Emerging Challenges at the Interface of Mathematics, Environmental Science and Spatial Ecology

Steve Cantrell (Miami),
Robert Holt (Florida), Mark Lewis (Alberta)

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1 Overview and Recent Developments

Traditional mathematical models in ecology, epidemiology, evolution, and related areas typically assume that the environment is uniform in time and space and that the transport of organisms, chemicals, genes, and pathogens through the environment is random. In reality, many environments are heterogeneous in time and/or space and many physical processes and behavioral responses involve nonrandom transport.

Incorporating heterogeneity and nonrandom transport into models for biological processes and then analyzing such models leads to significant new mathematical challenges. There are three unifying features that many of those challenges have in common: (i) The first is that quantities of interest that can be computed readily for random transport in homogeneous environments are, at present, difficult or even impossible to compute or analyze for parameter dependence when there is heterogeneity and/or biased movement; (ii) The second, which often gives rise to the first, is that the mathematical methods and physical or biological insights that allow us to understand simple models cannot be used in the presence of heterogeneity, anisotropy, or nonrandom transport; for example, it is easy to obtain an explicit formulae for the principal eigenvalues of the relevant Laplace operators in simple geometries and uniform space, and these immediately lead to a simple formulation for the minimal size required for a region to sustain a diffusing population with given growth and diffusion rates. On the other hand, there are no such formulae for the principal eigenvalue of a periodic parabolic operator with advective terms and variable coefficients, and there are few results on how the eigenvalues of such operators depend on parameters. Thus, it is much harder to determine the minimal habitat size needed for persistence in environments with semi-realistic patterns of spatial variation. A significant reason for this limitation in our current understanding is that orthodox analytic methods (such as the variational formulation of eigenvalues) can no longer be used, so progress requires the development of new methods; (iii) The third feature concerns the nonlocal nature of many transport processes which can include long-distance displacement or jumps. When transport is nonlocal, local partial differential equation models must be extended to include nonlocal interactions, resulting in integrodifferential or related integrodifference equations. Here, standard mathematical tools for classical spatial models based on partial differential equations, such as regularity theory, maximum principles or the existence of principal eigenvalues, do not necessarily apply. There is considerable empirical evidence that nonlocal dispersal occurs in some populations, but its significance has rarely been addressed outside of the context of invasion theory. New mathematics will be needed for the analysis of nonlocal dispersal models in other contexts. We envisage that the workshop help define and develop the new mathematics needed for such analysis.

Properly addressing these important issues will not only require new mathematical ideas but also close and on-going interaction between researchers who analyze models (mainly mathematicians) and those who pose questions and formulate models and attempt to link model to data (mainly biologists). Our workshop brought both groups together to identify important analytic challenges associated with models for environmental heterogeneity and nonrandom transport and to develop new mathematical approaches to addressing them. New mathematical challenges have come to the fore in various ways; to illustrate the nature of these challenges and to frame the problems more concretely, we the following describes a number of specific examples.

The rate of spread of a diffusing population into a uniform environment can, typically, be determined by a direct calculation based on a linear analysis, and such an analysis can often be extended to interacting populations. There are some abstract mathematical extensions of these notions to variable and stochastic environments, and there has been some empirical work on the topic, but analytic computations or estimates of spread rates are available only in a few special cases. Similarly, the basic reproduction number for epidemiological models, R_0, can be computed explicitly by matrix theoretic methods, assuming a nonspatial context and a temporally constant environment. Recently, there have been extensions of R0 theory to include infinite-dimensional models and temporally periodic environments. However, in practice, it remains a challenge as how to calculate the quantity in variable or spatially complex environments. Quantities such as R0 and spread rates that play a critical role in our understanding of models can sometimes be characterized in terms of eigenvalues for certain operators or matrices or as Floquet coefficients, but determining those analytically in terms of model parameters in the context of spatio-temporal heterogeneity presents many difficulties that will require new mathematical ideas to resolve. By mixing top mathematicians and quantitatively skilled environmental scientist together in the workshop, we not only addressed the above challenges mathematically but to also provided insight back to the questions of environmental concern that originally inspired the mathematical models.

Additional new mathematical challenges have recently arisen from issues of pressing environmental concern with anisotropic and directional movement. Examples include streams and rivers, where diffusion is augmented by downstream advection plus anthropogenic water flow manipulation, and terrestrial environments where structures such as roads can lead to movement anisotropy. Advection has been treated in connection with various purely physical processes, and anisotropic diffusion has been studied in the context of image processing, but neither of those areas of research addresses how spatial effects interact with nonlinear population or community dynamics. In the case of models with advection, standard methods based on variational principles do not apply directly, so alternative methods must be developed. These were the subject of discussion and development at the workshop.

Finally, we also considered the impacts of environmental change on populations from the context of optimal dispersal strategies. How should individuals within a population adjust their movement behavior in response to increasing environmental heterogeneity (both spatial fragmentation and temporal fluctuations in environmental conditions)? The issue of the evolution of dispersal strategies under changing environmental conditions is a question of very substantial interest in theoretical biology. It is also of urgent applied interest given the growing evidence for rapid evolutionary shifts in dispersal rates in organisms subsequent to land use changes and alterations in climatic range limits. There has been work on this problem from a number of diverse mathematical viewpoints, ranging from game theory, adaptive dynamics, to optimization to mathematical quantitative genetics, but each of those approaches emphasizes certain aspects of the phenomenon and ignores others. A major mathematical challenge in this area is the development of a synthesis of the different modeling approaches that has the capacity to address topics ranging from mechanistic descriptions of movement under environmental heterogeneity, to the evolutionarily and convergent stability of dispersal strategies, all within a unified framework.

