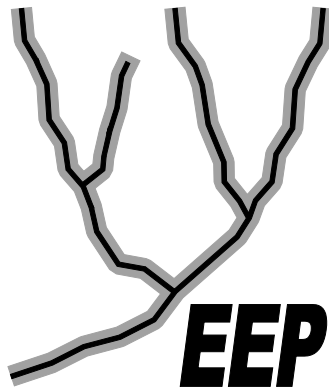


Young Scientists Summer Program 2010

Four Research Projects

**Evolution and Ecology Program
International Institute for Applied Systems Analysis
Laxenburg, Austria**



Ecological and evolutionary impacts of disturbance regimes on vegetation structures

Maud Comboul

*Department of Civil and Environmental Engineering,
University of Southern California, Los Angeles, USA*

Goal

To investigate the demographic and evolutionary consequences of different disturbance regimes on vegetation structures using an individual-based spatially explicit dynamical model.

Background and motivation

Understanding vegetation dynamics and worldwide vegetation structures is crucial for predicting how plants respond to climate change and how their response feeds back into the atmosphere. The latter occurs through changes in the carbon cycle and in the albedo of the terrestrial vegetation cover. Acquiring a detailed understanding of vegetation dynamics is challenging, however, due to the many diverse processes that drive the ecology and evolution of vegetation structures. At the physiological level, light, moisture, temperature, and nitrogen availability are the key factors to which plants have to adapt. At the level of an individual tree, the neighborhood interactions that arise from competition for light and from soil processes influence the local conditions that in turn affect tree development. At the level of a stand or forest, natural and anthropogenic disturbances such as fire, disease spread, or logging greatly influence the size distribution and species composition of vegetation structures. In addition to the direct impact on forests, disturbance processes also affect the demographics and life-history strategies of trees, although little is known about those effects.

Disturbance regimes vary greatly from woodland to woodland. In tropical forests, for example, the typical disturbance is a single large tree toppling over, leaving a gap in the canopy for other trees to exploit. In contrast, disturbances in temperate forests are usually associated with fire and wind that sweep through large areas, destroying trees along their path. Human activities are also increasingly altering the natural disturbance patterns of forests, through logging or the prevention of forest fires. A better understanding of the ecological and evolutionary impacts of different disturbance regimes may not only help explain patterns in worldwide vegetation, but also elucidate the long-term implications of anthropogenic impacts. Field studies have attempted to observe the adaptive response of plants to disturbances, but interpreting such data is difficult when neighborhood interactions and disturbance regimes lead to antagonistic selection pressures. As an alternative to field studies, theoretical investigations based on dynamical forest models have the potential to yield insights into the impacts of disturbance regimes on phenotypically plastic and evolutionary processes of plants. Numerical analyses of disturbed forest dynamics may furthermore help craft policies that will support nature conservation and sustainable exploitation.

While dynamical forest models have the potential to yield important insights into the impacts of different disturbance regimes, the complex mechanisms involved in forest dynamics are difficult to reproduce. Multiple temporal and spatial scales, ranging from those of tree-to-tree interactions to those of global environmental change, make forest modeling a challenging task: should the focus be on individual trees, on patches of significant scale, or on vegetation

landscapes? Forest dynamics have been modeled at all three levels: gap models (JABOWA, Botkin et al. 1972; FORET, Shugart and West 1979) describe forest growth on a coarse grid, representing patches of trees. Horizontally, patch properties are homogeneous; yet, a patch's vertical structure accounts for each tree the patch contains. Patches change independently of one another, because inter-tree distances are ignored. The lack of horizontal interactions in gap models motivated the developments of models with refined grid resolution that explicitly account for exact tree locations (SORTIE, Pacala et al. 1993). In such models, grid points are either empty or occupied by individual trees, and interactions among trees occur over influence zones defined according to tree morphology. The spatially-implicit Perfect Plasticity Approximation (PPA, Purves et al. 2008) is based on the assumption that projected tree crown area can completely cover the canopy. Strigul et al. (2008) showed that the simplified dynamics described by the PPA agree well with those of a more detailed spatially explicit individual-based model. The LANDIS model by Mladenoff (2004) was developed during the 1990s in an effort to study forests at a landscape scale. LANDIS runs on a mesoscale grid, with each cell representing a forest stand in terms of age classes of different tree species. While providing the necessary tools for studying a forest's interactions with natural and anthropogenic disturbances, the LANDIS model lacks the mechanistic complexity of individual-based models. In summary, spatially explicit models of the dynamics among individual trees are promising tools for studying forest dynamics, but remain under-explored because of the associated high computational cost (Levin et al. 1997; Busing and Maily 2004). Even so, individual-based models are likely to offer the best choice for simulating disturbed forests, as they avoid unrealistic assumptions about the horizontal homogenization of disturbances that have to be made in patch-based models.

The aim of this project is to explore the ecological and evolutionary impacts of different disturbance regimes on forests. We will develop an individual-based spatially explicit model of forest dynamics with trees characterized by two salient functional traits: leaf mass per area and height at onset of reproductive investment. For different disturbance regimes, we will explore the short-term ecological impacts and the longer-term evolutionary impacts of disturbances. The anticipated results will be critically compared with earlier findings obtained by Falster et al. (in preparation) for a spatially implicit size-structured metapopulation model with disturbances.

Research questions

The present effort will address the challenge of elucidating impacts of different disturbance regimes from three complementary angles: demographic consequences, evolutionary consequences, and methodological requirements.

- How do different disturbance regimes affect salient aggregate statistics of forest structure, such as leaf area index and standing biomass? How do disturbance regimes influence the ecological coexistence of different tree species?
- Can different disturbance regimes cause changes in the predicted range of trait values?
- How do the results obtained for the proposed individual-based spatially explicit model differ from those obtained by Falster et al. (in preparation)? In particular, will our individual-based model lead to trait distributions that markedly differ from those obtained by Falster et al.?

Finally, if time permits, we will analyze multiscale aspects of forest dynamics using a coarse-graining approach. We will first try to obtain statistical information about tree-to-tree interactions and use those statistics to characterize a coarse-grained process. If successful, we will attempt to use these results to simplify aspects of the full model to reduce the associated computational costs.

