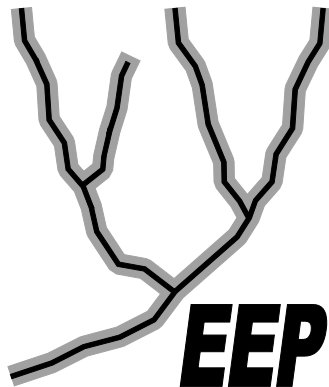


Young Scientists Summer Program 2012

Six Research Projects

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



Modeling soil microbial dynamics in carbon and nitrogen cycling

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Goal

To determine the relative importance of different mechanisms that influence carbon loss from soil under variable soil-moisture conditions.

Background and motivation

The soil contains more carbon than the atmosphere and plants combined (Scurlock and Hall 1998). This carbon is important for maintaining soil fertility, controlling erosion, and the long-term storage of carbon that could be released into the atmosphere. As greenhouse-gas concentration in our atmosphere increases, the rate at which this carbon is released into the atmosphere as carbon dioxide (decomposition) has been given new importance. Specifically, if predicted shifts in climate increase carbon release, positive feedbacks with soil-climate-atmosphere could emerge and alter the trajectory of climate change (Singh et al. 2010). These scenarios call for clarification of relationships between new climates and soil processes, and for a better understanding of the mechanisms that control these patterns. This information could help decrease uncertainty in current ecosystem models and better predict carbon-flux and climate-change trajectories and adaptive strategies.

One particular circumstance in which overall carbon-dioxide (CO₂) flux has been shown to deviate from rates predicted using empirical relationships arises in response to drying and rewetting cycles (Yuste et al. 2007; Boroken and Matzner 2009). The loss of CO₂ from soil may be higher when soils are exposed to fluctuation in soil moisture than when soil moisture is more constant (Clein and Schimel 1994; Miller et al. 2005; Jarvis et al. 2007). Understanding this phenomena, called the “Birch effect” (Birch 1958) is especially important because future climates are expected to be characterized by more variable rainfall (IPCC 2007), including longer drought and larger rewetting events. Identifying the mechanisms that control CO₂ dynamics under drying and rewetting could improve estimates of global carbon budgets and reduce error in predictions of soil CO₂ flux under future climates.

Although the large pulse of CO₂ that occurs after rewetting a dry soil has long been described, the mechanisms that underlie the Birch effect are still unclear. Most discussions divide mechanisms into those controlled by physical factors and those influenced by the biology of the soil microbial community (Xiang et al. 2008; Navarro-García et al. 2012; Manzoni et al. 2012). Physically, moisture alters carbon and nitrogen diffusion rates, which can prevent microbial access to substrate. In addition, a large rain event can break up large soil particles, which contain stored, but not accessible, carbon. Precipitation changes are also likely to alter microbial physiology (Schimel et al. 2007) and community dynamics (Evans and Wallenstein 2012). Dry conditions are physiologically stressful for microorganisms (Schimel et al. 2007), and changes in how microbes allocate carbon under drought may affect their response to a sudden rewetting event. In addition, some microbial species may be outcompeted by other species under drought (Drenovsky et al. 2004). Resulting community shifts could alter biological potential and therefore the biogeochemical functions microbes mediate (Allison and Martiny 2008).

A few studies have tried to compare the relative importance of these mechanisms for explaining CO₂ flux, but methodologies and the inability to objectively compare mechanisms in a controlled structure have made this challenging. Manzoni et al. (2012), in a recent meta-analysis, found that physical constraints (diffusion) may be more important in controlling respiration at different moisture levels than physiological constraints, but did not specifically look at rewetting pulses or at mechanisms in great detail. This study also found that the relative importance of mechanisms may differ in litter and soil, suggesting substrate availability may affect which mechanisms are important. A recent modeling study found that explicit inclusion of enzyme pools in a model could help predict CO₂ pulses after drying and rewetting, but model behavior depended on the length of drought and magnitude of rewetting (Lawrence et al. 2009). Other studies have found that drying and rewetting can significantly alter microbial community structure, and microbial communities with a history of drying-rewetting may respond differently to this moisture pattern (Fierer et al. 2003). These studies provide an excellent foundation on which to test these mechanisms in one model structure and systematically assess each mechanism's potential to influence CO₂ pulses after rewetting.

Research questions

I will address the following questions:

- What is the relative influence of physical and biological mechanisms on the CO₂ pulse observed after rewetting a dry soil?
- How does the importance of these mechanisms change with variation in substrate availability and pulse variability?

Methods and work plan

Model structure

I will test these questions using an individual-based model developed by Christina Kaiser. This model describes carbon and nitrogen dynamics during soil decomposition on a two-dimensional grid of microsites (cells). Being spatially explicit, it provides a good structure to test questions of microscale physical access and diffusion limitation. In addition, the model includes three microbial functional groups that mediate biogeochemical flux, each with a different set of traits. Spatially explicit cells host competitive interactions among groups, as well as the growth, death, and metabolism of microorganisms.

I will induce drying-rewetting events in the model by altering diffusion parameters, and by implementing parameters that determine water level. Water level will be a state variable describing water level in any one cell. Changes in water level will be the result of a constant inflow that stops under drought, occurs to random cells under rewetting, and spreads to other cells through a diffusion gradient, similar to the concentration of substrates changes from cell to cell.

I will then extend the model structure to implement each mechanism described below, and compare CO₂ released under drying-rewetting and constant moisture conditions to see how the difference between these two scenarios, which measure the magnitude of the Birch effect, varies among mechanisms. I will first examine the effect of a single drought and rewetting, and then, if time allows, extend this analysis to look at several consecutive drying-rewetting events.

Mechanisms to implement and test

1. Physical disruption of aggregates

Aggregates, or pieces of soil stuck together, contain organic matter that is physically unavailable to microorganisms when in larger pieces. A large rain event is likely to break up soil aggregates, increasing carbon available for microorganisms (Denef et al. 2001; Navarro-García et al. 2012). I will test this mechanism by first making the distribution of primary substrate among cells uneven. Some substrate may be concentrated into a few grid cells, while others may have little or no primary substrate. Upon rewetting, this carbon will be “broken up” into more cells and thus accessed by more microorganisms.

2. Osmolyte release from microbial cells

Microbes can tolerate drought conditions (osmotic stress) by producing solutes inside the cell to balance water potential inside the cell with that outside the cell (Schimel et al. 2007). These solutes can subsequently be released and used as mineralizable carbon when rewetting occurs. To test whether this physiological drought-tolerance mechanism influences CO₂ flux under rewetting, I will implement a new part of the model that describes the water level and solute concentration outside and inside the cell. When microbes are under water stress (so solute concentration is high outside the cell relative to its inside), microbes will allocate more of the carbon they take up to producing osmolytes inside the cell (as part of the carbon pool inside the cell). Thus, under drought, more carbon will be allocated to maintenance respiration compared to enzyme production or growth. In turn, these osmolytes can be released under rewetting, when more water dilutes any solute still present (Harris 1981; Kieft et al. 1987; Schimel et al. 2007).

3. Altered microbial community traits

To test whether altered community structure could contribute to the Birch effect, I will first create two functional groups that differ in their ability to produce enzymes (cheaters and non-cheaters), go dormant, and produce osmolytes (drought tolerance). I will run the model under drought to identify which of these two functional groups outcompetes other groups. I will then subject this community to a rewetting pulse, and compare the resultant response to that of a community that has experienced constant conditions for the same period of time (evenly distributed community).

