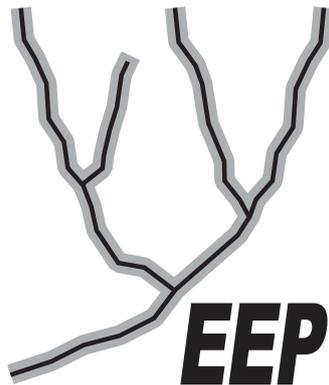# Young Scientists Summer Program 2013

Six Research Projects

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

EEP

The joint evolution of cooperation and information gathering

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Goal

To study the joint evolution of cooperation and information gathering in social systems in which agents receive payoffs from multiple interactions with other agents.

Background and motivation

There are (at least) two contexts in which information and memory are known to affect how agents in a social system interact with each other. First, reputation, reciprocity, and ostracism can help to stabilize cooperation when defection might otherwise dominate, and these mechanisms require that the agents in the system gather, store, and use information about their peers (Kreps et al. 1982; Nowak and Sigmund 1998b; Panchanathan and Boyd 2004; Nowak 2006; Alonso-Sanz 2009; Tavoni et al. 2011). Second, in economics, models in which consumers have imperfect information (a phenomenon called rational inattention) predict that consumers' ability to make optimal decisions about their interactions with sellers will be constrained (Sims 2003, 2006; Luo and Young 2009; Matejka and Sims 2011). Additionally, when consumers do not have perfect information, they may behave more randomly (Sims 2003) and the whole system may fluctuate more (Luo and Young 2009) compared to models in which consumers do have perfect information. Such findings highlight that systems with agents who have perfect and complete information and memory behave differently from those in which agents have imperfect information or memory. However, the quality and quantity of information that agents gather and store can vary extensively. The strategies that agents use to gather information are under selection and will evolve according to how much they benefit the agents who use them. By studying their evolution, we can understand how cooperative behavior is constrained by the evolution of information gathering.

Adaptive dynamics has been used to model both the evolution of memory strategies (Kerr and Feldman 2003) and cooperation (Killingback and Doebeli 2002; Doebeli et al. 2004; Zimmerman and Eguiluz 2005; Nowak 2006, Zhong et al. 2008). Kerr and Feldman (2003) studied agents who remember information about the environmental stimuli they encounter and observed evolutionary branching: the population could become dimorphic with agents having information-gathering strategies that differed in how much information was stored in memory. In models of cooperative behavior, cooperation, defection, or a stable mixture of the two strategies may evolve, and which of these three possibilities occurs depends on the number of interactions the agents engage in, as well as on the structure of their interactions (Nowak and May 1993; Killingback and Doebeli 2002; Zhong et al. 2008; Tanimoto 2009). There have been qualitative discussions of the co-evolution of memory and cooperation (Ambrose 2010) and quantitative studies of the co-evolution of interaction networks and cooperation (Tanimoto 2009). However, there are few existing models of the co-evolution of information gathering or memory and cooperative behaviors. In this project, I will model the co-evolutionary dynamics of both behaviors. If the co-evolutionary dynamics lead to high levels of cooperation stabilized by information gathering, this will provide evidence that mecha-

nisms like reputation-based behavior and reciprocity that support cooperation do not need to be externally imposed, but can emerge from an evolutionary process.

Research questions

By studying the co-evolution of cooperation and information behavior, I can study how each type of behavior affects the evolution of the other and what combinations of behaviors emerge from the joint evolutionary process. I will address the following questions:

- How does the evolution of cooperation depend on the ability or inability of agents to remember previous interactions and to change their future behavior accordingly?
- How does the evolution of information-gathering behaviors depend on the population size and distribution of cooperation strategies in the population?
- Can evolution lead to information-gathering and memory strategies that are socially optimal with respect to the level of cooperation they support in a population?
- Does evolutionary branching of information-gathering strategies occur and, if so, under what circumstances?

Methods and work plan

Model overview

I will model the evolutionary dynamics of a population in which agents receive payoffs from multiple interactions with other agents. Every agent in the population will have two types of traits, determining a cooperative behavior and a suite of information-gathering behaviors. These traits will affect each agent's fitness and consequently how the frequencies of different traits in the population change over time.

Cooperative interactions

I will use the donation game as a model system for cooperative interactions. When two agents play, one is randomly chosen to be the donor and one to be the recipient. The donor can either donate or not. If he donates, then he incurs a cost c and the recipient receives a benefit b. If he does not donate, neither player's overall payoff changes. Each agent will have a rule that determines how to behave that depends on what he knows about his partner, sometimes called an "action rule" (Nowak and Sigmund 1998b; Nakamura 2011). There will be three types of agents in a population: unconditional cooperators, unconditional defectors, and discriminating agents who use information about the recipient's reputation to decide how much to donate.

The agents will play the game multiple times. Which agents interact with each other will be determined in one of two ways:

- The agents interact randomly in a well-mixed population.
- The agents interact according to a fixed interaction network.

I will begin with a finite well-mixed population and subsequently add more complexity. The population size and, in the case of an interaction network, the structure of their interactions will be key parameters affecting the evolution of information gathering and cooperation.

Information behaviors

Each discriminating agent will observe the behaviors of other agents, use these observations to update his beliefs about the reputation of the observed player, store the reputations in

memory, and use these reputation values to choose a cooperative strategy. These behaviors will be quantified through a set of parameters. Each agent will observe games going on (within some distance in the case of an interaction network) with a probability p_o. (The agent might also make observations of his own experiences as a recipient, and I will consider both possibilities.) The agent then uses these observations to form and update reputations about each of the other agents. In order to distinguish between a neutral reputation and a lack of information, the agents will have two pieces of information: the total number of observations and the reputation value. There are three ways in which reputations will be updated.

- First, the reputation will be an integer that is incremented up or down according to whether a cooperative or defective behavior is observed, the so-called "image scoring" social norm (Nowak and Sigmund 1998b).