Methods and work plan

Spatial representation

Forests will be represented as a spatio-temporal point process (Särkkä and Renshaw 2006; Comas and Mateu 2008) in continuous two-dimensional space. To avoid boundary effects, we will use periodic boundary conditions, i.e. the spatial domain will be the two-dimensional torus obtained by identifying the opposite sides of the unit square. The state of a forest at a given time is therefore represented by a configuration of (marked) points on the unit torus.

Physiological model

The life cycle of a tree is characterized by dispersal, establishment, growth, reproduction, and death and is driven by the tree's energy budget. The available light determines the amount of carbon dioxide that the tree can assimilate at the leaf level via photosynthesis. The assimilated energy is then redistributed and used for the respiration of the living tissues supporting the tree, dry matter production, and reproduction. We follow the physiological model developed by Falster et al. (in preparation). For this project, two functional traits are considered: *leaf mass per area* (LMA) and *height at maturation*. Well-supported empirical scaling relationships link the size of a tree with the masses of its various structural tissues. The level of shading induced by neighborhood competition defines the leaf assimilation rate, which we multiply by the leaf density to obtain the assimilation rate for each tree. Respiration is defined to be proportional to the total mass of the living tissues. Net production, which is partially allocated to growth of the various tissues and partially to reproduction, is obtained by subtracting the expenses for respiration and leaf turnover from a tree's total carbon dioxide assimilation. Allocation to reproduction depends on the height at maturation of the tree and determines the rate of offspring production.

Neighborhood competition

In our model, competition between trees is exclusively based on light availability. This process is asymmetric in the sense that taller trees shade smaller trees. We assume that the extent to which one tree shades another depends on their sizes and horizontal distance. Shading among trees will be computed by assuming that trees have 'flat tops', i.e., have crown composed of a single layer of leaves at the top of the tree (Strigul et al. 2008). Higher layers shade the layers beneath if they overlap horizontally. The shading intensity will be weighted with opacity coefficients to account for the vertical separation between tree crowns. As a potential future extension, we may add one or more layers of foliage to better reflect the true vertical structure of tree crowns.

Environmental stochasticity

Tree configurations are driven by a birth-death-growth-interaction model. Following a continuous-time Markov process, changes in the pattern of tree locations are determined by birth and death events. New individuals are recruited into the population at a rate that depends on

the reproductive rate of each tree and on seedling survival, and are removed from the population at a rate that depends on wood density and a shade-tolerance factor as well as on disturbances.

Disturbance regimes

Disturbance processes cause the death of individuals. We assume that the time between disturbances is exponentially distributed and that the center of a disturbance occurs at a random point in space (corresponding to a spatially homogeneous Poisson process). A disturbance destroys a fraction of all trees located within a given distance from its center. A disturbance regime can thus be characterized by three parameters:

- The rate of occurrence of the disturbance.
- The extent of the disturbed area.
- The probability that any given tree within the disturbed area dies.

By taking the product of these three parameters, we obtain the intensity at which the forest is disturbed. In this way, we can represent a wide array of disturbances, ranging from a single tree fall (small area with a high probability of tree death) to wind disturbing large forested regions (large area with a low probability of tree death).

Evolutionary dynamics

To assess evolutionary effects on a tree population, we introduce mutations in the two considered functional traits (LMA and height at maturation). The resultant evolution of the distribution of those trait values is then observed through time.

Model implementation

We plan to implement the model in C++. Because individual-based models can be computationally burdensome, it is imperative to store the forest's state efficiently. One possibility is to divide the torus into m^2 coarse cells such that it suffices to compute the interactions between same-cell and neighbor-cell trees. This representation will reduce the determination of all vital rates from quadratic to linear complexity in the total number of trees. Initial forest configurations will be generated randomly. At each fixed time step, we must compute the energy budget and update the state of every tree in the forest. While it is unnecessary to store the point configurations in time, it is important to store the distributions of traits, sizes, and locations. To visualize the results, we intend to use R or Matlab.

Relevance and link to EEP's research plan

The analyses described here are relevant to evolutionary studies of biological populations under global change and human interventions. This project therefore contributes to EEP's research project on *Evolving Biodiversity* by addressing the selection pressures exerted on ecological systems through local interactions and different disturbance regimes.

Expected output and publications

This research is intended for publication as a co-authored article in an international scientific journal.

References

- Acevedo F, Urban DL & Shugart HH (1996). Models of forest dynamics based on roles of tree species. *Ecological Modelling* 87: 276-284
- Botkin B, Janak JF & Wallis JR (1972). Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60:849-872
- Busing RT & Maily D (2004). Advances in spatial, individual-based modeling of forest dynamics. *Journal of Vegetation Science* 15: 831-842
- Busing RT (1991). A spatial model of forest dynamics. *Vegetatio* 92: 167-179
- Comas C & Mateu J (2007). Modelling forest dynamics: a perspective from point process methods. *Biometrical Journal* 49:176-196
- Comas C & Mateu J (2008). Space-time dependence dynamics for birth-death point processes. *Statistics and Probability Letters* 78: 2715-2719
- Falster DS, Brännström Å & Dieckmann U. Ecological and evolutionary analysis of size-structured metapopulations under asymmetric competition. In preparation
- Falster DS, Brännström Å, Dieckmann U & Westoby M. The influence of four major plant traits on vegetation structure and function. In preparation
- Frelich LE (2002). *Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests*. Cambridge University Press
- Gavrikov V & Stoyan D (1995). The use of marked point processes in ecological and environmental forest studies. *Environmental and Ecological Statistics* 2: 331-344
- Levin SA, Grenfell B, Hastings A & Perelson AS (1997). Mathematical and computational challenges in population biology and ecosystems science. *Science* 275: 334-343
- Mateu J, Uso JL & Montes F (1998). The spatial pattern of a forest ecosystem. *Ecological Modelling* 108: 163-174
- Mladenov J (2004). LANDIS and forest landscape models. *Ecological Modelling* 180:7-19
- Pacala SW, Canham CD & Silander JA (1993). Forest models defined by field measurements: I. the design of a northeastern forest simulator. *Canadian Journal of Forest Research* 23: 1980-1988
- Purves DW, Lichstein JW, Strigul N & Pacala W (2008). Predicting and understanding forest dynamics using a simple tractable model. *Proceedings of the National Academy of Sciences of the USA* 105: 17018-17022
- Särkkä A & Renshaw E (2006). The analysis of marked point patterns evolving through space and time. *Computational Statistics and Data Analysis* 51: 1698-1718
- Shugart HH & West DC (1979). Size and pattern of simulated forest stands. *Forest Science* 25: 120-122
- Stoyan D & Penttinen A (2000). Recent applications of point process methods in forestry statistics. *Statistical Science* 15: 61-78
- Stoyan D & Stoyan H (1998). Non-homogeneous Gibbs process models for forestry – a case study. *Biometrical Journal* 40: 521-531
- Stoyan D, Kendall WS & Mecke J (2008). *Stochastic Geometry and its Applications*. Wiley
- Strigul N, Pristinski D, Purves D, Dushoff J & Pacala S (2008). Scaling from trees to forests: tractable macroscopic equations for forest dynamics. *Ecological Monographs* 78: 523-545