4. Accumulation of dissolved organic carbon under drought

An accumulation of dissolved organic carbon (DOC) is likely to result in higher CO₂ flux rates, and therefore represents a fourth mechanism. However, the same pattern may also occur as the result of other mechanisms. Therefore, I will test the importance of this mechanism by first determining under what conditions DOC accumulates. I will start by examining whether fluctuation of diffusion causes this pattern due to limited access of DOC from microbial groups. However, it is also possible that this pattern can only occur when enzyme turnover or production are altered, or if one of the previous mechanisms is implemented. Specifically, an un-even distribution of primary substrate, as described in (1), is likely to portray the effect of diffusion on carbon availability more realistically (resulting in “resource islands” as opposed to well-mixed soil).

Mechanisms under different resource and moisture-fluctuation scenarios

If time allows, I would also like to test the influence of resource status and timing of drying-rewetting on the relative importance of the aforementioned mechanisms. In the models above,

primary substrate (resources) will not be limited. In another model, I can give this pool a starting value, and allow it to be depleted throughout cycles. Similarly, I can record the relative changes in total CO₂ loss, and the strength of the Birch effect, under longer drought, and more intense (greater moisture) rewetting.

Calibration

This model has been calibrated with data from litter, which possesses different chemical and biological properties than soil, which will be more highly affected by rainfall pulses. I will calibrate this model using data on soil organic carbon and nitrogen, microbial biomass, and dissolved organic matter I have collected during my Ph.D. studies from two sites in the US. I can also use data from additional sites to calibrate, as these site properties are commonly reported in soil-experiment publications.

Analysis of response variables

I will view model runs graphically, but will assess the relative importance of mechanisms quantitatively by analyzing the response-variable output, written to a data file. I will concentrate on three metrics to evaluate the relative importance of mechanisms:

- Overall carbon release among mechanisms under a single drying period followed by rewetting.
- Magnitude of the Birch effect, quantified by subtracting CO₂ loss from each pulse in the fluctuating model from that in the model with constant soil-moisture conditions.
- If I have enough time to investigate multiple drying-rewetting pulses, I will compare the difference between the peak CO₂ loss in the last (5th) pulse, and the first pulse. This will provide an indicator of how long the Birch effect persists, as some mechanisms may play a larger role during earlier pulses, and have different long-term implications.

In certain scenarios, I will also monitor other variables (e.g., DOC accumulation, change in microbial biomass and community composition) to verify that the focal mechanism is correctly executed, and to qualitatively describe dynamics that accompany the mechanism.

Work plan

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

- Gain familiarity with model structure, coding, and execution.
- Extend the model structure to induce drought and rewetting environmental conditions by altering the diffusion constant; examine differences between fluctuating moisture and constant moisture.
- Apply variations in water level and make the primary substrate unevenly distributed among cells.
- Implement each mechanism individually and record CO₂ loss for constant and fluctuating moisture conditions.
- Repeat analysis with multiple drying-rewetting pulses, at low and high substrate, and at low and high moisture variability, and record how the relative importance of each mechanism is altered.

Relevance to EEP's research plan

My work relates more generally to the ways in which disturbance affects communities and the competitive interactions that drive their composition, which are major interests of the EEP Program. My research will advance EEP goals and complement other EEP studies on adaptation, relationships of scale, and disturbance ecology. This work is also novel in its approach and implications, and could generate more interest in theoretical modeling in the field of microbial ecology.

Relevance to ESM's research plan

My work will contribute to IIASA's Ecosystem Services and Management (ESM) Program's goals to develop more accurate carbon budgets and to more precisely monitor carbon emissions. In addition, this work is closely related to theories of ecosystem thresholds and climate-biogeochemical feedbacks to ecosystems. Most ecosystem responses to climate are nonlinear, and an improved understanding of the mechanisms that control these functions can help us identify in what situations thresholds and feedbacks will occur.

Expected output and publications

The work from this project is expected to result in a publication as a coauthored article in an international journal.

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A management model for Alpine fish populations under temperature stress

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Goal

To predict the effects of management interventions on an Alpine whitefish population (*Coregonus* sp.), considering life-history variability and its interdependence with slowly rising water temperatures, using a stochastic matrix model calibrated with empirical catch data.

Background and motivation

The Alpine lakes are home to stenothermic coldwater fishes, such as economically important whitefish species (Salmoniformes: Coregonidae: *Coregonus* spp.). Many populations are subject to fishery management interventions, which affect population densities, survival rates, and recruitment through stocking and harvesting. Population dynamics are also influenced by life-history and environmental variability, leading to substantial fluctuations in stock abundances. Additionally, slowly rising water temperatures due to a climatic change in the Alps are affecting life histories and habitat quality. Suitable habitats may increasingly be limited by very warm surface layers during summer stratification and simultaneous high oxygen depletion in deepwater layers (Fang et al. 1999; Ficke et al. 2007; Elliot and Bell 2010). On the other hand, warmer habitats probably promote growth periods and affect mortality (Casselman 2003).

Mathematical models can provide detailed insights into how environmental changes and management actions (such as stocking and harvesting) influence individual life histories and population growth rates. Matrix models are common mathematical tools for projecting fish populations. They provide extensive opportunities for analyzing demographic dynamics and can readily be extended by relevant mechanisms, such as harvesting, stocking, and density dependence (Quinn and Deriso 1999; Caswell 2001). In general, matrix models describe demographic development over discrete time steps (e.g., years) and discrete life-history stages (e.g., age or size classes), which are characterized by two specific vital rates (effective fecundity and mortality). A limitation of using deterministic matrix models for projecting fish populations is that they cannot account for natural variability among individuals and variable environmental conditions affecting vital rates. Incorporating such variability and uncertainty into matrix models by allowing stochasticity in the vital rates is therefore an important step towards increased ecological realism.

Research questions

I will address the following questions:

- To what extent does stochasticity affect projections by a matrix model for whitefish populations?
- How do changes in somatic growth rates induced by management interventions affect a population's dynamics?

- Which combination of management actions (stocking and/or harvesting) maximizes production?
- To what extent are increasing lake temperatures expected to affect coldwater fish stocks?

Methods and work plan

During my research at IIASA, I will develop a matrix model that includes density dependence and stochasticity for a whitefish population (*Coregonus* sp.) of the pre-alpine Lake Irrsee in Austria. The model is then used to assess the impact of growth changes as well as increased and decreased mortalities for adult and juvenile fish due to stocking and harvesting. Finally, I study the consequences of rising water temperatures by beneficially and/or detrimentally modified vital rates and reduced oxythermal habitats.

Model structure

Matrix models make the assumption that all individuals within a demographic class are equivalent. Conventional age-structured matrix models move all surviving individuals to the next age class after one year, while length-structured models move individuals to the next length class depending on their somatic growth rates. The latter can lead to inaccurate projections when the model has an insufficient number of length classes (numerical diffusion). Although age is a natural demographic property in the life history of fish, body length is probably the better indicator of life-history state, because vital rates and management interventions usually directly depend on length. Inclusion of both demographic classifications might be considered most realistic, but also complicates the model. Since sexual maturity is the property that most commonly depends not only on length, but also explicitly on age, I will first study the probabilistic maturation reaction norm (PMRN) to see whether a purely length-structured model is appropriate.

If so, I will develop a length-structured matrix model with density dependence, which projects population growth over time as

$$\mathbf{n}_{t+1} = s\mathbf{A}\mathbf{n}_t,$$

where \mathbf{n} is a vector of class abundances across length classes (i.e., the length distribution) in the population at time t (measured in years) and s describes the effect of density dependence (next subsection). The projection matrix is of the form

$$\mathbf{A} = \begin{pmatrix} S_{r,1} & F_2 & \cdots & F_x \\ S_{g,1} & S_{r,2} & \cdots & 0 \\ 0 & S_{g,2} & \cdots & 0 \\ \vdots & & \ddots & \vdots \\ 0 & 0 & \cdots & S_{r,x} \end{pmatrix},$$

where F_i is the effective density-independent fecundity in length class i , describing the reproductive contribution by an individual in length class i to the population's first length class 1 when population density is low. Annual density-independent survival probabilities are divided into 'survive and remain in the length class' (S_r) and 'survive and grow to the next length class' (S_g), until the maximum length class x is reached. Also these transition probabilities apply to a population at low density and can be calculated with the semi-empirical growth-model method developed by Rogers-Bennett and Rogers (2006), which uses the von Bertalanffy growth function.

