

# **Young Scientists Summer Program 2011**

## **Six Research Projects**

**Evolution and Ecology Program  
International Institute for Applied Systems Analysis  
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# Effects of temperature and precipitation on vegetation structure

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## Goal

To theoretically investigate the consequences of changing temperature and precipitation (water availability) on salient aggregate properties of single-species forest dynamics.

## Background and motivation

Current informal estimates place the number of species inhabiting our planet around 1.7 billion. This impressive diversity is the result of evolution over millions of years, in which many more species emerged that are now extinct. Though countless factors affect this evolutionary process, climate has clearly played an important role in determining which species lived on and which species went extinct.

Climate on earth has changed several times during the past millions of years, according to studies using a broad range of proxies such as ice cores, pollen, and tree rings (LaMarche 1974; Dansgaard et al. 1993; Lara and Villalba 1993; Briffa et al. 1995; Petit et al. 1999; Fowell et al. 2003). These changes have mainly been due to natural factors, such as solar cycles and biotic influences. Since the last century, however, one single species is shifting the natural atmospheric equilibrium: human impacts are causing an unprecedentedly quick elevation of atmospheric carbon-dioxide levels, leading to an elevation in the earth's average temperature. Although every living organism is affected by these changes, plants may be particularly at risk, as they are not able to migrate at the same timescale as the climate changes. Instead, plants largely have to rely on metabolic, physiological, and ecological strategies to compensate for environmental changes.

In an effort to secure understanding of how plants adapt to changing climate, a number of studies have considered changes in observables such as phenological characters and physiological rates, but due to methodological limitations, most of these studies only analyzed a limited period of a plant's life. These limitations make it difficult to obtain a complete picture of how species adapt in response to environmental changes. Furthermore, it is difficult to elucidate which responses are occurring in response to natural processes and which are related to anthropogenic influences. Quantitative models can help address these challenges, by integrating the impacts of a variety of environmental factors on the life cycle of a tree. This yields a particularly promising approach to studying the vegetation consequences of climatic changes. Naturally, such models need to be informed by empirical data. For this purpose, and also to address the other questions above, it is important to obtain long-term records of how vegetation has changed in response to climatic conditions.

Dendrochronology (from the Greek *dendros* = trees, *chronos* = time, and *logos* = knowledge) is a well-established science that can be used to infer growth rates under different environmental conditions (Schweingruber 1989; Stokes and Smiley 1996). It provides accurate and long series of data that provide yearly records of changes in environment conditions at a study site. As one example, tree-ring width (one of the characters used in dendrochronol-

ogy) shows strong correlations with temperature and precipitation across different landscapes throughout the world (Lara and Villalba 1993; Briffa et al. 2001; Briffa et al. 2004).

Although most of dendroclimatic studies have considered trees of temperate species, some tropical tree species have been shown to be especially suited for this kind of study. Worbes (2001), Schöngart et al. (2002, 2004, 2005, 2006), and Oliveira et al. (2009) have all shown that many tropical species are particularly suited for dendroclimatological analyses (in addition to unpublished works on the genera *Cedrela*, *Hymenaea*, and *Podocarpus* that also show promising results).

In this project, I will incorporate dependences on temperature and precipitation in an established model of plant growth developed by a former YSSP participant (Falster et al. 2010). The extended model will be used to study how emergent properties of vegetation, such as net primary productivity (NPP) and total biomass, are expected to change in response to future changes in temperature or precipitation changes.

## Research questions

The present study aims to elucidate the effects of changes in temperature and precipitation on vegetation structure. In particular, the following questions will be addressed:

- How do different temperature and precipitation regimes affect salient aggregate statistics of vegetation structure, in particular, average height, leaf-area index, net primary productivity, and biomass density?
- Which factor – temperature, precipitation, or stand age – is most limiting for tree development?
- How will tree stands develop under plausible future environmental scenarios?
- Do temperature and precipitation significantly interact in determining the population dynamics of trees?
- If time allows, I will also consider how different temperature and precipitation regimes affect evolutionary dynamics of leaf mass per area and height at maturation.

## Methods and work plan

### *Dendrochronological data*

We have available two datasets of tree-ring width measurements for two different tropical tree species (*Cedrela fissilis* – *Meliaceae* and *Hymenaea courbaril* – *Leguminosae*). These datasets have already been used to build chronologies of approximately 110 years, and both have been demonstrated to show significant relationships with climate (*Cedrela* mainly with temperature, *Hymenaea* mainly with precipitation). These relationships, between tree rings and temperature/precipitation, are well described by linear models with normally distributed residuals.

### *Photosynthetic effects of temperature and precipitation*

The rate of photosynthesis is well known to vary with temperature and precipitation. For temperature, this relationship is accurately represented by an initially exponentially increasing function, usually with a saturating maximum, and it is related to the optimal temperatures of the chemical reactions of this process (Bernacchi et al. 1992, 2001; Taiz and Zeiger 2004). On the other hand, water availability acts as a limiting factor on photosynthesis since it affects the

opening or closure of stomata, which changes CO<sub>2</sub> fluxes, and thereby alters photosynthetic rates and the transport of photoassimilates (Taiz and Zeiger 2004).

### ***Model adaptation and extension***

The vegetation model by Falster et al. (2011) will be adapted and extended to account for temperature and precipitation. As the relationships between tree rings and temperature/precipitation are well described by linear models with normally distributed residuals, a reasonable first assumption might be that, for the ranges of these two variables represented in the dendrochronological data, temperature and precipitation have linear and additive effects on photosynthesis, and thus also carbon assimilation. However, this assumption may not be adequate, as there are known interaction effects between temperature and precipitation (for example, high temperatures augment soil-water evaporation, leaving less water available for the trees). Moreover, using such simple models might hinder considering the effects of climate changes that are falling outside of those that have occurred in the past.

To overcome these challenges, we will first explore the extent to which interaction effects are affecting growth dynamics, by exploring selected interaction models. Second, we will make the leaf photosynthesis parameter that describes light-saturated photosynthesis a function of temperature and water use. The leaf will operate at constant maximum water use if it has enough water, which depends on this leaf water use and total leaf area. If water availability for the tree is less than the maximum water use, stomata will close, which means that water use per leaf and photosynthesis decline in parallel. To account for effects on respiration, we will include a temperature-dependent factor in the maintenance respiration.

Finally, the vegetation model by Falster et al. (2011) has been developed for Australian conditions, and will thus need to be parameterized with Brazilian trees data. Fortunately, as both countries have similar vegetation and are both influenced by ENSO (El Niño Southern Oscillation), only a few adjustments may be needed to account for the differences.

### ***Model implementation***

The model will be implemented in Matlab using an upwind scheme to solve the non-local partial differential equations that underlie the population dynamics.