Dispersal and speciation in a complex habitat

Ben Haller

*Department of Biology,
McGill University, Montreal, Canada*

Goal

To investigate how speciation processes and resultant biodiversity patterns are affected by spatial environmental heterogeneity, dispersal, mate choice, and temporal environmental variability.

Background and motivation

For Darwin (1859), the origin of species was the “mystery of mysteries,” and it remains poorly understood even today. Speciation, as the process that generated much of the biodiversity in the world today, is fundamental to the nature of life on earth; it is thus clearly worthy of study in its own right. A better understanding of speciation also has consequences for conservation biology and for the mitigation of anthropogenic ecological disturbances. It has previously been shown that adaptation to a local environment together with local competition for resources can promote speciation (Heinz et al. 2009). This project will investigate the effects of spatial environmental heterogeneity and dispersal distance on speciation dynamics and the resultant biodiversity patterns. Time permitting, temporal environmental variability and the evolution of dispersal and mate choice may also be explored within this framework. This research will be conducted using an individual-based evolutionary model, building on previous work in IIASA’s Evolution and Ecology Program.

Speciation results, fundamentally, from the genetic divergence of populations. The dispersal of individuals between populations, or more precisely the gene flow that results when those dispersers interbreed with residents, is commonly thought to hinder such genetic divergence, and therefore to impede speciation, although there may be exceptions to this rule of thumb (Garant et al. 2007). Heinz et al. (2009) modeled the interaction between dispersal evolution and speciation, and found that the evolution of short-range dispersal promoted speciation. Payne et al. (in preparation) extended the model of Heinz et al. (2009) to include the evolution of conditional dispersal, which was found to inhibit speciation in sexual populations. These models involved only a linear environmental gradient, so that the effects of more complex spatial structures on speciation dynamics have yet to be explored in such a framework.

Assortative mating can promote genetic divergence by increasing the reproductive isolation of populations even when dispersal connects spatially distributed populations (Garant et al. 2007), and several theoretical models have explored this idea. Doebeli and Dieckmann (2003) found that the evolution of mate choice along an environmental gradient could lead to parapatric speciation. Yukilevich and True (2006) modeled the coevolution of dispersal and assortative mating in a “two-island” system representing secondary contact after allopatric divergence. Gavrillets and Vose (2009) observed adaptive radiation resulting from evolution in an “island colonization” model consisting of ecologically random patches, with the evolution of habitat preference and mate choice. Again, these models involved only simple or random spatial structures.

Real environments vary over time as well as in space. Species can cope with environmental variation through adaptation or range shifts. Some prior work has examined adaptation and range shifts in response to spatial or temporal variability (Kirkpatrick and Barton 1997; Pease et al. 1989; Polechová et al. 2009), but not in conjunction with the evolution of dispersal and assortative mating, and not in the context of a complexly structured spatial landscape.

The proposed research will thus synthesize previous work, while also examining scenarios that were left unexplored by previous studies. In particular, this project will examine the combined effects of both spatial structure and dispersal on speciation.

It is clear from both theoretical and empirical studies that dispersal, ecology, behavior, and adaptation are complexly intertwined (Pelletier et al. 2009), and that spatial and temporal variation in environmental conditions play an important role in driving evolution (Mathias et al. 2001; McPeck and Holt 1992). While modeling these factors in isolation is interesting, it is important also to examine them together, to understand how they interact with each other, to weigh their relative importance, and to build a broader picture of how speciation emerges from lower-level processes.

A better understanding of adaptation and speciation is of more than theoretical interest, because the factors that promote the generation of biodiversity are likely related to the factors that preserve existing biodiversity. Conservation of biodiversity in the face of rapid anthropogenic environmental change (such as deforestation, habitat fragmentation, and climate change) demands a better understanding of how environmental and ecological factors support biodiversity (Jackson and Sax 2010). Evolutionary responses to environmental and ecological change can be rapid, with important implications for conservation (Stockwell et al. 2003). Furthermore, specific conservation policies, such as assisted migration, wildlife corridors, and captive breeding programs, are precariously balanced atop our very limited understanding of the role of dispersal and gene flow in the persistence of populations, the maintenance of genetic diversity, and the promotion of local adaptation (Storfer 1999; Sutherland et al. 2004).

Research questions

The goal of this project is to improve our understanding of the process of parapatric speciation in heterogeneous environments. Previous research has established that a linear environmental gradient can drive speciation through the evolution of dispersal and mating distance (Heinz et al. 2009) and through the evolution of assortative mating (Doebeli and Dieckmann 2003). In this project, I will address the following questions:

- What effect does nonlinear variation of environmental conditions at different spatial scales have on local adaptation, range limitation, population persistence, and speciation?
- How do dispersal and mate choice coevolve and drive speciation, under different patterns of spatial variation?
- What effect does temporal variability have on these evolutionary dynamics, for different rates, magnitudes, and patterns of environmental change?

