

Integrodifference Equations in Ecology: 30 years and counting

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1 Overview of the Field

Many ecosystems experience drastic changes: species go extinct, non-native species invade, climatic conditions change, human activities disrupt habitat and dispersal pathways. Some ecosystems are closely managed for the benefit of humans: forestry provides essential material, and fisheries are indispensable for food security. Ecologists focus on understanding causes and mechanisms for current change to understand future impact of development and climate change. Ecosystem managers need solid scientific bases to reach decisions about land use and conservation. The spatial and temporal scales involved in these processes are typically too large to conduct detailed empirical work. Mathematical modeling of individual and population processes is essential to understand ecosystem function and predict ecosystem response to change. Ecosystem complexity, in turn, poses considerable challenges to mathematical theory and analysis of the resulting models. Novel quantitative tools are needed to meet these challenges.

Integrodifference equations (IDEs) are a class of spatially explicit, dynamical systems models that closely reflect the strongly seasonally synchronized life stages of many ecological species. In the simplest case, a generation consists of a growth phase and a temporally distinct dispersal phase. Particular examples include some invasive insects causing great damage in North America and elsewhere (e.g., Emerald Ash borer), and native species on the verge of extinction worldwide (e.g., Fender’s blue butterfly).

IDEs project the density of a population forward from one generation to the next by considering the stationary growth phase and the dispersal phase in sequence. In the simplest case, denoting $N_t(x)$ as the density of a population in (discrete) generation t at (continuous) spatial location x , we write the IDE to obtain N_{t+1} as

$$N_{t+1}(x) = \int K(x-y)F(N_t(y))dy. \quad (1)$$

Function F represents the growth phase of the life cycle, and dispersal kernel K is the probability density function of offspring location. Thus, IDEs constitute discrete, non-local, infinite-dimensional dynamical systems. They are a discrete-time analogue of reaction-diffusion equations (RDEs), and some of the mathematical theory for IDEs parallels that for RDEs. The non-local nature of the equations and the discrete-time setting makes some of this work considerably more challenging than for RDEs.

In 1986, Kot and Schaffer introduced IDEs as models for spatial ecological processes and laid the foundation for their analytical investigation and application [12]. Building also on previous analysis of IDEs in genetics [24], several pioneering papers then explored the qualitative behavior of IDEs, in particular stability properties, stochastic and chaotic dynamics, spreading speeds, traveling wave theory and pattern formation

[1, 2, 7, 9, 19]. In 1996, the discovery that IDEs can support accelerating waves of species invasions (a property that classical RDEs do not have) caught the attention of theoretical and empirical ecologists and immediately publicized IDEs in the ecological community [10].

Since then, a growing number of empiricists and theoreticians have worked to understand the qualitative behavior of these equations, and to connect the theory with observations [15]. IDEs were extended to include structured and interacting populations, stochasticity, spatial heterogeneity, genetic aspects and evolutionary processes. The purpose of the BIRS workshop was to review of the tremendous work being done worldwide and to bring together researchers in all related fields (analysts, modellers, theoretical and empirical ecologists) for a preview of developments and challenges to come. Specifically, the mathematical theory of IDEs has much to learn from and to offer to other areas of dynamical systems with non-local operators, such as integrodifferential equations, the emerging fields of integral projection models and impulsive reaction-diffusion equations, as well as spatial stochastic processes. Close interaction between analysts, modellers, and ecologist at the workshop ensured that model development remained relevant to empiricists and that empirical research focuses on required model input.

2 Recent Developments and Open Problems

Multispecies models: Most theory on IDEs considers single-species models, but realistic ecosystem descriptions need to include several species and their interactions. Such models are relatively simple to formulate but their analysis poses great challenges. Simple two-species competition models have monotonicity properties, so that comparison theorems allow analytical results. Yet, even those models show some surprisingly anomalous spreading speeds [14]. Three-species competition or predator-prey relationships generally do not allow comparison theorems, and little is known about spreading speeds and travelling waves in these models. Novel phenomena arise, such as the formation of spatial stable patterns [19] or cyclic and chaotic behaviour in the wake of an invasion [9]. Some of these emergent patterns are well understood in reaction-diffusion equations but they are only starting to be developed IDEs and many phenomena remain unexplored.

Movement behaviour: When multiple life stages are included in the model, there are often sessile stages, during which individuals do not move. The resulting next generation operator in the IDE model fails to be compact, and classical existence theorems for travelling waves fail. There is much recent interest in travelling wave theory for non-compact and non-monotone operators [3]. A completely new challenge from a modelling and analysis perspective is to include movement behaviour that depends on the presence of other species. In reaction-diffusion systems, such questions lead to cross-diffusion models that are notoriously difficult to analyze. For IDEs only a single numerical study exists that poses more questions than it answers. A potential new way to study questions of cross-diffusion in IDEs is to connect them to impulsive reaction-diffusion equations by modelling seasonal movement explicitly.

Spatial Heterogeneity: Travelling wave solutions often serve as descriptions of species invasion and range expansion processes. To study spreading speeds one typically assumes that the habitat is spatially homogeneous. In reality, most landscapes are heterogeneous on many scales. Organisms often have clear habitat preferences and adjust their movement according to resource availability, landscape features or conspecific density. Prevention programs against invasive species might create additional heterogeneity through targeted removal of resources (e.g., host plants of forest invasive insects) or localized application of pesticides. How then does one model dispersal in such environments? And what are the effects of landscape variation and spatially localized intervention on the spread of an organism?

