STOCHASTIC AND DETERMINISTIC SPATIAL MODELING IN POPULATION DYNAMICS

The American Institute of Mathematics

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A.1 Adler, Fred

Why are there so many species, particularly in places like the tropics? In the 1970's, the ecologists Janzen and Connell independently proposed that a combination of specialized natural enemies and local dispersal might enhance the number of species in a region far above that caused by specialized natural enemies themselves. Common species suffer from the build-up of their natural enemies, but the realized effect of those enemies depends on their spatial distribution relative to the host species. Modeling this important idea requires analyzing spatially explicit models of ecological interaction and dispersal, a problem we only partially solved in earlier work (Adler & Muller-Landau, 2005). Current work applies this approach to viruses, whose "natural enemies" are not pests but the immune response of their hosts, and where "distance" between different viral strains is genetic rather than physical.

The ultimate goal is to understand the evolution of facilitation and other spatially localized positive interactions between sedentary organisms. Evolution is no more than the long-term outcome of the population dynamics of organisms bearing different strategies. Work on ants (Adler & Gordon, 2003) and plants (Adler, 1996) provided some tools for looking at these questions, but further progress requires more powerful methods for dealing with space and the stochasticity inherent in spatial patterns. These methods depend on seeing the world through the eyes of the organisms and developing descriptions of space based on how individuals interact via resources.

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A.2 Allen, Linda

Since the work of Levins in metapopulation modeling, there have been many applications and extensions of metapopulation models (stochastic and deterministic) to ecology, evolution, and disease. In particular, stochastic modeling can be approached in various ways and involves some interesting questions. Some stochastic modeling approaches that have been used to study applications to metapopulations include continuous or discrete time Markov chains, cellular automata, networks, stochastic computer simulations and more recently, stochastic differential equations. The various approaches depend on the particular population and spatial setting. They also lead to some broad questions about model selection. For example, what stochastic spatial modeling approaches are appropriate for plants, humans, or wildlife when addressing questions about ecology, evolution or disease? How do you formulate an appropriate stochastic spatial model? For example, in a stochastic differential equation,

$$dX(t) = F(t, X(t))dt + G(t, X(t))dW(t)$$

how do you specify the diffusion matrix G when there is demographic and environmental variability? What advantages or disadvantages are there in each approach? In what situations is one approach better and when do multiple approaches provide the same answers?

A.3 Bilinsky, Lydia

Models of population dynamics have traditionally been employed at the level of collections of whole organisms, as in mathematical ecology and epidemiology. However, these models are now finding applications in the area of cellular physiology, where the "members" of the population may be molecular species inside a cell. The heterogeneous structure of a cell, and the statistical nature of molecular interactions often necessitate models that are stochastic and in which space is modeled explicitly. I seek to appropriate ideas currently being used in ecological and epidemiological modeling for use in modeling cellular processes. Because of their applicability to this area, I am especially interested in reaction-diffusion equations and continuous-time Markov processes.

A.4 Day, Troy

A topic that I find interesting is related to how space is often incorporated. Suppose, for example, that the population of interest is very large (infinite), such that we can model it deterministically. So say we have an ODE model for its dynamics.

Now suppose that we decide spatial distribution is important. How do we model this? One common approach when dealing with such infinite pops is to simple use a model like a PDE. Under this assumption, however, we are effectively treating each spatial location as 'infinite' as well, and this need not be true. In fact, we might assume that a population is globally finite, globally infinite but locally finite, or locally infinite. And, from an evolutionary standpoint at least, these different assumptions can have interesting consequences.

A.5 Dembele, Bassidy

Currently, I am using dynamical systems theory to study the impact of seasonal variations on malaria epidemics in Mali. I am using mathematical models and population data to predict the long term behavior of the disease in Mali. In our mathematical model, we are making a connection between the basic reproduction number and the persistence or extinction of the disease. We will use sensitive analysis to determine the important model parameters. In addition, we make connections with experimental studies on malaria in Badiangara (a village in Mali), where sulfadoxine-pyrimethane (SP) has been used as a temporary vaccine. We successfully fit their experimental data and define drug administration protocols that would optimize the effectiveness of SP as a malaria vaccine.

