Impact of climate change on biological invasions and population distributions

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1 Overview of the Field

The purpose of this BIRS workshop was to generate, develop and apply new tools for the analysis of invasions and population distributions under environmental change. Thus the mathematical problems that we addressed were intrinsically spatial. Not only do temperatures vary with latitude, the very processes of population spread and shifts in range boundary are modelled using equations with spatial operators. Hence the mathematical and scientific challenges are significant, but the potential payoffs are large, making this significant as a BIRS workshop.

The workshop focused on the following issues:

Shifts in species range boundaries under climate change: As temperatures continue to increase, temperature isoclines will move quickly, particularly in northern countries, at rates predicted to be in excess of 1000 meters per year. Which species will keep up with shifting temperature isoclines and which will fall behind, and how can this be determined using dynamical systems? Initial attempts to solve this problem have used nonlinear reaction diffusion equations in a fixed moving coordinate frame for temperature. However, the meeting provided the opportunity to discuss and develop more realistic models that include integral operators that allow for long-distance dispersal, variable-speed coordinate frames for temperature, and changing external environmental conditions. Other approaches included slowly decaying initial conditions, which can appear as the result of a colonization-retraction event, and then may lead to accelerating rates of spread. Mathematical analysis of such systems requires gradually varying travelling waves. However, most current approaches focus on asymptotic behavior with constant parameters and these applications will require time varying parameters and responses on similar time scales. Applications range from understanding the spread of mountain pine beetle from western to central Canada, to analyzing the potential for loss of endangered plant species due to climate warming to tracking the advance of pine processionary moth as it moves across Europe.

Thus, many types of biological invasions are induced by climate change. Several challenging mathematical questions are related to such biological invasions in general and require new, sophisticated, mathematical developments. The meeting was the occasion to evaluate the state of the art in mathematical modelling as well as to identify the key mathematical challenges that arise or that are required for further progress. One of aims was to bring together modelers, mathematicians and ecologists with this goal in mind.

Dynamics of invasive species under variable environments: One hallmark of recent global warming is an increase in climatic variability. How will this increased climatic variability affect spreading speeds for biological invaders? Analyses of integrodifference equations in temporally random environments have shown that spreading speeds depend crucially upon the precise form variability takes and upon statistical correlations in the joint processes of growth and dispersal. This analysis relies upon the abstract ergodic theory for nonlinear infinite-dimensional operators. At the same time practical experiments in growth chambers are underway to examine dynamics like this in a highly replicated fashion using flour beetles (*Tribolium*). The meeting allowed mathematicians and ecologists to compare theory with experiment and move the understanding of species' responses to global change forward.

Multispecies interactions under changing environmental conditions: Historical records show vast changes in the competitive interactions of plants as they shifted behind retreating ice sheets after the last ice age. One possible explanation is that some plants may have escaped spatially from their natural predators during vegetation shifts, allowing them to become "supercompetitors." Initial models for such systems have involved spreading speeds for multispecies integrodifferential equations, but these have not been fully analyzed. Indeed, mathematical analysis of such systems is particularly challenging due to the lack of a comparison theorem for estimating spreading speeds. This is a very active area of mathematical research.

This is but one of many ways that spatial interactions between species can be affected by climate change. Climate may also influence competitive relationships of animals, as evidenced by the northward shift of the red fox and the simultaneous range contraction of its competitor, the Arctic fox. Predator-prey impacts may be as simple as the decline of local polar bear populations due to the bears' limited ability to access their prey in a spatially varying melting sea ice habitat, or as complex as the climate-driven collapse of population cycles in a lemming-four-predator system in Greenland. Mutualistic relationships may also be disrupted by climate change. For example, changes in blooming phenology have resulted in temporal mismatches between the availability of plants and their pollinators. One of the goals of the workshop was to develop a framework to categorize the types of perturbations that climate change can induce on such multispecies spatial interactions and to investigate the kinds of mathematical analysis that are possible. This was achieved by bringing together ecological theoreticians and mathematicians adept in the analysis of multispecies population models to share recent results and chart a course for future research.

