Mathematical Models for Biological Invasions
November 27 - December 2, 2004

FOCUS OF WORKSHOP

The focus of the workshop is the interplay between new mathematical results on biological invasions and the application of these results to ecological systems. Here the interplay between the science and the math is crucial. Some of the lectures focus on the math, others on the applications.

LECTURES

Lectures are scheduled for 50 minutes. Approximately 30 minute of formal discussion will follow each lecture. *We ask that the lectures be designed for a broad audience, give a background to the area, and an overview of results, methods and their implications, rather than be technical in nature.*

DISCUSSION

We anticipate approximately 30 minutes of formal discussion time for each lecture. There is also time in the afternoons for informal discussion/break out groups (not currently scheduled). *If you are a Discussion Leader, please contact the speaker ahead of time for some background information on the lecture. Be ready to give a short introduction about the speaker and the area and to lead the discussion after the talk.*

MEALS

Breakfast (Continental): 7:00 – 9:00 am, 2nd floor lounge, Corbett Hall, Sunday – Thursday
*****Lunch (Buffet): 11:30 am – 1:30 pm, Donald Cameron Hall, Sunday – Thursday
*****Dinner (Buffet): 5:30 – 7:30 pm, Donald Cameron Hall, Saturday – Wednesday
Coffee Breaks: As per daily schedule, 2nd floor lounge, Corbett Hall
***Please remember to scan your meal card at the host/hostess station in the dining room for each lunch and dinner.**

MEETING ROOMS

All lectures will be held in Max Bell 159 (Max Bell Building accessible by bridge on 2nd floor of Corbett Hall). Hours: 6 am – 12 midnight. LCD projector, overhead projectors and blackboards are available for presentations. *Please note that the meeting space designated for BIRS is the lower level of Max Bell, Rooms 155-159. Please respect that all other space has been contracted to other Banff Centre guests, including any Food and Beverage in those areas.*

SCHEDULE

Saturday, November 27

16:00 Check-in begins (Front Desk – Professional Development Centre - open 24 hours)
17:30-19:30 Buffet Dinner, Donald Cameron Hall
20:00 Informal gathering in 2nd floor lounge, Corbett Hall
Beverages and small assortment of snacks available on a cash honour-system basis.

Sunday, November 28

7:00-8:45 Breakfast
8:45-9:00 Introduction and Welcome to BIRS by BIRS Station Manager, Max Bell 159
9:00-9:15 Short introduction: Mark Kot/Mark Lewis/Pauline van den Driessche
9:15-10:35 Hans Weinberger. *Spreading speeds and traveling waves for multispecies systems.*
Discussion Leader: Paul Fife
10:35-11:00 Coffee Break, 2nd floor lounge, Corbett Hal
11:00-12:20 Hal Caswell/Michael Neubert. *Challenges and successes in applying invasion theory to dispersal and growth data sets.*
Discussion Leader: Ingrid Parker
12:20-13:30 Lunch
13:30-14:30 Guided Tour of The Banff Centre; meet in the 2nd floor lounge, Corbett Hall
Free Afternoon
17:30-19:30 Dinner
19:00-20:20 James Clark. *Fecundity: Why it controls invasion speed and how to estimate it.*
Discussion Leader: Mark Lewis

Monday, November 29

7:00-9:00 Breakfast
9:00-10:20 Chris Cosner. *Prey invasion in the presence of a generalist predator.*
Discussion Leader: Markus Owen
10:20-10:50 Coffee Break, 2nd floor lounge, Corbett Hall
10:50-12:10 William Fagan. *Spatial dynamics of consumer resource coinvasions.*
Discussion Leader: Steve Cantrell
12:10-13:30 Lunch
13:30 Group Photo; meet on the front steps of Corbett Hall
Free Afternoon
17:30-19:30 Dinner
19:30-20:50 Katriona Shea. *Optimization of dispersal study design.*
Discussion Leader: Tim Reluga