Few papers have dealt with IDEs in heterogeneous landscapes. They all assume temporally static, spatially periodic heterogeneity, employ relatively simple dispersal kernels and assume spatially continuous solutions of the IDE [4, 8, 22, 25]. Recently, novel dispersal kernels were derived from random walk models in patchy landscapes. These kernels are discontinuous, as are the resulting solutions of the corresponding IDE [17, 18]. A novel analytical framework is needed to study discontinuous solutions, emergent travelling waves and related spreading speeds.

Temporal variation: Temporally varying landscapes are models for global change of climatic conditions. Initial research for IDEs with moving habitat patches unveils how dispersal may facilitate or hinder a

species' ability to keep up with climate change [26]. Several talks at the workshop elaborated on this topic and presented new results that include stochasticity and stage structure (see Section 3.3 below).

Stochasticity and data: Although deterministic models were successful in predicting the speed of invading populations, they do not capture the patchy spread and variation in invasion speeds observed in real systems. Stochastic models are crucial for quantifying the variability in spread rates, yet despite their importance, there is relatively little work on stochastic IDEs. Extrinsic stochasticity (caused by environmental factors) and intrinsic variability (based on demographic processes) affect spread rates in different ways: the latter typically reduces invasion speed while the former may increase spread [6, 11, 16].

Great efforts are underway to collect more data on individual movement and population abundance, for example with respect to climate change scenarios, in conservation settings, and in model microcosms. To link these data with models in a meaningful way, models need to incorporate the stochasticity inherent in the data. Therefore, we need to extend the analysis and tools above and developed new techniques to better understand the behaviour of stochastic IDEs and to quantify the variation in spreading speed and other ecologically significant quantities.

Non-local operators: Several other mathematical modelling frameworks are closely related to IDEs, yet researchers from these fields only recently started to interact with one another.

Reaction-diffusion equations with non-local terms appear in various places in the literature. The non-local operator may describe non-local interaction or movement, depending on the ecological question. No systematic theory of these equations is currently available, however, there is much recent interest in studying the qualitative dynamics of these equations, for example, the study of accelerating waves through tracking of level sets or the generalization of the theory of λ - ω -systems from reaction-diffusion systems.

Integral projection models (IPMs) project the density of a population forward in discrete generations, while individuals are continuously structured by state (e.g., size) [5]. IPMs are formulated very similarly to IDEs but details (e.g., typical shapes of the kernels) and research questions are quite different. In a spatial setting, when individuals are structured by continuous state and location, IPMs and IDEs are merged, and the resulting model has both aspects, e.g., kernels that represent progression through states and kernels that represent movement in space.

Impulsive reaction-diffusion equations were only recently studied in an ecological context [13]. In their simplest linear form, these equations can be equivalent to linear IDEs, but their nonlinear extensions typically are not. The study of impulsive reaction-diffusion equations in ecology is only in its infancy, but it is clear that many questions and challenges are closely related to those for IDEs.

3 Presentation Highlights

3.1 Mathematical theory of population dynamics of invasion in a static environment: Analytical advances

Since the pioneering results of Weinberger (1982) much of the analytical advancements in IDEs focused on establishing results pertaining to travelling wave solutions of IDEs. This is still an active area of research and new analytical approaches to tackle the emergent challenges were presented in the meeting. Maximum principles are at the heart of proofs for many wave speed results and as such a one of the biggest challenges in this area is establishing travelling wave results for non-monotone systems where a maximum principle can not be applied. New analytical approaches are required and we saw the emergence of some of these in the meeting.

Bingtuan Li (*Multiple invasion speeds in IDE competition models*) proved the existence of multiple propagation speeds in his study of competition models. Consequently, the order of invading species in competitive systems can change with the lead invader being replaced by its competitor later in the invasion process.

Xiaoqiang Zhao (*Bistable travelling waves for monotone discrete time recursive systems*) established the general theory for their existence waves in bistable systems and then took a dynamical systems approach to

establish global stability results of these waves. He illustrated these results with a two species competition model and pointed out that an open problem in these systems is to determine the sign of the wave speed. Crucially, the sign of the wave speed determines which species is the winner of the competitive interaction. It is therefore one of the most important quantities for our understanding of species invasions.

Lenhart (*Optimal control of integrodifference equations*) developed the basic theory for applying spatio-temporal control to integrodifference equations. The underlying ideas were based on the *Pontryagin Maximum Principle* (distinct from the classical maximum principle for IDEs), best known in the context of controlling systems of ordinary differential equations. Although such optimal control theory was previously extended to spatio-temporal models such as partial differential equations, the development and application of optimal control theory to integrodifference equations is new. Applications were made to optimal harvesting and to the management of gypsy moth invasive insects.

Weinberger (*Spread in a two-allele genetic system*) presented developments in the new mathematical theory for spatial spread of a genotype with a two-allele genetic system. Classical theory, going all the way back to R.A. Fisher, has focused on one-allele systems. Weinberger showed very recent work on extending the theory and developing it further for the two-allele case. Although Weinberger was unable to travel to the meeting due to health reasons, it was a great honour to have him participate via Skype as one of the founders of the field of mathematical analysis of integrodifference equations.