Shifting patterns of vegetation under climate change: As rainfall patterns change, some regions are predicted to come under increasing drought. One response of vegetation to dry conditions is to form distinct spatially heterogeneous vegetation bands. These bands of "tiger bush" can be found in many semi-arid regions throughout the globe. Formation of vegetation bands can be understood, with the aid of mathematics, as a pattern formation problem in the context of plant growth and competition for water. Here nonlinear advection-reaction-diffusion models, that describe the processes, can predict the wavelength of vegetation bands and also explain how the vegetation bands slowly shift across the landscape. Hysteresis effects are also present: the nature of the bands depends not only on rainfall levels, but also on whether the level is increasing or decreasing. More significantly the process of desertification itself appears to exhibit hysteresis, making it difficult to revegetate once a threshold has been passed. Here mathematical models can actually be used to identify factors to predict imminent desertification. This workshop further developed the theme of vegetation patterns as indicators of environmental change with the use of mathematical models.

The meeting brought together researchers in dynamical systems with researchers in ecological and environmental modelling. Not only did the mathematical analysis inform the science. The science itself led to new mathematical challenges and insights, particularly in the following areas:

- Long range dispersal and non standard diffusion are topics that clearly are important perspective for modelling in ecology processes under climate change. Ecological problems represent a wealth of mathematical challenging problems that requires both insights in modeling and mathematical developments at the forefront of research.

- Likewise, careful analysis of the role of heterogeneity in dispersal shape and speed in the presence of environmental change is an important topic for ecology that the meeting focused on.

- In many instances it can be argued that dispersal involves several scales. The meeting developed mathematical approaches that combine multiscale diffusion that are important for having more realistic models.

- The models that have been introduced to study the impact of climate shift often rely on reaction-diffusion models with forced speed. In such models the ability of a population to survive mostly depends on its growth and dispersal capabilities. However, it is known that populations can also adapt themselves to new environments. Models that takes adaptation phenomena into account were proposed at the meeting. These models will enable us to understand the intertwined effects of growth, dispersal and adaptation in the success of a biological invasion.
- New mathematical developments are required to effectively study of reaction-diffusion systems with forced speeds for interacting species.
- Questions of model calibration and parameter identification much need to be set on more firm ground. Models that combine stochastic terms with evolution equations will be much relevant in this perspective.
- The genetic consequences of range expansions have not yet received much attention from mathematicians and modelers. However, range expansions are known to have an important effect on the shaping of genetic diversity of many species, and generally lead to a loss of genetic diversity along the expansion axis. More general model involve systems that take into account a population with varying traits. In mathematical terms this brings a new degree of complexity that combine reaction-diffusion equations with genetically evolving populations. Various classes of models are included in this framework for instance integro-differential equations modeling long-distance dispersal events.

In summary, the meeting provided a synergistic research environment, where researchers that do not usually interact will come together and experience cross-disciplinary opportunities for developing and applying methods of dynamical systems to population dynamics under environmental change. This workshop was also part of the Canadian Thematic year on ”Models and Methods in Ecology, Epidemiology and Public Health”.

2 Recent Developments and Open Problems

In recent years the effort to understand the impact of climate change on biological populations has led to a trove of mathematical and modeling developments. Much of this work has been focused on developing the mathematical tools and results to answer questions that arise when models incorporate a variety of biologically important aspects. For example, underlying environmental heterogeneity clearly plays an important role, and human activities strongly affect this heterogeneity. Global change also means that a focus on dynamic solutions, rather than on equilibrium behavior, is appropriate. Additionally, global change is increasing the variability in climate, emphasizing the need to incorporate different aspects of stochasticity. The challenges are great because the biological problems can, in many cases, only be adequately described by equations with strong nonlinearities.

Many new results have been achieved and many interesting and important open problems arise from these efforts and from the needs to understand the dynamics of biological populations under the influence of climate change. These works and problems range over a variety of directions: from the most fundamental partial differential equations including climate change effects in population dynamics models to the analysis of observations and experiments, to essential risk management questions, to modelling environments, to developments of predictive tools along with uncertainty understanding and quantification.

Nonlinear partial differential equations describing biological populations taking into account the climate change effect have been introduced in the works of Potapov and Lewis Potapov and Lewis (2004) and Berestycki, Diekmann, Nagelkerke and Zegeling Berestycki et al. (2009). These involve equations of which the prototype is:

$$\frac{\partial u}{\partial t} - \Delta u = f(x - ct\mathbf{e}, u)$$

where $\mathbf{e}$ is a given direction of propagation, c is a given parameter that represents the exogenously given velocity of the climate change. Such a model describes a population that is sensitive say to temperature conditions and, in one dimension, the variable could be thought of as representing the latitude. Typically, f is taken to be negative outside of a region - the range of the population. Various criteria have been introduced for the persistence of the species, including the notion of critical length given c or that of maximal velocity.