Density dependence

Intraspecific density dependence in population growth is important when modeling natural fish populations subject to limited resources and habitat. Survival, effective fecundity, and growth are often differently affected by increasing or decreasing population abundance. In the model approach for whitefish, I consider the simplest form of density dependence, which acts on all vital rates equally. The best population-level indicator accounting for compensatory processes is biomass, because of its importance for fish bioenergetics. In the model, population biomass at time t is given as

$$B_t = \sum_{i=1}^x w_i n_{i,t},$$

where w_i is the average weight of individuals in length class i . This is used to define the density-dependent coefficient s (preceding subsection) via the Ricker equation (Ricker 1954),

$$s = e^{R_{\max} (1 - B_t/K)},$$

where R_{\max} is the maximum observed population growth rate and K is the carrying capacity of whitefish biomass for Lake Irrsee.

Stochasticity

Since environment and population dynamics are variable processes, it is desirable to incorporate different types of stochasticity into matrix models.

First, demographic stochasticity, which plays a major role in very small populations, could be added to the model. However, the studied fish population contains at least 60,000 individuals, which means that the expected demographic noise is on the order of 1 %. I will therefore neglect this type of stochasticity.

A second stochastic process is variable growth, which is already part of the matrix structure, being captured by the transition probabilities between length classes. If this stochasticity becomes large, the projection matrix \mathbf{A} needs to incorporate additional transitions through which a fish can grow by more than one length class per year.

Importantly, I will consider a third type of stochasticity, which is caused by environmental fluctuations leading to annual variability in vital rates (i.e., environmental stochasticity in the elements of \mathbf{A}). This can be implemented by drawing, for each year, the realized rates from suitable probability distributions with means given by the deterministic model described above and with widths that reflect the magnitude of the environmental fluctuations. The statistical covariances between these realized rates is expected to be substantial and cannot be neglected, since fish of similar length mostly live in the same habitat and experience the same seasonal fluctuations in a similar way. However, coregonids live essentially in only two habitats during their life: small fish live close to banks and the surface, while large fish are pelagic or live in the deep water. This allows a major simplification of the covariance structure: we assume that all fish sharing a habitat experience fluctuations in the same way, regardless of their length.

Management interventions

With reference to my third research question, I will test the effects of different management strategies by adjusting the survival probabilities of pre-recruits and adult spawners, to reflect the impacts of fishing and stocking. Furthermore, I will analyze potential consequences of warming habitats for future population development and management by increasing growth

rates and simultaneously decreasing the habitat's carrying capacity, so as to account for smaller oxythermal refugia for coregonids.

Data availability

Since the year 2000, the Irrsee population is studied by means of gillnetting and hydro-acoustics, carried out by the Federal Institute for Water Ecology, Fisheries, and Lake Research in Scharfling, Austria. Harvesting and stocking data is provided by the angler association Sportanglerbund Vöcklabruck and temperature and oxygen data are available from monthly water samples. The fishery management, which is in the hands of the Sportanglerbund Vöcklabruck modified fishery regulations between 1996 and 2002 due to very low catches (Gassner et al. 2004).

Since the year 2000, fish biomass (hydro-acoustic data) and catch-per-unit-effort (CPUE) of gillnets have shown an increasing trend, resulting from angling restrictions. From this increasing trend it was concluded that during 2000 to 2004 lower average abundance and density prevailed compared to the period from 2005 to 2009. Also different von Bertalanffy growth functions were observed for these two periods, with lower growth during the second period, indicating density-dependent effects and/or truncation effects in age and/or size resulting from angling.

Calibration

The matrix model will be constructed on the basis of an already derived life-history table for the Lake Irrsee population from a 10-year catch series by gillnets with various mesh-sizes ($N = 2,013$). The demographic distribution of the population is estimated through correction for the size selectivity of gillnets according to their mesh sizes, using the maximum-likelihood-based SELECT method (Millar and Holst 1997; Millar 2000). Survival per length class can be calculated from simple regressions between the abundances of length classes. The reproductive output that survives from birth by a parent in length class i to the first length class is the effective fecundity

$$F_i = fw_i g_i m_i q,$$

where f is the weight-specific fecundity, which is defined as the number of eggs per unit body mass, w_i is the average weight in length class i , g_i is the sex ratio in length class i , m_i is the ratio of mature to immature individuals in length class i , and q is the survival probability from the egg stage to one-summer-old fish. Additionally, empirical data from literature and observed values from the Lake Irrsee population will be used for specifying variation in vital rates.

Work plan

I will use the model platform 'R' for the following work steps:

- Estimation of the probabilistic maturation reaction norm for age and size at maturation.
- Matrix-model construction considering density dependence and stochasticity.
- Calibration of the model using data from Lake Irrsee.
- Testing management interventions by modification of vital rates.
- Testing potential changes induced by increasing water temperatures.

Relevance and link to EEP's research plan

The assessment of population trends is increasingly important in the context of conservation, management, and harvesting of marine and freshwater fish. At IIASA, the Evolution and Ecology Program and its international network activities have focused on fish populations, in particular through the collaborative network projects FishACE, ADAPTFISH, and UNCOVER.

My research can contribute to this topic with my developed population projection matrices and the data set on lake whitefish (*Coregonus* sp., $N = 2013$). This species is a good model organism for studying population dynamics under environmental and anthropogenic influences. In general, fish populations in lakes provide manageable conditions for studies in population ecology, because these populations are very often closed or almost closed, as individuals do not migrate between ecosystems or populations. Coregonid populations are very well studied and density-dependent and density-independent processes are known. However, comprehensive population models for coregonids are still missing and could elucidate ecologically and evolutionarily relevant dynamics.

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 expect this work to be a part of my Ph.D. thesis.

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Effects of climate-induced changes in river flows on Japanese seabass

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Goal

To evaluate the effects of climate-induced changes in river flows on the population dynamics of the estuarine Japanese seabass, *Lateolabrax japonicus*.

Background and motivation

Concerns are mounting about the consequences of global climate change. The earth's average temperature is currently rising and, among other changes thereby brought about, it is expected that this will increase the concentration of heavy rain (Allan and Soden 2008). Not all climatic changes can be traced back to anthropogenic impacts. In fact, there is ample evidence for naturally occurring decadal climatic oscillations, such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO). As a changing climate affects all life on this planet, including major renewable resources, it is important to understand its consequences.

Fishes are major renewable resources that are affected by climate change. Marine fishes have population dynamics that are particularly sensitive to mortality in early life stages, because few individuals survive this stage (Hjort 1914), and climate change affects many environmental factors that are important determinants of larval mortality, such as temperature, salinity, predator density, and prey density. The population dynamics of coastal marine fishes are furthermore influenced by freshwater inflow (Gillson 2011). Rivers affect the coastal water flow and thus the transport of larvae, and they function as important nurseries. Differences in freshwater flow may influence survival and recruitment of estuarine fishes by controlling the retention of egg and early-stage larvae in the estuary, and by affecting the overlap of temperature and salinity zones preferred by later-stage larvae (North and Houde 2001).

The study of fish population dynamics has historically focused more on understanding the temporal than the spatial dynamics of populations, and environmental changes are traditionally assumed to affect all individuals equally. However, there are often groups of fish within a population that have group-specific migratory pathways and habitats; such groups are called contingents (Secor 1999). The presence of contingents can affect overall population dynamics, because the different habitats experienced by individuals in contingents can impact their abundance, growth, reproduction, maturity, recruitment, and survival (Kerr et al. 2010).