3.2 Mathematical theory of population dynamics of invasion in a static environment: New phenomenon and methods

The modeling of biological invasions was one of the earliest uses of integrodifference equations. Indeed, this was the application that first caught the attention of ecologists and that put integrodifference equations on the modeling map.

At this point, the basic theory of biological invasions in a static environment is well established: We know how to predict invasion speeds for a variety of dispersal kernels, in both one and two dimensions, for simple unstructured populations with compensatory growth and for age- and stage-structured populations. In addition, although open questions remain, we have made substantial progress in understanding invasions with depensatory growth (Allee effects) and/or with population interactions, such as competition. In addition, integrodifference equations have now been applied to a large number of invasive species ranging from weeds to trees and from birds to butterflies.

Given this background, one might think there would be little new mathematical theory about invasions in a static environment presented at this meeting. Nothing could be further from the truth. Six speakers presented stimulating talks that either offered new tools for old problems or that offered new insights regarding previously unstudied or understudied phenomena. In this section, we briefly summarize each of these talks, in the order that they were presented.

Mark Kot (*Models for the spread of white pine blister rust*) started the meeting by describing models for the spread of white pine blister rust. This is a fungal pathogen that is threatening a large number of valuable conifers. The pathogen has a complicated life cycle: It has two obligate hosts and numerous (spore) dispersal stages. All of the dispersal stages have different length scales. Kot showed how moment generating functions, used as integral transforms, and the method of steepest descent could be used to streamline the analysis of the complicated set of governing plant-host and pathogen equations. The resulting methods for predicting invasion speeds can be easily extended to other important systems such as host-parasitoid systems.

Many simple integrodifference equations generate invasions with constant asymptotic invasion speeds. And yet, many field studies and laboratory experiments show tremendous variability in invasion speeds. It is natural to assume that this variability is due to either demographic or environmental stochasticity. Michael Neubert (*Invasion variability in "simple" integrodifference equation models*) began his talk by asking whether this is necessarily the case. In particular, he asked whether it is possible to construct simple, deterministic IDEs with variable invasion speeds. He answered this question by considering three ways in which persistent variability in invasion speed can arise in scalar, deterministic, spatially homogeneous, and temporally constant models. In his most notable example, Neubert showed how overcompensation in back of an invasion can interact with the pushed waves associated with a strong Allee effect to generate variability in wave speed.

Tom Miller (*Ecological dynamics of colliding populations at habitat ecotones*) started his talk by telling us about ecotones. Ecotones are transition zones between adjacent ecological communities. These zones occur, for example, between forests and tundra and between shrublands and grasslands. In simple invasions, exotic species invade open space, but in ecotones, we often see the collision of invasion waves for foundational species from different communities. Miller described a system of integrodifference equations with intraspecific competition, interspecific competition, and dispersal, and he showed how this system provides insight into the dynamics of ecotones. He then connected his model back to empirical data from an ecotone involving creosote bush and black grama grass from the Chihuahuan desert of New Mexico.

Nathan Marculis (*Neutral genetic patterns for expanding populations*) asked “How do growth and dispersal affect genetic diversity in expanding populations?” He then showed that one can study the inside dynamics of an integrodifference equation and track the fate of neutral genetics fractions as the population expands. For pulled waves arising from compensatory growth and mesokurtic kernels, the neutral fraction at the front of the wave dominates the solution for all time. This leads to a strong founder effect. In contrast, pushed waves arising from strong Allee effects lead to slower spread but higher genetic diversity. Finally, fat-tailed dispersal kernels give rise to complicated patterns of genetic diversity that are still poorly understood.

In working with age- and stage-structured IDEs, we often calculate annual spreading speeds for invasive organisms. Mark Lewis (*Generational spreading speeds for integrodifference equations*) argued that we may, in fact, find it easier and more useful to calculate generational spreading speeds. In particular, Lewis showed how the next-generation operator of demography can be generalized to spatiodemographic models by separating the spatial fecundity and survival operators. This procedure can dramatically reduce the degree of the dispersion relation that one must then solve for the spreading speed. Lewis illustrated these ideas using spatiodemographic data for the weed teasel.

Finally, Frithjof Lutscher (*Spreading phenomena in integrodifference equations with overcompensatory growth function*) reported on his detailed studies and analyses of the complicated invasion dynamics that occur with overcompensatory growth. He showed that one can observe several traveling wave profiles with differing speeds. For example, one can observe a metastable solution for invasion into open habitat that is followed by stable traveling two-cycle. Lutscher focused his attention on the second-iterate operator for the integrodifference equation. He showed that this operator has a pair of stacked fronts. He generalized the concept of spreading speed to this operator, and he related his observations to the phenomenon of dynamic stabilization.

Although the basic theory of invasions in a static environment is indeed well understood, the above talks illustrate that there is still much work to be done. The presence of differing growth dynamics (compensation, overcompensation, and depensation), age and stage structure, genetic diversity, population interactions, and short and long-distance dispersal all leave us with many challenges.

3.3 Mathematical theory of population dynamics of invasion in a dynamic environment

A growing body of literature, empirical and theoretical, studies spreading phenomena as necessary adaptations for populations to keep track of their preferred climate zones under global change scenarios. Current estimates predict a global mean shift in the location of a population’s suitable habitat by 0.42 km/yr. The mathematical modelling of invasions in dynamic habitats is a rapidly emerging area of IDE research, with significant results being reported at the meeting.

