Young Scientists Summer Program 2014

Five Research Projects

Evolution and Ecology Program
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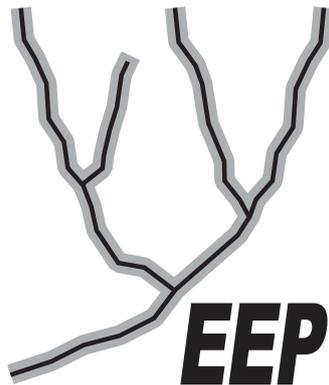
Climate change and malaria incidence in South Africa

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Goal

To understand the impact of temperature and precipitation changes on the distribution of three *Anopheles* species mainly responsible for the transmission of malaria in Africa, and so prepare a prediction of malaria incidence over the next decades.

Background and motivation

Every year, malaria infects around 200 million and kills over one million people, most of whom are children and almost 90% of whom live in sub-Saharan Africa (Update on Malaria in Southern Africa, 2003). Malaria has serious economic impacts in Africa, slowing growth and development and perpetuating the vicious cycle of poverty, because it afflicts primarily the poor who tend to live in malaria-prone rural areas in poorly-constructed dwellings that offer few, if any, barriers against mosquitoes (UNICEF update, 2013). It is caused by several species of single-celled *Plasmodium* parasites transmitted by female mosquitoes, of which the most dangerous and most commonly found in Africa is *P. falciparum.* All mosquito species that transmit malaria belong to the genus *Anopheles,* and approximately 40 species are able to transmit malaria well enough to cause significant human illness and death (Malaria Atlas Project). Malaria transmission in tropical Africa is sustained by three main vectors which are *A. gambiae, A. arabiensis and A. funestus* (Cinzia et al., 2011), while *A. arabiensis and A. funestus* are the main causes in South Africa (Yijun et al., 2010).

In order to effectively combat the thriving effect of malaria transmission in a population, it is important to make a critical assessment of the existing malaria models, and study their evolution and efficacy in describing the host–parasite biology (Mandal et al., 2011). However, over the years, mathematical models have been greatly used to provide an explicit background to understand malaria transmission dynamics in human population. Several efforts have been made since 1970 to expand and develop the Ross-Macdonald model. Recently, Reiner et al. (2013) compiled a bibliography of 325 publications from 1970 through 2010 that included at least one mathematical model of malaria-borne pathogen transmission and used a 79-part questionnaire to classify each of 388 associated models according to its biological assumption. Their analyses revealed a growing acknowledgement of geographical, ecological and epidemiological complexities in modeling transmission, but also that most models during the past 40 years still resemble the Ross-Macdonald model. The questionnaire focuses on three essential components common to all of these models, which are: mosquitoes, hosts and encounters between them. Concerning mosquitoes, they found that 62% of the models explicitly modeled the mosquito populations with at least one variable. Of those, many implemented various aspect of mosquito biology with constant per capita rates: 87% assumed a constant death rate and 74% a constant blood feeding rate. The aquatic phase of mosquito life cycle was often excluded as pathogen latency was completely ignored in 38% of the model. Also, 61% of those models that explicitly included mosquitoes and implicitly considered the aquatic phase assumed that mosquito density was constant. Similarly, 37% of the models did not incorporate host population dynamics. The mosquito–host encounters were also assumed to be well-mixed as 78% of the models agreed

on homogeneous distribution. This assumption is impractical at large spatial scales, but only few of the models considered two or more spatial locations.

There is a big concern that climate changes may make malaria parasites spread over more provinces in South Africa and Africa at large, thereby exposing more populations to malaria. Studies have shown that climatic factors such as temperature, rainfall and relative humidity play a vital role in malaria transmission. This is either through changes in the duration of mosquito and parasite life cycles or influences on human, vector or parasite behavior (Gubler et al. 2001; Koenraadt et al. 2004). In spite of this sensitivity of transmission to changes in these factors, there is still extensive debate as to the exact role that climate plays in driving malaria epidemics (Patz et al., 2002; Hay et al., 2005 and Pascual et al., 2008). For instance, the recent study of Li (Li, J, 2011) shows that it takes 1, 3 and 10 days for eggs of some mosquitoes to hatch at temperatures of 30, 20 and 10°C, respectively, as water temperature regulates the speed of mosquito breeding. Alonso et al. (2010) found that the development of the parasite within the mosquito (sporogonic cycle) also depends on temperature which takes about 9–10 days at temperatures of 28°C, but stops at temperatures below 16°C. The study also revealed that the minimum temperature for parasite development of *P. falciparum* is approximately 18°C and the daily survival of the vector is also temperature-dependent as temperatures between 16 and 36°C keep the daily survival high to about 90%. It has also been shown that temperature fluctuations between 15°C to 35°C have negative influence on development and survival rate of *A. funestus* but no significant influence on *A. arabiensis* (Lyons et al., 2013). Moreover, *A. arabiensis* develop consistently faster than *A. funestus* while *A. gambiae* shows fastest development at a constant temperature of 28°C and highest survival at 24°C (Lyons et al., 2013). In addition to these, Bomblies (2012) showed in a numerical study that intra-seasonal rainfall patterns account for 39% of the variance in simulated mosquito abundance. The result is validated over Niger Sahel village where malaria is endemic but highly seasonal.

Rainfall generates water pools serving as mosquito breeding sites, where mosquitoes lay their eggs, which later develop to adult mosquitoes if the pools are sustained for at least 14 day (Yazoume et al., 2009). It is also believed that if the average monthly relative humidity is below 60%, the life of mosquito is shortened and no malaria transmission (Pampana, 1969). The studies of Lindblades et al. (1999, 2000) show that land use changes alter malaria transmission parameters. The findings suggest that elevated temperature near cultivated swamps area, combined with occasional excessive precipitation, have intermittently encouraged populations of *A. gambiae* as well as *Plasmodium* transmission in the highland valleys of South-western Uganda. In addition to this, a number of studies (Manga et al., 1997; Klinkenberg et al., 2008; Yadouleton et al., 2010 and Sovi et al., 2013) confirmed that land use change can increase the level of malaria transmission. They found that mosquito biting rates are higher in villages where creation of fishponds and regional market-gardening are well developed than in villages located far from agricultural development areas. Fishponds and water reserves for watering vegetables also serve as breeding sites for *Anopheles*.