### ***Influence of climate on forest dynamics***

After the model has been implemented, the available dendrochronological data will be used to parameterize the dependence on temperature and precipitation. Since the trees of the dendrochronological dataset are from well-mixed forests, we will examine several constant light environments sampled from an assumed heterogeneous forest.

Once the model has been parameterized, we will explore how the modeled stands grow under the three future temperature scenarios proposed by IPCC (2007). If possible, we will also investigate the potentially interacting effects of changes in water availability. The outputs will be compared with the original model by Falster et al. (2011), as well as with literature data.

### ***Work plan***

The first step in this work will be to test, using R, if there are significant interaction effects of temperature and precipitation on tree growth. We will then adjust the photosynthesis parameter as a function of temperature and/or precipitation, initially as a linear additive effect. After

this, we will parameterize the new version of the model with the available data (biomass, tree density, diameter distribution, etc. – if possible) from the sampling sites.

Once the model has been properly parameterized, the new model will be implemented in Matlab, accounting for population-level feedbacks. After implementing the model, we will finally investigate how the modeled stands grow under different future temperature scenarios.

## Relevance and link to EEP's research plan

This project, which is an extension of a previous YSSP project by Daniel Falster in 2006, will contribute to EEP's ongoing research on *Evolving Biodiversity*, by establishing a framework in which the impacts on vegetation of changes in temperature and precipitation can be assessed.

## Expected output and publications

The results of this project are intended to be published as a coauthored article in an international scientific journal.

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# Comparing methods for identifying optimal forest management

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## Goal

To compare the performances of a spatially explicit individual-based model and a model based on the perfect-plasticity approximation in predicting forest dynamics under different harvesting regimes.

## Background and motivation

The past few decades have seen a considerable increase in the number and level of detail of individual-based models (IBMs) of forest dynamics. These models forecast dynamics by predicting each individual's birth, dispersal, growth, and death and how these events are affected by spatial competition for resources with neighbors. Individual-based forest simulators have also been used for forest management (Busing and Maily 2004).

Despite their usefulness, IBMs have one important disadvantage: they require too much computational resources to be used at a large scale. For this reason, a number of approaches have been recently developed based on differential equations, rather than on algorithms (Adams et al. 2007; Strigul et al. 2008; Purves and Pacala 2008). A notable advance in this area has been the development of the perfect-plasticity approximation (PPA; Strigul et al. 2008), which builds on the assumption that trees experience full light above the canopy height, defined as the maximum height at which the canopy can be closed, and a constant level of reduced light below the canopy height. In turn, the canopy height is a dynamic variable, and thus depends on demographic parameters.

Strigul et al. (2008) showed that a spatially explicit IBM that implements the perfect-plasticity approximation (PPA) gives results similar to those of a spatially implicit PPA model. The latter describes forest dynamics by the von-Foerster equation for the density of a size-structured population, together with an integral condition for the canopy height. They also compared predictions based on the PPA with results from the IBM SORTIE (Pacala et al. 1993). The SORTIE model describes trees as having a rigid cylindrical crown located directly above the stems. Quite unrealistically, full crown interpenetration is allowed, i.e., availability of space in the overstory is not a limiting factor. Pacala and Deutschman (1995) derived a mean-field approximation of the SORTIE model, but the comparison between the two approaches failed, suggesting that spatial effects cannot be described simply through averaged quantities. Interestingly, Strigul et al. (2008) compared the mean-field approximation based on the PPA with an extended version of the SORTIE model, which also accounted for crown plasticity and phototropism, and found the two to be in good agreement.

As the aforementioned findings indicate, the PPA is a promising tool for understanding forest dynamics. However, until now it has been developed and studied only for natural forest systems. In this project, we will explore its validity for describing managed forest under different types of harvesting. This will be done in three steps. First, we will develop a spatially-explicit IBM of forest dynamics that accounts for crown plasticity and management. Second,



we will derive a PPA approximation corresponding to this IBM. Finally, we will compare and critically evaluate the results of the two approaches.

## **Research questions**

The two foci of this research project are comparison of different harvesting regimes and of methods for describing forest dynamics under management. The main research questions are summarized below:

- How do different harvesting regimes affect yield and harvesting costs, in particular as summarized by the resultant economic revenue?
- Given the high spatial symmetry underlying the PPA, can we expect that it gives a good description of forest dynamics under spatially symmetric cutting (e.g., clear-cutting)? Is the PPA also applicable under more complex, spatially heterogeneous harvesting regimes?
- Time permitting, we will also attempt to determine optimal management regimes that balance economic revenue with impacts on ecological and cultural ecosystem services.

## **Methods and work plan**

### *Model structure*

The spatially explicit individual-based model we will examine describes the dynamics of each tree in continuous time by considering birth, dispersal, growth, and death. Growth rates and mortality rates are affected by neighborhood competition, either through explicit light limitation as determined by the Beer-Lambert law, or through a proxy in the form of a competition index based only on mutual distances among trees (e.g., Pretzsch 2009). As we focus on a managed forest, birth and dispersal are determined entirely by the applied management regime.

The baseline submodels for tree growth, mortality, and mutual shading (i.e., light competition) will be defined according to two possible choices. The first option is to follow the physiological model developed by Falster et al. (2011), which has already been implemented as an IBM in a previous YSSP project. The second option is to develop the physiological submodels based on the SORTIE model. Crown plasticity will be added following Strigul et al. (2008).

### *Model implementation*

Each tree has a horizontal position within the given plot. To avoid boundary effects, we consider periodic boundary conditions. The total time of a model run is divided into a discrete number of time steps, and the status of each tree is updated after each time step. As a large amount of computing time is required to identify each tree's neighbors, we will superimpose a discrete spatial grid on the plot such that the search for the neighbors of a focal tree can be limited to the neighboring cells of the focal tree (Pacala and Silander 1985; Bercé 2002).

### *Harvesting regimes*

We will analyze the effects of different harvesting regimes on yield and harvesting costs, as summarized by economic revenue. The price of a harvested tree will be assumed to increase with stem diameter (and thus also with height). The harvesting cost will, at least initially, be assumed to be proportional to the number of harvested trees. Later, we may consider includ-

ing fixed expenses associated with harvesting operations, increased expenses associated with selective harvesting, and possibly also costs representing losses in cultural and ecological services.

The harvest regimes and control parameters to be analyzed are:

- A simple clear-cutting cycle, described by its frequency.
- Managed harvesting described by the frequency of harvesting and the fraction of trees removed at uniform spatial density.
- Selective harvesting based on size, described by a size-selectivity curve.
- Spatially non-uniform harvesting, described by a probabilistic model for the frequency of harvesting, as well as for the location, size, and shape of the harvested area.

### ***Model visualization***

Individual-based models can produce a large amount of data. Often, the most effective way to describe, explore, and summarize a large set of numbers is to visualize the information (Tufte 1983). Therefore, an important part of this project is devoted to the visualization of results. We plan to use OpenGL, a 3D graphics library in the C programming language, to provide a visualization of the modeled forest dynamics.

