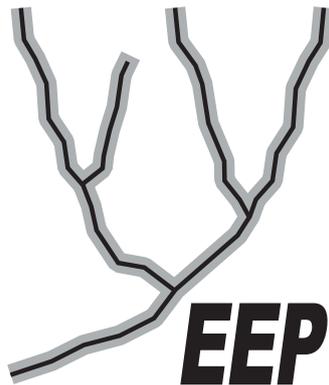


Young Scientists Summer Program 2016

Five Research Projects

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



Land-use change effects on infectious disease transmission: The case of Chagas disease in Colombia

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Goal

To investigate the effect of land-use change on Chagas-disease infection risk in Colombia, considering the expanding economy of oil-palm plantations.

Background and motivation

In 2012, the World Health Organization (WHO) defined the *2020 goals* program for controlling the burden of morbidity of neglected tropical diseases (NTDs). Chagas disease is a NTD in Latin America, with a burden of 10.000 deaths per year (Rassi *et al.*, 2010). It is caused by the cell parasite *Trypanosoma cruzi* and it is transmitted to mammal hosts by various species of so-called kissing bugs. In Colombia, recent estimates suggest that 1% of the population is infected and 15% is at risk (Moncayo *et al.*, 2009). Without treatment, Chagas disease can cause serious heart and digestive complications leading to death.

Control strategies, which include house spraying with insecticides, have reported successful outcomes in regions where the main vector is strictly domestic. This is, for example, the case of the vector *Triatoma infestans* in the Antiplano region in Bolivia (Salvatella *et al.*, 2014). However, re-infestation after spraying occurs in the Orinoco region located in Colombia and Venezuela. *Rhodnius prolixus*, the main vector in this region, is found in both domestic and sylvatic habitats, where it is strongly associated with palm trees (Abad-Franch *et al.*, 2015; Sanchez-Martin *et al.*, 2006). Thus, it is suspected that an inflow of vectors from the sylvatic populations thwarts control efforts.

Oil-palm plantations were established in Colombia during the 1960s. Currently, oil-palm is the most relevant crop used for biodiesel production in the world. Colombia is the main producer in Latin America and policies have been established to ensure that Colombia contributes significantly to the future biodiesel markets (Castiblanco *et al.*, 2013). One of the target regions is located in the Orinoco, known as an endemic area for several tropical diseases. This expansion of oil-palm plantations provides suitable habitats for the Chagas disease vector *R. prolixus* (Abad-Franch *et al.*, 2015) and thus may have a significant impact on endemic levels and infection risks. More generally, land-use change may similarly interact with many vector-borne diseases (Gottdenker *et al.*, 2014).

For Chagas, the WHO goal for 2020 is to reach regional elimination (WHO, 2012). Supporting policy development with quantitative research is one of the main approaches recommended by the WHO for achieving their 2020 goals (Hollingsworth *et al.*, 2015). Therefore, considering the expanding economy of oil-palm plantations in Latin America, the aim of my study is to analyze the effect of land-use change on Chagas-disease infection risk in Colombia. This study will also pave the way to a wider understanding of land-use change effects on vector-borne diseases in general and thus potentially support many other WHO vector-control initiatives.

Research questions

I will address the following questions:

- Which land-use characters predict best vector availability and Chagas incidence?
- Specifically, how does Chagas incidence depend on the co-occurrence of plantations and grass land?
- What are the expected health costs incurred by the expansion of the oil-palm economy in Colombia?
- How much can informed arrangement of oil-palm plantations reduce these costs?

Methods and work plan

These questions will be addressed by using Chagas disease incidence in Colombia and geographic information systems coupled with a statistical model.

Data

Colombia's land cover map at a 30 m resolution pixel using Landsat Thematic Mapper (TM) and Thematic Mapper Plus (ETM+), is available from Gong *et al.* (2013). I will process this map for identifying the land cover types of interest, such as oil-palm monocrops, forests, and human settlements. Environmental information regarding monthly temperature and precipitation is accessible from WorldClim. Furthermore, the Geographic Institute of Colombia Agustín Codazzi, has developed maps on economic factors such as roads, agricultural production, harvested agricultural area, and social factors relating to illiteracy, population density, population distribution, unsatisfied basic needs, health social security and vaccination coverage (all at municipality level except roads) among others. Maps must be processed for the same projection and sample resolution.