Malaria incidence depends critically on the availability of suitable mosquito vector populations. Predicting the distribution of mosquito species under climatic and land use changes is therefore the first, important, step to predicting malaria incidence.

Research questions

I will address the following questions:

- Which factors should be considered in a mosquito model, and how can they be included?
- How should the interface between mosquito and disease model be designed to maximize its usefulness?
- How do the predictions from a malaria model with a more intricate mosquito module differ from that of a simple model?

Method and work plan

In this project, a generalized malaria model will be designed based on a literature analysis following the study of Reiner et al. (2013). The model will summarize and incorporate some of the lapses in the previous models mentioned in the study. It will also analyze the impact of temperature and rainfall on the activities and life history of prominent *Anopheles* species which are responsible for malaria transmission in South Africa. The model will be prepared to predict malaria incidence over the next decades, and also to accommodate further development and expansion.

Below I list some components which may be included in our model (Reiner et al., 2013).

- Aquatic mosquito ecology
- Spatial dynamics
- Adult mosquito ecology
- Mosquito infection dynamics
- Host population dynamics
- Mixing and biting
- Movement patterns
- Male mosquitoes
- Recovery from infection
- Feeding rate
- Mosquito survival

Mosquito ecology

To construct a pragmatic malaria model, it is important to understand some activities of mosquito in which some are briefly mentioned below.

Life cycle

A mosquito goes through four stages of life. It starts out as an egg, laid in damp soil or on the surface of standing water. Once the egg hatches it goes through four growth stages as a larva, finally forming a pupa. Male mosquitoes usually emerge from pupa stage before female ones and form large swarms. Female emerge later and seek out of the males where they mate and acquire sufficient sperm to fertilize several batches of eggs. The aquatic stage is climate-dependent, mostly on rainfall and temperature (Martins et al., 1995; Paul and Edwin 2010). For instance, the suitable temperature for immature stage development rate for *Anopheles gambiae* is 28°C and between 22°C and 26°C for adult emergence (Bayoh and Lindsay, 2003). High rainfall tends to flush away the breeding site (Tompkins et al., 2011).

Feeding

Male mosquitoes do not feed on blood and may live several months feeding on plant and nectars. The female mosquitoes go in search of enough protein to produce eggs. *Anopheles* species prefers to feed on humans (anthropophily) or animals such as cattle (zoophily). Anthrophilic *Anopheles* are more likely to transmit the malaria parasites from one person to another. Most *Anopheles* mosquitoes are not exclusively anthropophilic or zoophilic. However, the primary malaria vectors in Africa, *A. gambiae* and *A. funestus*, are strongly anthropophilic and, consequently, are two of the most efficient malaria vectors in the world.

Mosquito biting rate

The rate at which mosquito bite is strongly affected by temperature (Paaijmans et al., 2013; Nakazawa et al., 1999). After obtaining a full blood meal, the female will rest for a few days while the blood is digested and eggs are developed. This process depends on the temperature, but usually takes two to three days in tropical conditions. Once the eggs are fully developed, the female lays them in a suitable location and resumes host-seeking. The cycle repeats until the female dies.

Daily mosquito survival

Temperature also plays a role in determining the mortality of vector. High air temperatures increase vector mortality, but the relationship is uncertain, especially at the high and low temperature bounds of transmission (Li, 2011). This leads to an exponential model of mortality, which has the advantage of huge mathematical simplicity, and is also widely used in analyses of mortality and survival in natural population.

These and other activities and functions will be considered in developing the ecological and epidemiological model.

Model structure

The first phase of this project is to develop and analyze a climate-based ecological model for mosquito population dynamics. The model will consider the aquatic stage of mosquito that is Egg, Larva and Pupa. The adult stage will be subdivided into Susceptible, Exposed, and Infected mosquitoes. Several parameters in both stages will depend on temperature and rainfall as land use and population changes will be a possible extension part of this model.

The second phase will be to build an epidemiological model which can fit in with the developed ecological model. The human component will also consist of a classical system of ordinary differential equations where the population will be subdivided into Susceptible, Exposed, Infectious and Recovered humans.

The third part will be to construct a compatible interface between the ecological and epidemiological model. This interface involve the force of infection and the rate at which female mosquito acquire the parasite from infectious human. Some activities (such as contact rate and biting rate) in this interface will be climate-dependent. Thereafter, the result would be validated over malaria epidemic provinces in South Africa.

Work plan

I intend to carry out the following activities during and after the summer program.

June: Literature analysis on malaria and climate, preparation of background and basic material, formulation of the ecological mosquito model, definition of the interface between mosquito and epidemiological model

July: Implementation of the mosquito model, validation with past data, projection of mosquito ranges for defined scenarios, link with a simple epidemiological malaria model

August – December: Finalizing and submission of a research paper

Possible extension

For the summer program, the aspect of climatic and ecological factors would be investigated, and the possible extension of this project would be to incorporate land use and population changes into the model.

Relevance and link to EEP's research plan

I will use mathematical modeling to examine the impact of climate and ecological factors on malaria transmission in South Africa and Africa. The socio-economic importance of malaria will also be investigated. This project will thus contribute to EEP's research on evolutionary epidemiology, the dynamics of adaptation in health and diseases and IIASA's project on poverty and equity.

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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Impact of shocks on the global seafood trade network

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Goal

To evaluate the response of global seafood trade to environmental and policy shocks and assess the resulting implications for food security.

Background and motivation

The 1996 World Food Summit described food security as a "situation that exists when all people, at all times, have physical, social, and economic access to sufficient, safe, and nutritious food that meets their dietary needs and preferences for an active and healthy life." Recently, food security policies, goals, and studies have focused on access to sufficient food calories. Since fish and other aquatic food (seafood) comprise a relatively small share of calorie intake, seafood is often ignored in food security discussions (Muir 2013). However, as the source of almost 20% of the global animal protein consumed by humans (FAO 2012), aquatic foods can play an important role in nutrition. This is especially true for many impoverished countries (Kent 2003). For example, while Africa has the lowest average per capita supply of animal protein of any major region, seafood provides the highest percent of animal protein intake of any region (Tacon and Metian 2009). Consequently, it is important to consider the role of seafood in food security.