### ***Work plan***

The work plan is as follows:

- Definition of the basic physiological submodels that will be implemented in the IBM, following either the SORTIE model or Falster et al. (2011).
- Implementation of the OpenGL functions for visualization.
- Inclusion of crown plasticity in the IBM.
- Alternative description of shading and crown plasticity through the use of neighborhood competition indices.
- Inclusion of harvesting.
- Comparison with the PPA approach.

## **Relevance and link to EEP's research plan**

Human-induced changes have the potential to profoundly alter the ecological environment of a species and thus also play a major role in shaping observed ecosystem patterns. Predicting the effects of such impacts may allow for better and more sustainable management of natural resources. This work thus aims to link ecological research with policy-relevant questions.

## **Expected output and publications**

The results of this research project are intended for publication as a coauthored article in an international scientific journal. In addition, the developed visualization tool will be made available for future studies of spatially explicit vegetation dynamics.

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# **Biodiversity dynamics under intransitive competition and habitat destruction**

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## **Goal**

To investigate how biodiversity is affected by intransitive competition and habitat destruction in spatially structured and well-mixed populations.

## **Background and motivation**

Species are faced with a multitude of risk factors for extinction including small carrying capacity, large environmental variation, habitat loss, climate change, and invasive species (Drake 2006; Kuussaari et al. 2009). These factors naturally occur at certain baseline levels, but modern humans have contributed to an astonishing increase in the degree to which they exacerbate risks of biodiversity loss. This increase has been so large that we may be in the midst of a so-called sixth great extinction, in which the percentage of biodiversity loss may rival that of the mass extinction events at, for example, the ends of the Ordovician and Cretaceous periods (Leakey and Lewin 1995). With evidence pointing to a decline in ecosystem functioning related to extinctions (e.g., Rovito et al. 2009), it is of great importance to understand how species respond to the aforementioned threats. Pimm and Raven (2000) note that habitat destruction is the leading cause of extinction; hence, a focusing of efforts on understanding this phenomenon may provide great rewards for guiding conservation efforts that limit the magnitude of biodiversity loss and mitigate the associated negative consequences on ecosystem functioning.

Most work in this area is rooted in the metapopulation model of Levins (1969) and is more recently based on a model with multiple competing species introduced by Tilman et al. (1994). Refinements to this latter model have been proposed over the years, to include additional features (such as Allee effects; Chen and Hui 2009) or to relax assumptions (such as allowing imperfect trade-offs between competitive abilities and colonization rates; Banks 1997). Against this background of previous work, arguably the most pressing challenges arise from the need to account for the effects of spatial distributions and of intransitive competition.

While the model of Tilman et al. (1994) assumes a well-mixed environment, habitat loss is usually spatially correlated and produces distinct spatial fragments. Also, it has already been shown that local, as opposed to global, competition allows for a greater number of coexisting species (Laird and Schamp 2008). Therefore, it is necessary to understand the consequences of local competition in the context of habitat destruction.

In addition to the question of local versus global competition, another fundamental assumption built into the model of Tilman et al. (1994) is that of a hierarchical ranking of species in terms of their competitive abilities. In contrast, it may often be the case that competitive abilities do not follow a hierarchical ranking: the simplest such situation involves an invasion relationship such as  $A \rightarrow B \rightarrow C \rightarrow A$ , where  $x \rightarrow y$  indicates that an individual of species  $x$  outcompetes an individual of species  $y$ . This is most commonly illustrated by the rock-scissors-paper game and is known as intransitive competition. Sinervo and Lively (1996)

observed such competition in *Uta stansburiana*, a species of lizard in which individuals express one of three color morphs that exhibit differential territory use and sexual selection strategies. Buss and Jackson (1979) also documented intransitive competition in a coral-reef environment with various subsets of twenty species interacting with each other.

By allowing for intransitive and local competition in a habitat-destruction model we may refine predictions of the response of species in such circumstances and provide useful guidance for conservation efforts.

## Research questions

This project aims to further our understanding of how biodiversity is jointly affected by intransitive competition and habitat destruction. In particular, I will address the following questions:

- Which features of competitive interactions best explain variation in coexistence?
- How is the biodiversity of communities with intransitive competition affected by habitat destruction?
- How do these results differ in spatially structured and well-mixed populations?

If time allows, the effects of two additional model refinements will be explored:

- How are predicted dynamics and outcomes affected by uncertainties in the result of competition between two species?
- What impact does temporal variation in site quality have on the predicted dynamics and outcomes?

## Methods and work plan

This project will be based on the intransitive competition model and simulation approach introduced by Laird and Schamp (2008), in conjunction with the habitat-destruction model of Tilman et al. (1994).

### *Spatial structure*

Following Laird and Schamp (2008), species occupy a lattice with periodic boundaries. The spatially explicit version of this model has a (Moore) neighborhood consisting of the eight cells surrounding a selected focal cell. In the well-mixed version, the neighborhood of a focal cell is the entire lattice, thus obviating any effect of spatial structure.

### *Site destruction*

To account for spatially correlated site destruction, in lieu of purely random habitat loss, a spatial point process is employed to generate a clustered distribution of lattice cells classified as destroyed. At a later stage, we may also consider temporal dependencies, such as autocorrelations, among destroyed sites.

### *Competition between species*

We assume that the outcome of competition between two species is predictable, with one of the species always outcompeting the other. This is represented in the form of a matrix with elements  $a_{ij}$  that for any two species  $i$  and  $j$  indicate which one is competitively superior,

$$a_{ij} = \begin{cases} 1 & \text{if species } i \text{ outcompetes species } j, \\ 0 & \text{otherwise.} \end{cases}$$

Additionally, to indicate that a species does not compete among itself, we set  $a_{ii} = 0$  for all  $i$ . To reflect the assumption that there is always a unique winner in a competition between two different species, we require  $a_{ij} + a_{ji} = 1$  for all pairs  $(i, j)$  with  $i \neq j$ . In the mathematical literature, a matrix satisfying these conditions is known as a tournament.

### ***Tournaments***

For competition described by a tournament, a number of possible indices exist for measuring intransitivity and for otherwise describing the structure of competitive interactions. Laird and Schamp (2009) noted that, while previously studied intransitivity indices were excellent predictors of coexistence, there was still a degree of unexplained variance. Hence, in an effort to determine which measures of a tournament best explain variation, a number of indices will be explored. Candidate indices include, but are not limited to, number of cycles, average cycle length, distribution of cycle lengths, girth, distribution of in- and out-degrees, and Fiedler value. Also, for comparison, indices examined by Laird and Schamp (2009) will be included: Slater's  $i$  and  $j$ , Bezembinder's  $\rho$  and  $\delta$ , Petraitis's  $t$ , and Laird and Schamp's relative-intransitivity index.