Regarding Chagas disease incidence, the National Institute of Health has recorded at the municipality level, the number of new cases per week since 2012. Additionally, during the National Control Program of Chagas Disease in Colombia (1997–2001), kissing bugs of seven species were collected at the village level (Guhl *et al.*, 2005).

For predicting the oil-palm monocrop effect in Chagas disease, I will use the projections developed by Castiblanco *et al.* (2013) regarding the probability for expansion of the oil palm in Colombia, future scenarios by 2020 considering biofuel blend goals and the expectations of the Ministry of Agriculture in Colombia.

Underreporting

Neglected tropical diseases are known for low reporting. Infected people typically live in rural remote areas where the health authorities are barely informed. Additionally, early disease symptoms may be mistaken for any number of other ailments and heart complications are only evident after 20 to 30 years. Therefore, estimating disease underreporting at the municipality level in Colombia is a crucial step for preparing the data.

I will address this matter by using disease incidence, kissing bug presence and health center quality in each municipality. First considering kissing bugs presence, I will be able to develop species distribution models (SDM) using the maximum entropy method (Maxent) (Phillips *et al.*, 2006) and assign an arbitrary score of disease likelihood to each municipality. Afterwards,

by ranking the reporting quality of the health centers and controlling by the municipality population, I will estimate a correction factor (CF). Using the latter, the expected number of cases of the disease at the municipality level could be determined.

Statistical model

To study the possible effects of land cover and land-use change in Chagas disease in Colombia, I will use a generalized linear model (GLM) where Chagas disease incidence at the municipality level is the dependent variable. Environmental, economic, and social data of Colombia will be used as predictor variables. Moreover, the kissing bugs distribution predictions will be considered for feeding the input data.

Oil-palm plantations, forests and human settlements are considered as suitable habitats/landscapes for kissing bugs. Spatial heterogeneity of land-cover in each municipality regarding on how segregated or integrated these different environments are, is an essential variable for feeding the statistical model. Therefore, using the land cover information and spatial statistics such as variogram models (Garrigues *et al.*, 2006), I will describe the degree of spatial dependence of the landscape. A matrix of correlation lengths between habitats will be associated to each municipality.

Finally using the statistical model and the projections of oil-palm plantations in Colombia, Chagas disease new cases in Colombia could be predicted. Thus, I will determine total treatment costs for the infected population by projecting incidence for the next years. For 2008, the treatment of a chronic Chagas disease patient for lifetime averaged to \$11,619 (Castillo-Riquelme *et al.*, 2008).

Work plan

I am planning to work on this project in five stages.

- Gathering statistical model inputs (land cover images, cleaning maps, SDMs and Chagas disease incidence in Colombia)
- Processing land cover images
- Development of correlation length matrices at municipality level using variogram models
- Estimating the underreporting of Chagas disease in Colombia
- Implementing the linear regression model (GLM) for determining the effect of land-use change in past and current disease transmission

Possible extension

The proposed extension of the project is the development of a diffusion model to improve the projections of Chagas disease infection risk generated by the statistical model. Using oil-palm suitability (Castiblanco *et al.*, 2013), current land-cover, insect biology and presence, the possible habitat expansion of kissing bugs in Colombia could be predicted. Here, I will implement a reaction–diffusion model with logistic growth for modeling the population dynamics of the insect.

Relevance to EEP's research plan

Being involved in the research program of EEP is a great opportunity since the disease dynamics describes a complex ecological system and mathematical approaches are needed. This project aims to contribute to the EEP's ongoing vector-modeling research, by using tools in ecological modeling regarded to Chagas disease ecology and epidemiology.

Expected output and publications

The results of this project will be a chapter of my PhD thesis and hopefully a co-authored article in a scientific international journal.