Popatov and Lewis (Potapov and Lewis, 2004) have considered competing species and derived a critical length. Berestycki et al. (Berestycki et al., 2009) have considered single species with general terms f and have derived critical length with predictions on the distribution of the population, explaining why climate change can bring about both range expansion as well as retraction. The effect of geometry when there is an Allee effect is discussed in (H. Berestycki and Nadin, 2008). Ongoing work (Berestycki et al., 2013c) describes the formation of gaps between competing species under the influence of climate change.

Several striking open problems arise in this context that are strongly motivated by modelling questions . Several of these were discussed at the meeting:

- Models of general systems of interacting species. To what extent do species interactions infleunce the geographic distributions.
- Effects of one-dimensional fast diffusion lines on persistence under climate change
- Climate change velocity varying over time
- Development of models that change from a continuous description to a stochastic individual based description at low density levels as an alternate way to describe extinction effects under the Allee effect.
- More general formulations involve varying diffusions, transport terms and several time dependence though a general type of equations

$$\frac{\partial u}{\partial t} - \nabla \cdot A(x,t)\nabla u + q(x,t) \cdot \nabla u = f(x - ct\mathbf{e}, t, u)$$

- The space itself may consist of networks of regions of different dimensions such as for the water network that involves interconnected streams, rivers and lakes
- Taking into account changes in the environment either as a result of a deterministic evolution or by stochastic variations (e.g. Fagan et al. stochastic patches environment)
- New models for phenology matching and climate change. A way climate change affect ecosystems is by modifying tje periods in time over which species interact.

The evolution of the biotope under the influence of a changing climate is a fundamental question for any description of biological populations dynamics. The process of desertification is studied in the more general formulation of looking for patterns arising in water limited vegetation development. Systems of nonlinear partial differential equations have been proposed by E. Meron et al. (Bel et al., 2012; Gilad et al., 2007; Sheffer et al., 2013) to approach these questions, taking in particular into account the positive feedback mechanisms that are involved. These equations lead to pattern formation that are analyzed through bifurcation analysis. Both the formal analytical bifurcation and numerical simulations agree with different patterns of patches seen in nature. In this context, an explanation is given in (Sheffer et al., 2013) for the formation of “fairy circles” in African lands. These systems of PDE’s reveal a rich structure and lead to many open problems from a mathematical standpoint.

3 Presentation Highlights

The mathematical challenges associated with modeling range boundary shifts and invasions under climate change were reviewed by Mark Lewis in the final talk of the meeting (*Mathematical challenges for modelling range boundaries and invasions in the context of climate change*). These challenges are broken down into different sections below.

3.1 Mathematical theory of the population dynamics of invasions in a changing climate:

Classical models for dispersal and invasion typically assume that the underlying environment is stable. Furthermore, they typically focus on a single species or a pair of interacting species, with fixed attributes and interactions. With climate change to the environment, these and other assumptions of existing frameworks often will not be valid. Modeling the impacts of climate change on biological invasions thus provides novel mathematical challenges, which were a major focus of this meeting.

Chris Cosners talk (*Challenges in modeling biological invasions and population distributions in a changing climate*) set the stage by outlining numerous challenges that would need to be addressed to enable existing frameworks for considering climate change impacts on species distributions and biological invasions. The talk in particular emphasized (i) the need for reaction-diffusion models to include the specific structure of environmental change (e.g., to understand potential future phenological mismatches between focal species), (ii) to include multiple species (e.g., for understanding future changes in species competition and niche partitionings), (iii) to extend previous dispersal models that were phrased for homogeneous landscapes to complex topologies (e.g., as given by lake/river networks), and (iv) to incorporate evolutionary processes into dispersal models to account for potential adaptations, and thus changing attributes of the modeled species over time.

Henri Berestycki (*Can a species keep pace with a changing climate?*) outlined a simple reaction-diffusion model that includes an environmental forcing term which allows considering gradual shifts in the environment (Berestycki et al., 2009). Through its principal eigenvalues, the model allows determining conditions that lead to population persistence or extinction, depending on whether the species can shift its range fast enough to track changes in the environment. The model, while simple, allows incorporating various biological complications to enhance realism, and could thus form a basis for representing the effects of a changing climate on invading populations (Fagan et al., 2009).