Ying (Joy) Zhou (*Integrodifference equation models for populations in dynamic habitats*) pioneered some of the initial work in this area and presented her most recent advances covering two scenarios: 1) habitat location shifting with climate change and 2) a seasonally expanding and contracting habitat as associated with, for example, dry and wet seasons. In both cases the problems can be formulated as an IDE of the following type

$$n_{t+1} = \int_{-\infty}^{\infty} \underbrace{k(x, y)}_{\text{dispersal kernel}} \underbrace{Q_t(y)}_{\text{habitat suitability}} \underbrace{f(n_t(y))}_{\text{population dynamics}} dy \quad (2)$$

This equation can be transformed into a time-autonomous system in both cases, allowing for population persistence conditions to be determined. Moreover, the presenter demonstrated that these persistence results,

which apply to compact operators on a bounded domain (fixed habitat range) can now be extended to unbounded domains allowing for more realistic habitat suitability models to be considered. Importantly, these results also extend to ‘fat’ tailed dispersal kernels provided $Q_t(y)$ decays fast enough. Analytical results for IDEs in which dispersal kernels are not exponentially bounded are still quite sparse, so progress in this area is an important advancement.

Juliette Bouhours (*Climate change and integrodifference equations in variable environments*) extended the framework given by equation (2) to the stochastic case in which habitat suitability depends on a random variable, as does population growth rate. The random variable describes the uncertainty associated to the speed of climate change. The theorem she presented stated the dichotomy that a population in such a stochastically varying environment would go extinct with probability either 0 or 1. The condition determining extinction depended on the geometric average of the local population growth rate and dispersal kernel.

In contrast to Zhou and Bouhours, who focus on long-time asymptotic behaviour of equation (2) Austin Phillips (*Will transient dynamics help or hurt species during climate change?*) instead focussed on the short-term transient dynamics. In doing so, Austin presented four metrics for quantifying transient dynamics. Importantly, he demonstrated that long transients can be associated with critical slowing down in invasion speeds, which has important implications for species ability to keep pace with a moving environment.

Complementing the approaches of Zhou, Bouhours and Phillips, James Bullock (*Population spread and the velocity of climate change*) constructed virtual species from a statistical model of life-history and dispersal data. This new approach tackles the challenge of sparse population data. The synthesised life-history and dispersal parameters for the virtual species enabled the presenter to estimate invasion speeds from IDE models enabling him to broadly identify classes organism that would struggle to keep pace with climate change.

Taken together, these results suggest IDE research in there area is able to offer many important ecological insights regarding the vulnerability of species to climate change. Moreover, the talks demonstrated that there are number of key mathematical challenges that emerge from looking at this particular ecological problem.

3.4 Integrodifference equations: heterogeneity, data and numerics

The focus of sections 3.1-3.3 has been on IDEs which are solved on spatially homogeneous domains. Real spatial domains are typically a long way from this idealised homogeneous view. Moving away from this abstraction one has to decide how much detail to then include. Alan Hastings (*Ecosystem engineering and IDEs*) and Elizabeth Crone (*Combining models and data to set guidelines for butterfly conservation*) both advocated for the value of including the ‘key features’ of the landscape and biology and discussed periodic landscapes of alternating habitat types to address questions of species persistence in such landscapes. Both gave examples where the IDE theory was used to successfully inform conservation policy. In the case of Hastings this was in the design of marine reserves and in the case of Crone this was to quantify the minimum size of protected habitat areas for an endangered butterfly species. These talks illustrate that there are many questions beyond those related to spread that can be usefully addressed using IDEs.

With the increasing availability of fine resolution satellite data detailing the location of habitat types and GPS data of movement at large spatial scales we would also like to be able to understand population dynamics at a landscape level and move away from the idealised heterogeneous landscape. Two of the speakers specifically addressed the challenges associated to studying IDEs on such large spatial scales (of the order of 100s of kilometres). James Powell (*Invasion speed in highly variable landscapes: multiple scales, homogenization and the migration of trees*) presented a seed dispersal problem whereby seeds were dispersed by animals that made movement choices on the scale of the local habitat changes (10s metres), but moved distances of 10s kilometres. At the landscape scale the heterogeneous habitat resulted in an IDE describing seed and tree distribution which contained an anisotropic dispersal kernel. Analytical results for IDEs with anisotropic kernels are limited and many proofs rely heavily on the kernel symmetry. Powell addressed this challenge by using the technique of homogenisation to “average” out the effects of the local scale and produce an IDE description of the landscape scale dynamics. The resulting homogenised IDE contained an isotropic dispersal kernel allowing classical travelling wave solution results to be employed in the study of the tree invasion speeds.

The homogenisation approach offers a powerful method of including crucial biological detail while maintaining analytical tractability. However, one would still like to numerically simulate the dynamics of movement over landscapes and this challenge was picked up by Steven White in his talk on *Predicting species*

spread in heterogeneous landscapes with IDEs. The usual approach to numerically solve an IDE on a 2D heterogeneous landscape is to define a fixed spatial grid and to use either fast Fourier transforms or quadrature to carry out the integration in equation (1). The problem with this approach is that it places heavy demands on RAM and CPU time. and to overcome this the presenter illustrated a new adaptive algorithm. The adaptive algorithm used a coarse spatial grid at the far front or far rear of an travelling wave solution where the solution will show little spatial variation and so can be accurately solved with only a few grid points, but at the wave front where the solution changes rapidly a fine spatial grid is used. As time is updated the location of the fine spatial grid is also updated. Similar ideas are used to solve PDEs, but this is the first time an adaptive approach has been developed for IDEs. The technique leads to an order of magnitude improvement in computational efficiency.