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Network analysis of anthropogenic pollinator declines

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Goal

To assess the resilience and vulnerability of plant-pollinator networks and investigate the effects of species extinctions and other anthropogenic stressors.

Background and motivation

Mobile animals facilitate pollen transfer between plants in almost every ecosystem on earth (Ghazoul, 2005). While self-compatibility in reproduction is widespread, many wild plants rely on pollinators to produce fruit and seeds. In wild plant populations, 62–73% of investigated plant species showed evidence of pollination limitation, or the circumstance where plants would produce more seeds and fruit with more pollination (NRC, 2007). Yet, anthropogenic impacts on ecosystems around the world correlate with declines in pollinator diversity (Martins *et al.*, 2013; Williams *et al.*, 2015) and parallel loss of interacting plants and pollinators (Biesmejer, 2006; Moeller *et al.*, 2012). This disruption of vital pollination interactions threatens food security as well as biodiversity and other plant derived ecosystem services (Potts *et al.*, 2010).

Current declines and response to anthropogenic impacts differ between species, and the population dynamics of many species are not monitored. The clearest and most investigated declines are observed in the managed European Honey Bee, *Apis mellifera*. In European Honey Bees, Colony Collapse Disorder (CCD) is responsible for mysterious, very high colony losses in many countries, where average colony losses in the United States have been around 30% since 2006, with some statewide average losses of 40–50% (Ellis *et al.*, 2010). While some potential causal factors for CCD may affect honey bees alone (Moritz and Erler, 2016), several factors such as *Varroa* mites, viruses, and neonicotinoid pesticides that explain significant variation in colony loss occurrence have also been observed to impact colony health of bumble bees (Parmentier *et al.*, 2016; Sánchez-Bayo *et al.*, 2016). Population dynamics of thousands of solitary bee species are not often tracked, however, habitat loss and fragmentation are frequent factors that explain the extirpation of bee species and community decay (Martins *et al.*, 2013; Williams *et al.*, 2015) and increasing use of pesticides around the world are also observed to affect native pollinator populations (Hladik *et al.*, 2016). Phenological studies of plant and pollinator activity have emphasized the risk of decreased plant and pollinator fitness due to phenological mismatches stemming from climate change (Solga *et al.*, 2014; Forrest, 2015).

One common, holistic approach to investigation of linkage between plant and pollinator populations is network analysis (Bascompte *et al.*, 2006; Memmott *et al.*, 2004). To describe the structure of plant-pollinator networks a variety of indices have emerged which summarize the connectivity and fill of interaction matrices, as well as other properties such as modularity and asymmetric dependency (Dormann *et al.*, 2009). Network robustness has been evaluated by removing species from networks and summarizing the additional effect of secondary extinctions on the network (Memmott *et al.*, 2004; Ebenman and Jonnson, 2005), yet as applied to plant-pollinator networks, this approach dramatically simplifies the flexibility of shifting foraging behavior. In contrast to other types of trophic networks, some studies have concluded that

plant-pollinator networks are more robust and secondary extinction risk is low due to the architecture of their static structure (Memmott *et al.*, 2004; Bascompte *et al.*, 2006). A dynamical model approach can incorporate more realistic processes like network rewiring and competition (Brännström *et al.*, 2012; Bewick *et al.*, 2013). Without further work to compare the relationship between static network structure and dynamic behavior, it is unclear what assertions can be made regarding the resilience conferred by network structure.

In this study I will build a population dynamical model of plant-pollinator networks and apply this model to eighteen montane meadows where plant and pollinator interactions were surveyed between 2011 and 2015. These community interaction models will be subjected to anthropogenically driven declines of targeted species groups representing the effects of various real-world threats. We will test the influence of anthropogenic and competitive pressures on network behavior and vulnerability by measuring resulting consequences for plant and pollinator fitness expected to impede or maintain functionality of ecosystems.

Research questions

I will address the following questions:

- How do anthropogenically driven pollinator declines cascade through dynamical community networks?
- Which structural indicators best predict network behavior under various extinction scenarios?