- Second, I will consider higher-order social norms in which the reputation of the recipient also affects how the donor's reputation is updated, e.g. the Sugden or Kandori social norms (Nowak and Sigmund 1998a, Panchanathan and Boyd 2004; Ohtsuki and Iwasa 2006; Uchida and Sigmund 2010; Nakamura and Masuda 2011).

- Finally, the agents will use Bayesian inference to update their expectations about their co-player's probability of conforming to their social norm. Each agent then uses its previous observations to form and update a prior, and the initial prior could be part of the suite of evolving traits.

In each round, the agents may lose some of their memories. Specifically, there is a probability p_r of remembering a piece of information, such that at each time step each observation or reputation stored in an agent's memory will be retained with probability p_r. The number of time steps a piece of information is stored in memory then becomes a random variable.

When the agents are given the opportunity to donate, they will use a threshold T to decide whether to donate or not: if the recipient's reputation is below the threshold, the discriminating agent does not donate. A discriminating agent's behavior towards an unknown recipient can be more or less cooperative, and for this I will consider a range of possibilities.

I will impose a cost on increased information gathering and storage through a cost function $c(p_o, p_r)$, such that $c(0,0) = 0$ and c is an increasing function of both p_o and p_r. Although there are many plausible choices of cost function, I will at least initially assume that the cost function is given by a quadratic polynomial.

Evolutionary dynamics

There are two types of traits under selection in this model: cooperative behavior and information behaviors. There are three types of cooperative agents: unconditional cooperators, unconditional defectors, and discriminating agents who use information about the reputation of their co-players to decide how to behave. The information behavior, as described above, will be a two-dimensional trait consisting of p_o and p_r, which are used in conjunction with the threshold T. I will assume there is a timescale separation such that the frequencies of the cooperative types change on a fast demographic timescale and the information traits and threshold change on a slower evolutionary timescale.

On the fast timescale, the traits of the discriminators are fixed and each agent has a fitness that depends on the payoffs from his cooperative behavior, the cost of his information behavior, and the frequencies of the three cooperative types. I will use replicator dynamics to model how these fitnesses lead to equilibrium frequencies of the cooperative types. The size of the

population, the number of interactions in a single generation, and, in the case of an interaction network, the structure of the network, will affect these replicator dynamics. On the slow time-scale, the frequencies of the cooperative types will be equilibrated and a discriminator with a given information behavior will have a fitness that depends on this equilibrium. I will then use these fitnesses in an adaptive dynamics framework to model the evolution of the information behaviors themselves.

Work plan

In summary, I will begin with a base model that extends previous game-theoretic models of cooperation through the addition of the evolution of information gathering and then systematically make modifications to the model in the following steps:

- I will begin by assuming that the population is finite, well-mixed, and that agents are equally likely to interact with any of the other agents. Initially, the agents will update the reputations using image scoring as in Nowak and Sigmund (1998b). I will study the evolutionary dynamics of information behaviors (probability of observation p_o, and probability of remembering p_r) and the threshold reputation level T, as well as the resultant levels of cooperation that the evolutionarily equilibrated information behaviors support.

- Second, I will consider higher-order social norms, e.g., Sugden and Kandori norms.

- Next, I will make the modification that the agents use Bayesian inference to update the reputations of the other agents, and possibly include the prior belief as an evolving trait.

- Finally, I will introduce a fixed interaction network that determines which players interact with each other.

Relevance to EEP's research plan

By studying the co-evolution of cooperation and information gathering, I will elucidate how memory can promote and stabilize cooperation and how to design systems that promote cooperation. This project will thus contribute to EEP's research on the evolution of cooperation, in particular to the project "Equitable Governance of Common Goods".

Expected output and publications

The results of this research project are intended for publication as a coauthored article in a peer-reviewed scientific journal and inclusion as a chapter of my PhD thesis.

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The impact of concurrent partnerships on HIV transmission dynamics

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Goal

To gain qualitative understanding of the impact of concurrent partnerships (multiple partnerships of one and the same individual overlapping in time) on HIV transmission dynamics using a simplified model that captures such concurrent partnerships.

Background and motivation

Infectious diseases, such as HIV, influenza, and measles, are part of modern life. Especially in sub-Saharan Africa (SSA), HIV has a large impact. Mathematical modeling can play an important role in increasing our understanding of transmission pathways (Grassly and Fraser 2008). It can be applied in different ways. Firstly, models can be defined whose aim is to provide a "proof of principle"; such models have a simple structure and show the effects of a specific mechanism. In many aspects, such models will not be realistic, but can transparently demonstrate the impact of the considered mechanism on transmission dynamics. Another strategy is based on defining models that are more realistic, such that they can be reasonably fitted to available data. Both strategies are useful and should be followed in order to give guidance to epidemiologists and behavioral scientists for future field studies. In this project, we will follow the first strategy to obtain qualitative insights into the impacts concurrent partnerships have on HIV transmission dynamics.

In most of the world, HIV remains concentrated in high-risk groups such as injecting drug users and sex workers, while in SSA, HIV is widespread among heterosexual populations. For a long time now, there has been a debate on concurrent partnerships as a driver of the HIV epidemic in SSA (Halperin and Epstein 2004; Lurie and Rosenthal 2009; Go and Blower 2012). Concurrent partnerships could lead to a sexual network in which many individuals are connected to each other, allowing HIV to spread quickly through the population. This potential impact of concurrency has been demonstrated by simulation studies (Morris and Kretzschmar 1997; Eaton et al. 2010; McCreesh et al. 2012). However, empirical findings regarding this impact are inconclusive. For example, while Kenyon and Colebunders (2012) reported a positive correlation between HIV prevalence and concurrent partnerships, Tanser et al. (2011) found no evidence in their cohort study to suggest that concurrent partnerships are an important driver. In an ecological study, Reniers and Watkins (2010) even reported a negative correlation between HIV prevalence and population-level prevalence of polygyny (men have more than one wife, while women are monogamous), which led them to discuss the possibility that some forms of concurrency might actually have a protective effect on the spread of HIV.