Odo Diekmann and Laurent Desvillettes (*Can climate change lead to gap formation?*) further incorporated species competition into a diffusion framework, and showed that with spatial heterogeneity in competition advantage, a gradually shifting environment can lead to the formation of a gap between the distributions of competing species (Berestycki et al., 2013a,b).

In contrast to previous models that assumed one scale of diffusion, Luca Rossi (*Fisher-KPP propagation in the presence of a line with fast diffusion*) proposed a new diffusion framework that allows describing the influence of roads on biological invasions (Berestycki et al., 2013c). The system is characterized by fast diffusion along roads, slow diffusion outside of roads, and shows that the asymptotic speed of propagation in the direction of the road is enhanced if the ratio between the two diffusivities is above some threshold (Berestycki et al., 2013d). The speed of propagation in a given direction will hereby also depend on the angle formed with the road, and diffusion enhancement does not occur above a critical angle.

Alex Kiselevs talk (*Role of chemotaxis in enhancement of biological reactions*) emphasized the need to not only consider random diffusion and passive advection in dispersal models, but also active and directed movement, for example, through the influence of chemotaxis (Kiselev and Ryzhik, 2012, 2013). The approach was illustrated using the example of coral breeding, where diffusion-advection models underestimate reproduction success, but incorporating chemotaxis can yield much more realistic estimates.

Ehud Meron (*Pattern formation a missing link in the study of ecosystem response to climate change*) underscored the need for incorporating feedback loops between biotic and abiotic factors in climate change impact models, as, for example, found in the interaction between root growth and water accumulation near patches with plant growth (Gilad et al., 2007). These interactions can lead, for example, to vegetation pattern formation, thus shaping water-limited landscapes. Phrasing these biological details in spatially explicit vegetation models not only reproduces observed patterns, but can also outline how pattern formation processes can affect ecosystem response to environmental change (e.g., gradual and incipient regime shifts induced by droughts and disturbances) (Dakos et al., 2012). A particularly powerful utility of this approach is its ability to use spatial patterns as indicators of regime shifts (Bel et al., 2012).

In contrast to the previous talks and most existing models for spatial changes in population distributions under climate change, (Joy) Ying Zhou (*Niche deficits in varying climate warming scenarios: will the deficit go through the roof?*) adopted an integrodifference approach rather than partial differential equation (PDE)-based diffusion-advection models (Zhou and Kot, 2011). Two advantages of this approach are its amenability to analytic analyses and its versatility in describing spatially heterogeneous recruitment rates, dispersal patterns, and varying speeds of climate warming. Joy Zhou showed, for example, that non-autonomous models can be reduce to autonomous ones when the speed of warming is constant, that the dominant eigenvalue of a linear integral operator can be used to determine whether the population goes extinct or converges to a travelling pulse solution, and how the approach can be used to calculate niche deficits, defined as the distance by which populations lag behind their changing niche. Niche deficits were in particular shown to be drastically different between the constant- and accelerated-warming cases, once again emphasizing the need to consider the climatic details of warming (Zhou and Kot, 2013).

3.2 Mathematical theory of the genetic aspects of invasions:

It is widely acknowledged that climate change may not only change population distributions, but also affect genetic diversity, both directly through novel adaptation pressures and indirectly through the influence of range shifts on the spatial distribution of different genetic traits. The mathematical modeling of these effects is still in its infancy, but some remarkable progress was made through a series of four talks.

Lionel Roques (*The dynamics of the genetic structure of range-expanding populations*) introduced reaction-dispersion models that can outline spatial changes to genetic diversity in range-expanding populations through decomposing the global model into subclasses corresponding to different genetic traits (Bonnefon et al., 2013). Several applications of the approach were given. The presenter showed, for example, how strong Allee effects can lead to so-called pulled waves where all genetic traits move more or less at the same speed and genetic diversity is conserved throughout the range; without an Allee effect, by contrast, pushed waves are observed with decaying diversity as some traits will move faster than others (Roques et al., 2008, 2012).

Francois Hamel (*Inside structure of pulled and pushed fronts*) expanded on the mathematical underpinnings of this work, in particular showing how the stability characteristics of the reaction term determine whether pulled or pushed wave fronts are observed (H. Berestycki and Nadin, 2008). This framework gives a more complete interpretation of the pulled/pushed terminology, and can be extended to the case of general transition waves.