Participating to the Stochastic and deterministic spatial modeling in population dynamics workshop would give me an excellent insight into the area of stochastic modeling and be an outstanding opportunity for me to explore these working methods not only to apply to my previous work on malaria but also to study other models. A workshop of this type is of great interest to me and I look forward to attending to it.

A.6 Hilker, Frank

My current interests in modelling spatial population dynamics are as follows.

- Rate of spread and the type of spread pattern in biological invasion and epidemic spread: This typically involves reaction-diffusion equations, and I am particularly interested in the reversal of travelling wave fronts. The underlying question is if the introduction of a natural enemy (like a predator or pathogen) can be an effective biocontrol agent (see [1] for a synthesis and [2] for an example). Mathematically, this involves bi- and tristable differential equations with cubic nonlinearities.

- Stochastic partial differential equations: External noise is known to have constructive effects such as coherence resonance, that is to induce regular oscillations. What roles can noise play in spatiotemporal settings, especially if the dynamic deterministic 'skeleton' exhibits complex traits such as excitability, multistability or limit cycles (see [3,4] for an example).
- In spatially fragmented or structured landscapes, the spatially implicit metapopulation concept thinks of independent (sub-)populations in habitat patches. Though the populations are connected by species dispersal, the spatially implicit approach ignores both local population dynamics and the spatial arrangement. An example is the classical patch occupancy model by Levins [5]. Spatially realistic models such as the incidence function model [6] take into account some basic spatial information, but remain simple and are supposed to be easily parameterisable. Spatially explicit models in form of individual-based (or agent-based) models [7] consider great detail in both spatial and population dynamics. Can the different hierarchies in description and modelling be used to derive insights in essential processes and the identifying useful concepts? (See [8] for an example.)
- Last but not least, I believe that this workshop is an excellent opportunity to extend my tool set of modelling techniques. I look forward to learn new methods and to fruitful interactions on pros and cons of various modelling assumptions.

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A.7 Lanchier, Nicolas

Most mathematical models introduced in the biological literature that describe inherently spatial phenomena of interacting populations consist of systems of ordinary differential equations, thus leaving out any spatial structure. The spatial component, however, is identified as an important factor in how communities are shaped, and spatial models can result in predictions that differ from non-spatial models. The aim of my research is to understand the role of space in ecology, epidemiology and population genetics through the mathematical analysis of a class of stochastic processes known as interacting particle systems. These processes are ideally suited to investigate the consequences of the inclusion of a spatial structure in the form of stochastic and local interactions. This includes generalizations of the contact process and the voter model in spatially heterogeneous environments and on inhomogeneous graphs.

Currently, I am especially interested in identifying mechanisms that promote coexistence in models based on interacting particle systems (including both stochasticity and space in the form of local interactions) and would be glad to discuss about this problem for a wide variety of deterministic and stochastic models. Here is a list of articles in which some of these mechanisms have been identified in the framework of interacting particle systems. There are three important factors: spatial heterogeneity, temporal heterogeneity, and topological structure of the graph.

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A.8 Leviyang, Sivan

I am interested in questions of inference relating to subdivided populations. Specifically, given genetic data how much can be inferred about the structure of the underlying subdivided population. Current inference techniques for subdivided population center only on the existence of structure. There is, to my knowledge, no work on testing for population structure type. As a starting point, consider the classical island and 2-d stepping stone population models. Can a statistic be formed that can detect which of these population structures is present? More generally, what aspects of structure can be inferred through genetic data and which cannot? Does it matter if we assume a continuous population (in space) rather than discrete demes? What effect do different models of mutation have on this question?

A.9 Lutscher, Frithjof

My background is in deterministic models; one of my interests is in population persistence and spreading speeds: What is the effect of individual dispersal behavior, species interaction, and habitat heterogeneity on persistence and spread? As a step towards applicability and one bridge to experimentalists I am also interested in approximations or sensitivity: what are the relevant spatial scales and which can be averaged over? What if we only have incomplete information about the process? I use models with continuous space and either discrete or continuous time (integrodifference equations, integrodifferential equations or PDEs). Many of these modeling tools can be derived from a stochastic process in a certain limit and/or have a stochastic interpretation. I hope to learn more about these and other stochastic processes and the relevant mathematical methods for their analysis.