2 Presentation Highlights

Dr. Chris Cosner presented an overview of research on models for the evolution of conditional dispersal in spatially heterogeneous environments. Here partial differential equation models were coupled to methods from game theory to determine evolution of dispersal. Ideas such as evolutionarily stable strategies, convergent stable strategies and neighborhood invaders were developed in the context of infinite dimensional dynamical systems. Methods based on variational approaches for eigenvalues were developed. A repeating theme in the research was that, under temporally constant environmental conditions, evolution would select diminished dispersal or ideal free dispersal. A challenge for the future is how to incorporate temporal environmental variation into our understanding of evolution of dispersal. This was the subject of much discussion.

Dr. Wenxian Shen addressed the challenge of analyzing spatially heterogeneous dynamical systems with nonlocal dispersal. Much of the analysis investigated the principal eigenvalues of nonlocal dispersal operators in spatially heterogeneous domains. Here, spectral results rely upon constraints regarding the nonlocal operator and the explicity spatial environmental variation encountered. Conditions for population persistence and methods for analysis of spreading speeds and travelling waves were discussed.

Dr. Wei-Ming Ni reviewed some recent progress in spatially inhomogeneous Lotka-Volterra competition-diffusion systems. A two species reaction-diffusion system for Lotka-Volterra type competition was investigated for an environment with heterogeneous carrying-capacity. New results concerning which combinations of diffusion coefficients and interspecific competition coefficients result in either a globally attracting coexistence equilibrium or extinction for one of the species. It was shown that if two ecologically equivalent species compete there is a lower limit for diffusivity beyond which slower diffusion can be detrimental. This was compared to the homogeneous case where the slower diffuser always wins. Two open questions were presented regarding the single species equilibrium of a logistic-diffusion equation with heterogeneous carrying-capacity:

1. Is the L-1 norm of the difference between the population equilibrium and the carrying-capacity monotone increasing in relation to the diffusion coefficient; and,

2. For a fixed total carrying capacity, can the local carrying capacity be distributed in such a way that can yield an arbitrarily large total population at equilibrium?

Dr. Vlastimil Krivan used the ideal free distribution (IFD) and game theory models to study the dispersal of multiple species of omniscient animals in a multi-patch environment. Population dynamics were included into the model by assuming that the animals' adaptive dispersal behavior happened on a faster time-scale than the population dynamics. Predator-prey and Lotka-Volterra competition modules were considered. A variety of dynamics were exhibited including ESS coexistence states, and multiple alternative coexistence states at higher competition levels. It was shown that in some cases adding IFD dispersal can destabilize population equilibriums in multi-species models.

Dr. Robert Holt addressed the role of predation and evolutionary dynamics in determining species range limits. Most species have genetic variation, which allows them to adapt to spatially varying environmental conditions. Models of adaptation and population dynamics in continuous or discrete space show that the interplay of demography, selection, and dispersal (including gene flow) can influence the habitat use and geographical range of a species. A predator-prey model illustrates how the ecological factor of predation can alter the balance of these forces, and thus alter the evolutionary trajectory of a prey species. Sometimes, predation can shift the equilibrial distribution of a prey species and expand its range of habitats, but in other circumstances, predation can constrain prey invasion and hence range limits. Open questions include accounting for the fact that dispersal itself can provide a source of genetic variation; that dispersal is often not simply diffusive; and that predators themselves have genetic variation and can thus evolve. The specific topic of the talk centered around spatially heterogeneous population dynamics, which is exactly the topic of this workshop.

Dr. Henri Berestycki presented new developments regarding reaction-diffusion equations in heterogeneous media. His talk introduced definitions of a General Transition Wave (Front) and its global mean speed for a type of reaction-advection-diffusion equations with temporally and spatially varying diffusion, advection and growth functions in an unbounded domain. For reaction-diffusion equations of KPP and bistable types with spatially varying growth function but constant diffusion rate, the existence or nonexistence of the general transition wave have been given in R^n space and in more general unbounded domains with a star-shaped or compact obstacle. However, the existence of the general transition wave in the most general heterogeneous habitats still needs to be investigated and the computation approaches for estimating the mean speed also remain open. The general transition wave in non-local cases is also an interesting problem. The results greatly enrich the study of propagation patterns of population in general heterogeneous habitats.

Heterogeneity enters dynamical models in different ways, one of which is that individuals can switch between phases that may be connected to differential properties of the habitat. Dr. K. Hadeler analyzed diffusively coupled dynamical systems, which are constructed from two dynamical systems in continuous time by switching between the two dynamics. If one of the vector fields is zero, it is called a quiescent phase. His research shows that introducing quiescent phases damps oscillations or even causes them to disappear. In their most recent work, exponentially distributed sojourn times is replaced by general distributions that lead to novel types of delay differential (diffuse) equations. One of the question pointed out in the talk is that the quiescent phase is somehow similar to a refuge which has infinite capacity. In the classic non-spatial competing species models introduced by Lotka and Volterra, the competitive exclusion principle (CEP) plays a significant role. However, in the recent work, Dr. J. Lopez-Gomez proved that even in the simplest cases when the species disperse through random transport, the spatial heterogeneities can lead to a modification of the CEP that might explain the earth biodiversity through the existence of refuge patches for some of the competing species, where they can segregate when the intensity of the aggression from the antagonists increases. An interesting question arouse from the talk is that since the coexistence of species requires that the refuse size for each species should be large enough, the number of different species will be limited if refuses for difference species do not overlap between each other, which is permitted in their model. Then the question is what the maximum number of different species is if they are able to coexist in the same habitat.