The growing human population and increasing per capita demand for animal protein have fueled an ongoing debate about global food security (Tilman et al. 2011). The uncertainty surrounding the ability to meet these growing food demands increases when climate change is considered for both terrestrial (Schmidhuber and Tubiello 2007) and aquatic (Merino et al. 2012) food production. In addition to climate change pressures, there has been debate over the future trajectory of global fisheries (Worm et al. 2009). While the state of global fisheries is controversial, there are specific fisheries known to be in decline, with small unassessed fisheries in significantly worse condition than large assessed ones (Costello 2012). Global trade can allow countries to overcome such regional shocks to food supply, but the increasing reliance on international food trade exposes a country to higher risks of being impacted by external perturbations.

This project will evaluate how shocks spread throughout the global fish trade network and model the redistribution of trade flows under environmental and policy shock scenarios. These analyses are expected to reveal which countries are most vulnerable to environmental impacts on the seafood trade network and identify conditions under which environmental impacts that initially are regionally confined cause knock-on effects that propagate throughout the seafood trade network. This project represents a novel application of network analysis methods that will combine research in economics, ecology, natural resources, and systems analysis to add a seafood perspective to the ongoing discussions of global food production.

Research questions

I will address the following questions:

- To what degree do shocks spread through the throughout trade network?
- How might environmental and policy perturbations reshape seafood trade flows?
- Which countries are most vulnerable to perturbations to the seafood trade network?

Methods and work plan

This project will investigate how the global seafood trade network responds to environmental and policy perturbations from two angles: first, by studying how negative local impacts such as the collapse of a regional fishery cause contagious effects that spread through the trade network, and second, by evaluating how trade flows are redistributed under shock scenarios using an economic model. The implications for food security will be examined by comparing changes in national fish supplies to indices of each country's economic and nutritional fish dependency.

Spread of shocks in the seafood trade network

First, contagion within the seafood trade network will be investigated using a simple propagation model. Fish trade volumes from country i to country j are represented by w_{ij} (non-traded domestic production is w_{ii}). A node, k, will be randomly selected to have its exports decreased by a fraction s, with s equal to 1 for a complete collapse. Since each connected countries' imports from k are decreased by sw_{ki}, those countries' available fish will be reduced. As a result, this reduction is divided between consumption and exports proportionally to the original flows. This will be iterated a sufficient number of times to reach equilibrium and repeated with new initial node shocks. The resulting seafood supplies will be computed for each country. Countries which have the largest decreases and those which fall below an identified supply threshold will be identified. The parameter s will be varied to compare contagion under different degrees of perturbation.

Economic model of shocks in the seafood network

The above propagation model assumes that each country experiences an equal reduction in supply, which ignores changes in price and differences in the elasticity of demand. While this evaluates how a country's location in the fish trade network affects whether or not it could be reached by a given shock, it does not represent a likely redistribution of fishery products under a shock scenario.

In order to better assess changes in trade flows under a shock scenario, an economic model will be developed that includes fishery product demand elasticities, and maximizes exporters' revenues. To simulate a shock to the system, the production of a country (or of several countries) will be changed according to the scenario. For example, under a fishery collapse scenario, the production from the collapsed fishery will drop to zero. Remaining fishery production from that country will be exported or kept within that country. The trade flows will be determined by optimizing the exporter's revenue based on the elasticity of demand of the importers. Depending on the resulting flow changes, these importing countries then readjust their imports from other countries to which they are connected and adjust their own exports. This re-equilibration will proceed for stepwise away from the perturbed country until the system reaches equilibrium. Initially, this model will be developed using all fishery products, assuming complete substitutability and no transportation costs. The model will then be reformulated with fishery products in groupings that are more likely to be substitutable goods and with transportation costs.

This model will be a static network, where trade flow volumes change, but the structure of the network does not. Further, it will be assumed that countries cannot increase production on a time-scale relevant to the time-scale of the perturbations. This is because most capture fisheries operate at the highest production permitted and aquaculture requires investment and time to increase production. Within a longer timeframe, aquaculture production would be expected to change in response to the shocks studied.

This model will be used to evaluate the impact of environmental and policy shocks to the system. Shocks to the system will be modelled as decreases or increases in fishery product supply to the relevant countries. Fishery collapses will be modelled for several vulnerable fisheries as a complete removal of the fishery product from the relevant countries' production. Possible policy shocks to be considered include changes in tariffs, an introduction of other protectionist policies (such as prohibiting exports if fish supply falls below a given level), increases in transportation costs, and the establishment of a free-trade agreement.

Data availability

The United Nations' Comtrade data will be used to construct the trade network. Countries voluntarily report the origin or destination of imports, exports, reimports, and reexports to the United Nations on an annual basis. The Food and Agriculture Organization of the United Nations (FAO) has made its fishery database (FishStat) publically available. This database provides data on national capture fishery and aquaculture production and total national imports and total national exports from 1976 to 2009. These values are either reported by producing countries, or estimated by the FAO, with estimated values indicated in the dataset. Species production can be provided at the species-level, or grouped according to several schemes, and contains data on both the dollar value and volume. This allows estimates of seafood trade volume flows to be computed from the Comtrade dollar trade flows. The resulting dataset will be used to model the effects of environmental perturbations on the network. Volumes and prices will be used to calculate country demand elasticities. Food security outcomes will be evaluated by the change in the national fish supplies, and comparing these changes to national nutritional and economic fish dependency indices (Allison et al. 2009). The nutrition dependency index is constructed by comparing the contribution of fish protein to animal protein consumed, the employment dependency index represents the share of national employment in fishing-related work, and the macroeconomic dependency index represents the contribution of fisheries to national GDP and exports.

Work plan

- Evaluate the spread of shocks in the trade network using a simple propagation model
- Develop the economic model and perturb the network with environmental and policy shocks
- Compare the results of shocks on the seafood trade network to each country's economic and nutritional dependency on fish.

Relevance to EEP's research plan

This project will contribute to the Evolution and Ecology Program's work on the integrated assessment of fishery systems by examining the provision of aquatic food resources through the international trade systems. This project utilizes complex systems methods and applies modified ecological network methods to study the global seafood trade network.

Expected output and publications

The results of this research project are intended for publication as a coauthored article in a peer-reviewed scientific journal and will also be part of my Ph.D. dissertation.

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Signatures of speciation: From theoretical mechanisms to observable patterns

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Goal

To identify post-speciation genetic patterns – in terms of ecological, spatial, and reproductive differentiation among the resultant species – that allow inferring the underlying speciation processes, and in particular, distinguishing between adaptive speciation caused by local competition and coincidental speciation – its traditional alternative – in geographic isolation.