Jimmy Garnier (*Effect of climate niche shifting on the genetic diversity*) extended the analytic framework for the inside dynamics of traveling waves to assess the effect of climate shifting on the genetic diversity of range-expanding populations (Garnier et al., 2012). For this, he incorporated a heterogeneous environment that is moving with a constant speed into reaction-diffusion models, and evaluated under what conditions range-expanding populations can maintain sufficient genetic diversity at the leading edge to tackle founder effects.

Yuan Lou (*Evolutionary stable strategies for dispersal in heterogeneous environments*) complemented this series of talks by considering reaction-diffusion-advection models that allow for evolutionary changes in dispersal ability (Hastings, 1983; Cantrell et al., 2006; Cosner and Lou, 2003). He specifically addressed the question of optimality in dispersal, and thus which dispersal strategies would be evolutionarily stable. For this, he showed how the traditional concept of ideal free distributions (describing how individuals should distribute themselves in a resource-limited environment such that their individual fitness is maximized) can be applied to understand the evolution of dispersal in constant environments (Cantrell et al., 2010, 2012). The lack of an intuitive analogue of this important ecological concept for changing environments was discussed, thus outlining a key research direction for understanding evolutionary adaptations to climate change.

3.3 Mathematical theory of population stability under climate change:

One aspect of climate change is that it can be represented by a shift in underlying parameters in mathematical models. In many cases, small changes in underlying parameters produce only small changes in behavior. However, as is well known, there are parameter values where small changes lead to large changes in behavior, and these critical transitions, or regime shifts, can be very important aspects of biological dynamics under climate change. In particular, many ecological systems, such as coral-algal-grazer systems (Mumby et al., 2013), appear to exhibit hysteresis, which would be expected if a changing parameter was associated with a fold bifurcation (i.e., a saddle-node bifurcation). Studying these kinds of shifts, in the presence of noise, with the goal to predict when they occur, is an important problem. In her presentation, Mary Lou Zeeman developed the underlying basic ideas and related them to concepts of resilience, namely the ability of systems to withstand perturbations while remaining close to a desired state.

Turning the basic underlying ideas about resilience and the possibility of regime shifts into practical ones for making predictions that could be used as management tools, to either prevent a transition or adapt to a transition, is a substantial problem. In his presentation, Alan Hastings reviewed issues related to the existence and detection of regime shifts with special attention to the dynamics of invasions, both in spatial and nonspatial contexts. He developed statistical approaches that explicitly incorporated stochasticity and showed that a this model based approach appeared to be the best approach for detecting impending regime shifts (Boettiger and Hastings, 2012a,b, 2013). One important underlying idea was that since the goal is not to prove or disprove a scientific hypothesis, receiver operator curves are a very useful tool as a way to display the ability to distinguish between false and true psotives.

3.4 Importance of Phenology for understanding climate change impacts:

As emphasized in Chris Cosners introductory talk (outlined above), traditional reaction-dispersal models often disregard seasonality, but considering the effects of seasonality on organisms, and the effects of climate change on organisms via changes in seasonality, are key for understanding climate change impacts.

William Fagans talk (*Phenologically explicit models for population dynamics and species interactions under climate change*) outlined how issues of phenology (i.e., the timing of biological events such as budbreak, flowering, and egg hatch) may be influenced by climate change, and how these effects may affect population viabilities, population distributions, biological invasions, and interactions between different species, under future climate scenarios (Fagan et al., 2010). Drawing on a range of biological examples and data (e.g., butterflies and moths, plant-pollinator systems, plant-herbivore systems), he discussed how systems of non-autonomous ordinary differential equations can be used to explore the ecological consequences of phenological shifts, how non-autonomous partial differential equations can be used to study spatial phenomena such as critical patch size dynamics and species invasions that appear sensitive to phenology, and how these models could provide novel routes by which density-dependent processes may introduce Allee effects, bifurcations, and complex dynamics (Calabrese et al., 2008). These models are particularly relevant because they allow parameterization from exactly the kinds of empirical data that are available from field studies of biological timing.