Hantavirus is a recent emerging zoonotic disease that is carried by wild rodents. Based upon ODEs, continuous-time Markov chains and branching processes, Dr. Linda Allen presented patch models with three regions reflecting reservoir habitat, spillover habitat and the boundary between them. The key result is that interaction of the species in the boundary region spreads the disease, i.e. there is an amplification rather than a dilution effect due to increased contacts (aggressiveness). It is therefore possible for the spillover species to contribute to the maintenance of the disease in the wild. This is facilitated by the workshop theme of spatial structure. Furthermore, cross-species transmission may lead to host shifts when a new viral strain is able to reproduce in a new host. It was suggested that the model could be used as a starting point to identify in general necessary ingredients for diseases to spill over and back, as well as to suggest key processes to measure in the wild (Mark Lewis). With 16 ODEs, the model is rather complicated, and suggestions have been made how to simplify the model (time scale arguments / Bob Holt; focussing on states of new infection to reduce the NGM / Odo Diekmann). Connections were drawn to reaction-diffusion models with overlapping habitats and competitive interactions (Chris Cosner).

Bacteriophages are viruses that parasitize bacteria and the most numerous life form on the planet. Their spread can be observed on agar plates, where they wipe out bacteria after bursting. The speed of the spreading plaques can be seen as a surrogate for fitness and is therefore of biological interest. Existing models significantly overestimate the wave speed. Dr. Hal Smith presented a model in which the exponential distribution of the latent period is replaced by a fixed delay. The key result is the effect of this delay on the existence and speed of travelling waves. This has been accomplished by applying asymptotic spreading speed theory to a related scalar equation. It appears that this scalar equation can be connected to quiescence (Karl Hadeler). Alan Hastings suggested similarities to certain nematodes and Odo Diekmann to use the fundamental solution of the Laplacian. The rate of plaque advance could be further slowed down by fixing the life time of free virus (Bob Holt). Chris Cosner pointed out that there may be hidden Allee effects breaking down the linear determinacy. Lyme disease is a vector-borne disease and transmitted to humans by the bite of infected ticks. Dr. Xiao-Qiang Zhao based his presentation on a reaction-diffusion model that takes into account the vector's stage structure (Caraco et al., Am. Nat. 2002). Using monotone semiflows in bounded and unbounded spatial domains, the key finding is that host movement spreads the disease spatially. The model could be applied to spatially heterogeneous environments by making some parameters space-dependent. Tying in with spatial control management, the model could be modified to include control to make uniform disease persistence impossible. As an example, Mark Lewis referred to the culling of white-tailed deer in Alberta with the aim to control chronic wasting disease. Jim Powell pointed out that deer move very differently within and between habitats (also, prions are very persistent and should therefore be an interesting spread problem). Furthermore, it was suggested that the basic model might be modified to include frequency-dependent transmission (vector-borne disease) and passive movement of the vector proportional to the host movement.

Dr. Sergei Petrovskii tackled a major question of dispersal when realistic individual movement is taken into account. Specifically, given a point source release of N individuals at time t=0, with population density r(x,t), the main question is "what is the rate of decay for large $|x|$ as t evolves?" It is known that realistic movement often involves (at least for some ranges) a statistical distribution with fat tails, so the initial question can be rephrased in terms of: (1) What is the process behind fat tails? (2) Do fat-tails mean non-Brownian motion? (3) Is diffusion irrelevant? The answer to all questions is "diffusion prevails", and the method to reach this conclusion is via a diffusivity distribution function. The theoretical framework was put to test with real-world data, and results are encouraging; the next step is to widen the validation of this framework with more species.

The main question of the talk of Dr. William F. Fagan was how complex population-level patterns arise as a result of (1) population-level movement, (2) individual-level movement, and (3) dynamic resources. Resources vary according to amount, spatial variability, temporal variability, and resource predictability. The movement mechanisms are either non-oriented (diffusion), oriented (perception-based), and spatial memory (own history, communication, genetic inheritance, path integration, cognitive maps). It was noted that consumers evolved to use different mechanisms in different situations, leading to patterns of residency, migration, nomadism in which there is no pattern, and nomadism in which there is no repetition of terrain. The talk addressed the problem of how landscapes influence movement, and identifies, for several ungulate species, mechanisms of response to dynamic resources, and infotaxis, i.e. when information directs movement due to spatial memory, and communication. The main question opened is how to incorporate these phenomena into an analytical framework capable of explaining phenomena whose qualitative properties are well understood.

Dr. Roger Nisbet linked mathematics to a conservation problem in environmental sciences. Specifically, he used the Pacific salmon as a study case to illustrate that for species which encounter strongly varying spatial scales at different life stages, it is important to consider entire life cycle. Dynamic Energy Budget Theory (DEB) offers a good vehicle in which to take behavior, physiology and space into account simulataneously. A standard DEB model can represent the complete life cycle in a parameter-sparse way and provide a generic model. Comparison of salmon data with model predictions shows agreement on both inter-species level and intra-species level. The biological importance of considering varying spatial scales across different life stages wass highlighted throughout the presentation.