Background and motivation

Every living organism contains a unique set of biological information in its genome – genetic patterns resulting from ever-ongoing evolutionary processes. These evolutionary processes are affected by the ecological and biogeographical backdrop experienced by each individual, processes that ultimately might lead to speciation.

On the remote Tristan da Cunha archipelago (close to the Mid-Atlantic ridge) two endemic types of finches (*Nesospiza spp.*), originating from a common South American ancestor, are coexisting on two small islands (Inaccessible and Nightingale Island). Each island contains a thin-billed type and a thick-billed type, and each type is connected to a specific resource (Ryan et al. 2007).

These specific attributes of the Nesospiza system – a comparatively simple two-habitat, two distinct resource system with two species on Nightingale island and one species (with three hybridizing subspecies) on Inaccessible Island (for more information see Ryan 1992 and Ryan et al. 2008) – makes it extra interesting from a evolutionary point of view, since the empirical system might shed light on the connection between biogeographic and genetic patterns.

The main question of the Nesospiza project is if it is possible to disentangle and backtrack the evolutionary history of the finch species from the genetic patterns – what is the most likely speciation scenario: sympatric speciation on one island followed by dispersal to the other or allopatric speciation followed by back-colonization and secondary contact, or if there might be other scenarios?

To get a deeper understanding of the genetic imprint of different speciation scenarios, it is necessary to build a theoretical model. As this project focuses on some of the fundamental mechanisms of adaptive speciation in a spatially structured system, I will use eco-evolutionary modeling to generate genetic data, using the speciation cube (Dieckmann et al. 2004) as a conceptual tool to visualize the evolutionary pathways to full speciation, given specific eco-evolutionary scenarios (see Fig. 1).
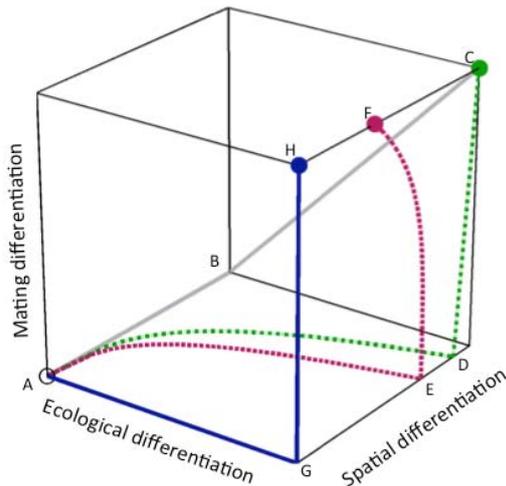
Fig. 1. The speciation cube, adapted from Dieckmann et al. (2004), with some sample speciation scenarios included. During the speciation process an ecological, spatial, and reproductive differentiation will take place depending on factors such as geographic speciation mode and mating preferences. Each pathway in the speciation cube will give rise to different genetic signatures.

Research questions

The general objective of this project is to understand what signatures adaptive speciation – occurring through evolution of assortative mating – leaves on the genomic patterns of differentiation and to generate new testable predictions of biogeographic and genetic speciation patterns. The results should not only shed light on the connected Nesospiza project, but on speciation processes in general, and could inform applied biologists on the possibility to infer process from pattern. In order to accomplish this, two particular research questions should be answered:

- What is the genetic imprint of sym-, para- and allopatric speciation scenarios and how does this genetic signal differ between the different speciation scenarios?
- How can these theoretical results be used to infer process from pattern using the experimental data from the Nesospiza project?

Methods and work plan

Model description

The model will describe the genotypic and phenotypic evolutionary dynamics of sexually reproducing populations. The main point is to follow the entire population of individuals to generate a set of genomes that can be further analyzed.

The spatially explicit model will be defined in discrete time. Individuals will compete and reproduce only within habitats.

Environment and state variables

The environment consists of two discrete habitats (h=1, 2), each with two resources with abundances $R_{h,1}$ and $R_{h,2}$. In the absence of consumers, resources grow logistically. Each individual disperses at birth with probability δ ($0 \leq \delta \leq 0.5$) to the other habitat (Fig. 2).

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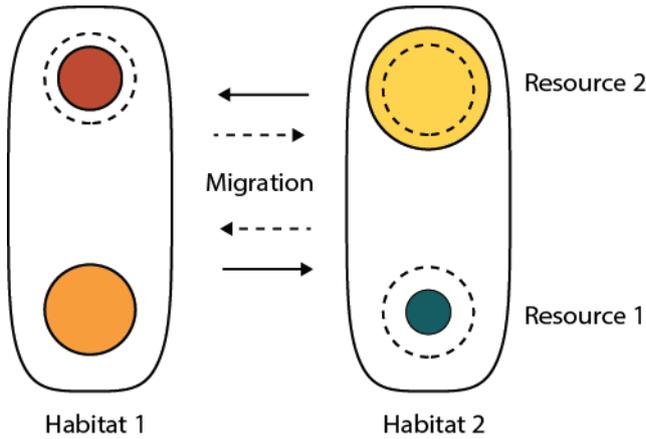
Fig. 2. The basic structure of the model.

Individuals

Individuals living in this environment differ by location and phenotype and will have two phenotypic traits, each of which will be determined by one set of diallelic diploid loci with equal additive effects. The first trait, x, is the ecological trait affecting local resource utilization and m is a mating preference trait, which will regulate the degree of choosiness when mating. Mating will vary from random ($m=0$) to assortative ($m>0$). In a more advanced setting, an additional display trait may be added.

At any moment in time, the state of the system (disregarding genetics) is given by the states (h_i, x_i, m_i) of all individuals $i = 1,\ldots,N$, where N is the current number of individuals.

Genetics

Each individual has three types of diallelic loci: x-loci, m-loci and a set of neutral loci where the neutral loci have no phenotypic effect. An elaborate genetic methodology developed by Varvara Fazalova will be implemented in steps, starting from the simplest case, where each locus is unlinked to all other loci, gradually increasing complexity.

Events

All individuals, i, go through three types of events each time step in the following order: dispersal, reproduction (with the possibility of mutation) and death.

Dispersal

Any individual disperses with a fixed probability to the other habitat with the probability δ.

Reproduction

Reproduction is only possible between individuals in the same habitat. All individuals are considered hermaphrodites and each individual will produce offspring in accordance to fitness (see fitness calculations below).