Until now, consensus indicators of concurrent partnerships are lacking, so different definitions and measures of concurrent partnerships are used across studies. This complicates the comparison of studies conducted in different settings and regions. Recognizing this detrimental state of affairs, UNAIDS has proposed a consensus indicator (UNAIDS 2010). In ad-

dition, Leung et al. (2012) introduced two natural definitions for measuring concurrent partnerships, referring to these as individual-based and partnership-based concurrency indices. How do these various indices relate to the disease dynamics? And what relation do different indices have with each other?

It is plausible that concurrency could enhance the initial spread of HIV through a population. But, once HIV prevalence has risen to higher levels, concurrency may have a different effect. In particular, it could potentially lead to stronger heterogeneity, with cliques either having a high local prevalence or consisting entirely of susceptible individuals, which might reduce further spread and the eventual overall prevalence. Therefore, it is important to consider the effect of concurrency on the basic reproduction ratio R_0, the initial exponential growth rate r when $R_0 > 1$, and the endemic prevalence.

Research questions

We will address the following research questions:

- How do we best compare populations with different levels of concurrency to study the relation between epidemiological quantities and concurrency indicators? In particular, which model parameters (or parameter combinations) should be kept fixed, or controlled for?

- How does concurrency impact initial spread and endemic prevalence? In particular, how do R_0, r, and endemic prevalence relate to the UNAIDS concurrency measure (UNAIDS 2010), the concurrency indices introduced by Leung et al. (2012), and other measures proposed in the literature (Boiley et al. 2012; Tanser et al. 2011)?

- How should concurrency indices be defined such that the impact of concurrency on transmission dynamics can best be captured? What characteristics does a measure for concurrency need to have in order to possess predictive value, and do concurrency indices in empirical literature have these characteristics?

Methods and work plan

This project will build on previous results in my current PhD research project. In Leung et al. (2012), a mathematical model of a dynamic concurrent partnership network was developed in the setting of a homosexual population. In this model, we defined and analyzed a dynamic process of link formation and dissolution, in conjunction with demographic turnover. We introduced two indices to measure the level of concurrent partnerships in a population and characterized these for our network. Subsequently, transmission of an SI infection was superimposed on the network and several epidemiological parameters were characterized (publication in preparation).

Dynamic sexual network

In this project, we will consider a heterosexual population consisting of men and women all of whom may concurrently engage in several partnerships. The partnership capacity n is the maximum number of simultaneous partners an individual may have, and it should be thought of as the implementation of a social norm. In many populations, the social norm is monogamy ($n = 1$). In some SSA populations, it is socially accepted to have a second steady partner next to one's wife or husband ($n = 2$) (Leclerc-Madlala 2009), while in others, polygyny is practiced (Reniers and Tfaily 2008).

For the mathematical modeling, it is convenient to think in terms of individuals having n "binding sites". These are either "occupied" or "free"; an individual with k occupied binding sites has k partners. The dependence between individuals is captured by the fraction of "free binding sites" F^m (belonging to males) and F^f (belonging to females). These "free binding sites" then govern the partnership dynamics in the population.

In total, the dynamic network model has four parameters: the partnership capacity n, the death rate μ, the separation rate σ, and the partnership-formation rate ρ.

Concurrency indices

In the course of the concurrency debate, a lot of different definitions and measures of concurrent partnerships have been introduced. Some of these even failed to measure concurrent partnerships and measured sequential partnerships instead (Boiley et al. 2012). Here we focus on three concurrency indicators.

First, the UNAIDS indicator (UNAIDS 2010) for concurrency is defined as the proportion of all adults in the population having more than one sexual partners at a point in time.

Second, Leung et al. (2012) defined two other measures of concurrency, κ_I and κ_P. In a heterosexual population, these measures of concurrency can be applied to males and females separately. The two indices have a natural and straightforward definition, one based on sampling individuals, and the other based on sampling partnerships.

The individual-based concurrency index κ_I^g has the following operational definition: sample an individual of gender g (male or female) at random from the pool of all individuals of gender g having at least one partner, and then count how many partners this individual has. This index can thus be interpreted as the expected number of partners of a non-single individual minus 1.

The partnership-based concurrency index κ_P^g has the following operational definition: sample a partnership at random from the pool of all partnerships, focus on the partner of gender g and count how many partners it has besides the partner in the sampled partnership.

Note that the UNAIDS indicator (UNAIDS 2010) for concurrency does not take the number of concurrent partnerships into account (nor does it make a distinction between male and female concurrency). Of course, due to difficulties with empirical work it might be desirable to use an index that is less informative than theoretically motivated measures like κ_I and κ_P. However, can the UNAIDS measure capture the same dependency of the disease dynamics as κ_I and κ_P?

Infectious disease dynamics

To study HIV dynamics, we superimpose an SI-infection on the dynamic sexual network, i.e., individuals are either susceptible or infectious, and, once infected, individuals remain infectious until death. This introduces an additional parameter for the transmission rate β.

The infectious disease model allows for a characterization of R_0 (via a Markov chain describing the dynamics of the binding sites of an infectious individual), r, and endemic prevalence (by using the independence of binding sites as far as partnership dynamics are concerned).

We may consider extensions within the framework of this model. One example of such an extension is allowing for one-off encounters next to steady partnerships. In this project, we will also explore the feasibility of such extensions.

Relationship between concurrency indices and HIV transmission dynamics

Concurrency is really a network property that is closely related to other network properties. In order to isolate the effects of concurrency, certain other parameter (or parameter combinations) need to be kept fixed, or controlled for. Different choices can be made here. We would not like a change in, e.g., R_0 to be caused mainly because the mean number of partners changes. So one of the questions is: how do we best compare populations with different levels of concurrency to study the relation between epidemiological quantities and concurrency indicators?

The model for this project has five parameters. By scaling time, we can reduce this number to four. Next, we could choose a one-parameter path in the four-dimensional space, by, e.g., fixing β and two partner statistics such as the mean lifetime number of partners and the mean partnership duration. Letting the one remaining parameter change, we could then explore how concurrency measures and epidemiological quantities co-vary.