The Japanese seabass, *Lateolabrax japonicus*, is a euryhaline fish distributed in temperate coastal waters of Japan and Korea. This species is often dominant in coastal areas, where it is commercially important. Japanese seabass spawn in deep offshore areas in winter, and larvae are then transported inshore and reside in the bottom layer in coastal areas and estuaries. My data shows that the survival rate of these larvae is strongly affected by the winter river discharge in the Tango Sea, Japan, and that the discharge of the Yura River, which is the largest river in the Tango Sea, is correlated with an important climatic indicator, the Aleutian Low Pressure Index (ALPI). This suggests that the population dynamics of the Japanese seabass are influenced by climatic change as expressed by ALPI. As the temperate seabass has a relatively long lifespan of over 10 years, it is difficult to detect the effects of ALPI by regression

analysis. A population-dynamical model is better suited for elucidating the effects of climate change on Japanese seabass: first, such models are capable of predicting integrated effects across several cohorts and provide mechanistic insights into their causes, and second, delays between environmental changes and their population consequences are emerging dynamical properties of the model, rather than being merely assumed or being estimated as a parameter.

In this project, I will use a population-dynamical model inspired by Kerr et al. (2010) to examine the effects of variable river discharge on the population dynamics of the Japanese seabass.

Research questions

I will model the population dynamics of Japanese seabass and evaluate the consequences of changes in river discharge. Specifically, I will address the following questions:

- Does the winter river discharge significantly affect the population dynamics of Japanese seabass?
- How well can the model reproduce population-fluctuation patterns of Japanese seabass in Japanese coastal waters?
- Will the increased frequency of concentrated heavy rain in the spring and summer seasons cause a decrease in the abundance of Japanese seabass through the change of mortality in the river nursery area?
- How would destruction of river nursery areas (e.g., by building estuarine weirs) affect the Japanese seabass?

Methods and work plan

Study site and model species

I have studied the ecology of Japanese seabass in the Tango Sea, Japan. The Tango Sea is located in the northern part of Kyoto Prefecture, Japan, facing the Sea of Japan. It is approximately 336 km² and is semi-enclosed. The Tango Sea is approximately 60 m deep at its center and 80 m deep at the mouth.

The Japanese seabass spawn in deep offshore areas during winter months, from December to February. Larvae are transported inshore and reside in the bottom layer of the water in coastal areas and estuaries. Fuji et al. (2011) showed that juvenile seabass with poor growth ascend the river, while others reside in the sea until April. Juveniles then distribute in the river and the adjacent surf zone from May to July (Fuji et al. 2010, 2011). After August, juveniles in the river return to the sea. Following two years of growth, a small portion still use rivers as foraging areas from spring to autumn, and return to the sea in winter, while most individuals spend all their time in the sea.

Methodological overview

As a first step, I will carry out a regression analysis on the relationship between Yura River discharge and Japanese seabass landings. This will establish a baseline against which predictions by a population-dynamical model can be compared. As a second step, I will adapt and extend an existing population-dynamical model by Kerr et al. (2010) to account for river discharge and mortality. Kerr et al.'s model links two age-structured contingents through a

common stock-recruitment relationship. The model includes river discharge, but the representation is simplistic (only high, low, and drought conditions) and will therefore be extended.

Recruitment

Recruitment is determined by the fecundity of the spawning adult population and by larval mortality. Newborn larvae initially experience density-independent mortality that decreases with the mean winter river discharge during February. After settlement in the coastal area, the larvae experience density-dependent mortality (Ohmi 2002; Shoji and Tanaka 2007), and the surviving larvae eventually migrate to nursery areas. Specifically, the density of surviving larvae recruited to nursery areas is

$$D_{t,0} = \frac{e^{-Z_{t,0}}}{V_c} \sum_{a=2}^{a_{\max}} N_{t,a} p_a s_a f_a.$$

Here, the sum represents the number of newborn larvae and is taken over all reproductive ages. In the sum, $N_{t,a}$ is the number of seabass of age a at time t . To arrive at the number of newborn larvae, we multiply with the fractions p_a and s_a of these individuals which are mature and female respectively, and finally we also multiply with the average fecundity f_a of the mature and female individuals of age a . This fecundity is calculated from the data in Makino et al. (1999), and accounts for the survival probability from egg to larvae. The mortality rate during the larval stage, $Z_{t,0}$, will be described as a linear function of the mean winter river discharge during February and of the logarithmic density of larvae. The number of surviving larvae is converted to density by division with the coastal water volume V_c .

Partial migration

Having survived the larval stage, the population diverges into two groups which are respectively found in the surf zone and the river. These two groups experience contingent-specific mortality that is driven by environmental conditions (i.e., stream flow). In the surf zone, the dynamics are given by

$$D_{t,1,s} = \frac{V_c}{V_s} D_{t,0} (1 - c) e^{-Z_{t,1,s}},$$

while the corresponding expression for the river is

$$D_{t,1,r} = \frac{V_c}{V_r} D_{t,0} c e^{-Z_{t,1,r}}.$$

Here, c is the proportion of individuals that form the river contingent. This proportion is assumed to be fixed and approximately equals one-third according to my field data. The quantities $Z_{t,1,s}$ and $Z_{t,1,r}$ are the contingent-specific mortality rates. The juvenile mortality rate in the surf zone is assumed to be constant, while the mortality rate in the river is assumed to depend linearly on the river flow in the spring-summer season, assuming a juvenile period of 90 days (Fuji et al. 2011). Finally, V_s and V_r are the accessible water volumes in the surf zone and river, respectively. At age 1, the two contingents mix in the sea, where they subsequently experience the same conditions. The resultant density of individuals of age 1 is given by $D_{t,1} = (V_s D_{t,1,s} + V_r D_{t,1,r}) / V_a$, where V_a is the water volume available to adult individuals.

Survival as adults

The density of adult individuals, with ages 2 and older, is assumed to decrease as a consequence of density-independent mortality,

$$D_{t+1,a+1} = D_{t,a} e^{-Z_a}.$$

When useful, we can transform the density to an abundance by multiplication with the water volume available to adult individuals, $N_{t,a} = V_a D_{t,a}$. The total age-dependent mortality is determined as the sum of fisheries-induced mortality and natural mortality, $Z_a = F_a + M_a$. The fisheries-induced mortality is described by

$$F_a = F_{\max} / (1 + e^{-\frac{a-a_{50}}{w}}),$$

where F_{\max} is the maximal fishing mortality rate and age a_{50} is the age a at which F_a equals half of F_{\max} . The parameter w determines how steeply the fishing mortality rate increases with age.

Catch dynamics

To compare the model output with observed fisheries landings, we determine the catch of seabass in year t as

$$C_t = \sum_{a=2}^{a_{\max}} V_a D_{t,a} (1 - e^{-Z_a}) \frac{F_a}{Z_a} W_a,$$

where a_{\max} is the maximum age of Japanese seabass and W_a is the mean body weight at age a , as determined by an empirically estimated allometric relationship. and represent, as before, the fishing mortality and the total mortality.

Available data

The following data sets are available for this study:

- Yura River discharge (from 1954 to 2012).
- Aleutian Low Pressure Index (ALPI; from 1900 to 2008).
- Fisheries landing of Japanese seabass around the Tango Sea (from 1956 to 2010).
- Maturity and sex ratio of adult individuals from my empirical data.
- Average fecundity and hatch rate from Makino et al. (1999).
- Adult growth and length-weight relationship from my empirical data.
- Total adult mortality)rate from the catch curve and my empirical data.
- Planktonic larval mortality from my empirical data.
- Density-dependent settlement larval mortality from Shoji and Tanaka (2007).
- Juvenile (age-1) mortality in the river from my empirical data.
- Fraction of dispersive juveniles (river juveniles) from my empirical data.