Here are some more detailed questions that I am interested in:

1. Spreading speeds depend crucially on the tails of the dispersal distribution. These are notoriously hard to measure. How sensitive are the results with respect to measurement uncertainty? In addition, the probability of long-distance dispersal is so small that stochastic effects should play a role. Which?

2. Simple dispersal kernels seem reasonable descriptions for non-animated dispersal (e.g. wind-borne seeds). What are adequate descriptions of animal dispersal? Are kernels still useful? For example: how do home ranges, habitat preferences or energy budgets influence dispersal?

3. Modeling dispersal is a crucial element in such equations. How does spatial heterogeneity affect dispersal? What are the appropriate scales and which can be averaged out? When are network models more appropriate and how do their predictions differ?

Some of the work I have done (reprints sent to AIM and available through my website www.mathstat.uottawa.ca/∼fluts037/)

- approximations of spreading speeds by variance and kurtosis of the dispersal kernel (BMB 2007), extension to non-zero mean (MEPS, in press)

- density-dependent dispersal: the probability of leaving a site increases with local density. Spreading speeds, persistence in fragmented habitat, mechanism for coexistence of competitors (JMB 2008)

- approximation of persistence conditions by average dispersal success, critical patch size and patch arrangement (Ecol Appl 2006)

- spread and persistence in the face of advection (e.g. rivers, longshore ocean currents, dominant wind direction). Spread and persistence conditions (TPB 2005, SIAM 2005); effects of periodic heterogeneity (BMB 2006); advection-mediated coexistence and reversal of competitive outcome (TPB 2007).

- spread in periodically heterogeneous landscapes: averaging, spatial scales, effect of fragmentation, patch-leaving rate depending on patch quality (Ecology, in press)

A.10 Manore, Carrie

I am working with a zoology student and his advisor (S. Moore, E. Borer) on a population and disease model for Barley Yellow Dwarf Virus (BYDV) infecting native and invasive grass species in California. They have shown that the virus may play a key role in the success of invasive annuals over native perennials. We are using patch, or metapopulation, models that include both competition between species and a shared disease as well as migration of the aphid vectors between patches.

I would like to discuss how to incorporate different types of movement into the patchy model. For example, aphids disperse both locally within a patch and over large distances and may move in only certain directions between patches. How can this be modeled most simply? There is also a much slower rate of migration for the plant species that I am currently neglecting, but that may be important in the dynamics of invasion by non-native plants.

It would be interesting to incorporate stochasticity into the spatial population models for BYDV. I think both stochastic and deterministic models may be key in helping to answer the underlying question of how mechanisms such as spatial configuration and disease affect the coexistence of species. This is particularly useful for studying endangered species and/or invasive species as in the case above.

A.11 Miller, Judith

A basic question about the genetics of an invading population is: If a mutation arises during an invasion, what is the probability that it will survive in the population as $t \to \infty$, and what will be the long-term spatial distribution of the mutation if it does survive? (If reproduction is asexual, this is equivalent to a question about competition between two invasive species.)

Invasions can be modeled as contact processes (among other things). It is a nontrivial achievement to prove a theorem about a two-type contact process giving conditions that imply $P(\text{mutant survival}) > 0$ or $P(\text{mutant survival}) = 0$. But we can hardly blame biologists for wanting a more precise estimate of $P(\text{mutant survival})$. What probabilistic and/or deterministic models and methods could supply such estimates?

More generally, I am interested in deterministic models for the spatial moments of population densities and joint densities, averaged across all possible realizations of an evolutionary process. How can such models be derived, analyzed and simulated in order to shed light on quantitative questions like the one above?

A.12 Mubayi, Anuj

I am interested in studying geographical invasion of vector borne diseases Visceral Leishmaniasis and Chagas that affect millions in developing world. In particular, my Leishmaniasis research focuses on Indian state of Bihar and Chagas study focuses on the state of Texas in US. I will now explain briefly the two research interests.