### ***Model dynamics***

Following the habitat-destruction model of Tilman et al. (1994), we consider parameters describing the colonization rate  $c_i$  and the mortality rate  $m_i$  of species  $s_i$ . Slightly modifying the model of Laird and Schamp (2008), in addition to choosing a focal site and conducting a competition event, our model includes mortality and sites may be classified as destroyed. This will better mimic the various mechanisms explored by Tilman et al. (1994).

For a given tournament matrix, and with the lattice initially being randomly populated (possibly including destroyed or unoccupied cells), model dynamics will proceed as follows:

- Choose a focal site  $i$ , with  $s_i$  denoting the species, if any, occupying that site. Increment the iteration count. If  $i$  is classified as a destroyed or unoccupied, repeat this step.
- Choose a random neighboring site  $j$  of  $i$ ; if  $j$  is occupied,  $s_j$  denotes the species occupying this site. (In a future refinement of this model, the possibility of "smart" dispersal may be included by favoring unoccupied sites when selecting a neighboring site.)
- Realize the result of the interaction between  $i$  and  $j$ :
  - If  $j$  is destroyed, do nothing.
  - If  $j$  is unoccupied, colonize  $j$  with probability  $c_i$ .
  - If  $j$  is occupied and  $s_j$  is superior to  $s_i$  ( $a_{ji} = 1$ ), do nothing.
  - If  $j$  is occupied and  $s_j$  is inferior to  $s_i$  ( $a_{ji} = 0$ ), colonize  $j$  with probability  $c_i$ .
- With probability  $m_i$ , let  $s_i$  die, and thus change  $i$  to unoccupied.

### ***Model implementation***

A simulation tool will be developed in C/C++ with an OpenGL graphical front-end. Following Laird and Schamp (2009), we use a square lattice of size  $N \times N$  cells.  $N^2$  iterations of

the steps above constitute one generation, and 500 generations embody one replication. During the course of a replication, the time to the first extinction and either the time to monoculture or the species richness after 500 generations will be recorded. Multiple replications form a data set, and results will be derived from the analysis of that set.

### **Work plan**

I aim to complete my research project through the following steps:

- Develop the simulation tool, including its basic functionality and graphical front-end.
- Use the simulation tool to generate data. These data will then be used to identify the measures of intransitivity that best explain variation in coexistence. This will be achieved either based on an analysis of variance (ANOVA) or a generalized linear model (GLM).
- Use the simulation tool to investigate how biodiversity is affected by intransitive competition and habitat destruction, as well as how these results compare or contrast in spatially structured and well-mixed populations. Additionally, the well-mixed model might be examined using a system of ordinary or stochastic differential equations.
- If time allows, extend the simulation tool to account for uncertainty in competitive outcomes and then use this extended simulation tool to explore the consequences of this refinement.
- If time further allows, implement an additional extension of the simulation tool to consider and explore the consequences of temporally varying site quality.

### **Relevance and link to EEP's research plan**

This project aims to further our understanding of the ecological consequences of habitat destruction. It will therefore contribute to EEP's research project on *Evolving Biodiversity*.

### **Expected output and publications**

The results of this research project are intended for publication as a coauthored article in an international scientific journal. I also intend this work to be a part of my Ph.D. thesis.

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# Indirect reciprocity with costly information

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## Goal

To study the evolutionary dynamics of indirect reciprocity based on reputation information when sharing and maintaining such information is costly.

## Background and motivation

Humans are characterized as reciprocal animals cooperating with each other even though such behavior is costly. Why costly cooperation is frequently observed in many species, including humans, has been an evolutionary mystery, which is widely studied by using game theory. The Prisoner's Dilemma (PD) game and its variants are typically used for examining cooperative behavior in social dilemmas. In a PD game, players have a choice to cooperate or to defect: although mutual cooperation maximizes their social welfare, defection is always the dominant strategy. Therefore, additional mechanisms are required for stabilizing cooperation, such as repeated encounters or a structured population (e.g., Nowak 2006).

Indirect reciprocity is a particularly important mechanism for sustaining cooperation when individuals rarely interact with the same partners (Nowak and Sigmund 2005); such one-shot interactions are increasingly ubiquitous in human societies (e.g., anonymous encounters in online marketplaces such as amazon.com and ebay.com; Bolton et al. 2004). For indirect reciprocity, reputation information plays a key role (Alexander 1987). In a canonical model of reputation-based indirect reciprocity, individuals possess reputation scores determined by their past actions toward other individuals (Nowak and Sigmund 1998a, 1998b). Individuals helping others are regarded as good and those cheating are regarded as bad. Individuals help others when those have a good reputation, but not those when they have a bad reputation. Consequently, helping others to maintain a good reputation is more beneficial than cheating to gain a momentary profit. Recently, evidence for indirect reciprocity has been found in animals (Bshary and Grutter 2006; Akçay et al. 2010).

Sharing information about reputations is crucial for the mechanism of indirect reciprocity. In practice, however, it often is costly to share information about the reputations of individuals. For example, while amazon.com adopts a feedback mechanism to assess each seller, customers often do not submit such feedback, because for them this involves extra work. More in general, collecting, sharing, and maintaining information is costly, so the availability and quality of information may suffer from a tragedy of the commons (Hardin 1968; Ostrom 1990). Individuals, or a marketplace as a whole, may try to address these challenges by charging fees before allowing individuals to access reputation information, which can lead to the emergence of a reputation market operating alongside the dynamics of indirect reciprocity.

Most previous studies in biology have ignored the costs involved in sharing information about the reputation of individuals. In contrast, several studies in economics have treated the issue of costly observation (Ben-Porath 2003; Miyagawa et al. 2008). Most of them, however, only considered the case in which observing others and getting information about the reputation of those individuals is costly. In the present study, we will explore a general model in-

cluding two types of cost: costs for obtaining information and costs for exchanging information. Moreover, we will consider extensions in which individuals exchange reputation information, and may be motivated to contribute false or inaccurate information to others.

## Research questions

In the present study, we will investigate the dynamics of indirect reciprocity based on costly reputation information. We will identify conditions for sustaining cooperation and examine the following specific aspects:

- Competition among reputation providers. In a population with pairwise interactions and communication, we consider many reputation providers. If the quality of information offered by a reputation provider is high, every reputation customer will be motivated to obtain information from this provider. We will thus explore competition among reputation providers and identify conditions for the emergence of hub providers.
- Modes of exchanging reputation information. Individuals can deal with reputations either through a centralized institution (e.g., the assessment system in amazon.com) or through pairwise communication (e.g., gossip). We will examine which of those two modes is more efficient.
- Deficient information. Several animals implement their systems of indirect reciprocity by direct observation (Bshary and Grutter 2006; Akçay et al. 2010). Humans, however, often adopt indirect observation, not the least since we can communicate with each other using complex language (Dunbar 1998; Nowak and Sigmund 2005; Sommerfeld et al. 2007). We will investigate conditions for cooperation when reputation may mistakenly spread via gossiping, or when reputation providers offer false or inaccurate information.