Methods and work plan

The starting point for this research project is the individual-based spatially explicit model of Heinz et al. (2009). Briefly, this model simulates the evolution of individuals that inhabit a two-dimensional space in which environmental conditions vary along one spatial dimension, forming a linear ecological gradient, while the other spatial dimension is ecologically neutral.

Each individual has three genetic traits: an ecological trait that governs the individual's fitness at any given position along the ecological gradient, a dispersal trait that governs its natal dispersal distance, and a mating trait that governs the strength of its preference for spatially proximate mates over more distant mates. I intend to work with both an asexual and a sexual model version (the asexual version does not include the mating trait). Individuals are born at a constant rate, and die at a rate that depends on the strength of competition exerted by other individuals in the environment, so that selection is frequency-dependent. Offspring inherit parental traits with mutation. For different strengths of competition and slopes of the environmental gradient, evolutionary outcomes range from a homogenized mixture of long-range dispersers to distinct "species" that maintain separate identities on the landscape through short-range dispersal and a strong preference for local mates.

Prior to the YSSP, I have already replicated the results by Heinz et al. (2009), to establish a baseline and platform upon which I will build. During the YSSP, I will modify this model to address the stated research questions. Work will proceed in four stages, allowing the investigation of as many questions as time permits.

In the first stage, natal dispersal distance and mating distance will be held constant, so that only the ecological trait is allowed to evolve. Nonlinear spatial heterogeneity will be modeled by letting the local carrying-capacity density of the environment change among locations according to four parameters: the average slope and curvature of the gradient's deterministic component, as well as the amplitude and spatial autocorrelation distance of the gradient's stochastic component. On this basis, I will characterize the spatial structures and dispersal distances for which speciation can occur.

In the second stage, the evolution of dispersal and mating distance will be enabled. Different types of spatial variation may be expected to promote the evolution of different types of dispersal and mating behavior, with consequences for the likelihood of speciation under different spatial structures.

In the third stage, the evolution of assortative mating will be added to the model, by integrating a trait that governs the strength of assortative (or disassortative) mating (Doebeli and Dieckmann 2003). Mate choice will be based either upon the ecological trait or upon an additional ecologically neutral marker trait. These mating traits will either replace or supplement the mating-distance trait of the Heinz et al. (2009) model, which does not permit the evolution of assortative mating. This extension will allow exploration of the joint evolution of dispersal and assortative mating under different spatial structures, and of the way in which this evolution promotes or hinders speciation.

In the fourth stage, time permitting, temporal environmental variability will be modeled. Oscillations in local carrying capacity may be used to simulate seasonal variation, while gradual linear change in carrying-capacity densities could simulate climate change. We will assess the effects of these temporal patterns on speciation, dispersal evolution, and mate-choice evolution.

There are different ways to detect speciation, since speciation is really a process, and not just an instantaneous event. The lines drawn between species therefore depend on the considered species concept and other arbitrary choices (Coyne and Orr 2004). To add an additional perspective to these decisions, I will incorporate unlinked neutral loci. These loci will be subject only to genetic drift, not to natural selection, and will therefore be useful in diagnosing the degree of reproductive isolation between different populations in the model, even though

neutral loci cannot always be used to diagnose speciation reliably (Thibert-Plante and Hendry, in press). Alternative quantitative methods for diagnosing the reproductive isolation of populations may thus be explored for comparison.

Relevance and link to EEP's research plan

This project extends work previously done as part of EEP's research projects on *Evolving Biodiversity* and *Adaptive Dynamics Theory* (e.g., Doebeli and Dieckmann 2003; Heinz et al. 2009; Payne et al., in preparation). It will contribute to the goal of distinguishing the key ecological factors that promote and hinder biological diversification.

Expected output and publications

The results of this research project will be published as a coauthored paper in an international scientific journal. I also expect this work to be a part of my PhD thesis.

References

- Coyne JA & Orr HA (2004). *Speciation*. Sinauer Associates
- Darwin C (1859). *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. J. Murray
- Doebeli M & Dieckmann U (2003). Speciation along environmental gradients. *Nature* 421: 259-264
- Garant D, Forde SE & Hendry AP (2007). The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology* 21: 434-443
- Gavrilets S & Vose A (2009). Dynamic patterns of adaptive radiation: Evolution of mating preferences. Pages 102-126 in Butlin RK, Bridle JR & Schluter D eds. *Speciation and Patterns of Diversity*. Cambridge University Press
- Heinz SK, Mazzucco R & Dieckmann U (2009). Speciation and the evolution of dispersal along environmental gradients. *Evolutionary Ecology* 23: 53-70
- Jackson ST & Sax DF (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution* 25: 153-160
- Kirkpatrick M & Barton NH (1997). Evolution of a species' range. *American Naturalist* 150: 1-23
- Mathias A, Kisdi E & Olivieri I (2001). Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* 55: 246-259
- McPeck MA & Holt RD (1992). The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140: 1010-1027
- Payne JL, Mazzucco R & Dieckmann U. The evolution of conditional dispersal and reproductive isolation along environmental gradients. In preparation
- Pease CM, Lande R & Bull JJ (1989). A model of population growth, dispersal and evolution in a changing environment. *Ecology* 70: 1657-1664
- Pelletier F, Garant D & Hendry AP (2009). Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society of London B* 364: 1483-1489

- Polechová J, Barton N & Marion G (2009). Species' range: adaptation in space and time. *American Naturalist* 174: E186-E204
- Stockwell CA, Hendry AP & Kinnison MT (2003). Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* 18: 94-101
- Storfer A (1999). Gene flow and endangered species translocations: a topic revisited. *Biological Conservation* 87: 173-180
- Sutherland WJ, Pullin AS, Dolman PM & Knight TM (2004). The need for evidence-based conservation. *Trends in Ecology and Evolution* 19: 305-308
- Thibert-Plante X & Hendry A. When can ecological speciation be detected with neutral loci? *Molecular Ecology*, in press
- Yukilevich R & True JR (2006). Divergent outcomes of reinforcement speciation: the relative importance of assortative mating and migration modification. *American Naturalist* 167: 638-654

Emergence and stability of cooperation in multi-public-good games

Balázs Könnyű

*Department of Plant Taxonomy and Ecology,
Eötvös Loránd University, Budapest, Hungary*

Goal

To study the emergence and stability of cooperation in public-good games in which each player may contribute to two different public goods.