Christina Cobbold (*Modelling the role of temperature in insect development and adaptation*) followed up on these issues by discussing evolutionary aspects of phenology. In particular, she discussed how developmental rate curves and the cold tolerance (i.e., the ability to survive winter freezing) of insects may evolve in response to temperature and phenological shifts, and how these effects can be extracted from climate-driven phenology models (Cobbold and Powell, 2011). These impacts can have wide-ranging consequences for population outbreaks and pest management, the survival of consumers reliant on insects for food, and the spread of insect-borne zoonotic diseases.

3.5 Importance of stochasticity for understanding biological invasions

Up to here, all talks were largely deterministic, whether they dealt with seasonal or non-seasonal effects. Weather and climate, however, are inherently stochastic. Moreover, climate change is likely to not only change the means and ranges of temperature and other abiotic variables, but also their stochastic distributions. The next set of talks thus focused on introducing stochastic events into models of the ecological impacts of climate change.

Kim Cuddingtons talk (*Suboptimal conditions, stochasticity, and probability of establishment*) emphasized that climate change may not only affect the intra- and inter-annual variance of environmental conditions, but that the autocorrelation signature of environmental signals may also change **citations needed**. Using a series of modeling and experimental approaches, she demonstrated how increased autocorrelation of environmental signals can increase the invasion risk for populations that may otherwise be considered low risk.

Rebecca Tysons work (*The effect of extreme temperature events on developmental dynamics*) further emphasized how extreme temperature events, such as sudden and brief periods of warm temperatures during an otherwise cold season, could have a strong effect on the developmental dynamics of insects that depend on temperature cues for development **citations needed**. Using a phenological model for development, she investigated how annual oviposition date and mortality of insects are affected by extreme temperature events.

Furthermore, she outlined applications for pest management using the example of a biocontrol agent released in southern Alberta where extreme temperature events called Chinooks are common in winter.

The particular importance of stochasticity for understanding and predicting climate change impacts on ecosystems was further emphasized in work on both experimental (Brett Melbourne: *Spatial spread in invasion and climate change: stochastic models and biological experiments*) and field systems (Michael Bonsall: *Noise, demographic sampling and population dynamics of the large skipper butterfly*), as outlined below.

3.6 Linking experiments with mathematical models to predict invasions:

One advantage of mathematical models is their power to outline likely impacts of climate change before they can be observed. The next logical step from these thought experiments are laboratory experiments, which–unlike field observations of climate change impacts on ecosystems–can be replicated numerous times, and are thus useful to explore hypotheses concerning the biological mechanisms of change, as well as test and improve mathematical models.

Brett Melbourne (*Spatial spread in invasion and climate change: stochastic models and biological experiments*) used a highly replicated experimental microcosms for red flour beetles, *Tribolium castaneum*, to develop and test mechanistic stochastic models for spatial spread under climate change (Melbourne and Hastings, 2008). The models were devised for the population and landscape levels by scaling up from stochastic processes at the level of individuals, and were tested in various experiments, including spread into a novel habitat, spread in spatially heterogeneous landscapes, and shifting habitats as expected under climate change. An advantage of this approach is the ability to control demographic, genetic, and environmental factors, and to closely track population and genetic changes through time (Melbourne and Hastings, 2009). A further advantage is the ability to study variance in spread generated by biological processes, essential for understanding uncertainty in model predictions.

3.7 Application of mathematical models for understanding current invasions and range changes

Mathematical models can not only be used to formalize and analyze complex biological dynamics. It is precisely because of their ability to phrase complex biological hypotheses in a tractable framework that they can be used to disentangle climate change impacts from otherwise difficult-to-interpret biological data.

Amy Hurford (*Parameterization of a mechanistic model for species spread under climate change and the implications for 12 North American butterfly species*) applied a mechanistic model for species range shifts under climate change (Potapov and Lewis, 2004) to empirical data of 12 North American butterfly species to illustrate the potential use of this theory for global change biology (Leroux et al., 2013). The framework explicitly defined the ecological processes contributing to range shifts via biologically meaningful dispersal, reproductive, and climate envelope parameters, and Amy Hurford presented methods for estimating these parameters with widely available species occurrence and abundance data. The model estimated that the climate envelopes of her study species are shifting north at a rate of 3.25 km/yr (1.36 km/yr), and predicts species persistence in light of current climate change and habitat loss.