Bihar has one of the highest prevalence and mortality levels of Kala-azar (or Indian Visceral Leishmaniasis) but the magnitude of the problem is difficult to assess because most of the cases are handled by private health providers who are not required to report them. We study the impact of underreporting using district level reported incidence data from the state of Bihar. The average reproduction number estimates for the state of Bihar range from 1.1 (2003) to 4.3 (2005) with some districts' estimates supporting values less than one in the two years. It is estimated that the proportion of underreported cases declined from about 88% in 2003 to about 73% in 2005. However, our estimates show that at least 5 districts had still over 90% levels of underreporting in both years. Estimated underreporting is then adjusted to reported incidence data and high-risk districts are identified. Four out of eight (in 2003) and three out of nine (in 2005) districts are miss-identified as high-risk by reported data. Total of seven (in 2003) and five (in 2005) districts are not even there in the list of high-risk districts according to reported incidence suggesting significantly different targeting of resources. This study uses a separate dynamical system for each district. Each system was unconnected to the other system. However, high migration and variations in climatic conditions between districts might affect obtained estimates of reproduction number and underreporting. How can we incorporate these factors in a spatial model that can use available incidence data? If such a model can be developed then how are these estimates affected?

On the other hand, Chagas disease affects millions in latin America including Mexico. The prevalence levels of the disease is now growing and spreading in US, which may be because of the changing climatic conditions, land use and movement of individuals. The transmission dynamics of Chagas disease, caused by parasite Trypanosoma Cruzi, varies widely across Americas, due to variations in parasite strains, species of vector, climate and geography. The native strains of T. Cruzi in southeastern US (including Texas) are not known to cause Chagas disease. But the movement of individuals and changing climatic conditions are affecting the dynamics of Chagas disease in US. There have been experimental studies that demonstrate cross immunity between strains of T. Cruzi. That is, infection from low virulent Chagasic strains results in immunity against infection from high virulent Chagasic strains. The goals here are to study the extent at which the two groups (low- and high-virulent Chagasic strain) are present in Texas using available data and also to identify factors that affect the spread of the strains. How spatial model can incorporate two strains that compete in a common region (Texas) at the same time predominately existing in their separate regions (low-virulent strain in rest of the southeastern US and high-virulent strain in Mexico bordering Texas)?

There are some challenges associated with studying underreporting levels of Kala-azar in Bihar and competing Chagasic strains in Texas through spatial models. Especially when an appropriate data are unavailable. Hence, I would like to discuss how we could address the spatial issues mentioned above under these limitations?

I am also interested in social problem of alcohol drinking. In my Ph.D. dissertation, I used system of stochastic dynamical models much like a contagious disease to study the collective role of environmental contexts and social interactions on alcohol drinking in college population. This study has a major research goal of increasing our understanding of alcohol drinking dynamics and identifying interventions that can influence the existing drinking culture in communities. The research primarily focuses on the impact, on drinking dynamics, of individuals movement between low- and high-risk environments. That is, the model included two extreme forms of drinking environments. However, there is large variation in risk levels and mixing patterns in drinking environments. Understanding of variations collectively is required for effective intervention policies. I would like to use spatial stochastic model to incorporate these factors.

A.13 Renteria, Jorge

Rubus niveus was introduced to the Galapagos Islands in the 1970s. This species is a serious problem on Santa Cruz and San Cristobal islands, and has become a problem on Santiago and Floreana islands where its presence has been more evident after the eradication of introduced herbivores. Rubus niveus grows rapidly from seeds, it produces root suckers and canes root at the tips, creating daughter plants. It has invaded open vegetation, shrub land and forest alike. It forms dense thickets up to 4 meters high, replacing native vegetation, and threatening several native communities. In the agricultural zone, R. niveus has spread aggressively, transforming farmland into land useless for agriculture, causing serious economical problems. In Galapagos, management of R. niveus has focused on intensive herbicide control in infested areas but there is little evidence that repeated herbicide applications alone have consistently displaced R. niveus or facilitate the regeneration of native communities. In Galapagos, there had been studies on the ecology and control of R. niveus. These studies have produced information about reproduction, seed bank dynamics, seed dispersal and herbicide effectiveness. However, this information alone is insufficient to understand the full complexity of the Rubus invasion. The objective of this study is to evaluate the effects of canopy gaps in the invasion process of Rubus niveus through a population demographic model which allow the identification of key life-cycle stages survival and expansion of invading populations and can therefore be used to determine the most effective management strategy.

