

Mathematical Models for Biological Invasions

Discussion Questions

November 27–December 2, 2004

We invited workshop participants to submit open questions in the area of biological invasions. These open questions were the foundation for our discussion on the final day. A list is given below.

1 Mathematical Theory

1. Can we come up with a general theorem on the existence of spread rates, even when systems are not cooperative? (Hans Weinberger)
2. Just as there are well-known precisely defined kinds of stability, applicable to classes of dynamical systems, someone (if they haven't already done so) ought to come up with general well-defined notions of invadability of a given ecological community by another given community, which are applicable to broad classes of evolutionary population dynamics models. In the case of models of spatially distributed populations, some but not all of these definitions would involve propagative ideas (well represented in this conference). These definitions of invadability would be mathematical, but of course clearly tied to concrete events. Example: systems with traveling fronts connecting two "stable" constant states—the state being invaded could be considered invadable according to one definition, but not if something like the hair trigger effect is required. (Paul Fife)
3. Find a framework in which to study traveling waves for non-monotonic evolutions. Maybe take a clue from physics; there has been a lot of work, usually not rigorous, on non-monotonic invasions, sometimes invasions of or by a spatially or temporally oscillatory state. (Paul Fife)
4. I wish we would have a clear definition of an accelerating front. (Karl Haderler)
5. What error does one commit (with respect to critical domain size (leading eigenvalue) or speed of fronts if one replaces a kernel by its diffusion approximation? (Karl Haderler)
6. Is there any scaling (cf. Paul Fife's comment on Barenblatt: long time, but not too long) of time and/or space that would make a fat kernel biological meaningful. Remember: you try to investigate the behavior of a front for large time at distant space positions and at the same time you assume that the fat kernel reaches to infinity with high probability. No wonder there is singular behavior. (Karl Haderler)
7. How quickly do invasions reach the wave speed c^* , what role do transients play, and how do demographic and dispersal contributions shift as an invasion progresses? (Kat Shea)
8. What to do about overcompensation? (Mike Neubert)
9. What is the biological interpretation of the condition for invasion in the bistable equation? (I.e. $\int f(x)dx > 0$?) (Mike Neubert)
10. Why hasn't any mathematician written a paper, in plain language, that lays out exactly what we know about rates of spread in population models, exactly what we don't know, and exactly what we wish we knew? (This last part will be different for mathematicians and biologists.) (Mike Neubert)

11. What happen if we don't have a cooperative system? Can we still define an invasion speed? Mathematically, this is very challenging as Prof. Weinberger pointed out. The phenomenon of accelerating waves that Jan talked about is also very interesting. (Roger Lui)
12. Difference integral equations can formally be written as double integral equations using the Dirac measure in time concentrated at one. Jan Medlock's epidemic model with movement via an integral kernel can formally be transformed to a double integral equation with a Dirac measure in space concentrated at 0. (Horst Thieme)
13. Can the double integral equation theory be extended from Lebesgue densities to more general measures such that these models are not only formally covered, but become actual special cases? (Horst Thieme)
14. If a multi-species or multi-stage system is cooperative, certain useful results follow. If it is not, no one knows quite what to expect. Faced with this situation, some students of invasion (like me, for instance) go ahead and calculate properties of wave speed anyway. This reliance on faith seems touching, but dangerous. So, are there any calculations (hopefully simple) that would support one's belief in the existence of a wave, with a speed, in the absence of a demonstration of cooperativity? An obvious possibility would be a numerical simulation for a specific set of parameters, but does this really provide much comfort? Are there other, less obvious, calculations? If so, what are they? (Hal Caswell)
15. Is it true that the flows of integrodifferential equations do not compactify (although they may contract with respect to measures of non-compactness) and hence their qualitative analysis is technically more difficult than that of reaction diffusion equations ? (Karl Hadeler)