The mating probability between individuals i and j is p_{ij}. For assortative mating ($m>0$), $p_{ij} \sim N_\sigma(\Delta x_{ij})$ where $\sigma = m^{-2}$ and Δx_{ij} is the phenotypic difference between potential mates i and j (if $m=0$, $p_{ij}=1/(N-1)$). An elaborate methodology for gamete formation developed by Varvara Fazalova will be implemented in steps, starting from the simplest case where $L-1$ independent crossover events will occur (L being the total number of loci on the chromosome), gradually increasing complexity.

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After gamete formation, random mutations can switch alleles from 0 to 1 or vice versa with a small probability μ. The two gametes from the respective parents will then merge. This process is repeated to produce offspring, each with a specific genomic set.

Death

Each season, individuals may die with a fixed probability d. The surviving population will constitute the new parent generation.

Fitness calculations

The attack rate, $a(x_i, y)$, of an individual with trait value x_i (where x can be seen as bill depth in the Nesospiza system) on resource y (where y can be seen as seed mass) is written as a Gaussian function:

$$a(x_i, y) = a_0 e^{-\frac{(x_i - x_{\mathrm{opt}}(y))^2}{2\sigma_a^2}} , \tag{1}$$

where a_0 is the maximum attack rate, σ_a is the niche width (here used as a measure of the trade off-strength between the two resources), and $x_{\mathrm{opt}}(y)$ is the optimal x-value for consumption. A large value of σ_a corresponds to a weak trade-off (the consumer shows generalist behavior) and a small value to a strong trade-off (specialist behavior).

A simple way to take the resource dynamics into account is to assume logistic growth and subtract the total consumption (Ripa 2009). The per capita resource growth rate can thus be written:

$$\frac{dR_h(y)}{dt} \cdot \frac{1}{R_h(y)} = r \cdot \left(1 - \frac{R_h(y)}{K_h(y)} \right) - \sum_{i \in I(h)} a(x_i, y) , \tag{2}$$

where $R_h(y)$ is the abundance, r the intrinsic growth rate, $K_h(y)$ the carrying capacity and in which $I(h)$ are the individuals in habitat h. The total consumption is the sum of consumption from all individuals in habitat h.

Resource abundance is thus dictated by the carrying capacity, and since individuals only compete through resource utilization, different spatial settings can be studied by tuning the carrying capacity values of the respective resources, $K_h(y)$.

Further assume that resource dynamics are much faster than consumer dynamics, which implies the resource populations will always be close to their equilibrium abundance, $R_h^*(y)$, given the current consumers. The equilibrium abundance in the respective habitats is found by setting Eq. 2 equal to zero and solving for $R_h(y)$:

$$R_h^*(y) = K_h(y) \left(1 - \sum_{i \in I(h)} a(x_i, y) \right) , \tag{3}$$

where negative equilibrium abundances are set to zero. The resource dynamics are assumed to take place within a season in continuous time.

Given that the resource is at ecological equilibrium, the local per capita growth rate, w_h, of a consumer individual with trait x_i in habitat h can be written:

$$w_{h,i} = c \int a(x_i, y) R_h^*(y) dy , \tag{4}$$

where c is a conversion factor from resource to consumer (which, without any loss of generality, can be chosen as $c = 1$). The integral is over all resources in the respective habitat. We assume that the effective fecundity of a parent is proportional to $w_{h,i}$.

Initially, we consider two discrete resources:

$$K_h(y) = k_{1,h}\delta_{y1_h} + k_{2,h}\delta_{y2_h},$$ (5)

where k is the carrying capacity for the respective resource and δ_y is the Dirac delta function, indicating a peak in the resource spectra at seed mass y. In a second step, continuous distributions (Gaussians or from data) will be used.

Analysis and simulations

I will make individual based simulations from parameter areas of interest. Since testing and characterizing the full parameter set is too time consuming, an asexual model will be used to find settings in parameter space where speciation is possible (most likely, only a subset of the possible parameters will eventually lead to speciation if sexual reproduction is added). Methods from the adaptive dynamics framework will be used to analyze the asexual model (see, e.g., Metz et al. 1992, Geritz et al. 1998).

Using this information, I will look at the problem from two directions, from one point of view characterizing the signals from different generic modes, from another point of view parameterizing the Nesospiza system.

I will then use the distance in trait value between the two morphs under speciation as a measure of the ecological differentiation and a modified version of Pianka´s omega index (Pianka 1973) of niche overlap as a measure of spatial differentiation:

$$\Omega = 1 - \frac{\left(N_{1,1}\cdot N_{1,2} + N_{2,1}\cdot N_{2,2}\right)}{\sqrt{\left(N_{1,1}^2 + N_{2,1}^2\right)\cdot\left(N_{1,2}^2 + N_{2,2}^2\right)}},$$ (6)

where $N_{h,k}$ are the consumer clustered abundances after branching.

Finally, I will use either reproductive differentiation (with reproductive isolation as a measure) or mating differentiation (using mating behavior, e.g. the correlation between partner ecological trait values) or a combination of the two to get a measure of full speciation, given sexual reproduction.

I will use Matlab to code the system or, if necessary, a combination of Matlab and C to increase calculation speed.

Model output

To be able to compare the outcome of the model analysis with real data, a number of standard genetic statistic measures can be used to describe the level and patterns of diversity, on selected and neutral loci, for a given sample.

From the finch data, various kinds of genetic distance measures such as F_{ST} (e.g. Hudson et al. 1992) to measure average differentiation among populations, statistics using mutation frequency information, such as Tajima's D (Tajima 1989), or statistics using information from the haplotype distribution, such as EHH (Extended Haplotype Homozygosity), Sabeti et al. (2002). Finally a molecular clock (e.g., Bromham and Penny 2003) can be used to deduce the relative time of divergence for two species.

Different regions in model parameter space for selected and neutral loci will give different values for the standard measures – these patterns might be strong enough to give a clear picture of the road to speciation.

If every time step is accounted for, and every mutation is given a separate id, a full phylogenetic tree can be produced. Also, the speciation cube can be plotted for type examples, contrasting post-speciation genetic patterns to the underlying process.

Work plan

In summary, the following two parts have to be done in parallel to be able to reach my research goals:

Computational part

- Implementation of the model algorithm in Matlab.
- Performing runs of the model, summarizing the genome patterns of differentiation through genetic statistics.
- Visualization and interpretation of results. Evaluation of plausible speciation processes to understand their imprint on the resulting genetic patterns.

