Mathematical Models for Biological Invasions

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1 Background

The spread of introduced species is one of the most important applied problems in ecology. In North America, invasive exotic species are widespread, ranging from zebra mussels to Africanized honey bees to weedy plants. Although some invaders are thought of as beneficial, many become pests, and the associated costs are immense, exceeding $100 billion US per year.

Early models for invasive species were nonlinear reaction-diffusion equations such as Fisher's equation [8], which describes quadratic growth coupled to Brownian motion. Here the analysis of traveling waves and of the convergence of initial data to wave solutions has been a fruitful area of classical mathematical research [9]. The traveling wave speed, interpreted biologically as the rate of spread of the introduced population, has successfully predicted spread rates of many introduced species, but has failed dramatically with others.

¿From a scientific perspective, the field of invasion biology has matured greatly in the last few years as ecologists have tried to come to grips with the risks, damages, and spatial spread of introduced species. This is evidenced by new journals (eg, 'Biological Invasions'), large sections of meetings devoted to the subject of biological invasions (eg, Ecological Society of America annual meeting), and many new books and new text books on the subject. At the same time, quantitative biologists and mathematical modelers have become increasingly aware of the limitations inherent in the early quantitative models.

Ingredients missing in early models include: rare, long-distance dispersal events which cannot be described by classical diffusion, age- and stage-structured population dynamics, interspecific interactions and nonlinear stochastic effects. It is possible to include such ingredients in systems of coupled nonlinear reaction-diffusion equations, systems of integral-based equations, such as integro-difference (discrete-time, continuous space) equations, or as stochastic, interacting particle models.

Analysis of the resulting mathematical systems is a daunting task, and provides a modern-day challenge for applied mathematicians. Some progress has been made on such analysis of these systems, although, to date, results have not always been communicated widely. Moreover, a broad scientific impact requires a multidisciplinary effort which includes mathematicians, biologists and modelers.

The purpose of this meeting was to bring together a group of expert mathematicians and quantitative biologists with the following goals: (i) communicate recent advances in the mathematical analysis of invasion problems, and advances in the application of these results to real ecosystems (ii) propose future directions for research in the mathematics of biological invasions with a view to developing areas where the interaction between models and science is strong. Because the field of biological invasions is immense, we focused of four subareas where the interaction between models and science is already promising.

1. How do invader life-history details affect spread, and are there particular stages that are most sensitive to control measures?
2. How do secondary ecological interactions with other species impact spread, and what is the impact of the invader on these other species?
3. How can model inputs (such as dispersal kernels) be measured under practical field conditions, and how can model predictions (such as spreading speeds) be tested against field data?
4. What is the impact of rare, long-distance dispersal events on the rate of spread, and the precision of spread rate estimates?

Some results of these efforts give us a detailed understanding of biological invasions, including the spatial spread of disease, new methods to predict the response of vegetation to climate change, the spread of weed species through ecosystems, and new methods for spatial biocontrol of pest species.

Our workshop was roughly focused around the above four themes, and involved a range of participants, ranging from mathematicians to quantitative biologists. The synergistic interaction between mathematics and biology lead to advances in both fields.

2 Mathematical Theory

Several large classes of models for the growth and spread of multiple species can be unified into a simple recursion model of the form $u_{n+1} = Q[u_n]$. Here the operator Q takes the set of densities of the species at an initial time into the values at time later. This provides a generalization of the early partial differential equation (PDE) models of Fisher [8] , Skellam [21] and others, to include the possibility of non-Gaussian dispersal and discrete-time dynamics.

Hans Weinberger presented a survey of the qualitative spreading properties of solutions of such models in which all the species cooperate [11, 23]. The main results are that there are, in general, a slowest spreading speed such that no species spreads at a speed less than this number and at least one species spreads no faster, and a fastest spreading speed such that no species spreads more quickly and at least one species spreads no more slowly. These results were illustrated with some simple invasion models, one of which showed the development of ‘stacked waves’ of mutualistic species, moving at different speeds, and another that treated two-species competition models. More recent work on the existence of traveling wave solutions was discussed. Here the existence of a family of traveling wave solutions was shown, with the spreading speed characterized as the slowest speed of the family of traveling waves [1]. This recent work builds on the earlier theory developed by Roger Lui for recursion models [13, 14].