Dr. Thomas Hillen discussed how transport equations can be employed in spatial ecology to model movement in habitats with directional features that provide faster travel routes. Scaling methods for these transport equations that were previously considered separately (moment closure, hyperbolic scaling and parabolic scaling), are shown to lead to the same drift-diffusion limit, where the drift and diffusion are determined by the expected orientation of the habitat and its variance, respectively. Depending on the scaling, drift- or diffusion-dominated limits can be obtained. The parabolic scaling is only applicable if the expected habitat orientation is zero. Application to wolf movement shows that they prefer to move along seismic lineswhich enables them to spread out faster from a point compared to uniform movement. The talk brings together different mathematical tools for the modeling of an ecological phenomenon, and mathematics is linked with ecological data.

Dr. Otso Ovaskainen discussed animal movement and evolution of dispersal in heterogeneous space using the Glanville fritillary butterfly as an example. He proposed a simple model incorporating random walk and habitat selection for butterfly movement. Linear landscape elements such as corridors and barriers are explicitly considered in the model. He used diffusion-advection-reaction models to fit mark-recapture data. The model can be applied to predict the probability that a butterfly visits a specific meadow and to examine effects of a movement corridor. In the second part, he discussed two ways of modeling dispersal evolution: ESS and ESFD, and simulated the movement of an individual with short-ranged dispersal kernel and an individual with long-ranged dispersal kernel. The models are analyzed by moment closures or perturbation expansions. Furthermore, he discussed how life-history and land structure influence the evolution of dispersal. As for the connection to the theme of the workshop, this talk provides a good study example for animal movement and its evolution. More empirical evidence needs to be accumulated for validating and calibrating the evolutionary dispersal models.

Dr. Alan Hastings presented a talk on the stochastic aspects of dispersal and on the control of invasive species. He employed the stochastic Ricker model with various stochasticities: demographic stochasticity, environment stochasticity, demographic heterogeneity, and sex ratio stochasticity, to discuss species extinction. His group performed a series of experiments on red flour beetles to validate the model. His study suggested that typical deterministic models can be misleading. For instance, many species could be at much higher risk than we think. In the second part of his talk, he computed stochastic spread speed usinga stochastic modeling framework. In the last part, he discussed the management of invasive species (cost versus risk) and showed that an Allee effect slows invasion considerably. As for the relationship to the theme of the workshop, this talk was the only one discussing stochastic aspect of dispersal and the control of invasive species .

Dr. Donald DeAngelis discussed several ecological issues of significance a specific locale, namely the

Florida Everglades: (1) the ecotone dynamics of halophytic and freshwater vegetation types under rising sea levels, changing ground water salinity, and storm surges; (2) dynamics of fish under a hydrology with strong temporal dependence; (3) dynamics of highly mobile hydrology dependent species with small populations, such as the snail kite. The approach outlined is that of supplementing rigorous mathematical models (ODE, PDE, matrix) with less rigorous but flexible individual or agent based models.

Dr. Mark Lewis discussed issues related to the analysis of spatiotemporal models for steam and river populations. Such ecosystems consitute instances where biology meets physics, in that population dynamics are coupled to stream flow. In this regard, Dr. Lewis examined the role of spatial heterogeneity and flow rate in mediating predictions of persistence for both a single pelagic population in the drift and for a population with drfit and benthic states. Following was a discussion of biogeographic issues related to the “drift paradox”, in particular the interplay between upstream spread rate and the stream length needed to sustain a population. He then showed how the notion of net reproductive rate from epidemiology can be formulated in the current ecological context for a single pelagic species based on the concept of a next generation operator, and how this formulation can then recover mathematical results pertaining to biogeographical aspects of the drift paradox.

3 Scientific Progress Made

This meeting has highlighted important issues at the interface mathematics, environmental science and ecology. We had particular foci for each morning/afternoon of each day of the meeting, in discussing important, fundamental mathematical and ecological issues, around which the talks were built: dispersal, impact of spatial heterogeneity, invasion and spread, scale, determinism and stochasticity and real-world applications. The talks keyed-in markedly on each of these themes, much to the credit of speaker who made concerted effort to connect closely with the workshop themes.

Perhaps unsurprisingly, many of the connections that were made were unanticipated. In particular, the discussions generated new ways to connect seemingly disparate areas. For example, dynamic energy budgets were connected to optimal spatial movement modelling; analysis of detailed animal migration patterns was connected to transport equation models and their scaling limits; spatial competition models and analysis was connected to issues of biodiversity, spatial segregation, niche theory and promotion of spatial coexistence; the ideal free distribution and game theory was connected to predator-prey dynamics and evolution of species ranges. The list goes on.