Background and motivation

The evolution and maintenance of cooperation among unrelated individuals in non-iterated games have been a major focus of evolutionary studies over the last decades. Models of cooperation are traditionally cast in the framework of game theory. In cooperation games, individuals receive a payoff according to their and their partners' strategies. One of the best studied cooperation games, the Prisoner's Dilemma, describes the interaction between two players: defection is the dominant strategy if interactions between individuals occur randomly over a large population (Maynard Smith 1982). However, despite the apparent disadvantage of cooperators in such games, cooperation is ubiquitous in nature and in human societies. Understanding why cooperation nevertheless evolves therefore is a challenging and important problem.

Many human endeavors require simultaneous cooperation of many individuals. Moreover, there are several biological situations, for example the production of biofilms or enzymes within bacterial communities, in which cooperative tasks are carried out jointly by several individuals (Nowak and Sigmund 2002; Rankin et al. 2007). These situations can be modeled by n -player analogues of the Prisoner's Dilemma, called public-good games. In classical public-good games, each individual has a personal pool of resources and decides how much of these to contribute to the public good (Hauert et al. 2002a 2002b; Bach et al. 2006). The invested resources from all individuals are then pooled and multiplied by a factor r ($1 < r < n$, where n is the number of players in the group); the multiplied amount is equally shared between all players, irrespective of their individual investments. The highest total payoff would thus be obtained if all individuals invested all their resources (full cooperation). However, to reduce their own costs, individuals have an incentive to avoid contributing to the public good (full defection), thereby potentially gaining a cost-free share of the public good resulting from the investments of others. Hence, as in the two-player Prisoner's Dilemma, the dominant strategy is defection. Recently, Doebeli et al. (2004) have extended the classical public-good game to incorporate nonlinear dependencies in both individual costs and common benefits. With this extension, defection is not always a dominant strategy, and cooperation can consequently evolve even in well-mixed populations. Doebeli et al. (2004) further found that, under some conditions, gradual evolution in cooperative investments results in evolutionary branching and in the emergence of coexisting low-investing and high-investing strategies.

All studies described above are based on the assumption of a single public good. In several biological and social situations, however, a community consisting of n individuals might depend on several different public goods, with each individual contributing to none, some, or all of these. A case in point is the community metabolism of bacterial communities, or the simultaneous dependence of advanced human societies in many public goods. In this project, I

will therefore consider an extension of the classical public-good game that allows each player to contribute to two public goods.

Research questions

The main goal of this project is to develop and explore multi-public-good games. As in simpler cooperation games, the key goal is to identify the circumstances that favor the emergence of cooperation. We can break this up into the following more specific questions:

- How does the total cooperative investment develop within the group?
- What is the effect of different nonlinearities in benefits and costs on the emergence and stability of cooperation when considering interactions among public goods?
- Will division of labor with regard to alternative contributions to the public goods naturally emerge within groups? What are the conditions for the emergence of specialists (who produce one public good) and generalists (who produce more than one public goods)?

If time allows, we will explore these questions also in a spatial setting. Spatial structure has been shown profoundly to affect the incentives for cooperation in classic public-good games and may thus have similarly important implications for multi-public-good games. Other potential extensions are the inclusion of punishment and of changing player densities.

Methods and work plan

Game dynamics

To understand the dynamics of multi-public-good games, we consider an individual-based model in individuals within groups of n players ($n > 2$) can contribute to two public goods. We consider that these groups are assembled from a large population of $N > n$ players. At a constant rate, groups of n players are formed for which members are selected through an unbiased random draw from the population. Each player's strategy is characterized by the amounts x and y , respectively, it contributes to the first and second public good.

For each player i , total contributions X and Y determine the benefit B that is shared among the n players, while individual contributions x_i and y_i determine the costs C , resulting in the payoff

$$P_i = B(X, Y)/n - C(x_i, y_i),$$

where X and Y are the sum of x and y within a group,

$$X = \sum_{j=1}^n x_j \text{ and } Y = \sum_{j=1}^n y_j$$

The nonlinear functions

$$\begin{aligned} B(X, Y) &= b_1 A(X, Y) + b_2 A^2(X, Y), \\ C(x_i, y_i) &= c_1 a(x_i, y_i) + c_2 a^2(x_i, y_i), \end{aligned}$$

describe the benefits and costs of contributing to the two public goods. Without loss of generality, we can set $c_1 = 1$ by choosing the unit of contributions.

Contributions to public goods may interact synergistically or antagonistically, and may be essential or substitutable (Tilman 1980). In our model, we account for this range of interaction options by using generalized means,

$$A(X, Y) = \left(\frac{X^p + Y^p}{2} \right)^{1/p} \text{ and } a(x_i, y_i) = \left(\frac{x_i^q + y_i^q}{2} \right)^{1/q}.$$

In our analysis, we will consider all possible values for the parameters p and q , $-\infty < p, q < \infty$. As a result, the functions A and a can gradually be altered from the minimum norm ($p, q = -\infty$), to the harmonic mean ($p, q = -1$), geometric mean ($p, q = 0$), arithmetic mean ($p, q = 1$), and maximum norm ($p, q = \infty$) as special cases. In the particular case of perfectly substitutable public goods ($p, q = 1$), we recover the model studied by Doebeli et al. (2004), thus allowing the systematic comparison with earlier findings of the new results we will obtain.

Evolutionary dynamics

On a demographic time scale, players adopt the strategies of better-performing players. Two players i and j are randomly chosen and player i imitates the strategy of player j with probability $w_{ij} = 1/(1 + e^{-s(P_j - P_i)})$ depending on their payoff difference (Hauert et al. 2002a, 2002b; Sigmund et al. 2010), where $s > 0$ denotes the imitation strength (for $s \rightarrow \infty$, a more successful player is always imitated).