Experimental part

- Thorough literature review of the Nesospiza finch system.
- Assessment of the data situation of the Nesospiza project in Lund and gathering of relevant model parameter values.
- Review of which genetic statistics that are to be utilized to examine the genomic patterns of differentiation.

The latter part will be done continuously during summer in collaboration with P. Ryan, B. Hansson and M. Stervander.

Finally, a synthesis will be done, comparing the results of the computational part with the empirical *Nesospiza* data.

Data availability

I will primarily use information regarding habitat and ecology from Ryan (1992), Ryan et.al (2007) and Ryan (2008), morphological data from Ryan (2008) and Stervander (unpublished), and genomic data from Ryan et.al (2007), Ryan et.al (2013) and Burns et.al (2014).

However, three substantially larger and more comprehensive genomic data sets on the *Nesospiza* finches are provided by B. Hansson and M. Stervander at Lund University. Genetic data from these sets are currently being analyzed, and the Nesospiza project is to be finished in 2014. Whereas some aspects (e.g. finding candidate genes controlling beak size) are more difficult to assess, other parts can readily be analyzed. The Nesospiza project will be able to produce the appropriate information sought for in collaboration with the IIASA group.

Relevance to EEP's research plan

The project strives to understand some very fundamental evolutionary questions and connects directly to a better theoretical understanding of the eco-evolutionary dynamics of living systems. Also, since the outcome of the model will be compared to empirical data, this project will shed light on conditions promoting the formation of biodiversity, and from a conservation biology point of view, the maintenance of evolutionary processes.

Understanding the mechanisms underlying the origin of extant species may be of paramount importance for their future persistence and the efficiency of species management. For example, removing the environmental variation necessary for the ecological coexistence of two species may result in reverse speciation or the loss of one of the two species. Altering the environmental basis for efficient partner choice can have the same effect (Seehausen 2006). Taken together, a broad knowledge of the mechanisms of speciation may be necessary to successfully impede the current rapid decline in biodiversity on Earth.

Expected output and publications

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

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Ecosystem-based fisheries management of cod and sprat in the Baltic Sea

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Goal

To improve understanding of the effect of fishing on pelagic Baltic Sea fishes, I will examine a multi-species, multi-impact fisheries model with food-dependent growth and food-dependent seasonal reproduction.

Background and motivation

Overfishing has resulted in the collapse of many commercially exploited fish stocks (Myers & Worm 2003). To improve fish-stock management, the adoption of an ecosystem approach to fisheries management has been propagated (Garcia & Cochrane 2005). Large predatory fish are often the preferred and most profitable targets for the fishing industry. These predatory fish critically depend on prey fish for their survival and growth. Typically, these forage fish are also subject to commercial fishing. Even though it has become widely recognized that fisheries management should account for trophic interactions and multiple impacts in fishery systems (Gislason 1999; Walters et al. 2005), it is proving difficult to operationalize this approach (Persson et al. 2014; Möllmann et al. 2013). This hinders the reliability of predictions of the effects of fishing and the establishment of optimal exploitation targets in systems of interrelated stocks. In order to fully employ an ecosystem-based approach to fish-stock management, innovative tools are needed.

For a realistic assessment of the effects of trophic interactions and multiple impacts, several biological mechanisms need to be implemented: first of all, a realistic feedback between predator and prey, encompassing density-dependent life-history processes such as growth, reproduction, maturation, and predation mortality. Secondly, a community structure with realistic interactions, such that the dependence on different resources in different life stages is accounted for. That these factors are not only desirable but also essential to predict community responses to harvesting is stressed by theoretical and empirical evidence indicating that these factors may result in the occurrence of alternative stable community states with low and high densities of predator populations (the emergent Allee effect: Persson et al. 2007; de Roos and Persson 2013). While some contemporary modelling approaches are quite sophisticated, so far none of them include all the ingredients listed above (for a summary, see Persson et al. 2014, table 1).

The cod population in the pelagic Baltic Sea crashed in the 1990s and, while by ICES standards it is not 'collapsed', at present it has not returned to its old levels (ICES 2013). It is argued that the high cod biomass in 1980s and the low cod biomass in the mid-2000s may have represented alternative stable states. The decrease of cod in the system resulted in a 'trophic cascade' and drastic changes in the pelagic Baltic Sea community (Casini et al. 2008). In response to the decreased predation pressure of cod, sprat biomass exploded. This resulted in a decrease of zooplankton biomass and, through the reduction of zooplankton grazing, in an increase of phytoplankton biomass. Both empirical and theoretical evidence indicate that the alternative stable

states in the pelagic Baltic Sea might be explained by an emergent Allee effect in the cod population (Van Leeuwen et al. 2008; Gårdmark et al. 2014). The consideration of the factors summed up in the second paragraph above seems thus especially important for analysing the effect of fishing in the pelagic Baltic Sea.

In addition to overfishing, changing recruitment success is argued to be one of the causes for the collapse of cod and the increase of sprat in the Baltic Sea (Köster et al. 2005). Reproduction of cod and sprat are seasonal processes concentrated in a specific period of the year (Köster et al. 2003; Wieland 2000). Seasonality of reproduction leads to possible matches or mismatches between the early critical feeding period of young predator life stages and prey availability (Cushing 1990). Shifts in zooplankton availability within years and a resultant food shortage for cod larvae may have caused recruitment failure (Köster et al. 2005). However, recruitment success of cod is mainly based on estimates of age-2 recruitment, as this is when cod shows up in stock-assessment data (ICES 2013). The switch in cod from zooplanktivorous and benthivorous food sources to piscivory takes place well before this age (Sparholt 1994). Failure in the recruitment as measured in this age group could be caused by low availability of food in any of the food sources essential to reach this age. Seasonality in the reproductive output of the fish species and their timing of spawning relative to each other is therefore an important factor to investigate.

The effect of harvesting sprat on the emergent Allee effect in cod has so far not been tested in the Baltic cod-sprat system. Moreover, the obvious fact that both cod and sprat exhibit seasonal reproduction has not been accounted for. The aim of this project is to develop and examine these extensions in an improved fisheries model, to elucidate how the fishing of cod and sprat affects the Baltic Sea ecosystem.