Tuesday, November 30

7:00-9:00 Breakfast
9:00-10:20 Karl Hadeler. *The effects of quiescent states on dynamical systems and ecological models in particular.*
Discussion Leader: Horst Thieme
10:20-10:50 Coffee Break, 2nd floor lounge, Corbett Hall
10:50-12:10 Xiao-Qiang Zhao. *Spreading speeds and traveling waves for some population models.*
Discussion Leader: Yuzo Hosono
12:10-13:30 Lunch
Free Afternoon
17:30-19:30 Dinner
19:30-20:50 Jan Medlock. *Integro-differential -- equation models for infectious disease.*
Discussion Leader: Pauline van den Driessche

Wednesday, December 1

7:00-9:00 Breakfast
9:00-10:20 Frithjof Lutscher. *Relating invasions and critical domain size.*
Discussion Leader: James Watmough
10:20-10:50 Coffee Break, 2nd floor lounge, Corbett Hall
10:50-12:10 James Powell. *Invasion of mountain pine beetle due to climate change: A cautionary tale involving satellite data, integrodifference equations and phenology modelling.*
Discussion Leader: Andrew Liebhold
12:10-13:30 Lunch
Free Afternoon
17:30-19:30 Dinner
19:30-20:50 Rebecca Tyson. *Modelling recolonization of clear cuts.*
Discussion Leader: Andrew Edwards

Thursday, December 2

7:00-9:00 Breakfast
9:00-10:20 James Bullock. *Applications of invasion models to conservation questions: some worked examples.*
Discussion Leader: Mark Kot
10:20-10:50 Coffee Break, 2nd floor lounge, Corbett Hall
10:50-11:30 Closing: Kot/Lewis/van den Driessche
11:30-13:30 Lunch

Checkout by 12 noon.

** 5-day workshops are welcome to use the BIRS facilities (2nd Floor Lounge, Max Bell Meeting Rooms, Reading Room) until 4 pm on Thursday, although participants are still required to checkout of the guest rooms by 12 noon. **

Applications of invasion models to conservation questions: some worked examples.
Bullock, James (CEH Dorset Winfrith Technology Centre)

Invasion models are traditionally used to understand the spread of exotic species into new regions. However, their relative simplicity and clear outputs make such models appropriate for a wider range of ecological questions. Variation in the rate of spread of a population is of fundamental importance for managing species of conservation concern, whereby we often want to facilitate this spread. I present case studies in which we have used this approach 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? In our studies we are using the Neubert & Caswell modelling approach which combines the projection matrix approach widely used in applied population ecology with dispersal data to model wavespeeds.

Challenges and successes in applying invasion theory to dispersal and growth data sets.
Caswell, Hal (Woods Hole Oceanographic Institute **) and Michael Neubert** (Woods Hole Oceanographic Institute **)**

Combining stage-specific information on demography and dispersal, it is possible to predict invasion wave speeds. Such predictions are not the only, or even the most interesting, results of the model. We will discuss a variety of other analyses, with examples.

Fecundity: Why it controls invasion speed and how to estimate it.
Clark, James S. (Duke University)

When the scatter of seeds about a parent plant can include rare, long-distance dispersal events, fecundity makes a strong contribution to invasion speed. 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. 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. In this talk, I discuss the components of R_0 that must be inferred or predicted in order to anticipate invasion speed, and I provide perspectives on those components we can expect to predict well and those that will remain uncertain for the foreseeable future.

References (available at http://www.biology.duke.edu/clarklab/publications.htm)

Clark, J.S. 2004. Why environmental scientists are becoming Bayesians. *Ecology Letters* (in press).
Clark, J.S., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-competition hypothesis, *Ecological Monographs*, 74:415-442.
Clark, J.S., M. Lewis, J.S. McLachlan, J. Hille Ris Lambers. 2003. Estimating population spread: what can we forecast and how well? *Ecology* 84:1979-1988.
Clark, J.S., Lewis, M., and L. Horvath. 2001. Invasion by extremes: variation in dispersal and reproduction retards population spread. *American Naturalist* 157:537-554.

Prey invasion in the presence of a generalist predator.