The effects of quiescent states on ecological systems were discussed by Karl Hadeler. Quiescent states, with random switching in and out of these states, damp oscillations locally and can suppress periodic orbits. This was illustrated by the introduction of a quiescent state for the prey into the MacArthur-Rosenzweig model. Coupled reaction-diffusion equations with a quiescent state [6] can be analyzed by the methods in [11, 23] to yield spread rates and traveling fronts. Here the impact of the quiescent states can be dramatic on spreading speeds, often reducing the speed to a fraction of what it would be without the quiescent state. The mathematical methods in Hadeler’s research [6] have been recently applied to model the spread of West Nile Virus across North America [10]

Xiao-Qiang Zhao gave a historical survey of results on traveling waves and spread speeds for different population models. He summarized studies of monostable and bistable waves for a variety of different formulations (reaction-diffusion equations, integro-differential equations, etc.) and unified these with an integral equation approach. He gave rigorous results on the asymptotic spread speed and traveling wave speed for symmetric kernels [22]. This general method was illustrated by examples from the literature in which the spread speed and minimum wave speed were equal, and this value was estimated. Numerical simulations [24] of spreading speeds were presented.

Invasions of diseases into new territory is a worldwide problem, which traditionally has been modeled with reaction-diffusion equations. If dispersal is nonlocal, these equations can greatly underestimate speeds of invasion. Integro-differential models can incorporate nonlocal dispersal. Jan Medlock showed how to use knowledge about the dispersal of either disease propagules (distributed contacts) or infected hosts (distributed infectives) to model disease spread with integro-differential equations [16]. Both models have traveling wave solutions and the wave speed can be computed in terms of the moment generating function of the contact distribution or dispersal kernel. The magnitude of the force of infection determines which dispersal mechanism gives rise to faster wave speeds. A perturbation scheme can be used to approximate the wave shape. Integro-differential equations seem more flexible than reaction-diffusion equations for continuous time scenarios; they will clearly be the focus of much future work.

3 Development of the interface between model and data

The theoretical work of Lui [13, 14], cited above, was popularized and applied in an ecological context to stage-structured (matrix) models with dispersal by Neubert and Caswell [17]. Here the combination of stage-specific information on demography and dispersal makes it possible to predict invasion wave speeds. However, such predictions are not the only, or even the most interesting, results of the model. For example, analysis of sensitivity and elasticity of the speed to model parameters makes it possible for managers to determine where invasive species are most susceptible to control measures. These issues were discussed in detail by Mike Neubert and Hal Caswell. They also presented a large number of examples of successful application of the theory to biological invasions across biological taxa. Some of the work they presented was the output of a US NSF-funded "National Center for Ecological Analysis and Synthesis" working group.

Beneficial 'invasions' may be the goal when managing endangered species. Variation in the rate of spread of a population is of fundamental importance for managing the species of conservation concern, for which spatial spread is beneficial [20]. James Bullock presented case studies in which this approach was used to model and understand constraints on spread for a range of conservation questions: how we facilitate habitat restoration; how we speed up species re-introduction; what role do mutualisms have in population persistence and spread; and how do we predict risks from Genetically Modified Organisms? The methods used for the analysis in these studies was based on the Neubert and Caswell modelling approach given above [17].

When rare, long-distance dispersal events occur, spread rates of populations are very sensitive to the so-called 'tails' of the dispersal kernels (probability density functions for dispersal distance). Here, the rare, long-distance dispersal events are the ones that cause rapid spread of an invading population. At the same time, the spreading speed becomes highly variable, as it is uncertain precisely when the rare, long-distance dispersal will occur [3]. In this context fecundity (number of viable offspring produced) makes a strong contribution to invasion speed [4]. The importance of fecundity has been largely overlooked, because traditional models of diffusion are weakly influenced by net reproductive rate (R_0) and, thus, seed production. By contrast, fat-tailed dispersal kernels effectively translate small differences in fecundity over large distances [2]. Among the challenges for predicting invasion speed is the estimation of fecundity and of recruitment success in new landscapes. Together, these components of population success far from the resident population control the capacity to spread. Jim Clark discussed the components of R_0 that must be inferred or predicted in order to anticipate invasion speed, and provided perspectives on those components we can expect to predict well and those that will remain uncertain for the foreseeable future [5].

Although recent studies have highlighted the importance of detailed dispersal data for the accurate prediction of spread rates, there are few, if any, standardized methods for the measurement of dispersal. Katriona Shea reported on recent efforts to standardize dispersal study designs. These include simulation models to investigate the efficiency of different trap layouts; to assess the importance of trap areas, source strengths, and dispersal geometry; and to compare the effectiveness of trapping (Eulerian) and tracking (Lagrangian) approaches. For thin-tailed dispersal data, transects were especially effective, but for fat-tailed data sector sampling was more effective. Under constant environmental conditions tracking of seeds often required smaller sample sizes than trapping for reasonable goodness of fit. At the same time, tracking data, which is often of limited duration, is more susceptible to error from autocorrelation in the environment. Dispersal models based on limited samples should be used with caution in population dynamics.