We will explore the evolution of investments x and y into the two public goods using adaptive-dynamics techniques (e.g., Geritz et al. 2004; Doebeli et al. 2004). We consider a resident strategy $z_r = (x_r, y_r)$ and a mutant strategy $z_m = (x_m, y_m)$. The frequencies of these strategies are denoted by p_r and p_m , respectively, with $p_r + p_m = 1$. As a consequence of the imitation dynamics described above, the frequencies of the resident and mutant subpopulations will follow the replicator equations

$$\frac{dp_k}{dt} = sp_k[P_k(p_r, p_m) - \bar{P}(p_r, p_m)]$$

for $k = r, m$. Here, $P_r(p_r, p_m)$ and $P_m(p_r, p_m)$ are the average payoffs of the resident strategy and mutant strategy, respectively, while $\bar{P}(p_r, p_m) = p_r P_r(p_r, p_m) + p_m P_m(p_r, p_m)$ is the average payoff in the population.

From the replicator dynamics, we derive the invasion fitness of the mutant strategy, i.e., the initial per capita growth rate of a rare mutant strategy z_m in a population of individuals with the resident strategy z_r ,

$$S_{z_r}(z_m) = \lim_{p_m \rightarrow 0^+} \frac{1}{p_m} \frac{dp_m}{dt} = s[P_m(1,0) - P_r(1,0)].$$

If $S_{z_r}(z_m) > 0$, the rare mutant strategy can spread in the resident population.

The long-term evolution of the resident strategy z_r is then described by the canonical equation of adaptive dynamics (Dieckmann and Law 1996),

$$\frac{dz_r}{dt} = \frac{1}{2} n \sigma^2(z_r) \frac{\partial}{\partial z_m} S_{z_r}(z_m) \Big|_{z_r=z_m},$$

where $\sigma^2(z_r)$ is the covariance matrix of mutational steps in the strategy z_r . In the simplest case, mutations in x and y are independent, uniform with respect to the strategy, and have the same variance.

An equilibrium point $z^* = (x^*, y^*)$ of the canonical equation is called an evolutionarily singular strategy. If z^* is attracting, it is said to be convergence stable. If the invasion-fitness landscape $S_{z^*}(z_m)$ has a local maximum around $z_m = z^*$, z^* is locally evolutionarily stable. If z^* is convergence stable but not locally evolutionarily stable, it is an evolutionary branching point.

Relevance and link to EEP's research plan

One of the most difficult scientific questions is the emergence and stability of cooperation in nature. IIASA's Evolution and Ecology Program has a long track-record of developing new perspectives in this area. My project thus contributes to EEP's research project on the *Evolution of Cooperation*. The anticipated results will assist in understanding the mechanisms that underpin cooperation at all biological levels, from molecules to human societies.

Expected output and publications

The results of this project are intended for publication in a co-authored article in an international scientific journal.

References

- Bach LA, Helvik T & Christiansen FB (2006). The evolution of n-player cooperation-threshold games and ESS bifurcation. *Journal of Theoretical Biology* 238: 426-434
- Brännström Å, Gross T, Blasius B & Dieckmann U (2010). Consequence of fluctuating group size for the evolution of cooperation. *Journal of Mathematical Biology*, in press
- Dieckmann U & Law R (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34: 579-612
- Doebeli M, Hauert C & Killingback T (2004). The evolutionary origin of cooperators and defectors. *Science* 306: 859-862
- Hauert C, De Monte S, Hofbauer J & Sigmund K (2002a). Replicator dynamics for optional public good games. *Journal of Theoretical Biology* 218: 187-194
- Hauert C, De Monte S, Hofbauer J & Sigmund K (2002b). Volunteering as Red Queen mechanism for cooperation in public goods games. *Science* 296: 1129-1132
- Hauert C, Traulsen A, Brandt H, Nowak MA & Sigmund K (2007). Via freedom to coercion: the emergence of costly punishment. *Science* 326: 1905-1907
- Geritz SAH, Kisdi É, Meszéna G & Metz JAJ (2004). Adaptive Dynamics of specialization: ecological underpinnings. Pages 54-75 in Dieckmann U, Doebeli M, Metz JAJ & Tautz D eds. *Adaptive Speciation*. Cambridge University Press
- Maynard Smith J (1982). *Evolution and the Theory of Games*. Cambridge University Press
- Nowak MA & Sigmund K (2002). Bacterial game dynamics. *Nature* 418: 138-139
- Rankin DJ, Bargum K & Kokko H (2007). The tragedy of the commons in evolutionary biology. *Trends in Ecology and Evolution* 22: 643-651
- Sigmund K, de Silva H, Traulsen A & Hauert C (2010). Social learning promotes institutions for governing the Commons. *Nature*, in press
- Tilman D (1980). Resources: a graphical-mechanistic approach to competition and predation. *American Naturalist* 116: 362-393

Life-history model of sardine-anchovy cycles

Roktaek Lim

Interdisciplinary Graduate Program in Computational Science and Technology, Seoul National University, South Korea

Goal

To develop a simple life-history model for sardine and anchovy that can explain the mechanisms causing the globally observed cyclic stock fluctuations.

Background and motivation

According to the Food and Agriculture Organization of the United Nations, the catch of anchovy reached its peak in the 1970s, dramatically decreased in the 1980s, and recovered to the previous level in the 1990s. In contrast, the catch of sardine began to grow in the 1970s, reached its peak in the 1980s, and has dropped sharply in the 1990s. This oscillatory phenomenon, known as sardine-anchovy cycles, has been observed in at least four different oceanic regions. Both anchovy and sardine serve as major food resources around the globe, so their cycling strongly impacts seafood supplies, fisheries economics, and coastal communities.

Recent studies discovered that fluctuations in air temperature and ocean temperature were similar, in terms of phase and duration, to the oscillatory catches, suggesting that sardine-anchovy cycles are partly driven by climatic changes. In addition, interactions among these species, and also among cohorts within each species, have been suggested to contribute to the cycles. In general, however, the causal origin of sardine-anchovy cycles remains unknown, and no comprehensive model exists yet to describe these cycles. In this project, we will try to address this gap.