Cosner, Chris (University of Miami)

This talk is about some joint work with C. Magal, S. Ruan , and J. Casas.
The motivation is to use mathematical models to understand an invasion of France by a leaf miner which is preyed upon by a generalist parasitoid. We use reaction-diffusion models where both the parasitoid and the leafminer have logistic growth but with an additional Holling type 2 predator-prey term linking the models for the two species. This turns out to give a range of possible phase portraits for the dynamics, depending on parameters. Some of them rule out invasion by the leafminer altogether; others suggest the presence of pulled waves of invasion, still others suggest the possibility of pushed waves because the leafminers experience a type of Allee effect. In the cases where there are pulled waves the linear conjecture and simulations suggest how wave speeds should depend on the parameters in the system. The main point of interest is that it seems possible for a generalist predator to slow or stop invasions if it can persist without the invading prey species.

Spatial dynamics of consumer resource coinvasions.

Fagan, William F. (University of Maryland)

Ecological invasions take place within a food-web context, where species interactions may influence the spatial progress of an invading species. This talk will focus on the spatial dynamics of co-invading consumer-resource pairs. After presenting background theoretical material, I will focus on a specific case study involving native herbivorous insects attacking lupine plants at Mount St. Helens, Washington. Detailed data on the life history and interaction strengths of the lupine and one of its herbivores are used to parameterize a system of integrodifference equations to study recolonization of the volcano's primary successional landscape. Analyses yield several new insights into the spatial dynamics of consumer-resource co-invasions. In particular, aspects of plant population growth and the intensity of herbivory under low-density conditions can determine whether the plant population spreads across a landscape or is prevented from doing so by the herbivore. In addition, threshold levels of spatial extent and/or temporal advantage for the plant together define critical values of “invasion momentum,” beyond which herbivores are unable to reverse a plant invasion. These findings have implications for successional dynamics and for the use of biological control agents to limit the spread of pest species.

The effects of quiescent states on dynamical systems and ecological models in particular.

Hadeler, Karl (Universität Tübingen)

This is joint work with Thomas Hillen which started from earlier work with Mark Lewis on travelling fronts in the "split" logistic equation. The general message is that quiescent states damp oscillations locally (near stationary points) in a very predictable way (theorem available) but may also change global behavior.

Relating invasions and critical domain size.
Lutscher, Frithjof (University of Alberta)

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.

We propose some simple models for populations in environments with unidirectional flow, such as rivers and streams, and analyze the consequences of biased movement with respect to invasion speed and critical domain size. 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.

We then 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.

Integro-differential -- equation models for infectious disease.
Medlock, Jan (University of Washington)

Invasion of diseases into new territory is a worldwide problem. Examples include West Nile fever in the US, HIV in Africa and Asia, and dengue in Latin America. Traditionally, the spatial spread of disease has been modeled using a local process, diffusion, to model dispersal. However, if dispersal is non-local, diffusion can greatly underestimate speeds of invasion. In this talk, I will discuss integro-differential--equation models that incorporate knowledge about the dispersal of disease propagules and infected hosts to describe disease infection. These models are continuous-time analogues to the discrete-time integrodifference-equation models and share many of the same advantages.

Invasion of mountain pine beetle due to climate change: A cautionary tale involving satellite data, integrodifference equations and phenology modeling.
Powell, James (Utah State University)**,** Justin Heavilin (Utah State University), Jesse Logan (USDA Forest Service Rocky Mountain Research Station), Barbara Bentz (USDA Forest Service Rocky Mountain Research Station)

In this talk we explore the potential consequence of global warming on the distribution and outbreak status of mountain pine beetle (*Dendroctonus ponderosae*). Mountain pine beetle serve an important ecological role in North American pine forests, which have evolved with bark beetle disturbance as an integral part of an adapted system. The reproductive strategy of mountain pine beetles requires new hosts each year, and pines under attack defend themselves strongly. There is thus strong selective pressure for dispersed populations of beetles to mature and emerge simultaneously (synchrony), and at an appropriate time of year (seasonality). Interestingly, the development and timing of mountain pine beetle development seems to be under direct thermal control, operating without the benefit of diapause (which often serves to `time' the development of other insects). A very simple model for insect development uses a combination of linear developmental rates and temperature thresholds below which development can not occur.