Another way to study the relationship is by using statistical methods. For this, we can consider the following three sets of variables: (a) concurrency indices, (b) partner statistics, and (c) epidemiological quantities. The model's parameter space can be sampled randomly according to a probability density function, and for each parameter combination, the variables (a), (b), and (c) are determined. We can then study the resultant data set by, e.g., linear correlation analysis, generalized linear models, or nonlinear correlation analysis.

Work plan

To summarize, the work plan to answer the research questions of this project is as follows:

- Investigate the best strategy to compare models with different levels of concurrent partnerships.
- Explore correlations between epidemiological quantities and κ_I and κ_P and other measures numerically.
- Investigate literature on important empirical measures and study them in the network model described above (e.g., the UNAIDS measure).
- Investigate the relationship between (a) concurrency indices, (b) partner statistics, and (c) epidemiological quantities with statistical models.
- Investigate possible model extensions (e.g., allowing for some form of proportionate mixing or one-off encounters).

Relevance to EEP's research plan

This project will give insights into the impact of a network property such as concurrency on processes of contagion defined on dynamic networks, and will thus contribute to EEP's research project on "Systemic Risk and Network Dynamics".

Expected output and publications

The work from this project is expected to be a chapter in my PhD thesis. I also expect to publish the results of this project as a co-authored article in an international peer-reviewed scientific journal.

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Evolution of multilevel cooperation: Analogies between social and medical systems

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Goal

To better understand the evolution of dual cooperative behavior in multilevel systems.

Background and motivation

While cooperation is common at many levels of life, ranging all the way from micro-organisms to complex social structures (Maynard Smith and Szathmáry 1995), cooperative behaviors are fundamentally vulnerable to selfish defection. Hence, their prevalence in nature is often considered puzzling. In line with an expectation of prevalent defection, cancer can be interpreted as a disruption of cooperation within a multicellular organism, with tumors jeopardizing the multicellular common good through processes analogous to the tragedy of the commons (Hardin 1968) well-known from resource economics.

Traditionally, cancer is understood as a selfish cheater within its host. Multicellularity relies on cellular cooperation and the regulation of gene expression in each cell. In a cancerous cell, the regulation of certain critical actions has failed, providing fitness benefits for the individual cell at an expense for the multicellular host. While defecting the host, cancerous cells might still cooperate at other levels, e.g., within a tumor, and between the tumor and its microenvironment. Such a dual face of cooperation is also recognized in social systems, where it is related to the distinction between in-group behavior and out-group behavior, with a higher propensity for cooperation in the former case and a higher propensity for defection in the latter. More realistic models of cooperation, reflecting the complexity arising from multiple levels of selection and from discriminating among individuals, are thus of importance for understanding medical conditions and cooperation dynamics in the social world.

Concentrating on the evolution of dual cooperative behaviors in cancer and the social world, we will build a model to capture key characteristics common to both types of organizations. We plan to achieve this by combine two recently established approaches to the evolution of cooperation, focusing, respectively, on multilevel selection (Traulsen and Nowak 2006) and tag-based cooperation (Jansen and van Baalen 2006; Traulsen and Nowak 2007).

Research questions

We are interested in dual cooperative behavior in multilevel systems. Our research questions include:

- What selects for in-group cooperation in a multilevel system?
- When is it beneficial to invest into out-group cooperation?
- How can cooperation levels be raised, e.g., by altering a system's multilevel structure or by enabling the emergence of costly punishment?

Methods and work plan

Ecological dynamics

Our contribution will be to combine the two recently developed approaches of tag-based co-operation (Jansen and van Baalen 2006; Traulsen and Nowak 2007) and multilevel cooperation (Traulsen and Nowak 2006). We consider individuals that form assemblies with sizes $\{0,1,2,...,N\}$. Individuals play pairwise prisoner's dilemma games within the assembly and also, but less frequently, between the assemblies. Since we are interested in the in-group and out-group perspective, we assume that individuals carry a heritable tag, which is an arbitrary label recognized by other individuals.

The phenotypic trait of the individual is a strategy vector $S = (s_1, s_2)$, elements of which correspond to the investments put into a game played with an in-group individual or with an out-group individual, respectively. Individuals with the same tag in the same assembly obviously are in-group individuals, and individuals with different tag in different assemblies are out-group individuals. However, individuals that share either of the two, the tag or the assembly, but not both, can be considered as in- as well as out-group players. The decision how players discriminate their partner can be probabilistic, in which case we can study the effect of corresponding parameters on the evolution of cooperation.

Investing is always costly, and can be assumed either to decrease the birth rate b or to increase the death rate d of the individual. In addition, the benefit achieved from the games with a cooperative partner increases the reproduction rate b of the individual. In each assembly stochastic birth and death events occur based on the corresponding rates b and d. When the assembly reaches its maximum size N and a new individual is born (or immigrated), two events may happen. Either, a randomly chosen individual dies, or the assembly splits in two daughter assemblies.

Assuming that there are infinitely many assemblies, we can write the population model with a system ODEs describing the population size distributions.

Evolutionary dynamics

To study the evolution of cooperative behavior we apply the framework of adaptive dynamics (Metz et al. 1992, Metz et al. 1996, Geritz et al. 1997, Geritz et al. 1998). The main idea is to have evolutionary dynamics on the top of the ecological dynamics, both of which can be analyzed rigorously. The key concept in adaptive dynamics is invasion fitness, the sign of which answers the question whether a mutant may or may not invade the prevalent resident(s). To study the expected direction of evolution we use the fitness gradient.

The fitness gradient is the derivative of the invasion fitness with respect to the strategy of the mutant, evaluated when the mutant strategy is equal to the resident strategy. Strategies, for which the fitness gradient is zero, are called singular strategies. If all mutant strategies different from the resident strategy have negative invasion fitness, the singular resident strategy is also an evolutionarily stable strategy, ESS (Maynard Smith 1976).

In our model setting we will consider two cases, allowing and not allowing immigration between assemblies. First, let $p(i,j)$ denote the proportions of assemblies with i residents and j mutants. In general, we can write a system of differential equations describing the dynamics of $p(i,j)$. In order to calculate the invasion fitness of a mutant, it is enough to study the dynamics of such assemblies, where $j \geq 1$, when the resident population distribution is at equi-

librium and the mutant population is rare. This differential equation is linear, and can be written as $\mathrm{d}P/\mathrm{d}t = AP$. In case immigration between assemblies is not allowed, the invasion fitness of the mutant is the dominant eigenvalue of the matrix A.