Parameterization

Most of the model parameters can be directly estimated from the time series mentioned above. A few parameters, however, require additional attention. The juvenile (age-1) mortality in the surf zone is unknown. Mortality of other marine fish (red drum, *Sciaenops ocellatus*) of the same size is available from Purtlebaugh and Allen (2010) and will be used in lieu of the species-specific value. Furthermore, the age-specific fishing mortality rate is unknown. I will statistically infer the parameters for the fishing mortality rate based on the ability of the model to match actual fisheries landings. The total adult mortality rate Z_a is estimated from the catch curve. The natural mortality M_a can then be calculated as $M_a = Z_a - F_a$. Alternatively, M_a can be determined from the natural lifespan of Japanese seabass (Hoenig 1983). I will incorporate

both historical and projected river discharges and infer the relationship between river discharge and larval-juvenile mortality from empirical data.

Winter river-discharge fluctuations induced by climate oscillations

The Aleutian Low Pressure Index (ALPI) oscillates on a timescale of a few decades. This affects the long-term fluctuation of winter Yura River discharge. I will use the time series of winter (February) Yura River discharge for my population-dynamical model.

Flood events

I will assume that flood events caused by concentrated heavy rain lead to reduced survival of age-1 juveniles in the river, as inferred from my empirical data. This phenomenon was also reported by Shoji et al. (2006). The impacts of flood events on mortality are modeled as a relationship between the mortality of age-1 seabass in the river and the mean spring-summer river discharge as estimated from my empirical data.

Nursery destruction

Estuarine weirs partially prevent Japanese seabass juveniles to use rivers as nursery areas. The building of estuarine weirs narrows the river nursery areas, causing increased density dependent mortality of juveniles. The impacts of estuarine weirs will be simulated by lowering the water volume V_r of the river nursery. I will assume the same relationship for density-dependent mortality (Shoji and Tanaka 2007) at the juvenile stage.

Work plan

- Conduct a statistical analysis to infer the relationship between Japanese seabass landings and Yura River discharges.
- Parameterize the population-dynamical model of white perch by Kerr et al. (2010) to describe the Japanese seabass.
- Attempt to reconstruct the fluctuation of fisheries landings in the Tango Sea. The objective is to minimize the sum of squared differences between the modeled catch C_t , and the observed landings, by adjusting model parameters. An autocorrelation analysis will be used to infer the periodicity.
- Examine plausible scenarios for future climatic changes that alter the river discharge in the spring-summer season and therefore increase the juvenile mortality in the river. I will also conduct numerical analyses to assess the consequences of nursery destruction.

Relevance and link to EEP's research plan

This project will contribute to EEP's ongoing research on fisheries management by developing a population-dynamical model of Japanese seabass that can assess consequences of future climate change.

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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Curbing corruption in public good games

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Goal

To study the evolutionary dynamics of the spread of corruption and its suppression under different incentive schemes for a rule enforcer.

Background and motivation

Although the “tragedy of the commons” is ubiquitous (Hardin 1968), field research on the governance of the commons and laboratory experiments of public good games show that cooperation can sometimes be maintained and the tragedy avoided (Ostrom 1990; Rutagi et al. 2010). Ostrom (1990) claims that the basic design principles for systems allowing long-lasting resource use include the successful establishment of a monitoring and sanctioning system. This is in line with theoretical studies emphasizing punishment as a mechanism for enforcing cooperation (e.g., Nakamaru and Iwasa 2006; Rockenbach and Milinski 2006; Nakamaru and Dieckmann 2009).

Corruption may arise when monitoring and sanctioning is delegated. It is a significant problem that disturbs ecosystem management in many places, such as forest management in Cambodia, Indonesia, Tanzania, etc. The phenomenon occurs widely and persistently at state and community levels (Corbridge and Kumar 2002; Véron et al. 2006; World Bank 2006). It ruins joint efforts, and leads to resource depletion and distorted distribution.

Previous theoretical studies deal with corruption between harvesting firms and public inspectors (Mishra 2006; Diarra and Marchand 2011). Here we consider the situation that a group of players establishes monitoring and sanctioning institutions that are run by hired rule enforcers. This approach is in line with a recent study showing that social learning can lead to the adoption of institutions (Sigmund et al. 2010). We assume that the group must provide funds for the rule enforcer. Also, we compare endogenous sanctioning systems with sanctioning systems imposed by an external authority (Vollan and Ostrom 2010).

Research questions

The focus of this research project is to identify institutional designs that curb bribery and maintain cooperation. We compare models with different incentive schemes for a rule enforcer. The main research questions are as follows:

- What counterforce can effectively curb corruption in a single-enforcer system?
- How does an incentive system that is voluntarily accepted by a group differ from a system enforced by external authority?
- Is the competition of multiple enforcers efficient in suppressing the tendency to accept bribes?
- Are systems based on multiple enforcers capable to punish corrupt behavior with the help of higher authorities that punish bribe acceptance?
- How does the magnitude of fines and bribes influence the dynamics of corruption?

Methods and work plan

Model overview

We develop and analyze a model of a public good game with a single rule enforcer. Bribery and its suppression are affected by the size of the fines imposed onto defectors, the size of the bribes offered to the enforcer, the acceptance and detection rates of bribes, and the punishment of corrupted behavior. We consider alternative reward systems that influence the detection of defection and the detection of bribery.

Public good game

We assume that players either cooperate (C: doing no harm to the commons) or defect (D: resource overuse with harm to the commons). Cooperators also decide whether to participate in the implementation of sanctions by paying a fee for an enforcer. Defectors decide whether to pay the fine or to offer a bribe to the rule enforcer. An enforcer chooses whether to punish defection or to accept bribery.

Paying for enforcement

We will consider the following four modes of paying for enforcement:

- (A) Cooperators who agree to use enforcers pay their fees. The detection rate depends on the amount of the fees collected from these cooperators.
- (B) Cooperators pay the fee for an enforcer. Moreover, the enforcer takes a certain fraction of the fine imposed on the defector. The effort is proportional to the amount of the fee and the collected fine.
- (C) An exogenous higher authority supports the enforcer.
- (D) Cooperators pay a fee for several enforcers instead of for a single enforcer. While this costs cooperators more than a single enforcer, the resultant competition among enforcers may be beneficial.

Punishing a bribed enforcer

Contingent on the mode of paying for enforcement, we will consider the following three modes of punishing a bribed enforcer:

- (A), (B) Bribe detection depends on the efforts of the group members. The enforcer is fined when bribe acceptance is reported, and fired when defection is prevalent.
- (C) If the officer is introduced from outside, the corrupt behavior is discovered and fined by the external authority with a fixed probability.
- (D) Competition between enforcers may reduce the fee for bribe detection. The enforcers are fined when bribe acceptance is reported, and fired when defection is prevalent (as the case of a single enforcer). A higher authority can be introduced to punish the corrupt behavior of enforcers.

Work plan

- We start from a basic model with just two players, which describes the situation with a single (honest) enforcer, in order to understand the effect of enforcer use.
- Then, we study the possibility of corruption in same setting. We compare the case of a voluntarily accepted institution with the case of an institution introduced by an exter-

nal authority. The model with multiple players will be studied based on those results.

- We plan to extend our model to the case of multiple enforcers. The goal of the extension is to identify the conditions under which competition among enforcers works as an efficient suppressor of bribe acceptance. A higher authority of enforcers can support and organize the monitoring and sanctioning of enforcers.
- Time permitting, we might replace the discrete strategies considered above with continuous strategies.
- We compare the results of different institutions described above and explore the implications in realistic settings of resource management.

Relevance and link to EEP's research plan

Curbing of corruption is critical for maintaining joint efforts in resource use. Thus, this project contributes to EEP's research on the evolution of cooperation.

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 Ph.D. thesis.