## Methods and work plan

### *Model overview*

We extend the canonical model of indirect reciprocity with binary reputations (Nowak and Sigmund 1998a, 1998b) in a population of  $M$  individuals. In this model, each individual as perceived by each other individual has a simple reputation: good (G), bad (B), or unknown (U). Specifically, each individual has its information storage represented by a vector of reputations of others. Each element of these vectors represents the relevant individual's reputation. Observing a game and exchanging the resultant information impose cost on individuals. Each individual who needs reputation information pays a cost when consulting a reputation provider.

Below, we first describe a multi-provider model as an individual-based model to be studied by numerical analysis. In this model,  $N$  denotes the number of existing reputation providers, so that  $N = 1$  represents a monopolistic situation (recovering the canonical model of indirect reciprocity), while  $N = 2$  represents a duopolistic situation. If  $N$  is large, there is competition among many reputation providers. We will successively analyze the one-provider and two-provider models, before addressing the general case of  $N$  providers. In particular, the one-provider and two-provider model can be studied by mean-field analysis. Model extensions for studying additional research questions are described at the end of this section.

### ***Donation game***

We consider a sufficiently large population, in which individuals encounter each other and play the so-called donation game. In a one-shot donation game, two individuals are selected uniformly randomly and participate in the game. One serves as a donor, and the other serves as a recipient, while  $N$  reputation providers serve as observers.

The donor either cooperates (C) with or defects (D) against the recipient. The donor makes a choice (C or D) according to its strategy (ALLC, ALLD, or DISC) and the recipient's reputation (G, B, or U). ALLC donors always cooperate, ALLD donors always defect, and DISC donors cooperate if the recipient's reputation is G or U (so-called trustful discriminators). The donor pays a cost  $c$  and the recipient gains a benefit  $b$  if the donor cooperates ( $0 < c < b$ ), whereas the payoffs of the game are 0 if the donor defects.

### ***Information exchange***

Prior to deciding whether to cooperate or defect, a DISC donor requests the recipient's reputation from a reputation provider and pays a cost  $\beta > 0$  to the provider. If the provider knows the recipient's reputation (G or B), the donor sticks to this provider after the game. Otherwise (U), the donor changes to a randomly chosen other provider after the game. Tolerances to a larger number of unsuccessful requests can be considered, and non-uniform distributions can be specified for choosing the new provider.

At the same time, all providers may observe the game. An observer  $i$  decides whether or not to do so according to its observation probability  $q_i$ . If the provider observes, it pays a cost  $\gamma > 0$  and updates its reputation information concerning the donor. If the provider does not observe, the donor's reputation in the provider's information storage changes to U. Note that a donor never uses its own information storage for playing the donation game. In this way, we exclude effects of direct reciprocity.

### ***Errors***

We can introduce errors of implementation and/or perception, with donors choosing their actions mistakenly and/or observers failing to update their information storage correctly.

### ***Assessment rule***

The reputations of individuals are updated based on their past actions and the assessment rule used by the population. We consider second-order assessment rules that assign reputations G or B to donors depending on whether these donors used strategies C or D toward recipients and on whether these recipients had reputations G or B. We may explore various assessment rules such as so-called image scoring and simple standing.

### ***Update rule***

After sufficiently many games, we determine the average payoffs of all individuals (including the providers) and update their strategies accordingly. We assume that individual  $i$  adopts the strategy of individual  $j$  with probability  $1/(1 + \exp(-s(P_j - P_i)))$ , where  $P_i$  and  $P_j$  are the respective payoffs and  $s > 0$  controls the intensity of selection.

### ***Mean-field analyses***

Here we describe the method of mean-field analysis for large populations ( $M \gg 1$ ) with two providers ( $N = 2$ ). In this case, we consider replicator dynamics based on the payoffs of the

different strategies in the donation games (ALLC, ALLD, and DISC) and competition between the two reputation providers. We denote the fractions of individuals using strategies ALLC, ALLD, and DISC by  $x_1$ ,  $x_2$ , and  $x_3$ , respectively, the fractions of individuals using these strategies and having a good reputation by  $g_1$ ,  $g_2$ , and  $g_3$ , respectively, the strategies of the two providers by  $q_1$  and  $q_2$  (with  $q_1 > q_2$ ), and the fractions of individuals consulting each of the two providers by  $p_1$  and  $p_2$  (with  $p_1 + p_2 = 1$ ).

For the purpose of this mean-field analysis, the strategies of the two providers are fixed ( $q_1, q_2 = \text{const.}$ ), and we assume that reputations change and individuals switch providers sufficiently faster than strategies change ( $\dot{g}_1, \dot{g}_2, \dot{g}_3, \dot{p}_1, \dot{p}_2 \gg \dot{x}_1, \dot{x}_2, \dot{x}_3$ ). After sufficiently many donation games,  $g_1$ ,  $g_2$ ,  $g_3$ ,  $p_1$ , and  $p_2$  thus equilibrate. On this basis, we can calculate the payoffs of ALLC, ALLD, and DISC, which we denote by  $P_i$  for  $i=1,2,3$ . Using these payoffs, we can examine the replicator dynamics  $\dot{x}_i = x_i(P_i - \bar{P})$ , for each strategy  $i$ , where  $\bar{P} = \sum_i x_i P_i$  is the average payoff.

### ***Provider distribution***

In the multi-provider model, a reputation provider  $i$  has  $k_i$  customers. The emergence of hub providers can thus be investigated by studying the probability distribution of  $k_i$  through numerical analyses. If the distribution of  $k_i$  is non-Poissonian, this suggests that hub providers emerge. We will check, in particular, whether the distribution of  $k_i$  follows a power law, the characteristic of a scale-free distribution.

We will also check whether the number  $N$  of providers and the distribution of  $k_i$  converges to either of the following two extremes:  $N = 1$  with  $k_1 = M$ , corresponding to a centralized institution with global information storage accesses by all individuals, or  $N = M$  with  $k_i = 1$ , corresponding to pairwise communication among all individuals.

### ***Deficient information***

In a model by Nakamaru and Kawata (2004), individuals are checking the reliability of reputation information against their direct experiences, as a means of detecting deficient information. We will instead consider a model in which providers that contribute deficient information are detected by customers examining reputation information from multiple providers (Sommerfeld et al. 2008). We thus extend the basic multi-provider model through two modifications: (1) We allow providers, with a certain probability  $r_i$ , to avoid paying the cost  $\beta$  by providing reputation information not based on observation. Such providers evidently are unreliable. (2) Each donor asks a fraction  $f_i$  of providers about the recipient's reputation. The donor accepts the majority's opinion as the reputation of the recipient, and providers that contribute a minority opinion lose the donor as a customer.