Using a range of examples from laboratory microcosms to contemporary long-term field surveys and historical paleo-ecological records, Michael Bonsall (*Noise, demographic sampling and population dynamics of the large skipper butterfly*) further illustrated how theory and data can be linked to understand population and metapopulation dynamics under climate change (Jeffers et al., 2011). In particular, his work emphasized the importance of incorporating demographic sampling variability and environmental noise into data-linked models to avoid biased estimates of the importance of various ecological processes for population abundances and distributions (Chapman et al., 2012).

Claire Dooley (*Spatial patterns in population dynamics of large skipper butterfly*) then applied these approaches to study the importance of a number of different weather variables on butterflies in Great Britain **citations needed**. She found substantial spatial variation in the relative importance of density-dependent effects and weather factors for population growth, and highlighted the need to develop and test theoretical models that can account for spatial variation in both biotic and abiotic factors.

3.8 Using mechanistic models for predicting future range changes and invasions:

Ultimately, the field of ecology still lags behind climatology in its ability to provide quantitative predictions for the impacts of climate change on ecosystems. However, great progress is being made as outlined in the talks in the previous sections. Building on this background, a final set of three talks focused on using mechanistic models, parameterized and tested with empirical data, for predicting future changes to population abundances and distributions.

Huaiping Zhu (*Modeling mosquito abundance and West Nile Virus risk using weather and environment conditions in southern Ontario*) used surveillance, weather, and land use data to develop statistical and dynamical models for predicting mosquito abundance and West Nile virus risk in southern Ontario (Abdelrazec et al., 2013; Wang et al., 2011).

Paul Moorcroft (*Ecosystem futures: predicting the fate of Amazonian forests over the coming century*) investigated the likely future fate of the Amazon forest using a terrestrial biosphere model that incorporates fine-scale ecosystem heterogeneity (Medvigy et al., 2009; Medvigy and Moorcroft, 2012). The model used a PDE framework as pioneered by McKendrick and von Foerster to incorporate size- and age-structure among plants, and reproduced observed patterns of spatial variability in above-ground biomass and associated changes in forest composition and canopy dynamics with increasing dry season length (Moorcroft et al., 2001). His analyses imply that there will be immediate responses of Amazon forests to changes in climate characterized by a gradual, heterogeneous transition from high biomass moist tropical forests to seasonally dry and transitional forest types. These predictions contrast with previous predictions that were obtained without accounting for fine-scale water-limitation processes, and which suggested threshold-type abrupt responses of the Amazonian forest to climate change. Paul Moorcrofts work thus in particular emphasizes the need to correctly determine the scale at which climate change impacts ecosystems (Moorcroft, 2006).

Peter Molnars talk (*Metabolic approaches to predicting ecological impacts of climate change: parasites, polar bears and other arctic critters*) also took a mechanistic approach to climate change impacts, arguing that most impacts can be understood using bioenergetic approaches. Specifically, he discussed how models based on the Metabolic Theory of Ecology (MTE) can predict the direct effects of temperature changes on ectothermic organisms (Molnár et al., 2013), and how dynamic energy budget (DEB) models can predict climate change impacts on ectotherms or endotherms that are mediated through changes in habitat and resource availability (Molnár et al., 2010, 2011). For illustration, he applied MTE-models to arctic host-parasites systems and DEB-models to polar bears, showing how these approaches can provide quantitative predictions for changes in phenology, population viabilities and distributions. One of the most powerful aspects of bioenergetic approaches is their ability to estimate model parameters from physiological principles, even for data-poor systems, and in particular for yet unobserved environmental conditions. This ability could thus help parameterize numerous modeling approaches, and help understanding and predicting climate change impacts worldwide.

4 Scientific Progress Made

The meeting was characterized by a broad representation of views, with presentations ranging from a focus on mathematical issues to a focus on underlying biological and environmental questions. A major scientific outcome of this meeting has been to bring together scientists from such diverse background and have them interact. New mathematical models and methods have been proposed to approach biological questions, while biologists have come up with problems and observations or experiments that require new mathematical developments. This interaction has led to extremely fruitful discussions at the end of each lecture and also during the specific discussion sessions. We believe that bringing together these different points of view is a key element to progress in the field.