Methods and work plan

Plant-pollinator interaction survey

A survey of plant-pollinator interactions in 18 montane meadows of the Western Cascades, Oregon, USA from 2011–2015 provides empirical data in the form of plant and pollinator abundance measures and visitation frequency, that is required to model community dynamics. In this survey, the presence of all interactions between mobile animals and the reproductive structures of plants were recorded for fifteen minutes in ten 3m x 3m plots per meadow, for a total observation period of 2.5hrs per meadow visit. This visitation record is used to populate a visitation matrix between plant and pollinator species. Each meadow was visited every two to three weeks contingent on sunny weather until meadow plants dried out in August or September. During each meadow visit, flowering plant species in anthesis were also surveyed within the ten plots. This flower survey data provides the population abundance measurements for plant species, and pollinator abundance is estimated as the summation of the occurrence of pollinator species individuals across all observation minutes for a meadow. The five-year dataset includes 110 unique plant species and 556 unique pollinator species.

Model structure

We base our model on two types of empirical observations: visitations v_{tij} and abundances N_{ti} and M_{tj} for years $t = 1, \dots, T$, plant populations $i = 1, \dots, I$, and pollinator populations $j = 1, \dots, J$. The model construction proceeds in the following steps:

- First, we determine the preference matrix $P_{ij} = V_{ij}/(N_i M_j)$.
- To improve the full description of pollinator visitation preference and to reduce noise, we average the compiled results from all meadows over the years of observation, $V_{ij} =$

$\sum_{t=1}^T v_{tij}/T$, $P_{ij} = \sum_{t=1}^T P_{tij}/T$, $N_i = \sum_{t=1}^T N_{ti}/T$, and $M_j = \sum_{t=1}^T M_{tj}/T$.

- Using the simplifying assumptions that (i) visitations are equally redistributed by preference upon abundance changes, and that (ii) individual pollinators have a visitation capacity that decreases with abundance of preferred flowers with a Holling-type II function, the visitations for abundances n_{ti} and m_{tj} are approximated by $v_{tij} = D_{tij} P_{ij} n_{ti} m_{tj} \sum_k P_{kj} N_k / \sum_k P_{kj} n_{tk}$, with $D_{tij} = 1/(1 + H_j / \sum_k P_{kj} n_{tk})$.
- From these visitation frequencies, we obtain the total visitations for the plant and pollinator populations, $v_{Nti} = \sum_{j=1}^J v_{tij}$ and $v_{Mtj} = \sum_{i=1}^I v_{tij}$, respectively.
- The benefits plant populations derive from visitations $b_{Nti} = c_N \sum_k v_{tik} r_{tik}$, are proportional to visitations and the probability that a pollinator's subsequent visit is made to the same plant population. The simple, but phenomenological ansatz $r_{tij} = (P_{ij} n_{ti} / \sum_{k=1}^K P_{kj} n_{tk})^\beta$, where $0 \leq \beta \leq 1$, accounts for flower fidelity, may be replaced by a more mechanistic derivation.
- The benefits pollinator populations derive from visitations are proportional to visitations, $b_{Mtj} = c_M \sum_k v_{tkj}$.
- Benefits are normalized relative to the empirical observations, so that $b_N = b_M = 1$ for $v_t = V$.
- Using the simplifying assumptions that (i) the annual growth rates of plant and pollinator populations linearly increase with these benefits and that (ii) the annual growth rates of plant populations linearly decrease with the total abundance of plants, the dynamics of these populations are mechanistically conceptualized as scramble competition and approximated similarly to the Ricker model, by $n_{t+1,i} = n_{ti} \exp(-d_{Ni} + a_{Ni} b_{Nti} - c_{Ni} \sum_{i=1}^I n_{ti})$ and $m_{t+1,j} = m_{tj} \exp(-d_{Mj} + a_{Mj} b_{Mtj})$.