White also presented the results of a recent IDE literature search which demonstrated an exponential increase in the number of IDE publications over the last 30 years. Still a relative small number of these papers specially addressed applications. White posited that the poor uptake of IDEs by ecologists may be due to the difficulties in numerically solving IDEs, and unlike working with ODEs or PDEs the availability of off the shelf code is very limited. Harsch (*Increased applicability and engagement through interactive web application*) presented an ‘Rstudio’ and ‘Shiny’ interactive web application to allow and encourage users to solve IDEs and gain a greater appreciation of their potential use. The idea of developing web resources for people interested in working IDEs was met with a lot of interest at the meeting and became the topic of one the breakout discussion sessions (see section 5).

3.5 Relationships to other model types

A number of different modelling approaches are closely related to IDEs, and their analysis poses similar problems. One of the goals of this workshop was to bring the various communities closer together and make them aware of ideas and results available in related fields.

Nonlocal reaction-diffusion equations are similar to IDEs in that (long-distance) dispersal is modelled by an integral operator instead of (or in addition to) the diffusion operator. Jérôme Coville (*Propagation phenomena in nonlocal reaction-diffusion equations: An overview of the recent developments*) gave a much appreciated overview presentation of the state of the art of analyzing spreading phenomena with these equations. His presentation began with an exercise in model selection that demonstrated that these nonlocal equations may provide a better fit to observed data than diffusion equations. Then he presented past and recent theory on spreading speeds in homogeneous and periodic environments.

Integral projection models formally look like the IDE in (1) but instead of spatial location (x) consider the ‘location’ of an individual in state space, i.e., x can denote size of an individual. In contrast to IDEs, the state space is typically compact and the ‘kernels’ that arise have qualitatively different properties. Stephen Ellner (*IDEs as models for individuals: who gets into the 1%, and why?*) was instrumental in developing the theory and applications of integral projection models and recently published the first book on the subject. In his talk, he used several long-term data sets and demonstrated how these models can yield much more information that is currently obtained from them. His results show that ‘success’ in many plant and bird populations is more a matter of luck than of individual traits.

Bill Fagan (*Perceptual ranges, information gathering, and foraging success in dynamic landscapes*) presented yet another application of integral equations in ecology. He modelled movement of individuals as a mix of random diffusion and directed movement, where the direction was determined by the amount of resources that an individual perceived in a certain detection radius. He compared the effectiveness of different strategies in different landscapes of resource distribution.

4 Scientific Progress Made

Scientific progress was made via break-out sessions. Here conferees discussed new results, scientific challenges and future directions in an informal environment. We kept a record of these discussions with the view that they can help inform future research. Summaries are given below.

4.1 Dispersal kernels and inverse problems

Dispersal kernels are central to integrodifference equations. The use of kernels to describe dispersal is the key feature that makes IDEs attractive to ecologists. The varied shapes of dispersal kernels lead, in turn, to many interesting phenomena, such as accelerating invasions.

The use of dispersal kernels does, however, entail serious empirical and theoretical challenges. For many systems, for example, invasion speeds are determined by the tail behavior of the dispersal kernel, and the tail of the distribution is precisely where data is often missing. We held a break-out session to discuss the problems, progress, and prospects associated with dispersal kernels. The discussion was wide-ranging. We briefly summarize some of the highlights of the discussion below.

Everyone quickly agreed that the old approach of fitting a pre-defined curve (e.g., a Gaussian), or even a pre-defined family of curves to dispersal data is insufficient, because of the importance of tail data. This led to a discussion of the usefulness of empirical methods, such as empirical moment generating functions and empirical saddle-point methods, that avoid pre-selecting the dispersal kernel. Several participants then pointed out, however, these empirical methods do not really solve the problem of tail data.

This led to a free-wheeling discussion regarding available methods for extrapolating kernels to regions where we don't have much data. We don't, after all, want to simply make up the tail. One suggestion that was emphasized was the usefulness of purposely censoring one's dispersal data in order to plot the estimated invasion speed as a function of the sampling radius. Investigators can then make sure that their estimates are leveling off with sampling radius. If they are, there is then some hope that the estimates can be trusted. Several people asked whether bootstrapping, Bayesian methods, and information theoretic methods could help. Others asked if there was some way to weight available tail data more heavily.

This was followed by quick discussion regarding the need for tail data. Everyone agreed that the question matters. Tails appear to be important for invasion data, but even here, time scales matter. Are we talking about transient dynamics or asymptotic behavior? In contrast, tails do not appear to matter for critical patch size problems.

At this point, the discussion shifted to questions regarding the realism of dispersal kernels. Most of the dispersal kernels that we use are simple and idealized. Can we construct more realistic dispersal kernels without adding too much complexity? There was great enthusiasm for further work on mechanistic models, and several people spoke well of the Wald distribution for wind dispersal. Jim Powell then gave us a preview of his upcoming talk on homogenization methods for highly variable landscapes.