In case of immigration, the global model is actually a structured metapopulation model. Then the convenient proxy for the invasion fitness is metapopulation reproduction ratio $R^{\mathrm{mut}}_{\mathrm{metapop}}$, which uses the dispersing generations (Metz and Gyllenberg 2001).

Work plan

- I will implement the model and the methods necessary into a computer program.
- I will explore both population as well as evolutionary dynamics.
- Together, we will discuss how to interpret the results in the context of social world and possibly in oncogenesis.
- I will write the first draft on the manuscript, which will then be circulated and polished within the team.
- Finally, the work will be submitted and published in an international scientific journal. Optionally, a more popularly written article for a more general audience could be published (potentially in Finnish) too.

Relevance to EEP's research plan

My research interests arise from medical questions, in particular, from the evolution of cancer. Many analogies exist between oncogenesis and social systems, particularly concerning the evolution of cooperating and defecting behaviors. Cooperation, especially in the social world, is one of EEP's focal research areas. Extending the field of application from social systems to oncogenesis can enable interesting integrative discussions, and hopefully provide new ideas and insights for studying cooperation.

Expected output and publications

This project is expected to result in a publication as a coauthored article in an international peer-reviewed scientific journal.

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Species dispersal and the spatial insurance hypothesis as a coupled ecological-economic system

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Goal

To investigate the consequences of the close integration of coupled ecological-economic systems.

Background and motivation

International trade has promoted the exchange of goods and services but also facilitated the spread of pathogens and species (Costello et al. 2007). Although most introduced species cause little or no harm, the addition of new competing species may impact the biodiversity of the ecosystem, which has been linked to ecosystem functioning and the resultant flow of ecosystem services (Cardinale et al. 2012). One explanation for this effect lies in the spatial insurance hypothesis, which centers on the notion that stability of primary production in a meta-community increases with the biodiversity within each of its substituent communities (Loreau et al. 2003). Redundant species or phenotypes of an ecosystem process provide robustness to temporal environmental variation and change (Yachi and Loreau 1999). However, empirical evidence for the spatial insurance hypothesis is mixed. Several studies have found positive effect of diversity on ecosystem productivity and stability (van Ruijven and Berendse 2010, Thompson and Shurin 2012) while others have found a neutral or negative relationship (Valone and Barber 2008, van Ruijven and Berendse 2010, Aragon et al. 2011).

In an influential theoretical analysis, Loreau et al. (2003) provide an illustration and corroboration of the spatial insurance hypothesis. At low rates of dispersal, the dominant "optimal" species in each community in a meta-community competitively drives all others to extinction. This leads to low local biodiversity within the community but, if the "optimal" species is different in each sub-community, to high biodiversity across the meta-community. On the other hand, at high rates of dispersal, competition across communities will lead both to low local and low global biodiversity. The optimal species in average conditions will exclude all others. Intermediate dispersal rates increase local biodiversity within communities without significantly altering global biodiversity, leading to the highest primary productivity and stability (Loreau et al., 2003).

However, the Loreau et al. (2003) model and analysis does not account for the effect of human behavior on species dispersal and competition. Specifically, dispersal is a function of the trade of goods and services between spatially distributed communities: species are dispersed as objects of trade or "passengers". The species coexisting within those communities is dependent on human decisions to promote or suppress particular species. For instance, crops are promoted in agricultural systems while weedy pest plants are suppressed.

In this project, I will investigate the effect of incorporating this human component into the Loreau et al. (2003) framework, resulting in a coupled ecological-economic system. I will test its effect on biodiversity under several cases: 1) no humans present, 2) people derive utility ("well-being") from local, within sub-community species consumption, and 3) people obtain utility from local and across-community trade.

Research questions

In my research, I will address the following questions:

- What is the effect of the closer integration of a coupled ecological-economic system for local and global biodiversity?
- What roles do preferences, prices, and discounting play in the trade-related dispersal of species?
- What is the optimal rate of dispersal from the perspective of the individual country, and how does this differ from the optimal rate of dispersal for the global system?

Methods and work plan

During my research at IIASA, I will re-evaluate the original Loreau et al. (2003) model, then couple its ecological system to an economic model by incorporating anthropogenic dispersal via trade and the harvesting of species biomass for human consumption. I will then solve for the optimal trade and harvest that maximizes utility and test the effects of preferences, prices, and the discount factor on local and global biodiversity.

Assuming the same resource and consumption/environment dynamics as Loreau et al. (2003), we may specify the dynamics of species and resource biomass to be governed by the equations:

$$\frac{dN_{ij}}{dt} = N_{ij}(t)\big(e\, c_{ij}(t)\, R_j(t) - m\big) + a \sum_{k \neq j}^{M} \big(M_{ki}(t)\, n_{ik} - X_{ki}(t)\, n_{ij}\big) + q\, L_{ij}(t)N_{ij}(t)$$

$$\frac{dR_j}{dt} = I - lR_j(t) - R_j(t) \sum_{i=1}^{S} c_{ij}(t)\, N_{ij}(t)$$

for all species $i = 1, 2, \dots, S$ on community $j = 1, 2, \dots, M$ at time t. Species consume resources at a rate $c_{ij}(t)$, convert it to new biomass with efficiency e, and die at rate m. Resources increase by a fixed amount I and are lost at a constant rate l. Species consumption of resource biomass is defined as a non-autonomous function of species-specific traits and environmental variation given by:

$$c_{ij}(t) = \frac{1.5 - |H_i - E_j(t)|}{10}$$

$$E_j(t) = \frac{1}{2}\left[\sin\left(E_{\text{init},j} + \frac{2\pi t}{40000}\right) + 1\right]$$

where H_i is a species-specific parameter such that $H_1 = 1$ and $H_i = H_{i-1} - \frac{1}{6}$ for $i = 1, 2, \dots, S$. Environmental variation is assumed to be out of phase with each community. $E_{\text{init},j}$, a community-specific parameter, is drawn from a uniform distribution between $\pm 2\pi$. This results in a single "optimal" species possessing the highest initial consumption rate in each community.