Mathematically the structure of the meeting rested upon new developments in nonlinear infinite-dimensional spatial operators arising from reaction-diffusion-advection models, integrodifference and integrodifferential systems, games theory, stochastic processes and stochastic differential equations. These developments including methods of analyzing spectra and eigenvalues, comparison methods, construction of super- and sub-solutions, energy methods, dynamical systems theory, and functional analysis. Here the new mathematical models, arising from ecological, environmental and evolutionary questions, challenged mathematical theory to investigate fundamental model properties, such as well-posedness, spreading speeds, persistence, anisotropy, invasibility, and optimality. In several cases, classical ecological theory was turned on its head. For example we learned how evolutionary pressures actually allow predators to enhance prey growth and spread (R. Holt), quiescent stages in life history can actually destabilize systems , promoting temporal oscillations (K. Hadeler), and variation between individuals can have dramatic population-level effects, such as greatly magnified spreading speeds (S. Petrovskii).

In other areas no ecological theory existed, and the talks outlined new ways to use mathematics to develop this theory. For example the concepts of spatial learning and memory in animal movement are in their infancy. However, new mathematical models can explain how different spatial movement strategies result in characteristic movement patterns such as nomadism, range residency and migration (W. Fagan). We are just beginning to study optimal dispersal in nonautonomous nonlocal systems and there will be considerable mathematical challenges going forward.

Spatial and temporal scales have been a recurring element, arising time and again in different areas. The key element is being able to formulate mathematically tractable models where movement, demographic processes, and population structure are included at the level needed for scientific insight.

4 Outcome of the Meeting

The meeting brought together mathematicians and biologists in new ways. We held extensive break-out sessions and discussion that lead to a deepening of our understanding of the mechanistic construction and analysis of mathematical models. Indeed several entirely new areas of mathematical model development were suggested at the meeting. These include physiologically-based movement modelling etc.

Moving towards a more profound mechanistic basis for ecological and environmental models is a key element in the maturation of the field of mathematical ecology. This meeting has taken us on the first steps.

There are several ideas for follow-up meetings, including potentially, future meetings at BIRS.

5 Abstracts of Talks

Linda J. S. Allen, Texas Tech University, Spread of Disease from Reservoir to Spillover Populations

Interspecies pathogen transmission is a primary route for emergence of new infectious diseases. Spatial overlap of habitats leads to greater numbers of interspecies encounters which in turn may lead to pathogen transmission in a nave host or adaptation of the pathogen to create a new reservoir. Deterministic and stochastic patch models for spread of disease among reservoir and spillover populations are used to investigate the dynamics of interspecies pathogen transmission when habitats overlap.

Henri Berestycki EHESS-Paris and University of Chicago Reaction-Diffusion Equations in Heterogeneous Media

I will review several recent developments regarding the mathematical theory of reaction-diffusion equations in general non-homogeneous framework. Issues such as non-uniform stationary states, generalized transition waves and what determines the speed of propagation will be discussed. These topics are relevant for ecology modeling in heterogeneous environment.

Chris Cosner University of Miami Models for the Evolution of Conditional Dispersal in Spatially Heterogeneous Environments

Mathematical models predict that in environments that are heterogeneous in space but constant in time, there will be selection for slower rates of unconditional dispersal, including specifically random dispersal by diffusion. However, some types of unconditional dispersal may be unavoidable for some organisms, and some organisms may disperse in ways that depend on environmental conditions. In some cases, models predict that certain types of conditional dispersal strategies may be evolutionarily stable within a given class of strategies. For environments that vary in space but not in time those strategies are often the ones that lead to an ideal free distribution of the population using them, provided that such strategies are available within the class of feasible strategies.Problems in the evolution of dispersal have been addressed from two complementary mathematical viewpoints, namely game theory and mathematical population dynamics. This talk will describe some results and open problems from the viewpoint of spatially explicit models in population dynamics, including reaction-diffusion-advection models and models for nonlocal dispersal. Some of the results and problems are related to the evolutionary stability of dispersal strategies leading to an ideal free distribution and the mechanisms that might allow organisms to realize such strategies.

Donald L. DeAngelis U. S. Geological Survey and University of Miami Plant Herbivore Defense: Modeling Optimal Defense Allocation as a Function of Light and Nutrient Availabilities and Intensity of Herbivory

Woody plants allocate their acquired resources, energy (or carbon) and nutrients, to meet their several essential functions. In order to grow and reproduce, plants allocate resources to acquire solar radiation (grow leaf biomass) and to acquire nutrients (grow fine root biomass). Investment instem wood, beyond what is needed structurally by the foliage and roots, is provided to obtain a competitive advantage through height for capturing light. In addition to the allocation of resources to these essential functions, resources are usually allocated to chemical antiherbivore defense, or other types of defense, such as spines or thickening of leaf surfaces, because herbivory can significantly reduce growth and increase mortality, thereby reducing plant fitness. Optimization of physiological trade-offs between growth and defense has been termed a central dilemma of plants. However, despite extensive research on chemically mediated plant herbivore interactions over the past three decades, an improved synthesis of plant defenses as a part of plant resource allocation strategies is lacking. Although such a synthesis will ultimately depend upon on empirical examination of patterns of chemical defense over a broad variety of environments, the efficiency of this empirical research can be greatly increased by appropriate use of modeling. The purpose of this study is to interpret theory using a quantitative framework for determining optimization of trade-offs between growth and chemical (or other) defense in terms of phenotypic responses of a plant as a function of spatial and temporal variation, external conditions, including available solar radiation (influenced by the degree of shadiness), external nutrient input, and intensity of herbivory. The model treats plant components and the herbivore compartment as variables. The herbivory is currently assumed to be purely folivory. Three alternative functional responses are used for herbivory, two of which are variations on donor dependent herbivory and one of which is a Lotka-Volterra type interaction. All three are modified to include the negative effects of chemical defenses on the herbivore. In preliminary results, optimal strategies of carbon allocation are found and shown to vary with most changes in environmental conditions. Increased intensity of herbivory led to an increase in the optimal allocation of carbon with increasing intensity of herbivory. Decreases in available limiting nutrient generally led to increasing importance of defense. Increases in shading also led, in one of the models, to increases in defense allocation, though not in the other two. Because the plant defense was only in the foliage, increases in allocation to plant defense were usually accompanied by shifts in carbon allocation from foliage to fine roots, because the effects of herbivory on foliage decreased.