Research questions

- To what extent does the incorporation of food-dependent growth and food-dependent seasonal reproduction affect the model dynamics?
- What are the predictions regarding the effect of fishing on cod and sprat on the pelagic Baltic Sea system based on the model findings?
- Do the model outcomes compare to data about the pelagic community in the Baltic Sea?

Methods and work plan

Model structure

To analyse the effect of fishing on both Baltic cod and sprat, I will use and extend an existing stage-structured biomass model for the cod-sprat interaction in the Baltic Sea (Van Leeuwen et al. 2008). The basic assumptions of the model follow the bioenergetics approach introduced by Yodzis and Innes (1992). In addition, the model incorporates food-dependent growth and maturation, food-dependent seasonal reproduction, and size-dependent feeding interactions of six cod stages and four sprat stages, all with different sizes.

Seasonal reproduction

Seasonal reproduction is added to the model by implementing a storage component for each of the mature fish stages. As the reproductive storages are assumed to be part of the adult body, they experience the same processes (i.e., mortality, maturation) as the corresponding adult stage does. Reproductive energy is stored up to the spawning season. Spawning is either assumed to

be a set event that occurs simultaneously for all mature individuals in the population or follows a probability density function that is spread out over several days.

Trophic interactions

The predatory interactions between cod and sprat stages are size-based and derived from field data from the Baltic Sea. Sprat is fully zooplanktivorous, while cod changes its diet during ontogeny twice (Bagge et al. 1994; Sparholt 1994). Cod starts as a zooplanktivore, switches to benthos in a larger juvenile stadium and starts including fish in its diet just before maturity. The boundaries of the different size classes are chosen based on the piscivorous interactions, cod has six stages and sprat has four stages; the resources in the model are unstructured. There is no overlap in the zooplanktivorous diet of sprat and cod and sprat is assumed not to predate on larval cod.

Parameterization

For the type of model used in this project, each fish stage requires six parameters for the continuous energetic processes (maximum ingestion rate, maintenance rate, assimilation efficiency, half-saturation density, background mortality rate, and fraction of energy channelled to somatic growth). Of these, the maximum ingestion rate, background mortality rate and maintenance rate are size dependent and are estimated from scaling relationships with average adult body size, data on oxygen consumption, and individual growth functions. The half-saturation density is theoretically expected to be independent of body weight within a species. The assimilation efficiency of ingested food is based on the type of diet. The fraction of energy channelled to somatic growth equals 1 for juvenile stages and is for the adult stages estimated from the average weight of annual egg production. All of these parameters can thus be derived from estimates based on individual-level data; no population-level data are used for parameterisation. Only for the maintenance costs of storage of reproductive energy no estimate has been found, so we will test the effect of zero maintenance costs and maintenance costs equal to somatic maintenance for stored energy.

The timing of reproduction in cod and sprat can be tested based on data from egg surveys (Wieland 2000; Köster et al. 2003). The timing of spawning of sprat is relatively constant over the years, but peak spawning of cod is more variable.

Fishing scenarios

In the Baltic Sea, both sprat and cod are commercially exploited (ICES 2013). Based on the fisheries data that are available, I will determine realistic size- and density-dependent fisheries scenarios for the two species.

Available data

Data for qualitative validation of the model is available. Baltic cod and sprat fish stocks have been closely monitored over the last decades. Data on cod and sprat abundance, body condition, average sizes, and fecundity are available or can be derived from ICES data (Casini et al. 2006; Van Leeuwen et al. 2008).

Work plan

- Determine realistic size- and density-dependent fishing scenarios based on available fisheries data.

- Analyse model dynamics for different values of the parameters representing the resource productivity of the prey, fishing mortality of cod, and fishing mortality of sprat.
- Analyse model dynamics with seasonal reproduction for differences in the timing of spawning of cod and sprat. In addition, the effect of different values of the parameters representing the resource productivity of the prey, fishing mortality of cod, and fishing mortality of sprat will be analysed for the different spawning scenarios.
- Compare model outcomes to outcomes of "classic" fisheries models

Relevance and link to EEP's research plan

This project will contribute to EEP's ongoing research on fisheries management. It will do so by developing a strategic model of the pelagic cod-sprat Baltic Sea community.

The model incorporates food-dependent growth, food-dependent seasonal reproduction, and should enhance the understanding of the effect of multiple impacts and seasonal dynamics in fishery systems.

Expected output

I am planning to write a manuscript intended for publication in a peer-reviewed international scientific journal. In addition, I expect this manuscript to be a chapter in my PhD thesis.

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Seasonal life histories in changing environments

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Goal

To examine the evolution of a consumer's reproduction schedule in a stage-structured consumer-resource interaction using the theory of adaptive dynamics.

Background and motivation

Climate change has strong influences on ecosystems, biodiversity, and ecosystem services (Grimm et al. 2013). In particular, climate change is altering the seasonal dynamics of many species and the timing of their interactions with other species (Yang and Rudolf 2010). For example, both mammals and birds are strongly affected by ambient temperature and resource availability, especially in their timing of life-history transitions such as growth, reproduction, maturation, migration, hibernation, and molting (Caro et al. 2013).

In classical Lotka-Volterra consumer-resource models only the reproduction of adults is assumed to be resource-dependent. However, the maturation of juveniles can also be resource-dependent. De Roos et al. (2008) investigated a stage-structured consumer-resource model in which both maturation and reproduction are resource-dependent. On the one hand, in a continuous-time model when the resource is limited then the assumptions above lead to a bottleneck in the consumer population. Then either the maturation of juveniles or the reproduction of adults is limited by the resource availability. As a consequence, the growth rate and total biomass of consumer population are limited by resource as well. On the other hand, if the adults are not continuously reproducing but seasonally then the juveniles are less limited by their resource because the juvenile biomass only increases at certain time transitions. In other words, the bottleneck in the consumer population is released by the seasonal reproduction.

Seasonal reproduction has been studied by a number of ecologists (Pachepsky et al. 2008; Bronson 2009) and is often modeled by semi-discrete models which are a combination of both continuous and discrete dynamics (Mailleret and Lemelse 2009). It has been found that in a stage-structured model a consumer population with seasonal reproduction of adults can have higher biomass compared to a population with continuous reproduction strategy. The reason is that the bottleneck in juvenile stage is released and then more juveniles can mature to adults, avoiding a waste of resource in juvenile stage. It has been concluded that a consumer population with seasonal reproduction has higher efficiency on resource utilization than a continuously reproducing population. Then the question arises what the outcome will be if two populations with two different reproduction strategies are competing for the same resource. It is of great importance to investigate the eco-evolutionary processes through which individuals with altered seasonal reproduction schedule can invade into resident population, since this will enable us to assess how populations in seasonal environments will need to adjust their life histories in order to cope with changing seasonal patterns in their environments.