### ***Work plan***

We will attempt to examine the three research questions listed above in the indicated order, and proceed as far as time permits.

## **Relevance and link to EEP's research plan**

Indirect reciprocity is considered a main mechanism for the emergence and maintenance of cooperation, particularly in the human societies. This project, therefore, contributes to EEP's *Evolution of Cooperation* research project.

## Expected output and publications

The results of this project are intended for publication as a coauthored article in an international scientific journal. M.N. also expects this work to be a part of his Ph.D. thesis.

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# **Biodiversity dynamics in stream communities**

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## **Goal**

To investigate the evolutionary dynamics of traits concerning adaptation to the local environment and to analyze how environmental factors affect the biodiversity of aquatic insects in streams and rivers.

## **Background and motivation**

Stream and river ecosystems are especially vulnerable to various types of natural and anthropogenic disturbances, which threaten their capacity to provide important ecosystem services, like food and clean water. Water quality affects aquatic insects (or, slightly more generally, benthic macroinvertebrates) particularly strongly: these play a functional role in aquatic food webs (Song et al. 2007), and have therefore been widely used as indicators of ecosystem health (Hellawell 1986; Rosenberg and Resh 1993). Understanding how their biodiversity dynamics depend on environmental factors is thus a question of pivotal importance for the management of aquatic ecosystems.

Streams and rivers have characteristic longitudinal profiles of latitude and environmental factors (e.g., temperature, oxygen, pH, substrate size), which are typically steeper in the uplands, where the streams originate, and have a more gradual slope in the lowlands near a river's terminus. River segments may vary in length, from one kilometer to tens of kilometers, and this is the spatial scale of major floodplains and channel features. Homogeneous units recognized within a segment are called reaches. In practice, reaches are often defined as a repeating sequence of channel units, such as riffle–pool–run sequences (Frissell et al. 1986). A reach can be 100 m or less in length in a small stream, and several kilometers in a large river.

Aquatic insects are adapted to stream ecosystems morphologically and in terms of their life-history traits. They typically have a life cycle consisting of four phases (egg, larva, pupa, and adult), which they spend in two different environments: in the water (egg, larva, and pupa) and outside the water (adult). Sexual reproduction is the norm, but parthenogenesis also occurs. The larval phase is relatively long (on the order of years), while the phase as a flying adult outside of the water is relatively short (on the order of weeks); adults often do not engage in much more activity than finding a mate and laying eggs before they die. As a consequence of physical and biological processes, the particle size of organic material that enters the water upstream (mostly leaf litter) during its transport downstream becomes progressively smaller (Vannote et al. 1980). Being typical generalists, aquatic insects can be classified into only a handful of functional feeding groups such as shredders, collectors, scrapers, and predators, according to their role in the processing of this organic matter, by considering a number of factors: the origin and size of the food items infested, the general location from which the food is taken (from the substrate or from the water column), the mechanisms of food acquisition (enabled by morphological and/or behavioral adaptations), as well as the trophic level. Accordingly, the traits reflecting the adaptation of benthic organisms to local environmental conditions mostly allow inferring their feeding strategy.

Aquatic habitats can be characterized passably by a surprisingly low number of important environmental factors (Cummins 1964), including current velocity, substrate size, food availability, and physical and chemical properties (e.g., oxygen content, temperature, and pH). Current velocity is the defining feature of streams and rivers. Temperature affects all life processes. The substrate is important to aquatic insects as the surface on which they dwell. Dissolved oxygen and pH are especially influenced by anthropogenic and non-anthropogenic pollution.

The dynamics of benthic macroinvertebrate communities are empirically studied by analyzing species–abundance distributions (SAD; e.g., Magurran 2004). SADs are usually visualized as rank–abundance diagrams which graph, on a logarithmic vertical scale, the relative abundances of species ranked horizontally in order of descending abundance. Community responses to changes in environmental factors, such as caused those by pollution, impose characteristic signatures on the observed SADs (Qu et al. 2008).

In this project, I will model and analyze the biodiversity dynamics of benthic macroinvertebrate communities and their responses to pollution using an individual-based eco-evolutionary model that considers essential life events such as birth, death, random movement, downstream movement, and upstream flight, and includes the effects of both competition within the community and local adaptation to, or tolerance for, extrinsic environmental factors.

## **Research questions**

I will model macroinvertebrate biodiversity by considering realistic spatial variation in local conditions along streams and rivers, and compare the SADs obtained from the model to empirical SADs reported from Korean streams and rivers (Qu et al. 2008; Tang et al. 2010). Specifically, I will address the following questions:

- How do basic environmental factors and functional feeding groups enhance the biodiversity of macroinvertebrates in the modeled stream ecosystems?
- How well can a relatively simple eco-evolutionary model reproduce empirical biodiversity patterns observed in Korean streams and rivers?
- How does pollution affect the biodiversity of stream communities in the model?
- How well can the model reproduce biodiversity patterns of polluted Korean streams and rivers?

## **Methods and work plan**

### *Model overview*

I construct an individual-based eco-evolutionary model that considers essential life events of macroinvertebrates – such as random movement, downstream movement, upstream flight, birth, and death – as they occur in continuous time and space along a one-dimensional stream. Only larvae are explicitly modeled. An individual has several traits that describe its tolerance to local environmental conditions, as well as its movement behavior. I consider a stream or river of 10 to 100 km length from headwaters to mouth. Consequently, individuals that move out of this range downstream are lost, while individuals that attempt to move out of this range upstream remain in the headwaters region. The various events occur with a frequency that is determined by the ratio of their maximal rate to the sum of all maximal event rates. Given the

event type, a focal individual is selected with uniform probability; the event is then realized with a probability given by the ratio of the individual event rate to the maximal rate for that event type. Waiting times between possible events are sampled from an exponential distribution with the sum of all maximal event rates as the expected value (Allen and Dytham 2009).

### **Death**

Individuals  $i$  die with a death rate  $d_i$  that is proportional to the competition they experience, and inversely proportional to the local carrying capacity and their tolerance for the local environmental conditions,

$$d_i \propto \frac{\sum_{j \neq i} N_{\sigma_x}(x_i - x_j)}{K(x) \prod_e N_{\sigma_e}(v_{ie} - v_e(x))},$$

where  $i$  is the index of an individual,  $v_{ie}$  are the traits describing its tolerance to the various environmental factors  $e$  (such as current velocity  $v$ , temperature  $t$ , oxygen  $o$ , pH  $p$ , and substrate size  $s$ ; maybe also organic matter  $m$ ),  $v_e(x)$  are the corresponding longitudinal profiles of these environmental factors,  $K(x)$  is the longitudinal profile of the carrying capacity density of organisms that are maximally adapted to location  $x$ , and  $N_\sigma(d)$  is the normal function  $\exp(-\frac{1}{2}d^2 / \sigma^2)$  with standard deviation  $\sigma$ .