Dispersal arises as the result of imports (M_{ij}) and exports (X_{ki}). n_{ik} and n_{ij} indicate the ratios of species biomass in patches j and k respectively. Species are transported on imports and exports at a constant rate a. (For this first step we assume that communities are far enough apart that no natural dispersal occurs. However, extending the model to include natural dispersal will be straightforward, allowing us to consider, for example, climate-induced changes in species population range.) Humans may alter the biomass of species within their

community directly as the result of harvest or consumption: species are harvested at a rate given by the quantity of labor, $L_{ij}(t)$, with a catch ability or efficiency q.

I assume that humans determine the quantity of imports, exports, and labor according to an objective of maximizing utility or "well-being", which we define as a function of direct consumption of species within a sub-community (C_j), the consumption of species from imports (C_j^*), and the flow of benefits arising from sub-community biodiversity (B_j). Thus we can write the utility maximization problem as:

$$\max_{L_j, M_j} \int_0^\infty e^{-\rho t} U(C_j, C_j^*, B_j) \mathrm{d}t$$

subject to [1], [2], and $\sum_{k \neq j}^M p_k M_{kj} = \sum_{k \neq j}^M X_{kj}$ (balanced trade, where p_k is the price of species k in patch j). The utility function is defined as a CES utility function in direct consumption of species and imports, with the flow of benefits as a separate additive term.

$$U_j(C_j, C_j^*, B_j, t) = \left(C_j^\alpha + C_j^{*\,\alpha}\right)^{1/\alpha} + B_j$$

where α is a parameter that determines the rate of substitution between C_j and C_j^*.

An individual, sole proprietor (owner) of each spatially distributed community alters the quantity of imports and management of inter-community species to maximize expected utility. By utilizing a dynamic programming algorithm, we may solve for the optimal allocation of species biomass between direct consumption, trade, and biodiversity, taking in to account future benefits of species growth.

Since utility is a function of species consumption and the flow of benefits from biodiversity, the degree to which communities harvest species depends on the weight of benefits between species consumption and biodiversity flows. For instance, if the benefits of species consumption far outweigh those of biodiversity, communities will likely choose to limit trade with partner that will not supply beneficial species and suppress non-beneficial species within their community. Therefore, I will examine the effect of different sets of preference structures on the behavior of the model. I also test the sensitivity of the model to dynamic costs and endogenous prices of species harvest/trade, as well as the effect of discounting future benefits of species biomass.

The global problem differs from the local problem in two important respects. First, utility is aggregated across the meta-community (the well-being of all communities). Second, the effect of dispersal on species diversity in all communities is taken into consideration. Like the local problem, the global problem will be solved using dynamic programming, and the sensitivity of the results to variation in key economic and ecological parameters will be tested.

Due to the nature of the problem, analytical results are not tractable. Therefore, to observe the consequences on biodiversity of human choices to promote or suppress species in a fluctuating environment with anthropogenic dispersal, I resort to numerical methods using MatLab. I will also remotely access Arizona State University's Saguaro high performance computing environment. In previous research, Saguaro was able to decrease simulation time by over an order of magnitude.

Work plan

- Re-evaluate the original Loreau et al. (2003) framework, replicating the results and testing their robustness to different numerical approximation methods.

- Numerically simulate three cases of the coupled ecological-economic system: 1) no humans present, 2) humans derive utility from local, within sub-community consumption, and 3) people obtain utility from local and across-community trade.
- Test the effect of preference structure and discount rate on biodiversity.
- Implement endogenous prices for species consumption and trade.
- Compare the individual community manager case to the social planner problem.

Relevance to EEP's research plan

My project contributes to the IIASA's Evolution and Ecology Program's research plan by developing a general bioeconomic model to investigate a real, complex coupled socio-ecological problem. This will provide a framework for testing hypotheses regarding the consequences of the closer integration of human-ecological systems.

Expected output and publications

The results of this work are intended for publication in a coauthored paper in an international scientific journal. I also expect this work to be incorporated as a chapter of my PhD dissertation.

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Contingent dispersal and the formation of cooperative groups

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Goal

To analyze how density-dependent group formation facilitates cooperation.

Background and motivation

Cooperation can be observed at almost all levels of biological and social organization. That cooperation and altruism exist among non-relatives is puzzling, since simple theoretical models predict that, while cooperation is the most beneficial for a group as a whole, non-cooperation is always the most successful strategy for the individual. Previous studies investigating the evolution of cooperation have typically assumed that cooperative interactions occur in pairs, single groups, via nearest-neighbor interactions, or in multiple groups of random sizes (Nowak and May 1992; Durrett and Levin 1994; Doebeli et al. 2004; Sigmund 2010; Brännström et al. 2011).

In realistic large-scale systems, individuals constantly leave or join groups depending on social interactions. The sizes of groups and the composition of individuals in groups, which are formed by these kind of processes, have been shown to be important for cooperation (Nowak and May 1992; van Veelen et al. 2010; Cornforth et al. 2012). The dependency on social interactions implies directly that such processes are density-dependent. It has been shown that density-dependent and conditional dispersal are evolutionarily stable and important in both ecological and evolutionary processes (Kun and Scheuring 2006; Flaxman et al. 2011; Payne et al. 2011; Parvinen et al. 2012; Nonaka et al. 2013).

A few recent studies have considered cooperation in relation to various kinds of direct and indirect density-dependent dispersal (Pepper and Smuts 2002; Hamilton and Taborsky 2005; Cornforth et al. 2012; Garcia and De Monte 2013). However, the characteristics of density-dependent group-joining and group-leaving processes have not been explicitly studied, nor how they affect the level of cooperation.