Several people asked about kernels for resource-based dispersal and there was a fair amount of discussion regarding both spatial heterogeneity and two-dimensional kernels and anisotropy. Animal ecologists expressed some pessimism about the usefulness of fitted dispersal kernels, while plant ecologists expressed a great deal of optimism. This striking contrast helped highlight the important distinction between goal-directed movement and passive dispersal.

The discussion then turned to the inverse problem. What can we say about the shape of dispersal kernels given the shape, for example, of the invasion wave? The slope of the invasion wave does, for example, depend on the invasion speed, which is controlled, in turn, by the growth rate and the dispersal kernel. A few people were hopeful regarding the inverse problem but, in ongoing discussions after the session, several people were more negative. Indeed, one person suggested we can no more determine the shape of dispersal kernel from the invasions wave than we can determine a Leslie matrix from a stable age distribution.

Finally, we ended with a short discussion on other possible methods for incorporating dispersal data into integrodifference equations. This discussion included such topics as extreme value statistics, branching random walks, and gravity models.

4.2 Spatial heterogeneity

Spatial heterogeneity is ubiquitous in nature and often enhanced by human activities. How exactly the many forms of heterogeneity influence the processes of population growth and individual dispersal is still a source of many open questions. These ecological questions have spurred several analytical and numerical developments and much has been learned from reaction-diffusion models and from IDEs (see Section 2). The participants of the break-out session on spatial heterogeneity discussed where these developments could and should lead in the future.

4.2.1 Heterogeneity in local dynamics

The simplest possible scenario to study the effects of spatial heterogeneity is that of a static heterogeneous environment that affects only the local growth dynamics but not the dispersal of individuals. There is recent work on periodic landscapes (persistence of the population, existence of spreading speed), with special emphasis on piecewise constant periodic landscapes of two types of habitat (binary) where many explicit calculations are possible. The analytical tools of homogenization seem particularly helpful to gain ecological insights.

A first forward step towards a more generally applicable theory would be to extend the calculations to non-binary landscapes, for example to three habitat types such as “preferred habitat”, “secondary habitat” and “unsuitable habitat”. Based on previous experience, this step seems doable in a relatively short time period.

A second question is to extend the framework from periodic to random landscapes. This extension would be very important ecologically to explore questions of how landscape autocorrelation affects population distribution and spread. Non-periodic landscapes pose a huge analytical challenge since, for example, a spreading speed cannot exist. There is recent progress on this question for reaction-diffusion equations by using level-set methods. Developing corresponding theory for IDEs would be a great step forwards. For more applied questions, averaging over a random landscape could provide a reasonably simple theory and give relatively good answers to ecologically relevant questions. Some work on sparse landscapes has already been done.

A third question that emerged in this context asks how structured populations or multi-species assemblies respond to environmental heterogeneity. The analytical theory for structured populations often follows the theory for a single species closely (since the equations are order-preserving). For two competing species, the order-preserving structure remains so that some theory should be reasonably easy to obtain (one more applied study exists already). But theory for consumer-resource interactions is an even greater challenge than in homogeneous habitats, where there are still many open questions.

4.2.2 Heterogeneity in dispersal

The much more challenging aspect of heterogeneity in IDEs is to adequately model how environmental variation affects individual dispersal as represented by the dispersal kernel. One approach that was explored recently is closely related to impulsive reaction-diffusion equations (see above). The dispersal phase is modelled by a linear diffusion equation with spatially varying coefficients. From this diffusion equation, a dispersal kernel is derived. The kernels that arise this way are typically not convolution kernels. While some analysis has been carried out, many analytical questions are still open. An alternative approach could see the individual probing the environment in a number of places before deciding where to settle. This approach was implemented once, but has since not been used or studied in detail.

Once it is clear how to describe the outcome of dispersal in a heterogeneous landscape, the task is to study the effects of heterogeneity on population patterns. Can dynamic instabilities be caused by habitat heterogeneity? Can travelling waves or pulses or more complicated patterns be induced? How does heterogeneity affect spreading speeds? Homogenization approaches can be very helpful in the study of these questions.

4.2.3 Understanding the causes of patterns

Once we have a good understanding of which patterns can be created or influenced by heterogeneity and how, we can try and tackle an old yet every new and crucial question in ecology: How to distinguish between endogenous and environmentally driven variability? It is a mystery. So what should we actually do?

Typically, we cannot measure processes directly. Focusing on a few cases where the distinction between endogenous and environmental drivers matters and figuring out – via modelling – what we would need to know to distinguish, could be a first step. Finding a unique, measurable signature of a generating process would be the holy grail. In the meantime, one could look at the work on signature patterns in time series and see whether some of that can be translated into spatial signatures. But even if we cannot distinguish causes behind patterns, there may be value in pointing out that endogenous patterns are possible. More often than not, it is assumed that environmental variability is the cause of static patchiness.

4.2.4 The evolution of dispersal

Finally, a question that has garnered great interest in reaction-diffusion equations is that of the evolution of dispersal. Work on the corresponding question for IDEs has only barely been begun. There are some insights on the evolution of dispersal kernel shape using function-valued traits and the evolution of dispersal for persistence on bounded habitats. A yet unanswered question is whether there is an equivalent of the ideal free distribution for IDEs. Any progress towards this question would be a great achievement. The first step may be to study corresponding impulsive reaction-diffusion equations as an intermediate step.