Eco-evolutionary dynamics, which are used to study how ecological changes cause phenotypic changes in natural populations, have received a lot of attention during the past years

(Pelletier et al. 2009). This brings together biologists from empirical and theoretical back-grounds to bridge the gap between ecology and evolution and provides a series of contributions aimed at quantifying the interactions between these fundamental processes. From the view of theoretical biology, the theory of adaptive dynamics is a useful tool for studying long-term phenotypic evolution (Metz et al. 1996). The basis for using the theory of adaptive dynamics is a mathematical model that explicitly incorporates the traits undergoing evolutionary change.

In this project, I will investigate how seasonal reproduction can evolve, to gain insights into the evolutionary advantages of seasonal reproduction and to study how rare mutants can estab-lish themselves in an environment inhabited by a large equilibrium population of residents using the theory of function-valued adaptive dynamics (Dieckmann et al. 2006; Parvinen et al. 2006).

Research questions

This project aims to study the evolution of the seasonal reproduction schedules in a consumer population. In particular, the following questions will be addressed:

- How do different reproduction schedules affect the resource utilization of a consumer population?

- What are the conditions under which individuals with alterative reproduction schedules can invade established populations and how are these related to the conditions?

- What are the conditions for co-existence and evolutionary branching to occur?

- How are patterns of resource availability influenced by seasons affecting the evolution of the consumer population?

- What different dynamics will happen if we take into account multiple resources and ontogenetic niche shifts of consumers during their lifetimes?

- What role does climate change play in the evolution of population and what are the mechanisms on the individual level and the population level?

Methods and work plan

This project is based on the structured consumer-resource model constructed in De Roos et al. (2008), the method of Floquet theory introduced in Klausmeier (2008) and the theory of func-tion-valued traits developed in Dieckmann et al. (2006).

Stage structure

The consumer individuals are divided into juveniles and adults by their body size. Juveniles can only mature and adults can only reproduce. The maturation rate of juveniles and the reproduc-tion rate of adults are both resource-dependent. This is the basic assumption which ensures that different reproduction schedules will greatly influence the resource utilization.

Evolutionary traits

- If we consider a model for describing the evolution of a function-valued trait $x(a)$, which is the reproduction effort of adults at time a. There are two important components in the derivation of adaptive dynamics of function-valued trait: the invasion fitness f and the selection gradient $g(a)$. $f(x, x')$ is the average initial per capita growth rate of a mutant with trait x' arising in an established resident population and the sign of f dertemines whether the mutant can invade: a mutant with negative $f(x, x')$ cannot in-vade while mutant with positive $f(x, x')$ can. The selection gradient $g(a)$ is the strength

and direction of selection on trait x. The canonical equation of function-valued adaptive dynamics can then be derived.

- The competition between continuously reproducing individuals and discretely reproducing individuals is a specific situation. To make it more general we can consider a model describes the evolution of two traits s_1 and s_2, which are respectively the starting and ending time points within a year for adult individuals to exhibit discrete reproduction schedule (for $t \notin [s_1, s_2]$ they are continuously reproducing). By calculating the invasion fitness and the selection gradient of rare mutant individuals with traits s_1' and s_2' in an environment established by resident individuals with traits s_1 and s_2 we can obtain the invisibility region and trait phases.

Competition between mutants and residents

If an individual mutates in its reproduction schedule, this might result in a higher utilization efficiency of the resource. Then it will outcompete the resident individuals. In order to reflect this competition, we need to study the growth rate of a rare mutant individual with an alternative reproduction schedule in a resident population with a given reproduction schedule. Furthermore, the selection gradient is also determined by the competition between mutants and residents.

Seasonal resource

Besides the seasonal behaviors of consumers, the dynamics of the resource can also be seasonal, especially the growth rate of the resource depends on different seasons. Consequently, consumers reproducing at different parts of the year will face different ecological conditions. For example, the offspring will have different abundances of resource at different time during the year. Then the maturation rate of juveniles is affected and they will even starve when the resource is not sufficient to cover their maintenance. Therefore, different patterns of seasonal dynamics will greatly affect the development of the consumer population and individuals have to get adjust to the changing environment. It is thus of great importance to study the evolution of the consumer population in a periodic environment. Klausmeier (2008) introduced Floquet theory as a useful tool for calculating the invasion fitness of rare mutant in a periodic environment established by resident individuals and it will also be a mathematical approach in my project.

Climate change

Climate change not only affects the behaviors of consumers but also influences the dynamics of resource (Yang and Rudolf 2010). In other words, the resource availability for consumer individuals are time-dependent. Consequently, the growth rate of rare mutant individuals in resident population might also be affected by climate change. This will greatly influence the invasion fitness and the selection gradient and finally affect the evolution of the population.

Model implementation

The model will be numerically implemented in Matlab and C-based software.

Work plan

I am planning to complete this project through the following steps:

- Construct a simple model with one resource and one consumer population and develop

the numerical simulation tool.

- Investigate the invasion fitness and selection gradient of the model analytically as far as possible. Then compose this with numerical simulations using implementation tool.

- Consider a model with seasonal growth rate of resource and consumer population with two traits. Calculate the invasion fitness using Floquet theory and derive the selection gradient and the canonical equation, then numerically calculate the invisibility region and trait phases.

- Consider the influence of climate change on resource availability and analyze how these influences affect the evolution of consumer population.

- If time permits, I will take into account multiple resources and niche shift of consumer individuals and study how niche shifts influence the evolution of reproduction schedules.

Relevance and link to EEP's research plan

On the one hand, eco-evolutionary dynamics of living systems is one of the main projects of EEP and new tools are being developed to describe ecological and evolutionary transitions in realistically complex systems. On the other hand, the theory of function-valued adaptive dynamics has been developed by EEP (Dieckmann et al. 2006; Parvinen et al. 2006) and it is the main approach related to my project.

Expected output and publications

The results gained in this project are expected to be published as a co-authored article in an international scientific journal. Additionally, they are planned to yield one chapter of my Ph.D. thesis.

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