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The evolution of malaria incubation time

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Goal

To study the evolution of incubation times of *Plasmodium vivax* malaria and investigate the evolutionary constraints guiding the emergence of bimodality, and to identify and investigate the simplest suitable transmission model for *P. vivax* malaria that is in agreement with observed data.

Background and motivation

Malaria is a mosquito-borne infectious disease caused by one of several species of protozoan cell parasites of the genus *Plasmodium*, which have multiple developmental stages in humans and mosquitoes. While feeding on humans, infected female mosquitoes inject so-called sporozoites into the bloodstream, which infect liver cells, from where, sometime later, so-called merozoites are released back into the bloodstream. The time between the mosquito bite and the release of parasites from the liver is the incubation period. The merozoites then infect red blood cells and rapidly multiply in the bloodstream. Some of the merozoites mature into so-called gametocytes, which, after spreading back to feeding mosquitoes, reproduce sexually and ultimately produce more sporozoites that can again be transmitted to humans (Anderson and May 1992; Eisenstein 2012).

The parasite type *P. vivax*, which is common in temperate zones, can remain dormant in liver cells as a so-called hypnozoite, leading to an increased incubation period. It has been hypothesized for some time that the incubation time of *P. vivax* malaria has a bimodal distribution. Recent analyses of the incubation period of *P. vivax* malaria in Korea have confirmed that the incubation times are indeed bimodally distributed, with a clear distinction of short-term and long-term incubations (Nishiura et al. 2007; Nah et al. 2010a,b). Alving et al. (1952) suggested that this bimodality has evolved in response to the seasonality of the transmission period, which in temperate regions is restricted to a few summer months.

Despite widespread and sustained efforts, no convincing explanation for the regulation of incubation time has been presented to date (Huldén et al. 2008), even though important insights into the factors determining incubation time have been acquired. During the first decades of the last century, James and Shute (1926) and Schuffner et al. (1929) demonstrated experimentally that patients bitten by a large number of infected mosquitoes tend to experience a short incubation period, whereas patients bitten by only one or two infected mosquitoes tend to experience a long incubation period. While this may explain some of the variation in incubation time, it does not address the bimodality of its distribution. Several decades later, Ungureanu et al. (1976) claimed that the phenomenon of prolonged incubation periods is caused by the existence of two types of sporozoites in *P. vivax*, which might indicate the adaptive emergence of two coexisting strains from one single ancestor. The conditions that allow for adaptive diversification can be difficult to identify experimentally, but they can often be elucidated through the use of mathematical models (see, e.g., Dieckmann et al. 2002).

The classical mathematical models for describing the dynamics of malaria transmission are based on differential equations (Ross 1911; Anderson and May 1992). Ross's simplest

model gives the incubation period an exponential distribution, using ordinary differential equations in which the latent compartment decays exponentially in the absence of inflow from the infectious compartment. Meanwhile, Ross's delayed model describes the incubation periods of hosts and vectors with deterministic delay terms.

The aim of this project is to investigate the evolution of malaria incubation time. I will incorporate a bimodal distribution of incubation times in classical multistrain malaria models and conduct analyses of their adaptive dynamics to obtain insight into the factors that drive the evolution of malaria incubation time. If successful, my analysis will provide the first formal explanation for the documented bimodality in *P. vivax* incubation time.

Research questions

In this research, I seek to explain the regulation of the incubation times and look for the simplest suitable transmission model for *P. vivax* malaria. Specific questions are:

- Considering a simple model with two types (immediately infectious vs. delayed infectious), is coexistence possible, and for which parameter values?
- Can the bimodality of the incubation period reflect a genetic polymorphism, or is it better explained by alternative models involving probabilistic bet-hedging and/or plastic responses to the parasite density within a host?
- Which models are consistent with the empirical data?
- How do the model predictions based on ordinary differential equations differ from those based on delay differential equations, which may be considered more realistic? Is the difference relevant for the explanation of the empirical data?

Methods and work plan

I will construct *SEIS*-multistrain models based on Ross's malaria transmission model, starting with simplified assumptions about reinfection and incubation time. To build intuition about which conditions might favor adaptive diversification, I will first consider the coexistence of two strains representing the empirically documented bimodal distribution of incubation times. As a next step, I will calculate the invasion fitness of a mutant strain and conduct an adaptive dynamics analysis, finding evolutionarily singular trait values and assessing their evolutionary stability for reasonable ranges of model parameters. Specifically, I will look for parameter ranges that allow evolutionary branching, and thus, the emergence of two coexisting strains with different incubation times. I will finally investigate whether model predictions in these interesting parameter ranges are consistent with the empirical data. This procedure will be repeated for a hierarchical succession of alternative models with increasingly realistic assumptions until a complete picture of model suitability emerges.

A model with very simple assumptions

We start by assuming that each year is divided into a mosquito season, during which the parasite is transmitted via the mosquito population, and an off season, during which only birth and death in the host population and recovery of infectious hosts occur, but no new infections. While in reality there is always a certain delay between a mosquito bite and the resultant manifestation of the malaria infection (typically described in epidemiological models by an "exposed" state), here I assume that this delay can be neglected in the mosquito population (which means that mosquitoes become infectious immediately after biting), and that it can

also be neglected in the human population for the one parasite strain that has short incubation time (which means that humans become infectious immediately after being infected with this strain). In contrast, the other parasite strain has a long dormant (exposed) state in human hosts. Furthermore, I will neglect coinfections and strain-specific recovery rates. The mosquito population is not modeled explicitly. The size of the host population is assumed to be regulated by extrinsic factors, so that it suffices to consider the dynamics of the fractions of the population being susceptible, exposed, or infected with either strain, denoted below by S , E , I_s , and I_l , respectively, where ‘s’ (‘l’) stands for short (long) incubation time.

These simplified infection dynamics can be expressed via two systems of ordinary differential equations, one for the mosquito-active season and one for the mosquito-inactive season. Each system describes transitions between only four compartments. During the mosquito season, the dynamics are given by

$$\begin{aligned}\dot{S} &= B(1-S) - \Lambda(I_s + I_l)S + R(I_s + I_l), \\ \dot{E} &= \Lambda I_l S - (1/T + B)E, \\ \dot{I}_s &= \Lambda I_s S - (R + B)I_s, \\ \dot{I}_l &= E/T - (R + B)I_l,\end{aligned}$$

and during the off season by

$$\begin{aligned}\dot{S} &= B(1-S) + R(I_s + I_l), \\ \dot{E} &= -(1/T + B)E, \\ \dot{I}_s &= -(R + B)I_s, \\ \dot{I}_l &= E/T - (R + B)I_l,\end{aligned}$$

where B is the host’s birth rate, Λ is the transmission rate, R is the recovery rate, and T is the incubation time of the strain with long incubation time. Owing to the extrinsic population regulation, the rate R may be interpreted as additionally describing any infection-related negative fitness effects experienced by the host in the infectious state (e.g., infection-related mortality).

Alternatively, we may assume that exposed hosts become infectious after a fixed delay, or, in a further simplification, that they never become infectious within seasons, but that all exposed hosts turn into infected hosts at the beginning of the mosquito season (by letting $T \rightarrow \infty$ in the above equations and solving the mosquito-season equations with appropriately modified initial conditions). For this last case, a discrete-time approximation that steps from season to season may also be investigated.

A model with less simple assumptions

Under less simple assumptions, we explicitly include exposed states and incubation times for all strains, as well as infection dynamics in the mosquito population.