4.3 Temporal variation and stochasticity

External temporal variation and stochasticity are crucial elements to any reasonable ecological model. This is because ecological environments are notoriously variable in time. Therefore it is natural to ask how classical results regarding spreading speeds and critical domain size might change in temporally variable environments. Typical forms for the variation are either temporally periodic, or random.

However, these elements make the analysis of integrodifference equations a real challenge because the dynamics are nonautonomous. The simplest form of the model allows for the dispersal kernel K_t and growth rate r_t to be random variables, indexed by time t , taken from given distributions. Using these, the classical questions of spreading speeds and critical domain size can then be revisited for such models in the context of impacts of temporal variation and stochasticity.

Seminal work on the critical domain size problem came from a series of papers by Hardin, Web and Takac (eg. [7]). This work has been recently rediscovered and extended into new contexts, particularly in the context of species survival under climate change. Here the stochasticity means that it does not make sense to analyze eigenvalues of a linearized operator. Rather, calculations give rise to something similar to a Lyapunov exponent, from which it is possible to derive threshold conditions for persistence. Recent there have been attempts to extend this theory to infinite domains, but this work is ongoing.

Early work on the spatial spread problem for scalar models, concave down growth functions, and uncorrelated spatial variation was developed by Neubert, Kot and Lewis [20]. Here there is no longer a fixed spreading speed. Rather there is a distribution of spreading speeds, and under certain conditions it is possible to show that the distribution follows a normal distribution arising from a Central Limit Theorem result. However, these results assumed that the spreading speed nonlinear system could be characterized by the operator linearized about zero. Although this appears to be the case, there is no rigorous proof. Recent work has extended these results to stage-structured models and complex correlations in temporal fluctuations [23]. However, rigorous proof for conditions under which the spreading speed for the nonlinear stochastic operator can be determined by its linearization remains an open problem.

An alternate form of variability comes from variability in the behaviour of dispersing individuals. For example, each individual could disperse via a Gaussian dispersal kernel, with with a different variance. Thus the population dispersal kernel would no longer be Gaussian, but would require convolution of the Gaussian with the distribution for the variance. This kind of individual variability can then change the shape of the overall dispersal kernel from Gaussian to fat-tailed, leading to a dramatic effect on spreading speeds [21].

4.4 New model formulations

One of the main applications of the integrodifference framework has been to describe dispersing populations, the kernel in equation (1) then describes the probability of dispersal. For such dispersal models we are frequently interested in travelling wave solutions however integral projection models (IPMs) in which the kernel describes ageing or stage transitions results in an IDE problem where instead other questions emerge, such as finding the stable age distribution (equilibrium distribution) of the IDE. We held a break-out session to discuss other biological problems that might give rise from new types of IDEs and the corresponding new questions associated to the resulting equations.

Kernel-type functions can be used to represent a range of biological phenomena such as non-local interactions, whereby the kernel may be some description of distance-dependent decay in competition or communication among animals. The spatial influence of individuals can result in a kernel that changes sign as a function of proximity - this is a new type of dispersal kernel that has not been studied in the context of

IDEs, although these kernels have been adopted in non-local PDE models of group aggregation, migration, schooling and flocking. Exactly how many of the results from non-local PDE theory can be transferred across to the IDE framework remains an open question.

Other examples novel kernels that could generate new classes of IDE model include non-local transmission of parasites (i.e., representing an unobserved process), perception / information gathering / information exchange, kernels describing interactions with individuals of remote age / stage classes and kernels describing non-local but non-global interactions. Indeed in Alan Hastings' talk he presented a model of ecosystem engineers in which the kernel depended on the amount of occupied habitat which was determined by the density of the ecosystem engineers this also gave rise to an interesting new class of kernels and IDE problems.

Another area of discussion was formulating models of intermediate complexity to bridge from individual based models (IBMs) to IDEs and IPMs. IBM are close cousins of IDEs and allow detailed biological stochastic processes to be described, but lack some of the analytical tractability of an IDE. Bridging between the two frameworks of IBMs and IDEs could allow us to exploit the strengths of both frameworks. A mean field model of the IBM with a simple representation of deviations due to finite population size is one way in which this could be achieved. Another approach is to derive a stochastic difference equation with a Gaussian approximation to binomial process in IBM. Studies of stochastic IDEs are still in their infancy although there has been a recent push in the last few years to make progress in this area (see section 4.3).

Finally examining the underlying assumptions of IDEs one can ask how breaking these assumptions can also offer new classes of models not previously studied. For example, mixing continuous-time dispersal and population dynamics with discrete-time events gives rise to impulsive reaction-diffusion models, whose analysis is just in its infancy [13]. Also, by including vital rates or dispersal that depends on local conditions or time and including heterogeneity among individuals that affects rates or kernels lead to IDE models that are biologically important but are not addressed by the current theory and open up exciting new avenues of research.

5 Outcome of the Meeting

The most important outcomes from this meeting are most likely those that are currently intangible: the inspiration that occurred in talks and conversations over tea and coffee, between researchers who would otherwise never have met. Analysts recognized that many ecologists have used (variants of) integrodifference equations without calling them that. Ecologists recognized that theory is being developed to deal with scenarios that seemed to be accessible only to simulation before. The fruits of mutual inspiration will be visible only in a few years when new collaborations yield published results.