In this study we investigate how cooperation in a public goods game can be maintained in large systems by social interactions that are manifested as rapid group-joining and group-leaving processes depending on the individuals' group preferences, that is, the number of cooperators and non-cooperators. Since all individuals strive to maximize their own payoff, cooperators and non-cooperators alike share the interest of being amongst an abundance of cooperators.

Research questions

The main research questions are:

- What are the evolutionarily stable group-joining and group-leaving behaviors of cooperators and non-cooperators, respectively?
- What group structure of cooperators and non-cooperators do such behaviors give rise to?
- How do these behaviors affect the level of cooperation? Specifically, (1) can coopera-

tion invade a fully defecting population; (2) in such case, are there certain thresholds in the strength of group-leaving and group-joining behaviors that need to be met before cooperation can invade the population; (3) given that cooperation is already present in a population, can then group-leaving and group-joining behaviors maintain the cooperation; and (4) are there cases of group-leaving and group-joining behaviors where a cooperative population is immunized against invasion of defection?

Methods and work plan

Overview

A large number of individuals are distributed over a large number of social groups in which individuals engage in a local public-goods game. Individuals employ one of two strategies: they cooperate by investing into a common good for the group, or they defect by not investing but still utilizing the goods. Individuals may adopt the strategies of other group members based on their observed long-term success. Thus, a cooperator may choose to become a defector and vice versa. Depending on the local number of cooperators and defectors, individuals may decide to leave their group. Solitary individuals may decide to rejoin existing groups or form a new group by joining another solitary individual. Leaving, joining, and forming groups incur a cost. The traits that define individual leaving and joining behavior in response to local conditions are under selection.

Model description

1. Groups and games

The numbers of cooperators and defectors in local groups, X_c and X_d, respectively, are governed by stochastic processes. The games play out continuously in local groups and are thus dependent on local numbers of individual, such that

$$G_c(X_c, X_d) = B(X_c, X_d) - I$$
$$G_d(X_c, X_d) = B(X_c, X_d)$$

are the respective public goods game payoffs for cooperators and defectors, with $B(X_c, X_d)$ being the benefit of the game, and I the cost of investing.

2. Group formation

The probabilities per unit time that cooperators or defectors leave a group (of more than one individual) to become solitary are described by respective leaving-rate functions $L_c(X_c, X_d)$ and $L_d(X_c, X_d)$. That the probabilities per unit time that solitary cooperators or defectors joins a group are described by respective joining-rate functions $J_c(X_c', X_d')$ and $J_d(X_c', X_d')$, where X_c' and X_d' denote the individual numbers in the target group. The cost for performing these processes are assumed to be related to breaking up from groups and to establish in groups, and are thus proportional to the probabilities of doing so. The total payoffs for individuals in groups of more than on individual are

$$P_c(X_c, X_d) = G_c(X_c, X_d) - L_c(X_c, X_d),$$
$$P_d(X_c, X_d) = G_d(X_c, X_d) - L_d(X_c, X_d)$$

and the total payoffs for solitary individuals are

$$P_c^1\left(X_c', X_d'\right) = G_c(0,1) - J_c\left(X_c', X_d'\right)$$

$$P_d^1\left(X_c', X_d'\right) = G_d(0,1) - J_d\left(X_c', X_d'\right).$$

3. Imitation

The probabilities per unit time that individuals imitate the strategies of other individuals depend on the time-averaged payoff of the strategies, estimated as the ensemble average (as the system is ergodic). We will consider two possible scenarios of increasing complexity. First, we assume that individuals change strategy at a rate that depends only on the difference in average payoffs of the strategies. Second, we will assume that, at some rate, individuals compare their time-averaged payoff with randomly chosen other individuals in the group and change their strategies with a probability that is given by a function of the payoff-difference. Note that in the second scenario, imitation will only occur in groups with at least two individuals.

4. Invasion fitness

The group structure of the resident population is described by the probability distribution $p_{i,j}$ which denotes the fraction of groups with i cooperators and j defectors. The time evolution of $p_{i,j}$ is given by a master equation in which the transition processes are defined by rates of strategy imitation, group leaving, and group joining. The equilibrium probability distribution is thus given by the solution to $\dot{p}_{i,j} = 0$ and taking the average of all within-group payoffs over this distribution gives the time-averaged payoff of resident individuals. The mutant's long-term payoff is dependent on how large fraction of time is spent in different group types. Representing the mutant's movement between groups as a continuous-time Markov chain, we can determine the stationary distribution by solving a linear system. Taking the average of all within-group payoffs over this distribution then gives the long-term payoff of the mutant individual. The difference between the mutant payoff and the resident payoff will determine whether the mutant is able to successfully invade.

5. Assumptions on contingent dispersal

The leaving-rate and joining-rate functions are assumed to be positive functions that are typically linear, accelerating, decelerating, or sigmoidal. Various forms will be tested. The functions depend on traits such that the traits shape the functions, e.g., the slope, non-linearity, and inflection points (Kun and Scheuring 2006). If numerical analysis is not too computationally demanding, we will consider full vector-valued traits which do not artificially restrict the possible evolutionary outcomes.

Work plan

- First, we identify dispersal strategies which allow for the coexistence of cooperators and defectors.
- We then allow the dispersal strategies to evolve in order to understand what evolutionarily stable joining and leaving behaviors do emerge and how these behaviors affect the level of cooperation.
- If time allows, we will relax the assumption our definition on long-term fitness to see if this qualitatively gain different results, as well as make an attempt to formulate analytical models for a more rigorous investigation.

Relevance to EEP's research plan

The expected advances of this research will contribute to the knowledge on how cooperation in large populations is maintained. The proposed research will thus contribute to the EEP projects Equitable Governance of Common Goods and Eco-evolutionary Dynamics of Living Systems.

Expected output and publications

The results of this research are intended for publication as a coauthored article in an international scientific journal and will also be a part of my PhD thesis.

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Evolution of mediated cooperative interactions

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Goal

To investigate the evolution and stability of multi-player cooperative interactions through a strategic game theoretical model involving three players, in which a single focal player interacts with two lateral players.