Parameter estimation

Time series abundance data from the flower survey and pollination interaction survey will be used to parameterize the population growth models introduced above. Using an MCMC approach, maximum-likelihood estimates of parameters will be estimated, where the $3I + 2J$ parameters are non-negative. At least initially, we will use a single parameter for describing competition among plants, which will reduce the number of parameters to $2(I + J) + 1$.

Measures of network structure

Network structure has been described using a wide range of summary statistics. While such structural metrics are frequently calculated and discussed in ecological network analysis, they are rarely validated against dynamical models of network behavior. A set of structural indices will be calculated using the bipartite package in R statistical software and other literature for comparison against the observed vulnerability of the modeled networks. These indices will be used as independent variables to predict network behavior in the final statistical analysis of network behavior. The calculated indices represent the fullest variety of network structural metric statistics hypothesized to confer resilience to networks.

Anthropogenic impacts

To simulate the impact of anthropogenic pressures on functioning plant-pollinator networks, targeted pollinators will be identified, pooled, and impacted within the network each year. Anthropogenic forces will be applied to each meadow network to contrast the effect of various extinction cascades on network structure and resilience. The scenarios will include:

- Drought induced by climate change – decline of bumble bees and butterflies
- Reduction of early season flowers due to low snowpack and frost – early blooms decline
- Honey bee supplementation – increased abundance of honey bees
- Eusocial bee diseases – decreased abundance of colony bees including honey bee and bumble bee species due to viruses and *Varroa* mites
- Habitat loss – equal declines of all pollinator species

Measures of network response to anthropogenic impacts

Network resilience following extinctions will be measured in several ways that may be modified given different types of network behavior. If the network is permanently affected, useful statistics will include the time to network collapse, the proportion of species lost, and the robustness metric based on the proportion of links maintained within the network over time as pollinators are withdrawn from the network. The cumulative sum of remaining links across each time step will be calculated and standardized by network size to contrast the proportion of the networks preserved over a fixed period. If the network rebounds and reorganizes following the perturbations, some of these metrics may be less meaningful and other metrics may be more useful, including the temporal extent of network decline, the partner diversity and the network connectance, web asymmetry, and structural metrics post-impact.

Statistical analysis of indicators and network response following anthropogenic impacts

Structural metrics calculated for each empirical network will be compared to the network robustness and network response metrics post-impact to evaluate their usefulness as vulnerability indicator using the most appropriate statistical approach, e.g., multiple linear regression or Canonical Correlation Analysis (CCA). Before the statistical analysis, a final subset of structural metrics will be selected to minimize covariance.

Work plan

The envisaged work plan is as follows:

- Construct a preference matrix based on empirical observations of flower visitations and check this matrix against a matrix of flowering times
- Explore visitation, benefit and species abundance behavior in pilot model
- Build full scale model and equilibrate
- Calculate network structural metrics for empirical and equilibrated models
- Apply environmentally driven declines caused by specific anthropogenic forces
- Evaluate network resilience following extinction pressure under simulated anthropogenic forces
- Statistically contrast structural metrics and response metrics
- Write manuscript

Further extensions

The development of this community dynamical model provides a framework for characterization of species position within the network, and development of risk assessment for individual species. This model could be used to assess how pesticide use on different types of plant species may differentially influence the pollinator community. Characterization of risk of different plant species at different times through the season could provide information on how the timing of mowing, or pesticide application, may affect particular types of agricultural systems.

Relevance and link to EEP's research plan

This work is related to EEP interests in trophic network structure and correlation between vulnerability metrics and network resilience as measured through dynamical modeling approaches. EEP is also concerned with the effect of anthropogenic influence on ecological networks. Global pollinator declines underscore the pertinence of this theoretical exploration to important policy decisions regarding food security and sustainable ecological and agricultural systems.

Expected output and publications

The results of this work will be submitted to an international scientific journal for communication to a wide audience.

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Cultural evolution of low fertility at high socio-economic status

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Goal

To address the paradox in modern societies that socio-economic status is negatively correlated with fertility by broadening the framing from genetic evolution to cultural evolution.