We set the mosquito attack rate $\sigma(t)$ and the mosquito-to-human population ratio $m(t)$ to be periodic functions with the same period (normally, one year), reflecting the seasonal variation. With $t = 0$ corresponding to the beginning of the mosquito season, P denoting the period of $m(t)$, $t' = t \bmod P$ measuring time within a season, and $t' = L$ denoting the end of the mosquito season, we define

$$\sigma(t') = \begin{cases} \sigma & \text{for } 0 \leq t' < L, \\ 0 & \text{for } L \leq t' < P, \end{cases}$$

$$m(t') = \begin{cases} [\exp(-((t' - b)/c)^2 + (b/c)^2) + M_{\min}] / H & \text{for } 0 \leq t' < L, \\ M_{\min} / H & \text{for } L \leq t' < P. \end{cases}$$

Hence, the transmission rate from mosquitoes to hosts is obtained as $\Lambda = \sigma m \Delta$, and from hosts to mosquitoes as $\lambda = \sigma \delta$, with transmission probabilities Δ and δ . The parameters in the definition of the functions $\sigma(t')$ and $m(t')$ will, if possible, be inferred from empirical data. All strains have the same incubation time τ in mosquitoes.

Assuming that the ending of incubation periods can be described by a rate, we will consider the following system of differential equations,

$$\begin{aligned} \dot{S} &= B(1 - S) - \Lambda \sum_{j=1}^n i_j S + R \sum_{j=1}^n I_j, \\ \dot{E}_j &= \Lambda i_j S - (1/T_j + B) E_j, \\ \dot{I}_j &= E_j / T_j - (R + B) I_j, \\ \dot{s} &= \beta(1 - s) - \lambda \sum_{j=1}^n I_j s, \\ \dot{e}_j &= \lambda I_j s - (1/\tau + \beta) e_j, \\ \dot{i}_j &= e_j / \tau - \beta i_j, \end{aligned}$$

where $\Lambda = \Delta \sigma(t) m(t)$ and $\lambda = \delta \sigma(t)$, with the index $j = 1, \dots, n$ identifying each parasite strain. The system above already allows analyzing the adaptive dynamics of incubation times T_j as fixed traits characteristic of parasite strains. It can be modified to analyze

- bet-hedging strategies that switch with an unconditional probability q between two fixed incubation times,
- plastic responses to the current parasite density in a host via strain-specific function-valued traits describing bet-hedging strategies with conditional probabilities $q_j(\Lambda i_j)$, or
- plastic responses to the current parasite density in a host via strain-specific function-valued traits describing incubation times $T_j(\Lambda i_j)$.

Models with even more realistic assumptions

Since rate equations like those shown above imply exponential incubation-time distributions, it may be necessary to model incubation times via a delay term to achieve realistic model behavior. Both fixed and probabilistic delay times may be considered. Ultimately, also coinfection between different strains may be considered.

Model analysis

To study the evolution of incubation times, we apply the following analysis based on adaptive dynamics theory:

- Calculate a parasite's invasion fitness as its basic reproductive number using Floquet theory.
- Draw pairwise invasibility plots (PIPs).

- For a reasonable range of parameters, identify the evolutionarily singular strategies and their evolutionary stability.

Interfacing with empirical data

At the evolutionarily singular trait values, and for reasonable values of the remaining parameters, I will compare model predictions to patient data in Korea, where *P. vivax* malaria has recently become endemic again. The data will be acquired through the web-based statistics system of the Korea Centers for Disease Control and Prevention (KCDC), which includes the number of cases in each month since the year 2001 (KCDC 2012).

Work plan

First, I will analyze the first model described above to elucidate which evolutionary constraints guide the emergence of bimodality. Having successfully concluded this preparatory step, I will construct and analyze increasingly realistic models for the evolution of malaria incubation time. Finally, I will compare the results obtained with field data from the KCDC.

Relevance and link to EEP's research plan

I will use mathematical modeling to investigate the evolution of malaria incubation time. This project will thus contribute to EEP's research on evolutionary epidemiology and the dynamics of adaptation in health and diseases.

Expected output and publications

The results of this research project are intended for publications 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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Ecosystem vulnerability to species loss

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Goal

To assess the consequences of compartment collapses in real ecosystems.

Background and motivation

Loss of species has always occurred as a natural phenomenon, but the pace of extinction has recently accelerated dramatically as a result of human activity. Ecosystems are being fragmented, polluted, and impacted by exploitation, and innumerable species are in decline as a result. The degradation or disappearance of a species causes changes that propagate throughout the ecosystem of which it is part. Such an ecosystem will eventually reach a new equilibrium, but countless other species may become extinct in the process. An important challenge in ecology is to elucidate consequences of species loss for the composition and functioning of ecosystems.

Several authors have investigated how structural and functional aspects of ecosystems correlate with ecosystem stability. MacArthur (1955) argued that complexity should enhance the stability of ecosystems. May (1972), however, suggested the exact opposite: he showed that randomly assembled ecosystems become less robust as their complexity increases. Since then, a number of studies have brought forth theoretical arguments and experimental evidence supporting both of these positions (Lehman and Tilman 2000; Ives and Carpenter 2007), in what is known as the “complexity-stability” debate (Pimm 1984; McCann 2000; Dell et al. 2006). Among other salient insights, this debate has revealed that conclusions are crucially dependent on both the definition of stability and the criteria of complexity (Chen and Cohen 2001; Ives and Carpenter 2007). The most common stability criterion arguably is local stability, as used by May (1972). This gives a measure of an ecosystem’s ability to resist small perturbations. The main reason for the widespread use of local stability is that this criterion does not require specifying a full dynamic model, which is needed in order to assess resilience to large perturbations, including species loss.

The relationship between structure and stability has been explored for both empirically measured (e.g., Yodzis 1981; Pinnegar et al. 2005) and artificially generated ecosystems (e.g., MacArthur 1955; May 1972; Jansen and Kokkoris 2003). Such studies have assessed both local stability in the tradition of May (1972) and stability criteria that are based on responses to large perturbations. Surprisingly, however, few studies built on empirically measured ecosystems have considered the latter, more sophisticated, stability criteria (Worm et al. 2006). The reasons for this lacuna in the literature are not known, but the difficulty of constructing a proper dynamic model on top of empirically measured ecosystem data might be a root cause. The connectivity of most real ecosystems place them in the range that May (1972) identified as unstable. The dynamic stability of these ecosystems, therefore, hinges on finer details of structure and interaction strength, which may be hard to establish empirically.

The aim of this study is to fill this long-standing lacuna through an explicit and thorough consideration of dynamic stability in empirically measured aquatic ecosystems. This will be

facilitated by the application of modern dynamic ecosystem models in the same vein as Ecopath (Christensen and Walters 2004), rather than classical dynamical models in the tradition of Lotka and Volterra. Our principal objective is to investigate ecosystem stability under compartment collapses, elucidating how ecosystem topology influences stability. In full alignment with Ecopath, we mostly assume that energy flows between compartments are subject to donor control. Transcending the traditional focus on pulse or press perturbations of ecosystems (Pinnegar et al. 2005; Ives and Carpenter 2007), we systematically assume collapses of compartments and measure the consequences. We investigate ecosystem stability by calculating two primary variables for each compartment: the possible extinction time and the relative biomass loss that the compartment suffers if another focal compartment collapses (disappears). While the extinction time is often used as a stability criterion, the explicit consideration of relative biomass loss is less common. Based on these two primary indicators, we further calculate selected secondary indicators of stability. To our knowledge, this will be the first study that comprehensively addresses all of the aforementioned dimensions in an effort to elucidate the consequences of species loss in real ecosystems.

Research questions

The following research questions will be addressed:

- How does the collapse of one ecosystem compartment influence the remaining ecosystem compartments?
- How is an ecosystem's structure related to its vulnerability to compartment collapse?

Methods and work plan

General overview

Our investigations will build on a dynamic ecosystem model that predicts the changes in stock abundances following the collapse of one of the ecosystem compartments. Mathematically, this relates to the assessment of non-equilibrium dynamics of directed weighted connected graphs. The consequences of compartment collapses will be assessed based on biomass changes. We will determine correlations between measures of ecosystem structure and indicators of ecosystem vulnerability. The associations found through this analysis are expected to reveal which structural features are important for ecosystem vulnerability to species loss.