We are currently working on two review papers that shall summarize the results and open questions from this workshop and include the larger community in the quest to solve them. We aim one of the papers at a mathematical/analytical audience and the other at an ecological audience.

Equally important is the effort to collect current literature and simulation tools online through a mixture of website and wiki. Several possibilities of implementing such a resource were discussed at the meeting. Several researchers indicated that they are willing and able to fund some of these efforts.

All in all, we believe that this workshop will soon be viewed as the galvanizing event in the theory and application of integrodifference equations in spatial ecology. Its effects will be felt in novel collaborations, exciting research and increased visibility and accessibility of the field.

References

- [1] E.J. Allen, L.J.S. Allen, and X. Gilliam, Dispersal and competition models for plants, *J. Math. Biol.* **34** (1996), 455–481.
- [2] M. Andersen, Properties of some density-dependent integrodifference equation population models, *Math. Biosci.* **104** (1991), 135–157.
- [3] C. Castillo-Chavez, B. Li, and H. Wang, Some recent developments in linear determinacy, *Math. Biosci. Eng.* **10**(5/6) (2013), 1419–1436.

- [4] S. Dewhurst and F. Lutscher, Dispersal in heterogeneous habitats: thresholds, spatial scales and approximate rates of spread, *Ecology* **90**(5) (2009), 1338–1345.
- [5] M. R. Easterling, S.P. Ellner and P.M. Dixon, Size-specific sensitivity: applying a new structured population model, *Ecology* **81** (2000), 694–708.
- [6] S.P. Ellner and S.J. Schreiber, Temporally variable dispersal and demography can accelerate the spread of invading species, *Theor. Pop. Biol.* **82** (2012), 283–298.
- [7] D.P. Hardin, P. Takáč, and G.F. Webb, Asymptotic properties of a continuous-space discrete-time population model in a random environment, *J. Math. Biol.* **26** (1988), 361–374.
- [8] K. Kawasaki and N. Shigesada, An integrodifference model for biological invasions in a periodically fragmented environment, *Jap. J. Ind. Appl. Math.* **24** (2007), 3–15.
- [9] M. Kot, Discrete-time travelling waves: Ecological examples, *J. Math. Biol.* **30** (1992), 413–436.
- [10] M. Kot, M.A. Lewis, and P. van den Driessche, Dispersal data and the spread of invading organisms, *Ecology* **77** (1996), 2027–2042.
- [11] M. Kot, J. Medlock, and T. Reluga, Stochasticity, invasions, and branching random walks. *Theor. Pop. Biol.* **66** (2004), 175–184.
- [12] M. Kot and W.M. Schaffer, Discrete-time growth-dispersal models, *Math. Biosci.* **80** (1986), 109–136.
- [13] M.A. Lewis and B. Li, Spreading speed, traveling waves and the minimal domain size in impulsive reaction-diffusion models, *Bull. Math. Biol.* **74** (2012), 2383–2402.
- [14] M.A. Lewis, B. Li, and H.F. Weinberger, Spreading speed and linear determinacy for two-species competition models, *J. Math. Biol.* **45** (2002), 219–233.
- [15] M.A. Lewis, M.G. Neubert, H. Caswell, J. Clark, and K. Shea, A guide to calculating discrete-time invasion rates from data, *Conceptual ecology and invasions biology: reciprocal approaches to nature* (M. Cadotte, S. McMahon, and T. Fukami, eds.) 169–192, Springer 2006.
- [16] M.A. Lewis and S. Pacala, Modeling and analysis of stochastic invasion processes, *J. Math. Biol.* **41** (2000), 387–429.
- [17] J. Musgrave and F. Lutscher, Integrodifference equations in patchy landscapes I: Dispersal kernels, *J. Math. Biol.* **69** (2014), 583–615.
- [18] J. Musgrave and F. Lutscher, Integrodifference equations in patchy landscapes II: Population level consequences, *J. Math. Biol.* **69** (2014), 617–658.
- [19] M.G. Neubert, M. Kot, and M.A. Lewis, Dispersal and pattern formation in a discrete-time predator-prey model, *Theor. Pop. Biol.* **48** (1995), 7–43.
- [20] M.G. Neubert, M. Kot, and M.A. Lewis, Invasion speeds in fluctuating environments *Proceedings of the Royal Society of London, Series B: Biological Sciences* **267** (2000) 1603–1610.
- [21] S. Petrovskii and A. Morozov, A, Dispersal in a statistically structured population: fat tails revisited. *The American Naturalist* **173** 278–289.
- [22] Y. Samia and F. Lutscher, Coexistence and spread of competitors in heterogeneous landscapes, *Bull. Math. Biol.* **72** (2010), 2089–2112.
- [23] S.J. Schreiber and M.E. Ryan, Invasion speeds for structured populations in fluctuating environments, *Theoretical Ecology* **4** (2011) 423–434.
- [24] H.F. Weinberger, Long-time behavior of a class of biological models, *SIAM J. Math. Anal.* **13** (1982), 353–396.

- [25] H.F. Weinberger, On spreading speeds and traveling waves for growth and migration models in a periodic habitat, *J. Math. Biol.* **45** (2002), 511–548.
- [26] Y. Zhou and M. Kot, Discrete-time growth-dispersal models with shifting species ranges, *Theor. Ecol.* **4** (2011), 13–25.