### **Downstream movement**

Individuals drift downstream with a rate

$$r_i = \frac{r_{\max}}{1 + \exp(-\alpha(d_i - d_{\text{th},i}))},$$

where  $r_{\max}$  is maximal drift rate,  $d_i$  is the death rate of individual  $i$ ,  $d_{\text{th},i}$  is a corresponding threshold describing the death rate above which individual  $i$  is likely to drift, and  $\alpha$  describes the sharpness of this onset of drift around  $d_{\text{th},i}$ . Individuals drift for a duration  $\Delta t$  drawn from an exponential distribution,

$$\Delta t \sim \sigma_{t,i} \exp(-\Delta t / \sigma_{t,i}),$$

where  $\sigma_{t,i}$  is their average drifting duration. Their target location is found by integrating over the velocity profile  $v_v(x)$ .

### **Random movement**

Individuals move randomly with a rate  $r_m$ , changing their position by drawing a new position from a normal distribution centered on their old position with standard  $\sigma_{m,i}$ .

### **Flight**

At the end of each year, before reproduction, individuals may undertake a directed movement step along the stream. This describes the essence of their life phase as an adult, covering a distance

$$\Delta x \sim \sigma_{x,i} \exp(-\Delta x / |\sigma_{x,i}|),$$

where  $\sigma_{x,i}$  is their average flight distance. We interpret a negative value of  $\sigma_{x,i}$  as upstream flight and a positive value as downstream flight.



### ***Birth***

At their target location, each individual produces  $b \exp(-c\Delta x_i)$  offspring and dies. The discounting factor  $0 < \exp(-c\Delta x_i) < 1$  imposes a cost of dispersal, with  $c$  measuring the strength of this cost. With probability  $\mu$ , all offspring traits may undergo an incremental mutation relative to those of their parents; their trait values are then drawn from a normal distribution centered on the parental trait value, with different standard deviations for the different traits chosen so as to obtain in the population a stable coefficient of variation of about 1/2 in each trait. Immediately after their birth, offspring undertake a random movement step as described above (so as to prevent artificial crowding).

### ***Pollution***

We consider pollution by incorporating point sources that release organic matter or other substances into streams and rivers, thus affecting the downstream longitudinal profiles of environmental factors. Non-anthropogenic pollution mostly affects pH, while anthropogenic pollution causes a low availability of oxygen. The impacts of pollution on environmental factors are modeled by changing the longitudinal profiles of these factors in accordance with data observed in Korean streams and rivers.

### ***Empirical data***

Environmental factors (temperature, dissolved oxygen, pH, and substrate size) and the densities of benthic macroinvertebrates were recorded monthly over a period of 10 years for various streams and rivers, both clean and polluted, in Korea. The data was then analyzed by determining the SAD for each stream or river (Qu et al. 2008; Tang et al. 2010). The longitudinal profiles of environmental factors will be obtained based on information in the published literature in conjunction with the aforementioned empirical data from Korean streams and rivers.

### ***Work plan***

The work plan is as follows:

- Add environmental factors (current velocity, temperature, oxygen, substrate size, and pH) one by one to the model and observe their effects on biodiversity patterns.
- Compare the modeled SADs to the empirical SADs.
- Introduce pollution events and observe their effects on biodiversity patterns.
- Also for the polluted streams, compare the modeled SADs to the empirical SADs.
- Adjust the model until a satisfactory match of model results with empirical data is achieved.

## **Relevance and link to EEP's research plan**

This project extends work previously conducted as part of EEP's research project on *Evolving Biodiversity* (e.g., Doebeli and Dieckmann 2003; Heinz et al. 2009; Payne et al. 2011), interfacing these modeling approaches with empirical observations of the key ecological factors that promote or hinder the biodiversity of benthic macroinvertebrate communities in Korean streams and rivers.

## Expected output

I intend to publish this work as a coauthored article in an international scientific journal. I also expect this work to be a part of my Ph.D. thesis.

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# **Financial-market stability in the presence of heterogeneous adaptive agents**

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## **Goal**

To investigate the interplay between financial-market dynamics and emerging investor personalities of agents with the ability of self-adaptation and social learning.

## **Background and motivation**

The financial system is the core of our current economy. Financial markets, as the most important part of the financial system, provide an efficient way to trade assets of various kinds. Asset prices determine investor decisions and depend on them in turn, leading to complex dynamics that are prone to drastic fluctuations in both asset price and investor wealth; an issue that, although not new, has recently attracted mounting public attention. Traditional financial research has usually assumed that investors are homogeneous; in the real world, however, they are heterogeneous and adaptive. This means that they can adjust, over and over again, their beliefs and strategies according to the market situation and their own performance histories. Such adaptability is in fact necessary to achieve market efficiency, but it is also the force at the origin of great market tremors and financial crises.

Agent-based models allow analyzing the interplay between investor personalities and financial market dynamics without a need for artificially constraining the heterogeneity or adaptability of investors. To establish the proper context for such modeling efforts, we elaborate on these two key points in turn.

Investors are heterogeneous. In a real financial market, there are many participants, like fund managers, investment bankers, speculators, and individual investors, and these differ, e.g., with respect to their beliefs, motives, risk preferences, time horizons, and trading frequency. Wolf et al. (2007) showed that competition may result in stable coexistence of different explorative and risk-taking strategies in animals, leading to characteristic “animal personalities”. According to Simon (1956) and to Kahneman and Tversky (1979), economics and finance are witnessing an important (if actually slow) paradigm shift, from a representative, rational-agent approach towards a heterogeneous, bounded-rational approach.

Investors are adaptive. Based on empirical studies, Ippolito (1992), Del Guercio and Tkac (2002), Benartzi and Thaler (2007), and De Jong et al. (2009) found that investors change their behavior, which in turn affects market prices. Investors do this either through individual learning or through social learning. Chen and Yeh (2001) introduced a “business school” mechanism to implement social learning. Chang (2007) described a learning process via various individual and social learning factors. Ryuichi (2010) allowed agents to learn other agents’ decision parameters directly, which may be considered unrealistic, since such parameters are usually not observable as such and can be inferred from observable actions only with great uncertainty.

Social learning through imitation tends to reduce investor heterogeneity, creating a trend to “follow the herd”. This can often be a successful strategy, but it may also create market sit-

uations that greatly reward minority decisions. This is reminiscent of the El Farol Bar Problem of Arthur (1994) and the Minority Game of Challet and Zhang (1997), in which congestion entails low efficiency. This suggests that there is a collectively optimal level of social learning that preserves investor heterogeneity while still fostering market efficiency.