2 Development of the interface between model and data

1. Should we be paying attention to correspondence between projected spread rates and observed spread (from field data)? When and for what kinds of questions? Under what conditions should we de-emphasize this comparison? What can we learn from it? (Ingrid Parker)
2. Can some of the complicated behavior seen in plant-herbivore invasions on Mt. St. Helens be duplicated in simple models with a couple of PDE's or integro-difference equations? (Chris Cosner)
3. Patchy spread with more than one species motivated by the Mount St Helens system. This would involve something like random draws from a dispersal kernel in which a dispersed individual of species X starts a patch where it lands, which then starts to grow radially. The same type of process then occurs for species Y, but Y only succeeds if it lands on one of the patches of species X. Once a Y landed on a patch of Xs there would have to be some submodel for local growth of Y plus rules for how the newly founded patches of X and Y started sending off their own dispersers (or not). (Bill Fagan)
4. It seems that we lack a proper framework for 2D (and 3D) phenomena. Not only are the problems solved in 1D, but even questions are asked in a 1D shape (speed of invasion). The issue is first to know whether things essentially stay the same in 2D or not, and if not, in which shape can we ask the relevant ecological questions in 2D ? (Amaury Lambert).
5. There seem to be several open questions surrounding the choice of dispersal kernels to use in a model. These are of a more technical nature and not grand theoretical questions. What kernels are appropriate for a given dispersal mechanism(s). What are the appropriate statistics to use to estimate parameters in kernels. Most of what I am aware of in this area treats the kernels as mere statistical models and doesn't take into account the mechanisms. Surely there is a way to combine experiments on individuals (tracking) with experiments on populations (tracking). What is to be done with outliers, or extreme events. Should they be used in estimating a

dispersal kernel, or treated differently in a model. Eg, an integral equation model with either rare events as initial conditions or as a stochastic (rare) forcing. (James Watmough)

6. Given that long distance dispersal events are hard to quantify and measure, due to their stochastic nature, and that the effect of this data on the resulting dispersal kernel: little on parametric kernels; and large on spline type kernels, is unsatisfactory (Clark). How can this be resolved with the importance of LDD events on spread rate and wave speed (Neubert, Caswell etc)? Following Shea and Bullock's optimization method, can this be extended to determine the amount of effort that is worth expending on collecting LDD? Or should mechanistic models be investigated more fully? (Caroline Bampfylde)
7. Should we be paying attention to correspondence between projected c^* and observed spread? When and for what kinds of questions? When should we de-emphasize this comparison? What can we learn from it? (Ingrid Parker)

3 Development of new models and their analysis

1. "How much is enough?" There is a spectrum from simple mathematical toy models to highly complex simulation models, and similarly there seem to be simple field experiments and highly complicated ones. How much of all this information do we really need to understand and to make informed decisions? (Frithjof Lutscher)
2. Is there a simple model that can be used to determine conditions under which the intrinsic stochasticity in dispersal and environmental conditions make it impossible to estimate a spread rate with reasonable certainty? (Mark Lewis)
3. What happens in coinvasions or successive invasions involving prey and generalist predators or suites of predators? (Chris Cosner)
4. One of the main features of the Mt.St. Helens lupine-moth interaction is that moth feeding success is much higher on small lupine patches than it is on larger patches. In part the reason is that the nutrient content of larger patches is lower; however, the larger patch lupines appear to generate a substance that is toxic to the moth. It seems to me that one possible way to model such a scenario is to think of the interaction as predation at low resource levels and as competition at high levels. What are the implications for such a formulation regarding the invasion of consumer and resource across a spatial landscape? (Steve Cantrell)
5. I gather Okubo did something on invasion into a competitor, which I still have to find and read, but I'd be interested in how the degree of similarity between invaders and natives mediates invasion wave speed. Also, how the presence of different types of natural enemies in such competitive systems (generalists, specialists on the invader or on the native) would alter the dynamics. (Kat Shea)
6. Amaury Lambert and I talked about the following branching process problem, again based on the Mount St Helens system. The branching process considers how patches give rise to new patches (at rate B) and how patches are terminated by the herbivores (at rate D) There are old analytical results governing the probability of failure of the whole colony if B and D are constants. But consider the following scenario: After a patch is founded it continues to grow locally in size in addition to having the possibility of founding new patches. One way of treating this idea is to have B be some increasing function of patch age (the time since that patch was founded). Patch termination rate D would also have to be an increasing function of patch age to counter the increasing rate B and maintain the possibility for process failure. The interesting scenarios are ones in which B and D have different shapes, including the case where D is hump shaped (increasing faster than B for young ages but then below B for long ages [to capture the decline in lupine tissue quality]). This would be complicated analytically so one possibility would be to rephrase the problem as a hierarchy of branching processes where

at the fine scale individuals give birth to other individuals (at a constant rate B) but the D term operates against whole "limbs" (i.e., patches) of the process. There is a relevant book on this type of system called "Modeling extinction" which deals with theoretical treatments of extinctions in the fossil record trying to find ways of studying mass-extinction processes like those found in the geological record using mathematics. (Bill Fagan)