William F. Fagan and Thomas Mueller University of Maryland Migration, Nomadism, and Range-Residency: How Landscape Dynamics Link Individual Movements to Population-Level Patterns

To help synthesize existing research, I will outline a unifying conceptual framework that uses spatio-temporal resource dynamics to bridge the gap between individual-level behaviors and population-level spatial distributions. This framework distinguishes among (1) non-oriented movements based on diffusion and kinesis in response to proximate stimuli, (2) oriented movements utilizing perceptual cues, and (3) memory mechanisms that assume prior knowledge of movement targets. Species use of these mechanisms depends on life-history traits and resource dynamics, which together shape population-level patterns. Static and well-dispersed resources should facilitate sedentary ranges, whereas resources with predictable spatial distributions but seasonal variation should generate migratory patterns. A third pattern, 'nomadism', should emerge when resource distributions are unpredictable in both space and time. Extensive empirical datasets detailing animal movements, remote sensing imagery time series, and a variety of mathematical models will all be used to demonstrate the connections among individual movements, landscape dynamics, and population-level patterns.

K.P. Hadeler University of Tuebingen and Arizona State University Coupled Dynamics, Quiescent Phases, and Distributed Sojourn Times

Heterogeneity enters dynamical models in different ways. For example, consider a population distributed in space that evolves in time. The whole population can be subject to temporal (e.g. seasonal) changes of the habitat, individuals can move in a heterogeneous habitat, or individuals can switch between phases that may be connected to differential properties of the habitat. These different views of what happens to individuals lead to models that may appear similar but which may greatly differ with respect to stability of stationary states, properties of periodic orbits, and traveling waves. Phases of quiescence (resting phases) or reduced activity provide illuminating examples. In our most recent research (with Frithjof Lutscher) we replace exponentially distributed sojourn times (the usual Poisson assumption) by general distributions that lead to novel types of delay differential (diffusion) equations.

Alan Hastings University of California, Davis Spatial Population Dynamics and Control of Spatial Populations

I will discuss two related issues in spatial ecology. I will consider the dynamics of spatial spread when all appropriate sources of stochasticity are included. This work shows that calculations from typical deterministic models can be very misleading. A key issue is that in natural systemswe have only a single realization of a stochastic process. I will then consider how to optimally control the spread of invasive species, using the case of Spartina alterniflora as an example. This work shows the difficulties of drawing on rules of thumb to determine control strategies.

Thomas Hillen and Kevin J. Painter University of Alberta Kinetic Models for Movement in Oriented Habitats and Scaling Limits

Kinetic models for movement in oriented habitats are a useful tool if the environment shows some distinct directional features, such as roads, rivers, seismic lines, or row-plantations. Historically, kinetic models were considered for diluted gases (Boltzmann equations), and various scaling limits were developed. In my talk I plan to review the three most common scaling methods (i) parabolic scaling, (ii) hyperbolic scaling, and (iii) moment closure, in the ecological context. I will show how these scalings are related and I will discuss in which case which scaling is more appropriate. I will illustrate the theory on examples of movement in habitats with linear features, on attraction to a food source, and on life in a stream.

Robert D. Holt University of Florida Predation and the Evolutionary Dynamics of Species Ranges

Gene flow that hampers local adaptation can constrain species distributions and slow down invasions. Predation as an ecological factor mainly limits prey species ranges, but a richer array of possibilities arise once one accounts for how predation alters the interplay of gene flow and selection. In this talk, I will extend previous single species theory on the interplay of demography, gene flow, and selection, by investigating how predation modifies the coupled demographic-evolutionary dynamics of the range and habitat use of a prey species. I first consider a model for two discrete and heterogeneous patches, coupled by movement, and then a complementary model for species distributed along continuous environmental gradients. The latter involves an extension of familiar reaction-diffusion models, stemming back to Skellam. I show that predation can strongly influence the evolutionary stability of prey habitat specialization and range limits. Predators can permit prey to expand in habitat use or geographical ranges, or conversely cause range collapses. Transient increases in predation can induce shifts in prey ranges that persist even if the predator itself later goes extinct. Whether a predator tightens or loosens evolutionary constraints on the invasion speed and ultimate size of the range of its prey depends on the predator effectiveness, its mobility relative to its prey, and the preys intraspecific density dependence, as well as the magnitude of environmental heterogeneity. These results potentially provide a novel explanation for lags and reversals in species invasions.