Background and motivation

Cooperative interactions between species are ubiquitous and essential in the evolutionary diversification of life (Stachowicz 2001). Mutualistic associations have greatly facilitated the acquisition of novel traits and structures, and have contributed to the evolution of life as we know it (Bronstein et al. 2006; Douglas 2010). Yet, the evolution and maintenance of mutualisms has posed one of the most important and persistent theoretical problems in evolutionary biology. Often, both interspecific mutualisms in biological systems and analogous cooperative interactions in socioeconomic systems are cast within the framework of game theory, in which individuals receive a benefit according to both their own strategy and the strategy of their interaction partner. Players receive the biggest payoff by minimizing the costs associated with cooperating while maximizing the benefits received from their partner. In many cooperation games, such as the classic Prisoner's Dilemma (Trivers 1971), cooperation proves evolutionarily unstable and defection becomes the dominant strategy. Understanding the conditions that maintain cooperative interactions in nature has thus been an area of active research for decades, with many factors identified as stabilizing interspecific cooperation, such as spatial structure, partner choice and game iterations (Axelrod & Hamilton 1981; Boza et al. 2012; Nowak & Sigmund 2000).

While the majority of previous theoretical work has modeled mutualisms as interactions between two players, it is increasingly recognized that tight pairwise interactions are far less common in nature than associations among sets of potentially interacting partners. These "interaction guilds" often involve the asymmetric exchange of different services, frequently accompanied by evolutionary tradeoffs (Stanton 2003). In addition to the availability of multiple partners within a given interaction guild, many organisms engage in multiple concurrent mutualisms across trophic levels and interaction guilds. Moreover, the outcomes of these interactions can be context-dependent on both abiotic and biotic factors and can change over the course of an individual's development. The result is that in many biological and socioeconomic systems, cooperation occurs within the context of large interaction networks. While previous theoretical work has been instrumental in generating testable hypotheses about cooperative interactions in nature and improving our understanding of mutualism, their realism is limited by the simplification of these complex interaction networks into two-species models.

An important, and often overlooked, component of these networks is the emergence of indirect interactions (Ohgushi 2008), the dynamics of which cannot be captured with traditional pairwise approaches (Fath 2007). The present research will examine indirect cooperative interactions among three players by creating a strategic model of mediated mutualism. In this model, two players engage in an indirect interaction in which the interaction flows pass

through a central mediator rather than directly from donor to recipient. However, it is also assumed that the mediator may not be entirely neutral in this process, but rather strives to maximize its own payoff as well. Biological systems that may exhibit such indirect interaction structure include gut microbes determining the interactions of their animal hosts, or soil microorganisms conveying information and benefits among plants. In socioeconomics, an analogous process could be commercial trade, in which retailing groups mediate flows between consumers and the production of raw goods.

Research questions

The goal of this project is to develop and explore a strategic model of interspecific cooperation involving three players, in which a central mediating player can alter the interaction flows between two lateral players. Specifically, I will address the following questions:

- Under which conditions does a neutral player evolve to be a non-neutral mediator?
- Can the presence of a mediator facilitate evolutionary transitions between cooperative and exploitative interactions?
- How does the nature of the subgames between lateral players and mediator relate to the nature of the global game?
- Does the nature of the subgames determine the global interaction type (e.g., mutualistic, commensal, exploitative)?

Methods and work plan

In the proposed three-player system, M (mediator) will be a focal player that interacts with both player A and player B in the sense of a one-shot game; however, A and B do not directly interact with each other. Although A and B do not directly interact, they can indirectly affect each other's fitness via interactions with M. To begin, an individual-based model will be explored with three continuous traits, the selection gradients for which will be used to determine evolutionary dynamics. In addition to this base model, additional model extensions may be implemented as well, as described below.

Basic model structure

- Coexisting Players A and B each have one unit of resource of which I_i is invested into their interactions with M. The benefits received by all players are a function of these investments, and whatever is not invested into the interaction is retained by the players.
- The payoff functions for the players are given by:

$$P_A = (1 - I_A) + b_A(\frac{I_M}{2} + \lambda I_A),$$

$$P_B = (1 - I_B) + b_B(\frac{I_M}{2} + \lambda I_B),$$

$$P_M = b_A\left(\lambda\frac{I_M}{2} + I_A\right) + b_B\left(\lambda\frac{I_M}{2} + I_B\right) - I_M.$$

- The parameter $\lambda \in [0,1]$ determines the degree to which players benefit from their own investments. As such, this parameter determines whether the characteristics of the game are more like a Prisoner's Dilemma ($\lambda = 0$) or Snowdrift Game ($\lambda = 1$).
- The three continuous adaptive traits that will initially be considered are the invest-

ments of the players (I_A, I_B, I_M). As benefit functions, step (threshold) and saturation functions will be tested.

Model extensions

If time permits, the following extensions of this model will be implemented.

- While the benefit functions will initially be set as equal, these could later be changed such that players A & B have separate benefit functions, as such an asymmetry may be considered more realistic in many cases.
- Comparisons will be made between models in which players invest or extract benefit before versus after these parameters undergo nonlinear transformation via benefit functions.
- Environmental noise (e.g., implementation and sensing errors) could also be introduced into the model.
- Finally, reactive strategies in a game played for an indeterminate number of rounds may be explored.

Work plan

In summary, I will take the following steps to reach my research goals:

- Implement an individual-based model in Python
- Identify benefit functions that allow cooperation.
- Analyze how cooperation regime depends on game character
- Characterize subgames for regimes of the global game
- Prepare materials for report and manuscript

Relevance to EEP's research plan

Cooperative interactions have been an important focus of EEP research at IIASA for many years. The proposed work will build upon the EEP's previous research on evolutionary models of cooperation by including additional interaction complexity and elucidating differences between two-player and three-player systems. The resulting model will not be specific to any particular biological system and therefore will be generally applicable.

Expected output and publications

My aims in conducting this research are to contribute new insights into the ecological and evolutionary dynamics of biological species interactions in nature and structurally analogous socio-economic and political processes, and to generate predictions for future empirical research in insect–microbe cooperative systems. As such, it is envisaged that the work from this project will result in a coauthored publication in an international journal.

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