7. Analytically treat the case of co-invasions of predator and prey in the integrodifference case even if it is not tractable for PDEs and thus falls outside of the Weinberger-Li-Lewis general theory. (Bill Fagan)
8. Treat analytically cases where species interactions manifest through changes in each others movement terms rather than through the growth terms. So what is the effect of a mutualist like a seed disperser or a natural enemy like a seed predator on invasion success or wave speed. (Bill Fagan)
9. The focus is overwhelmingly on deterministic models (even if they sometimes have to be interpreted as integrated stochastic models). However, the role of stochasticity (demography but also dispersion) is ubiquitous in ecology and has not to be missed, et least because you might ask what is the probability that an invasion will succeed. The recent interest of some of the audience into branching random walks instead of PDE or IDE (Kot, Medlock, Reluga, Neubert, Caswell...) suggests that the community is mature for dealing more often with stochastic versions of known models, but also hopefully with truly new stochastic models. (Amaury Lambert)
10. Stochastic models - especially random environment and how they affect invasion speed. Prof. Haderler mentioned in his talk that a lot of work has been done in this area but I am unaware of any papers on this subject. Is this related to LDD that Prof. Clark talked about? (I am not talking about nonhomogeneous environment.) (Roger Lui)
11. A more complete theory of the functional response is needed that takes into account: use of a spatially distributed resource, and the effects of multiple predator and prey species, and does not assume dispersal, reproduction and predation are independent. (James Watmough)
12. I'm wondering how much we can learn about predator invasions from what is known about epidemiology. For example, we know that a susceptible population at K but spreading outwards can be invaded by a pathogen in the interior and the wave of infecteds will follow the wave of susceptibles, etc. We also know that for the disease, $R_0 < 1$ can invade and that immunization can reduce the density of susceptibles below the level necessary for an epidemic. (Kevin Drury)
13. How can integro-differential equation models for disease spread best be used to model disease control strategies? (Pauline van den Driessche)
14. If we consider a population where females and males disperse differently, is the spread speed of the travelling wave determined by the parameters of the less-readily dispersing sex? (Rebecca Tyson)
15. What proportion of "attempted" invasions fail, and how does invasion failure fit into the framework of wave speeds via the linear conjecture? Is it simply that failure is due to an overall negative growth rate, or should we be looking for threshold effects, which do not allow the use of the linear conjecture? There was some discussion to the effect that many invasions do fail, or require multiple initiating events, so this would appear to be a common feature. (Markus Owen)
16. What do our models tell us about types of intervention that may be desirable? E.g. control measures or conservation measures. (Markus Owen)

17. One thing I was thinking about was types of models other than pde's. Alan Hastings briefly mentioned cellular automata and interacting particle systems in his 1996 Ecology paper. I think that there is some analytical theory concerning these approaches - it's not just all simulation.
Also these approaches might be more amenable to incorporating detailed landscape data into a model. With all the GIS data that there must be now, this might be worthwhile. (Andy Edwards)
18. My question has to do with can we identify the extent to which dispersal makes a species a better invader. Most ecologists normally think that dispersal is a plus but (1) during establishment, dispersal may amplify the effects of an Allee effect and decrease establishment rates (2) If range expansions functions via formation of coalescing colonies (e.g. Shigesada et al) then dispersal may decrease the rate of colony establishment (again by magnifying Allee effects) and thus lead to lower rates of spread. I guess the big question is when does dispersal have these negative effects. (Sandy Liebhold)
19. Some plants produce fruits with a surplus of nutrient in order to attract spreaders (apple), others produce seeds with just the right amount for germination but they produce much more seeds than they can ever be expect to be dispersed in order to attract spreaders by the mere amount (acorn). In such cases most seeds fall very close to the parent plant and the actual dispersal happens later. Dow we know how to average over positions of located seeds to get the true dispersal pattern? Does standard sampling underestimate dispersal rates ? (Karl Haderler)
20. An invader that is rather similar to existing species (example leaf miner) can be sure that the per capita mortality caused by a generalist predator does not exceed that of its competitors. Is it true that its invasion success will largely depend on exploitation of resources and reproduction and not so much on predation? In other words, can it hide amongst its competitors? (Karl Haderler)
21. Is it true that Europeans should not bother about invaders since their flora (and perhaps fauna) is relatively poor in comparison to North America? (Karl Haderler)