I am interested in defining the most appropriate methods to determine the key parameters to develop a population dynamics model for a invasive clonal plant species. This course will give the opportunity to present my project to the experts, get their comments and help me to refine my research project in order produce a realistic and applicable management plan for Rubus niveus in Galapagos

A.14 Schreiber, Sebastian

A fundamental question in population biology is under what conditions does a population persist in the long-term? For spatially structured models accounting for demographic or environmental stochasticity leads to many mathematical challenges including:

1) For models only accounting for environmental stochasticity, a crucial quanity is the dominant Lyapunov exponent of the matrix cocycle associated with linearizing the model around the origin i.e. extinction set. When this dominant Lyapunov is positive, persistence may be ensured in the sense of stochastic boundedness, as defined by Chesson. Alternatively when it is negative, extinction tends to occur with probability one. Estimating this dominant Lyapunov exponent is an exceptionally challenging task. One approach to estimate this exponent are weak noise limits ala Tuljapurkar. I can discuss another approach and would welcome hearing thoughts about other approaches. Of particular interest is the effects of temporal and spatial correlations on this dominant Lyapunov exponent.

2) When accounting for demographic stochasticity, extinction is inevitable. Hence, one natural question to ask is “what does persistence of the deterministic skeleton underlying the stochastic model imply about the stochastic model?” One possible answer is, roughly, “when the the noise is weak, the stationary distributions of the stochastic model when conditioning on non-extinction place most of their weight on positive attractors of the deterministic limit.” While I believe the techniques to prove such a statement exist, it has yet to be shown.

A.15 Tyson, Rebecca

My main interest in modelling dispersal of organisms in heterogeneous landscapes, coupled with population dynamics. I am interested in understanding how the population dynamics are affected by dispersal, and how heterogeneities in the landscape shape the dispersal effects. These questions are particularly interesting when the non-spatial population dynamics are cyclic. What is the importance of dispersal effects in the behaviour of cyclic populations in general? How does patchiness in the habitat/non-habitat landscape modify dispersal effects? Can we say anything, in general, about persistence of cyclic populations dispersing in a fragmented landscape?

Stochastic effects must clearly play a role in real populations, and so I am hoping to learn, at this workshop, how to include stochasticity and what modifications to the results are expected. I know very little about stochastic differential equations, and am looking forward to learning more about them. In the context of population dynamics, I would like to know if stochasticity fundamentally changes any of the patterns observed above, or if it behaves simply as added noise? Are the cycles of cyclic populations more or less robust (or unchanged) in the presence of stochasticity?

I have been approaching my dispersal questions through models developed to answer related questions about specific organisms: snowshoe hare and Canada lynx [ST], codling moth (an agricultural pest) [TNTJ, TTJ], tree squirrels [NTL], honeybees and mountain pine beetle. In the agricultural and forestry applications, I also ask how landscape heterogeneity arranged through anthropogenic manipulations affects organism distribution and persistence. I generally use advection-diffusion PDE models, but have also used discrete difference equations, ordinary differential equations, and individual-based models. I find that a variety of approaches is helpful for elucidating the basic behaviour of the underlying system.

I am also looking forward to learning more about integrodifference and integrodifferential equations, as I recognise that these are also important tools in dispersal modelling. Fundamentally, it is important to uncover behaviours that are true characteristics of the biological system, rather than the mathematical structure of the modelling approach. This leads me to ask how the answers to my questions above vary with the modelling approach taken?

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A.16 Yakubu, Abdul-Aziz

Im interested in hybrid stochastic and deterministic ecological and epidemiological models. In particular, how do we incorporate the impact of climate change in standard ecological and epidemiological models?