Stocks and flows

We consider a system of n ecosystem compartments numbered $1, \dots, n$, which are connected through directed energy flows. To account for primary production and exchange of energy with compartments that are not explicitly represented, we also consider energy flows to and from the external environment. Formally, we ascribe the index 0 to the environment.

The compartments are divided into two groups: living and non-living. Living compartments correspond to biotic components of ecosystems, while non-living ones correspond to abiotic factors, e.g., detritus. Without loss of generality, we number the living compartments $1, \dots, l$, and the non-living compartments $l + 1, \dots, n$.

We assume that each compartment i has an equilibrium stock $x_i^* > 0$. The energy flow $f_{ij} \geq 0$ corresponds to the rate at which energy flows from compartment j to compartment i . Due to energy dispersion, a fraction of the energy flow f_{ij} coming from compartment j to compartment i dissipates to the environment, so that $h_{ij} = \lambda_{ij} f_{ij}$ is the flow from compart-

ment j that arrives in compartment i . Here, $0 < \lambda_{ij} \leq 1$ is the dissipation coefficient, or trophic efficiency, associated with the flow connecting compartment i to compartment j . We refer to f_{ij} and h_{ij} as outflows and inflows, respectively.

We assume that the ecosystem is initially in equilibrium, i.e., that the total outflow from each compartment k compensates its total inflow. Mathematically, this means that $\sum_{i=0}^n f_{ik} = \sum_{i=0}^n h_{ki}$ for all $k = 1, \dots, n$, and that the flows do not vary in time.

Determination of energy flows

We assume that the energy flow from compartment i to compartment j is a function of their respective stocks, $f_{ji} = \varphi_{ji}(x_j, x_i)$. As the environment is not associated with a stock, we assume that the flows to and from the environment and compartment i are functions only of that compartment's stock, i.e., $f_{0i} = \chi_i(x_i)$ and $f_{oi} = \psi_i(x_i)$, respectively. As there are two groups of compartments, living and non-living, a total of four types of interactions are possible:

- Living-to-living (L-L)
- Living-to-non-living (L-N)
- Non-living-to-living (N-L)
- Non-living-to-non-living (N-N)

To model these flows, we consider three types of regulation strategies:

- Law of mass action. The energy is proportional to the stocks of both energy donor and energy recipient. Note that this assumption mostly describes ecological interactions of “predator–prey” type. Thus, $f_{ji} = \alpha_{ji}x_jx_i$, where the α_{ji} are non-negative constant parameters.
- Recipient control. Under recipient control (also known as top-down control), flows are given as $f_{ji} = \alpha_{ji}x_j$.
- Donor control. Under donor control (also known as bottom-up control), flows are given as $f_{ji} = \alpha_{ji}x_i$.

We use bottom-up control to model L-N flows and flows to the environment, while flows from the environment are modeled using recipient control. For the remaining flows (L-L, N-L, and N-N), we will consider each of the regulation strategies considered above and select the one that seems most appropriate for our specific study systems.

Collapse dynamics

The collapse dynamics unfolds over discrete time periods $t = 0, 1, \dots$. At time $t = 0$, one of the ecosystem's compartments is assumed to disappear together with all related flows (both inflows and outflows). As transferring energy from one compartment to another takes one time step, the effect of the disappearance of the compartment is propagating over the system with time.

Given an initial condition, i.e., values of $x_i(0)$, $f_{ij}(0)$, $h_{ij}(0) = \lambda_{ij}f_{ij}(0)$ for all $i, j = 0, \dots, n$, energy conservation suggests that the change of a given compartment i 's stock over each subsequent time period for each compartment is given by the difference of its total inflow $\sum_{j=0}^n h_{ij}(t + 1)$ and its total outflow $\sum_{j=0}^n f_{ij}(t + 1)$,

$$x_i(t + 1) = x_i(t) + \sum_{j=0}^n h_{ij}(t + 1) - \sum_{j=0}^n f_{ij}(t + 1).$$

Note that this implies a one-period time delay in the reaction of a compartment's stock to changes in its total inflow and total outflow.

Utility of compartments

There are both economic and ecological reasons for assuming that the present value attributed to the future state of a considered stock declines the further that state is removed into the future. First, viewing a stock as a natural resource, it is natural to discount future values to reflect the relative value of alternative investments. Second, it is likely that the species making up the network's compartments can adapt to future changes through changes in their diet, thus inducing considerable uncertainty about predicted stocks far in the future.

For these reasons, we define a compartment's present utility as the discounted sum of all future stocks abundances,

$$u_i = \sum_{t=0}^{\infty} (1 + \rho)^{-t} x_i(t).$$

Here $\rho > 0$ is a given discounting factor. Thus, at equilibrium the compartment's utility is given by

$$u_i^* = \sum_{t=0}^{\infty} (1 + \rho)^{-t} x_i^* = (1 + \rho^{-1}) x_i^*.$$

Writing u_{ik} for the utility of compartment i following the collapse of compartment k , we define the change in compartment i 's utility as $\Delta u_{ik} = u_{ik} - u_i^*$. The ratio $r_{ik} = \Delta u_{ik}/u_i^*$ measures the relative change in utility of compartment i resulting from the collapse of compartment k . Accordingly, $r_{ik} < 0$ means that compartment i loses discounted biomass in comparison with its initial equilibrium, while $r_{ik} > 0$ means that compartment i gains discounted biomass in comparison with its initial equilibrium. By definition, $r_{ik} \geq -1$.

Measures of ecosystem structure

Measures of ecosystem structure are calculated based on the data describing an ecosystem's initial equilibrium. These are:

- Number of compartments in the ecosystem
- Connectivity of the ecosystem graph
- Maximum trophic level in ecosystem
- Fraction of weak links
- Evenness of links
- Evenness of stocks

The two measures of evenness are defined based on entropy considerations. The measures above can be assessed at the ecosystem level and at the meta-ecosystem level. The last three of measures can also be assessed at the compartment level.

Indicators of ecosystem vulnerability

Indicators of ecosystem vulnerability are calculated based on biomass losses, extinction times, and the concept of information entropy. These are:

- Total entropy (sum of compartment-specific entropies of biomass changes)
- Average relative change (average of elements in the matrix of changes)
- Average relative loss (average of negative elements in the matrix of changes)
- Average relative gain (average of positive elements in the matrix of changes)

- Number of extinct compartments in the ecosystem
- Fraction of extinct compartments
- Average time to extinction

The indicators above can be assessed at the compartment level, the ecosystem level, and the meta-ecosystem level.

Empirical data

I will carry out collapse-impact assessments for empirically quantified ecosystems. For this purpose, we will use a publicly available database of energy flows in ecosystems assembled by R.E. Ulanowicz (<http://www.cbl.umces.edu/~ulan/ntwk/network.html>). If time allows, we will also consider other databases containing weighted directed connected graphs, possibly even from other disciplinary fields (e.g., from finance).

Work plan

The envisaged work plan is as follows:

- Choose an appropriate energy-flows dynamics (donor-, recipient-, donor-recipient-controlled flows, or other) using an already developed software that projects ecosystem dynamics in discrete time.
- Identify promising vulnerability indicators reflecting the impact of compartment collapses on the remaining ecosystem compartments and the entire ecosystem.
- Analyze, qualitatively and quantitatively, these promising indicators, studying the relations between measures of ecosystem structure and these indicators of ecosystem vulnerability.

Relevance and link to EEP's research plan

This project will directly contribute to EEP's research plan by advancing the planned work on network dynamics and systemic risk. The project will be carried out in close collaboration with IIASA's Advanced Systems Analysis (ASA) Program.

Expected output and publications

The results of this research effort are intended for publication as a coauthored article in an international scientific journal. In addition, the developed software for analysis and visualization will be made available for future studies on related topics.

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