The Santa Fe Institute (SFI) artificial stock market model (Arthur et al. 1997) is an early and widely studied agent-based market model, designed to explore asset-pricing theory by employing heterogeneous agents. Such agent-based methods have recently become popular, because they enable a repeatable and controllable approach to otherwise intractably complex dynamics. Agents in the SFI artificial stock market achieve individual learning through updating their strategies via a genetic algorithm (GA). LeBaron (2001) revised the SFI model to include social learning via a strategy pool, which is not only more efficient but also better reflects reality. In this project, we will thus follow the latter approach.

## Research questions

Modeling a group of agents with different risk attitudes and the ability to learn from history and each other, I will address the following questions:

- Which population structures emerge, and how do they affect asset prices and wealth distributions?
- How does the introduction of social learning influence market dynamics?
- Can we identify population structures that promote or threaten market stability?
- What is the relationship between trading frequency and wealth distribution?

## Methods and work plan

### *Model overview*

Our model is agent-based and uses discrete time. Agents can divide their wealth over two assets: firstly, there is a risk-free bond (not modeled explicitly), paying a known interest rate; secondly, there is a risky stock, paying an uncertain dividend that fluctuates according to an AR(1) model. At the end of each period, the agents may reallocate their wealth; by selecting the number of stocks and bonds in their *portfolio*, they attempt to maximize the expected utility of their wealth. To assess this expected utility, the agents apply *forecasting* strategies to estimate the value of the stock in the next period; the number of stocks they want in their portfolio depends on the current and expected future *price*. To satisfy the *demand* thus created, the market offers a *trading* scheme that adjusts prices and demands accordingly. By continually comparing predicted and actual stock values, agents assess the usefulness of their forecasting strategies and *learn* to use good ones. All agent decisions are influenced by four evolvable traits characterizing an investor's *personality*.

### *Portfolio*

Agents divide their wealth between a bond and a stock. With  $x_t^i$  denoting the number of shares held by agent  $i$  at time  $t$ ,  $p_t$  the price of a share,  $d_t$  the dividend,  $r_t$  the risk-free interest rate (initially assumed to be fixed for all times,  $r_t = r_f$ ), the wealth  $W_{t+1}^i$  of agent  $i$  at time  $t+1$  is given by

$$W_{t+1}^i = x_t^i(p_{t+1} + d_{t+1}) + (1 + r_t)(W_t^i - p_t x_t^i).$$

The expectation of the share value  $v_{t+1} = p_{t+1} + d_{t+1}$  (and therefore of  $W_{t+1}^i$ ) depends on an agent's forecasting strategies (see below). Investment into the bond is modeled implicitly: wealth not allocated to the stock is implicitly invested in the bond. Agents attempt to maximize their utility

$$U(W_{t+1}^i) = -\exp(-\gamma^i W_{t+1}^i),$$

which represents constant absolute risk aversion (CARA) (von Neumann and Morgenstern 1944), with  $\gamma^i$  denoting the coefficient of absolute risk aversion of agent  $i$ .

### **Forecasting**

Each agent  $i$  has a list of strategies  $(a_j, b_j, c_j)^i$  to forecast the expected stock value as

$$E_t^i(v_{t+1}) = a_j^i(v_t) + b_j^i(v_t - v_{t-1}) + c_j^i,$$

which amounts to estimating stock values as an AR(2) process. In each period, agents reorder their strategies according to the squared deviation of their recently predicted stock value from the actual current stock value. Each strategy is thus assigned an updated weight index

$$w_{t,j}^i = (1 - \mu^i)w_{t-1,j}^i + \mu^i(v_t - E_{t-1}^i(v_t))^2,$$

where  $\mu^i$  describes the agent's propensity to accept new information. Agents pick a strategy for making the next forecast with a probability proportional to  $(w_{t,j}^i)^{-\sigma^i}$ , where  $\sigma^i$  describes the relevance the agent assigns to a success-based ordering of its strategies.

### **Price and demand**

It can be shown (von Neumann and Morgenstern 1944) that agents maximize their expected CARA utility by holding

$$x_t^i = \frac{E^i(v_{t+1}) - p_t(1 + r_t)}{\gamma W_{t-1,*}^i}$$

shares, where  $w_{t-1,*}^i$  is the weight index of the forecasting strategy the agent currently uses (which roughly reflects the historical variation in this rule's forecasting success, see its definition above). The demand thus generated depends on the current price  $p_t$ .

### **Trading**

The agents' respective demands are collected and trading prices are adjusted until supply meets demand. While trading is in this sense optimal, we allow for the possibility that agents do not have equal access to the market: in an attempt to mimic the situation in real markets, we thus assume that wealthier agents enter the market more frequently. Agents that do not enter the market within a given period do not participate in the price-setting scheme and cannot reallocate their wealth during that period.

### **Learning**

If the weight index of a strategy exceeds an agent's weight threshold  $\tau^i$ , the agent replaces this strategy by a new strategy drawn randomly from a set of centrally published strategies. This strategy pool contains  $n$  strategies,  $m$  of which are the  $m$  most successful strategies in the agent population and the rest are randomly generated strategies. Large values of  $m$  correspond to a high degree of social learning.

### ***Personalities***

For each agent, the vector  $(\gamma, \mu, \sigma, \tau)^i$  describes its “investor personality”. In each period, these personality traits are subject to mutations with small probability, upon which new trait values are drawn from Gaussian distributions of given widths centered on the old trait values.

### ***Model implementation***

The algorithm sketched above will be implemented in C, while the model output will be analyzed in Matlab.

### ***Work plan***

The work plan is as follows:

- Using a set of “reasonable” personality trait values, motivated by common sense, run the model with a monomorphic, non-evolving investor population, and visualize asset prices, wealth distribution, and strategies.
- Identify, if possible, model parameters that produce asset prices and wealth distributions with “realistic” qualitative features. Assess whether there are accompanying strategy patterns and how these can be interpreted.
- Let investor traits evolve and observe the resultant trait distributions. Vary model parameters to establish stable polymorphisms through evolutionary branching.
- Add social learning and observe its effects. Look for a critical level of social learning at which its costs (loss of heterogeneity, leading to an inability to react to market fluctuations) outweigh its benefits (ability to follow and stabilize trends).
- Document parameter choices and describe emerging patterns that appear to be correlated with stable/unstable market phases.
- Observe the effects of trading frequency on wealth distribution.

### **Relevance and link to EEP’s research plan**

*Poverty and Equity* is one of the three global problem areas on which IIASA research is planned to focus. In real financial markets, big investors often have a systematic advantage over small investors. With this project, we hope contribute to an increased understanding of the conditions required for the emergence of fair and equitable markets. By interfacing research on financial markets with recent advances in understanding the evolution of animal personalities, this interdisciplinary work is also related to EEP’s research project on *Evolving Biodiversity*.

### **Expected output and publications**

This research is intended to be published as a coauthored article in an international scientific journal.

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