4.1 Identifying new biological areas that that mathematical approaches at the meeting could be applied to

The study of spatial spread of invasive species can be traced back to the original partial differential equations studied initially by Fisher and Komolgorov et al about 75 years ago. These models were quite simple and made a number of assumptions. Yet, these models have brought deep and substantial mathematical challenges some still leading to intense mathematical research bringing together nonlinear PDE's, probability theory and statistical physics. ~~in proving that the traveling wave found was approached asymptotically~~. From the ecological modeling point of view, more complex models are needed. A number of presentations at the meeting identified recent progress on the understanding of spatial spread in many more complicated systems as reviewed in sections 2 and 3. Some of the advances have been motivated by the mathematical developments, while others were motivated by particular biological systems. Again, it is of great scientific value to bring these together.

At the meeting, a number of new biological systems were identified that the recent mathematical developments could prove useful in providing further insights into. For example, the presentation by Berestycki described new progress that indicated how different kinds of underlying heterogeneities in space would affect the rate of spread. There was discussion of the ways that these kinds of ideas could potentially be used to understand biological systems. The spread of flour beetles in laboratory microcosms could be used to test how well the mathematical results described the biological system. Suggestions were made for different experimental approaches that could shed new light on invasions and their mathematical description. The results of these experiments could lead to new mathematical formulations.

Meeting participants identified insect systems where pheromones played a role in movement that could be understood using results on heterogeneities in spread that emphasized the importance of chemotaxis that Kiselev presented. Discussions of results on spread in two dimensions where there was higher speed spread along a single direction also generated a number of other systems that could be understood using the mathematical results, including ones where the parameters had a very different biological meaning. Role of variability in spread

4.2 Identifying mathematical challenges that are required to understand biological issues

Many of the biological talks emphasized the importance of variability in both influencing the responses of species and ecosystems to global change and in influencing rates of spread. This emphasizes the importance of developing a much deeper understanding of the role of stochasticity in mathematical models of spatial spread. Suggestions were made during the meeting for coupling continuous reaction-diffusion equations for densities above a certain threshold with individual stochastic variability at low density levels.

Additionally, there were discussions of the importance not just of variability, but of large variability in biological systems. However, it was emphasized that mathematical techniques have typically focused on the role of small noise. Developing mathematical approaches for understanding the role of large noise represents a substantial challenge that arises in many different fields.

When understanding the impact of invasive species and climate change, another important issue is the impact of species interactions. Several lectures did already report on progress for the dynamics of spread with two interacting species. It is very clear that much further work is needed to understand the concept of spread when two and more than two species are involved. Scaling up to larger numbers of species is an important direction. Some new mathematical developments are called for and present serious mathematical challenges.

4.3 Identifying open questions

Several key open questions were identified both in the presentations and the formal and informal discussions that followed. These questions can be more mathematical or more statistical or more experimental in nature.

Considering systems of interactive species as described above is a first general question that will involve much research in the future.

Another such general question is that of translating notions of resilience and sustainability into careful mathematical descriptions. For understanding the impact of climate change such new developments are both important and challenging.

A key overall issue related to the problem of appropriate statistical methods that could be used to relate results from mathematical models to data collected. This naturally suggest the need for appropriate stochastic models of spread as noted above. Additionally there was extensive discussion, spurred by a number of talks, of the need to develop much further ways to deal with the relatively limited data sets available.

The effect of climate change and biotopes, such as desertification processes, leads to rather involved and new mathematical systems.

The question of the relevant amount of detail to include in descriptions of ecosystem response to climate change to allow prediction of future responses is also challenging. Understanding the behavior of more complex models, which may only be directly studied by simulation, through the development of rigorous mathematical analysis of parts of them will be important for obtaining more robust predictions.

All along the meeting, several specific open questions were identified that will lead to new and challenging mathematical research of which the following are examples. For models considering the effect of climate change, the questions arise of including a non-constant speed of climate change. Looking at more general diffusion where movement results not only from random dispersal but also form individual "intelligent" decisions leads to new forms of heterogeneity. Another effect of climate change that needs to be modeled is the separation of various periods in time for interacting species. Genetic diversity in biological invasions offers many interesting directions that could be related to experiments and observations.

5 Outcome of the Meeting

Because the area of applying mathematical methods to assess the impacts of climate change on species range boundaries and invasions is really quite new and growing very quickly, we are planning follow-up meetings in the next few years. We believe that this BIRS meeting will be the first of several high-profile meetings in the area.

A special issue of *Ecological Complexity* (Prof. Sergei Petrovskii Chief Editor) will be devoted to research arising from this meeting. The co-organizers of the BIRS meeting have agreed to be guest editors special issue.

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