Mountain pine beetle attacks on lodgepole pine are a major problem for forests in the western United States and, more recently, in Alberta and British Columbia. James Powell began by describing the ecology and phenology of pine beetles [12]. The development of mountain pine beetles is under direct thermal control, and success of attack depends upon the beetles' ability to emerge simultaneously at an appropriate time of year [19]. Before 1995, data on outbreaks in Sawtooth Valley in Idaho showed a declining period-two oscillation, but since 1995 data show exponential growth in the area of infestation. To describe these outbreaks, Powell developed a discrete-time model, the Red-Top Model, in which the pines are divided into three age classes. Two key parameters were estimated from the data. The presence of an Allee effect makes the calculation of the invasion speed difficult, even with good dispersal data. Predicted spread speeds match data for Sawtooth Valley, but are too low for current British Columbia outbreaks. Other factors such as wind dispersal and global warming may account for this discrepancy.

The most common method of harvesting forests is clearcutting, which presents a challenge to species that live in the forest, for example, tree squirrels in the dry interior forests of British Columbia. Rebecca Tyson presented a model for recolonization that includes a habitat quality depending on time since clearcutting. The model includes migration between patches and a patch selection function. Tyson applied the model to tree squirrels in both a two-patch system (mature and second growth forest) and a four-patch model that includes edge effects. In the latter case recolonization can take more than twice as long as forest regeneration. If the recutting schedule in based only on forest regeneration, then it is quite possible that even small mammal populations living in the forest are still a long way from recolonization.

4 Development of new models and their analysis

Are generalist predators effective biological control agents for invasive species? Chris Cosner described a model for an invasive leaf miner and a generalist parasitoid that attacks the leaf miner but that can survive without the leaf miner. Each species has its own carrying capacity, but there is a Holling type-II predator-prey term that links the dynamics of the two species. In addition, both species diffuse. The resulting reaction-diffusion model predicts a number of possible outcomes, depending on the parameters of the model. In some cases, there are pulled waves of leaf miner invasion. For other parameters, the predator induces an Allee effect in the prey and the leaf miner invades by means of pushed waves. Finally, the predator may prevent invasion by the leaf miner altogether. Cosner used this model to focus attention on the factors that lead to effective biological control by generalist predators.

William Fagan continued the theme of predator-prey interactions in ecological invasions by summarizing recent experimental and theoretical work on native herbivorous insects that attack invasive lupine plants at Mount St. Helens, Washington, USA [7]. Detailed data on the life history and interaction of the lupine and its herbivores have been used to parameterize a system of stage-structured integrodifference equations for the recolonization of the volcano's primary successional landscape. A key ingredient of these models is the presence of inverse density-dependent herbivory: herbivores that attack high-density patches of lupine encounter low nutrient quality and high toxicity. A preliminary analysis of this model suggests that Allee effects in the predator play a pivotal role and that too much plant "invasion momentum" prevents the herbivore from reversing the plant invasion. Fagan described the implications of this work for successional dynamics and the biological control of invasive species.

Species persistence in river ecosystems is a subject of ongoing concern, especially as these ecosystems are affected by human disturbance. Individuals in rivers and streams are subject to downstream-advection in their environment. The somewhat surprising observation that species can persist in such environments even though the individuals cannot actively move against the advection has been termed the "drift paradox" in the ecological literature. Mathematical models for populations in environments with unidirectional flow, such as rivers and streams, can be used to analyze conditions under which species can persist. In particular the models allow us to analyze the consequences of movement behavior of individuals with respect to invasion speed and critical domain size. As shown by Lutscher and coworkers in a series of papers [15, 18], it turns out that these two ecological quantities are related as follows: If the advection speed is so large that the critical domain size approaches infinity, then the population cannot invade upstream, and vice versa. As shown by Lutscher, it is possible to extend one simple model to include spatial heterogeneity, given by a "pool-and-riffle" environment in a river, and study the model with respect to persistence and traveling periodic waves.

5 Collaborative Research, Interchange and Open Questions

The workshop was the ideal venue for discussion and collaborative interactions. For every 50 minutes of lecture there was at least 30 minutes of formal discussion time. This was supplemented by more informal discussion in the afternoons. The afternoons were also used for informal "breakout sessions" in which groups discussed subjects such as: how to estimate observed population spread rates from data, and the formulation and analysis of stochastic models for population spread.

Collaborative research groups tackled specific applied problems where biological questions and mathematical theory came together. For example, two separate groups started work on deriving a simplified model for plant-insect recolonization interactions on the Pumice Plains region of Mt. St. Helens. The ideas for these groups followed on from the ideas presented in the talks of Bill Fagan and Steve Cantrell (above).

The organizers asked that workshop participants submit informal "open problems" as a basis for the final discussion for the workshop. The list appended shows the breadth and depth of the issues addressed at the meeting.

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