Research questions

The aim of my project is to develop a life-history model that reproduces the observed sardine-anchovy cycles and helps understanding the mechanisms that cause these stock fluctuations. Specifically, I will address the following questions:

- What class of models is best suited for describing sardine-anchovy cycles?
- What equations best describe the growth, maturation, reproduction, and mortality of sardine and anchovy?
- How are these equations reflecting density regulation, trait effects, and interspecific interactions?
- If the developed model can reproduce the observed cycles, what does this tell us about the mechanisms causing this global phenomenon?

Methods and work plan

Work plan

I will pursue the following steps to complete my research project:

- Develop suitable equations for a sardine-anchovy population dynamics model.
- Find the required parameter values from the literature or through own estimations.

- Refine the model specification until a good match with observations is achieved.
- Analyze the model to understand the causes of cycles.

Population dynamics

The life cycles of sardine and anchovy can be divided into two stages: first is the immature stage and second is the mature stage. Immature and mature individuals experience growth and mortality. Immature individual become mature through maturation, which may occur at different ages and lengths. Reproduction only occurs at the mature stage and results in the production of immature offspring.

Let $N_{i,a}(t)$ be the density of species i at age a in year t ($i = S$: sardine; $i = A$: anchovy),

$$N_{i,a}(t) = N_{i,I,a}(t) + \sum_{a_M=1}^a N_{i,M,a,a_M}(t), \quad \text{for } a = 1, \dots, A_i,$$

where I refers to immature individuals and M to mature individuals, a_M is an individual's maturation age, and A_i is the maximum considered age for species i . We assume that maturation can take place only after the age of immature individuals is greater than 1.

The densities of immature individuals change according to the following equation,

$$N_{i,I,a}(t+1) = \begin{cases} s_{i,I,0}(t) \sum_{a=1}^{A_i} \sum_{a_M=1}^a f_{i,a,a_M}(t) N_{i,M,a,a_M}(t), & \text{if } a = 1, \\ s_{i,I,a-1}(t) [1 - m_{i,a-1}(t)] N_{i,I,a-1}(t), & \text{if } a > 1. \end{cases}$$

where $f_{i,a,a_M}(t)$ is the fecundity in year t of an individual of species i at age a that has matured at age a_M , $m_{i,a}(t)$ is the maturation probability in year t of species i at age a , and $s_{i,j,a}(t)$ is the survival probability in year t in species i at maturation stage j from age a to age $a+1$.

The densities of mature individuals change according to the following equation,

$$N_{i,M,a,a_M}(t+1) = \begin{cases} s_{i,I,a-1}(t) m_{i,a-1}(t) N_{i,I,a-1}(t), & \text{if } a = a_M, \\ s_{i,M,a-1,a_M}(t) N_{i,M,a-1,a_M}(t), & \text{if } a > a_M. \end{cases}$$

Growth

We follow the growth model of Lester et al. (2004),

$$L_{i,I,0}(t) = 0,$$

$$L_{i,I,a}(t) = L_{i,I,a-1}(t-1) + h_i(t),$$

$$L_{i,M,a,a_M}(t) = \frac{3}{k_i g_i + 3} [L_{i,M,a-1,a_M}(t-1) + h_i(t)],$$

where g_i is the gonadosomatic index of species i , defined as the ratio of gonad weight and somatic weight, and k_i is the energy density of gonad tissue relative to somatic tissue of species i .

For conversion from length to weight, we use allometric relationships

$$W_{i,I,a}(t) = \alpha_i L_{i,I,a}^{\beta_i}(t),$$

$$W_{i,M,a,a_M}(t) = \alpha_i L_{i,M,a,a_M}^{\beta_i}(t),$$

where α_i and β_i are empirical parameters defining the allometric relationship for species i . The total biomass density B_i of species i in year t is given by

$$B_i(t) = \sum_{a=1}^{A_i} W_{i,1,a}(t) N_{i,1,a}(t) + \sum_{a=1}^{A_i} \sum_{a_M=1}^a W_{i,M,a,a_M}(t) N_{i,M,a,a_M}(t).$$

The average immature annual length increment $h_i(t)$ in year t is a function of the annual temperature $T_{G,i}(t)$ during the growth season of species i in year t and of the total biomass density $B(t) = B_S(t) + B_A(t)$ of sardine and anchovy in that year. We assume that growth diminishes with $B(t)$,

$$h_i(t) = h_{\max,i} R_{G,i}(T_{G,i}(t)) [1 + \gamma_i B(t)^{\delta_i}]^{-1},$$

where $h_{\max,i}$ is the maximum immature annual length increment in species i , γ_i and δ_i specify the density dependence of growth in species i , and $R_{G,i}(T_{G,i}(t))$ specifies the temperature dependence of growth in species i ,

$$R_{G,i}(T_{G,i}(t)) = \exp\left(-\frac{1}{2}(T_{G,i}(t) - T_{\text{opt},G,i})^2 / \sigma_{G,i}^2\right),$$

where $T_{\text{opt},G,i}$ is the optimal temperature for the growth of species i and $T_{G,i}(t)$ is given by

$$T_{G,i}(t) = \int w_{G,i}(\tau) T_i(\tau) d\tau,$$

where $w_{G,i}$ is the seasonal probability density of growth in species i and $T_i(\tau)$ is the temperature at time τ in year t .

Maturation

We assume that the maturation probability $m_{i,a}(t)$ depends on age a and length $L_{i,1,a}(t)$,

$$\text{logit}(m_{i,a}(t)) = c_{i,0} + c_{i,1} L_{i,1,a}(t) + c_{i,2} a,$$

where $c_{i,a}$ are constants specifying a linear probabilistic maturation reaction norm with constant width, and the logit function is defined as $\text{logit}(m) = \ln(m / (1 - m))$.

Reproduction

We assume that the per capita fecundity $f_{i,a,a_M}(t)$ diminishes with the total biomass density $B(t)$ of sardine and anchovy. High biomass density will raise food competition, which reduces surplus energy and thus energy invested in gonad development,

$$f_{i,a,a_M}(t) = \frac{g_i W_{i,M,a,a_M}(t)}{2W_{E,i}} e^{-B(t)/B_{0,i}},$$

where $W_{E,i}$ is the mean egg weight in species i and $B_{0,i}$ specifies the biomass density at which larval survival is reduced to $1/e = 36.8\%$.

