. Theoretical Population Biology, 52:179-197.

Benjamin Bolker and Stephen W.Pacala (1999). Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. American Naturalist, 153(6):575-602.

Richard Condit et al (2000). Spatial patterns in the distribution of tropical tree species. Science,288:1414-1418.

Noel A. Cressie (1991). Statistics for Spatial Data. John Wiley and Sons.

D.J. Daley and D. Vere-Jones (2003). An introduction to the theory of point processes. Vol. I: Elementary Theory and Methods. Probability and Its Applications. Springer Verlag, New York, second edition, 2003.

Ulf Dieckmann and Richard Law (2000). Relaxation projections and the method of moments. In Dieckmann, U. Law, R. and Metz, J.A.J., editors, The Geometry of Ecological Interactions, volume 1 of Cambridge Studies in Adaptive Dynamics, pages 412-455. Cambridge University Press.

Rick Durret (1999). Stochastic spatial models. In Vencenzo Capasso and Odo Dieckmann, editors, Mathematics Inspired by Biology, volume 1714 of Lecture Notes in Mathematics, pages 39-94, Springer-Verlag.

J.A. McFadden (1965). The Entropy of a point process. Journal of the Society for Industrial and Applied Mathematics. 13(4):988-994.

H. Flierl, D. Grünbaum, S. Levin and D. Olson (1999). From individuals to aggregations: the interplay between behavior and physics. Journal of Theoretical Biology, 196:397-454.

Toshihiko Hara and Tomasz Wyszomirski (1994)). Competitive asymmetry reduces spatial effects on size-structure dynamics in plant populations. Annals of Botany, 73:285-297.

Tomas Hillen (2004). On the L2 –moment closure of transport equations: The Cattaneo approximation. Discrete and Continuous Dynamical Systems-Series B. In press.

Richard Law, David Murell and Ulf Dieckmann (2003). Population growth in space and time: Spatial logistic equations. Ecology, 84(1):252-262.

Simon Levin (2002). Complex adaptive systems: Exploring the known, the unknown and the unknowable. Bulletin of the American Mathematical Society, 40(1):252-262.

David J. Murrel, Ulf Dieckmann and Richard Law (2004). Moment closures for population dynamics in continuous space. Journal of Theoretical Biology. In press.

Catherine A. Pfister and Forrest R. Stevens (2002). The genesis of size variability in plants and animals. Ecology, 83(1):59-72.

P.R. Moorcroft, G.C. Hurtt and S.W. Pacala (2001). A method for scaling vegetation dynamics: The ecosystem demography model. Ecological Monographs, 71(4): 557-586.

D.W. Purves and R. Law (2002). Experimental derivation of functions relating growth of Arabidopsis thaliana to neighbour size and distance. Journal of Ecology, 90:882-894.

Jacob Weiner (1985). Size hierarchies in experimental populations of annual plants. Ecology, 66(3):743-752.

Jacob Weiner, P. Stoll, H. Muller-Landau, and A. Jasentuliyana, (2001). The effects of density, spatial pattern and competitive asymmetry on size variation in simulated plant populations. The American Naturalist, 158(4): 438-450.