Vlastimil Krivan Czech Academy of Sciences The Ideal Free Distribution

The IFD is a game theoretical model that describes a theoretical distribution of a population in a patchy environment consisting of habitat or foraging patches. Under the IFD, payoff in all occupied patches is the same and individuals cannot increase their fitness by changing their strategy. Thus, the IFD is a Nash equilibrium of the underlying habitat selection game. Originally, this concept was defined for a single population that does not undergo population dynamics. In my talk I will discuss some extensions of his concept to situations with more interacting populations (e.g., two competing species), and with populations that undergo population dynamics. I will show that distributional models based on the IFD when combined with population dynamics can lead to new insights on the effect of adaptive animal behaviors on their population dynamics. Some of these simple models that combine population dynamics with distributional dynamics can be analyzed provided we assume time scale separation. In my talk I will focus on the situation where behavioral (distributional) dynamics operate on fast time scale when compared with population dynamics. The resulting models lead to piece-wise continuous differential equations that, in the case of two or three interacting species, are often analyzable.

Mark Lewis University of Alberta Analysis of Spatiotemporal Models for Stream Populations

Water resources worldwide require management to meet industrial, agricultural, and urban consumption needs. Management actions change the natural flow regime, which impacts the river ecosystem. Water managers are tasked with meeting water needs while mitigating ecosystem impacts. We develop process-oriented advection-diffusion-reaction equations that couple hydraulic flow to population growth, and analyze them to assess the effect of water flow on population dynamics. We present a mathematical framework, based on the net reproductive rate R_0 for advection-diffusion-reaction equations and on related measures. We apply the measures to populations in rivers under various flow regimes. This work lays the groundwork for connecting R_0 to more complex models of spatially structured and interacting populations, as well as more detailed habitat and hydrological data. This is achieved through explicit numerical simulation of two dimensional depth-averaged models for river population dynamics. This talk is is based on recent collaborative work with Frank Hilker, Jon Jacobsen, Yu Jin, Hannah McKenzie, and Peter Steffler as well as earlier collaborative work with Frithjof Lutscher, Ed McCauley, and Roger Nisbet.

Julian Lopez-Gomez Complutense University of Madrid Biodiversity through High Intensity Competition

Classical non-spatial competing species models, as introduced by A. J. Lotka and V. Volterra, predict extinction of some of the species when the level of the aggressions between antagonists is sufficiently large. As a byproduct, in non-spatial models the principle of competitive exclusion plays a significant role in describing the dynamics. Rather strikingly, even in the simplest cases when the species disperse through random transport, the spatial heterogeneities might explain the Earth biodiversity through the existence of refuge patches for some of the competing species, where they can segregate when the intensity of the aggression from the antagonists increases. If the refuge patches can support each of the species in the absence of competitors, some further adaptation mechanisms to the inherent territorial specificities might explain the extraordinary biodiversity of Gaia; possibly enhanced by some additional, eventually hidden, facilitative mechanisms between the species which might increment, even dramatically, the productivity and stability of the ecosystem, as it seemingly occurs in the tropical habitats. The importance of mathematical models in designing stable and productive ecosystems will become apparent when scientists can predict, by simply analyzing a prototype model, some hidden unexpected relevant phenomenology, like it was the prediction of the curvature of the light in Physics, by A. Einstein, one century ago. Here relies the great power of mathematics in dealing with real world problems. Besides estimating the relevant parameters of the models, mathematics provides with very simple toys to think about and order the available information in a rather systematic way.

Wei-Ming Ni University of Minnesota and East China Normal University Some Recent Progress in Spatially Inhomogeneous Lotka-Volterra Competition-Diffusion Systems

In recent years, lots of extremely interesting research in understanding the interaction among diffusion, directed movements and spatial heterogeneity have been done. In this talk I wish to report some of the recent progress in this direction.

Roger M Nisbet University of California Santa Barbara A Salmon's Perspective on Spatial Ecology

The dynamics of a population are determined by the interactions of individual organisms with their environment. However, different spatial characteristics of the environment are important at each life stage. I shall illustrate this by considering the full life cycle (egg/embryo, juvenile adult) of Pacific salmon. Eggs mature in gravel in upland streams, young fish grow in stream and river habitat before migrating to the ocean, and returning fish migrate upstream and spawn. Key physiological rates in all life stages can be described by a Dynamic Energy Budget (DEB) model that relates growth, development and reproduction to the fishs environment. The models qualitative predictions have been tested for five species: pink, chum, sockeye, coho and chinook. Practical application of the model to any particular salmon population requires considering processes at many spatial scales. Embryonic development and survival is influenced by spatial heterogeneity at the scale of 10-2m. Growth of young fish is influenced by the flow mediated dispersal of benthic macroinvertebrates that comprise their major food; food supply in upland streams will vary over 1-10m. Migrating juveniles face challenges of high temperatures and low water quality on a scale of 1-100km. Returning adults do not feed but face energetic challenges in upstream migration with large spatial heterogeneity in currents. I shall review how each is treated when working with the DEB model, and end with some general remarks on integrating multi-scale spatial and physiological heterogeneity into population models.