Mortality

When we calculate the annual survival rates $s_{i,j,a}(t)$, we consider two mortality rates, one describing natural mortality and the other fishing mortality,

$$s_{i,1,a}(t) = \exp(-M_{i,1,a}(t) - F_{i,1,a}(t)),$$

$$s_{i,M,a,a_M}(t) = \exp(-M_{i,M,a,a_M}(t) - F_{i,M,a,a_M}(t)),$$

where $M_{i,l,a}(t)$ and $F_{i,l,a}(t)$, respectively, are the natural mortality rate and fishing mortality rate of immature individuals in species i at age a in year t , and $M_{i,M,a,a_M}(t)$ and $F_{i,M,a,a_M}(t)$, respectively, are the natural mortality rate and fishing mortality rate of mature individuals in species i at age a in year t that have matured at age a_M .

According to Stearns (1992) and Hirshfield (1980), investments into growth and reproduction reduce an individual's survival,

$$M_{i,l,a}(t) = M_{b,i}(t) + \xi_i h_{\max,i},$$

$$M_{i,M,a,a_M}(t) = M_{b,i}(t) + \xi_i h_{\max,i} + \zeta_i k_i g_i,$$

where $M_{b,i}(t)$ is the baseline mortality rate for species i in year t and ξ_i and ζ_i are fixed constants for species i . The extra mortality rate $\xi_i h_{\max,i}$ is assumed to describe the trade-off between growth and survival in species i , while the extra mortality rate $\zeta_i k_i g_i$ is assumed to describe the trade-off between reproductive investment and survival in species i .

The ocean temperature might affect the baseline mortality rate. We assume that there is an optimal temperature for the survival of fish, so that if the ocean temperature is warmer or colder, the natural mortality rate will be increased,

$$M_{b,i}(t) = M_{\min,i} + (M_{\max,i} - M_{\min,i})(1 - R_{M,i}(T_{M,i}(t))),$$

where $M_{\min,i}$ is the minimum natural mortality rate and $M_{\max,i}$ is the maximum natural mortality rate for species i . $R_{M,i}(T_{M,i}(t))$ specifies the temperature dependence of mortality in species i ,

$$R_{M,i}(T_{M,i}(t)) = \exp\left[-\frac{1}{2}(T_{M,i}(t) - T_{\text{opt},M,i})^2 / \sigma_{M,i}^2\right],$$

where $T_{\text{opt},M,i}$ is the optimal temperature for the survival of species i and $T_{M,i}(t)$ is given by

$$T_{M,i}(t) = \int w_{M,i}(\tau) T_t(\tau) d\tau,$$

where $w_{M,i}$ is the seasonal probability density of mortality in species i .

We assume length-dependent fishing mortality rates $F_{i,l,a}(t) = F(L_{i,l,a}(t))$ and $F_{i,M,a,a_M}(t) = F(L_{i,M,a,a_M}(t))$ typical for trawl-type fishing,

$$F(L) = \frac{F_{\max,i}}{1 + \exp(-(L - L_{F,i}) / \sigma_{F,i})},$$

where $F_{\max,i}$ is the maximum fishing mortality rate in species i , $L_{F,i}$ is the length at which fish of species i experience half of this maximum fishing mortality rate, and $\sigma_{F,i}$ determines the steepness of the sigmoid selectivity curve for species i .

Evolutionary dynamics

To account for life-history evolution, we will try to consider selection pressures and selection responses using the techniques presented by Arlinghaus et al. (2009) and Matsumura et al. (submitted). Potentially evolving life-history traits of interest include the length increment $h_{\max,i}$, the gonadosomatic index g_i , and the intercept $-c_{i,0} / c_{i,1}$ of the probabilistic maturation reaction norm.

Relevance and link to EEP's research plan

This project aims to reproduce the observed global phenomenon of sardine-anchovy cycles and to understand the causal mechanisms underlying these long-term stock fluctuations. It will thus contribute to a better understanding of factors influencing the sustainable exploitation of living marine resource, and is linked to EEP's research project on *Evolutionary Fisheries Management*.

Expected output and publications

I intend to publish this work as a co-authored article in an international scientific journal.

References

- Arlinghaus R, Matsumura S & Dieckmann U (2009). Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). *Evolutionary Applications* 12: 335-355
- Chavez FP, Ryan J, Lluch-Cota SE, Niquen M (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299: 217-221
- Hirshfield MF (1980). An experimental analysis of reproductive effort and cost in the Japanese medaka, *Oryzias latipes*. *Ecology* 61: 282-292
- Lester NP, Shuter BJ & Abrams PA (2004). Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London B* 271: 1625-1631
- Matsumura S, Arlinghaus R & Dieckmann U. Evolutionary consequences of size-selective recreational harvesting on multiple life-history traits in pike (*Esox lucius*). Submitted.
- Post JR, Mushens C, Paul A & Sullivan M (2003). Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. *North American Journal of Fisheries Management* 23: 22-34
- Stearns SC (1992). *The Evolution of Life Histories*. Oxford University Press.
- Suda M & Kishida T (2003). A spatial model of population dynamics of the early life stages of Japanese sardine, *Sardinops melanostictus*, off the Pacific coast of Japan. *Fisheries Oceanography* 12: 85-99
- Suda M, Watanabe C & Akamine T (2008). Two-species population dynamics model for Japanese sardine *Sardinops melanostictus* and chub mackerel *Scomber japonicus* off the Pacific coast Japan. *Fisheries Research* 94: 18-25
- Takasuka A, Oozeki Y & Aoki I (2007). Optimal growth temperature hypothesis: Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? *Canadian Journal of Fisheries and Aquatic Sciences* 64: 768-776
- Yatsu A, Watanabe T, Ishida T, Sugisaki H & Jacobson LD (2005). Environmental effects on recruitment and productivity of Japanese sardine *Sardinops melanostictus* and chub mackerel *Scomber japonicus* with recommendations for management. *Fisheries Oceanography* 14: 263-278