In combination with seasonal temperature swings a natural consequence of this simple model of phenology is that oviposition and emergence will occur in fixed, attractive cycles corresponding to one, two, or half generations per year. The dynamical properties of the thermal habitat are therefore characterized by regions of adaptive, synchronous seasonality separated by regions of maladaptive, asynchronous seasonality, which (with host availability) set the limits of mountain pine beetle habitat and predict the potential for outbreak. These boundaries are moving upwards and northwards, with catastrophic consequences.

Spatial dispersal should condition the rate at which pine beetles are able to colonize new, thermally viable habitat. Over the past three years we have developed techniques to parameterize a dispersal/attack model, operating on a landscape scale, using aerial overflight data from aircraft or satellite. A technique based on estimating functions turns what would normally be a complicated optimization procedure for determining dispersal parameters into a one-dimensional root search. Vital parameters for attack effectiveness vary from year to year due to phenological responses, while mean dispersal distances remain relatively constant. In this portion of the talk we will survey the estimating function methodology and discuss some of the difficulties in using overhead imagery to generate parameter estimates.

Because of Allee effects in the model (based on the beetle's need to attack hosts in sufficient numbers to be successful), estimates of invasions speeds are not straightforward. We introduce a test function approach which allows us to overestimate rates of invasion progress. Unfortunately, even with heavy-tailed dispersal kernels, the rates of progress predicted by the parameterized models fall far short of the rates required to explain recent observations of mountain pine beetle outbreak in British Columbia. Indications are that either endemic populations previously `under the radar screen' have been released by warming climate, or that beetles are able to take advantage of wind and weather to occasionally disperse tens and hundreds of kilometers to thermally viable habitat.

Optimization of dispersal study design.

Shea, Katriona (Pennsylvania State University), Olav Skarpaas (Pennsylvania State University), and James Bullock (NERC Centre for Ecology and Hydrology, Winfrith)

The distribution and abundance of species are determined by the dynamics of individuals at a location (demography) and the movement of individuals between locations (dispersal). Although both processes are equally important, methods and protocols for studying demography are far better developed and more commonly used than those for dispersal, often because movement of individuals is much harder to study. This is partly due to a lack of guidelines for dispersal measurement and few attempts at optimizing sampling methods for particular questions. In this study, we used simulation models to investigate the efficiency of different sampling designs for dispersal measurement. In particular, we examine different trap layouts, and compare trapping (Eulerian) and tracking (Lagrangian) approaches under different circumstances

Modeling recolonization of clear cuts.

Tyson, Rebecca (Okanagan University College)

Managed forests around the world include a variety of harvesting strategies, in which the most common is clear cutting. A number of tree species are not amenable to other harvesting strategies, and so we need to study the recolonization process in clear cut areas. This study must go beyond a single clear cut and encompass several generations of trees in managed forests, so that the effect of repeated clear cuts can be assessed. Models of this process must involve population growth and dispersal in temporally varying environments where the carrying capacity can go to zero, and the death rate to 100%. This presents a number of mathematical challenges. As a case study, we present a model for the recolonization of clear cuts in BC by tree squirrels.

Spreading speeds and traveling waves for multispecies systems.
Weinberger, Hans (University of Minnesota)

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 Q is the operator which takes the set of densities of the species at an initial time into the values at time Δt later. We shall present a survey of the qualitative spreading properties of solutions of such models in which all the species cooperate. In particular, we shall explain the results of joint work with Mark Lewis and Bingtuan Li which appeared in the Journal of Mathematical Biology [45 (2002), pp. 183-218 and pp. 219-230]. The main results are that there are, in general, a slowest spreading speed c^* 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 c_f^* such that no species spreads more quickly and at least one species spreads no more slowly. We shall illustrate these results with some simple invasion models, one of which shows that one can also treat two-species competition models. We shall also discuss more recent work with the same collaborators which shows that c^* can be characterized as the slowest speed of a class of traveling waves.

Spreading speeds and traveling waves for some population models.
Zhao, Xiao-Qiang (Memorial University of Newfoundland)

In this talk, we first give a brief review of traveling waves, asymptotic speeds of spread, and convergence for monotone evolutionary systems. Then we show how to use the integral equations approach to obtain the spreading speeds and traveling waves for some continuous-time population models. We will also discuss the numerical computation of spreading speeds.