Otso Ovaskainen University of Helsinki Environmental Heterogeneity in Continuous-Space Continuous-Time Models

I discuss models of animal movement, population dynamics and evolutionary dynamics, focusing on the interplay between environmental heterogeneity and a biological process. I consider both theoretical approaches examining the link between the underlying assumptions and the emerging patterns, and statistical approaches aimed at interpreting data. I first discuss how mark-recapture data (e.g. on butterfly movements) can be fitted to diffusion-advection-reaction models. Here environmental heterogeneity is modeled either through a discrete set of habitat types (with habitat selection at boundaries) or through continuously varying habitat quality. Inclusion of linear elements (such as movement corridors or barriers) leads to a mixture of two- and one-dimensional diffusions. I then discuss how diverse ecological and evolutionary phenomena can be modeled by spatio-temporal point processes. In this framework environmental heterogeneity is modeled e.g. through a smoothed point field, allowing one to control parameters such as patch size, patch quality, and patch turnover rate. The spatial and stochastic individual-based models can be analyzed mathematically by constructing a perturbation expansion around the mean-field obtained at the limit of global interactions. As an example I discuss how the evolution of dispersal distance depends on landscape structure, life-history parameters and the approach taken to model evolutionary dynamics (adaptive dynamics vs. mutation-selection-drift balance).

Sergei Petrovskii University of Leicester A Tale of Two Tails: The Impact of Statistical Structure

The rate of decay in the population density at large distances from the species main range has been an issue of controversy, a subject of heated debate and a focus of intensive research for at least two decades. The traditional random walk/diffusion-based theoretical framework that predicts a thin Gaussian tail was eventually opposed by superdiffusion theories resulting in a fat tail with either exponential or even a slower power law rate of decay. Indeed, field data often show a decay rate slower than Gaussian. This issue is apparently very important for understanding invasion rates as a fatter tail normally results in a faster spread of the invading species. Here we show that the thin tail is, in fact, an artifact of an over-simplified description of the dispersing population and not an immanent property of the random walk diffusion. Specifically, we show that a fat-tailed dispersal curve arises naturally in a population of non-identical individuals, i.e. in a population with some inherent statistical structure. Therefore, contrary to a widely spread opinion, a thick dispersal tail is not necessarily a fingerprint of Levy flights or superdiffusion. A good understanding of population dispersal and biological invasions is hardly possible without knowing what happens on the microscale of the individual movement. Correspondingly, we then proceed to the analysis of animal's individual paths. Movement paths are characterized by the duration of bouts of continuous movements. Studies on different species have revealed that the distribution of bout durations often has a fat tail well described by a power law. The relation between this pattern and the underlying processes remains poorly understood though. Basing on the concept of statistically structured population introduced in the first part of the talk, here we formulate an approach that allows us to describe data on bout duration within a unified framework and show that a truncated fat-tail in the bout distribution of animal movement is an immediate consequence of the inherent statistical variation of individual traits.

Wenxian Shen Auburn University Nonlocal Dispersal in Spatially Periodic Media

The current talk is concerned with two separate, but related dynamical aspects associated to nonlocal dispersals in spatially periodic media, that is, the principal eigenvalue of spatially periodic nonlocal dispersal operators and the spatial spread and front propagation dynamics of monostable equations with nonlocal dispersal in spatially periodic habitats. First, a principal eigenvalue theory for nonlocal dispersal operators with space periodic dependence is developed, which plays an important role in the study of spatial spread and front propagation of spatially periodic nonlocal monostable equations and is also of independent interest. It is seen that a nonlocal dispersal operator with space periodic dependence has a principal eigenvalue for following cases: the nonlocal dispersal is nearly local; the periodic dependence is nearly globally homogeneous or it is nearly homogeneous in a region where it is most conducive to the growth of the solutions of the associated evolution equation. It is also seen that in general, a nonlocal dispersal operator may not have a principal eigenvalue, which reveals some essential difference between nonlocal and random dispersal operators. Second, by applying the principal eigenvalue theory mentioned above, it establishes some general theory about spatial spreading speeds and traveling wave solutions of spatiallyperiodic nonlocal monostable equations, including the existence of spatial spreading speeds and the existence, uniqueness, and stability of traveling wave solutions in any given direction with speed greater than the spreading speed in that direction. It is seen that the spatial spreading feature is generic for nonlocal monostable equations in the sense that the existence of spatial spreading speeds is independent of the existence of principal eigenvalue of the linearized nonlocal dispersal operator at the trivial solution. It is also seen that the spatial variation of the underline medium speeds up the spatial spread. The talk will also present some ongoing research on nonlocal monostable equations in locally spatially inhomogeneous habitats.

Hal Smith, Don Jones, Horst Thieme, Gergely Rost Arizona State University Spread of Viruses in a Growing Plaque

A reaction diffusion system with time delay is proposed for virus spread on bacteria immobilized on agar-coated plate. The delay explicitly accounts for a virus latent period of fixed duration. The focus is on the speed of spread of the plaque and on the existence of traveling wave solutions of the model equations, which represent a spreading plaque. We give a rigorous proof of upper and lower spreading speeds associated with the system and provide a proof of the existence of traveling wave solutions. Our spreading speeds give better quantitative agreement with experimental results than earlier, non-rigorous, results.

Xiaoqiang Zhao Memorial University Global Dynamics of a Reaction and Diffusion Model for Lyme Disease

In this talk, I will report our recent research on a reaction and diffusion model for Lyme disease. In the case of a bounded spatial habitat, we obtain the global stability of either disease-free or endemic steady state in terms of the basic reproduction number R_0. In the case of a unbounded spatial habitat, we establish the existence of the spreading speed of the disease and its coincidence with the minimal wave speed for traveling fronts. Our analytic results show that R_0 is a threshold value for the global dynamics and that the spreading speed is linearly determinate.

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