Background and motivation

Life-history theory predicts that individuals should behave to maximize their lifetime reproductive success, measured by the number of successful offspring. One would thus expect that parents with greater means have more children. Paradoxically, this is not the case: in modern societies socio-economic status is negatively correlated with fertility (Borgerhoff-Mulder, 1998; Bryant, 2007) with rich families reducing their fertility earlier than the rest of the population (Livi-Bacci, 1986). The demographic transition is the term used to describe the phenomenon observed in modern industrialized societies of reduced fertility despite overall increases in the availability of resources (e.g., Coale and Watkins, 1986; Robinson, 1992). As a result, over half of the global population now live in countries with below-replacement fertility (Wilson, 2004).

According to conventional demographic theory, socio-economic development is a key driver of fertility decline (Caldwell, 1982; Notestein, 1953; Lesthaeghe, 1983; Thompson, 1942; Cleland and Wilson, 1987; Easterlin, 1975, 1978). However, no single theory that attempts to explain the historical record on transitions has been sufficient so as to dominate its competitors (Mason, 1997). Each theory attempting to explain why some countries have undergone fertility transition whilst others have not provides important insights but has not been able to explain all known fertility transitions. This may be explained by the fact that each focuses on a single factor to explain the fertility transition, e.g., Caldwell (1982) concentrates on intra-familial wealth flows, whereas demand theory focuses on income (Becker, 1960).

Explanations based on biological evolution have traditionally focused on the trade-off parents face between the quantity and quality of their offspring (Lack, 1968). Reducing the number of offspring allows greater investment in each individual. Thus, parents may increase their relative reproductive success by producing a small number of high-quality offspring (Kaplan, 1996). According to this hypothesis, low fertility would be favored in environments in which a high level of parental investment is critical to the quality of the offspring (Irons, 1983; Turke, 1989). However, explanations along these lines assume that high-quality offspring will have high reproductive success; the fact that this does not seem to apply in modern societies is the very pattern that needs to be explained.

Biological inheritance describes the transmission of biological information exclusively from parent to offspring through DNA. The transmission of cultural information however, is not limited to parent and child but can be between generations or between members of the same group. Cultural transmission describes the process of acquisition of a trait from one individual to another individual through imprinting, imitation, observation, conditioning, direct teaching or a combination of these (Cavalli-Sforza and Feldman, 1981). Whilst it can be difficult to partition the process of transmission into purely genetic or purely cultural components (Laland

and Brown, 2002), many authors have argued that cultural evolution can be studied by adjusting the theory of evolution by natural selection (e.g., Campbell, 1960; Dawkins, 1976; Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Durham, 1991; Mesoudi *et al.*, 2004). The demographic transition has been explored using such theory. Boyd and Richerson (1985) suggest that lowered fertility rates are a consequence of non-genetic Darwinian mechanisms of inheritance where traits associated with high status individuals are preferentially imitated by others within the population. This does not however explain why influential individuals would choose to reduce their fertility. Why reproduction is sacrificed for socio-economic status is an important question to answer.

This project aims to investigate whether lowered fertility rates are a product of parents maximizing the wealth of their children. To expose motivations we employ in a novel way a dynamic state variable modelling procedure (Mangel and Clark, 1988) central to behavioral ecology. However, the fitness currency in our model will not be in terms reproductive success but instead in terms of wealth.

Research questions

I will address the following questions:

- Why are wealthy families frequently those with the smallest number of children in heterogeneous, post-transition societies?
- Can the paradox of low fertility at high socio-economic status be explained through the assumption that parents behave so as to achieve the highest possible social status for their offspring.
- Can the paradox of low fertility at high socio-economic status for all members of a population be explained using a cultural inheritance model?
- What patterns are predicted for fertility and wealth inheritance in modern society?
- If predictions are made that simulate the paradox, what are the key variables?

Methods and work plan

Model structure

We consider a large population in which the parents differ in their socio-economic status $0 \leq s \leq 1$ and in the endowment target $0 \leq e \leq 1$ they aim to provide to each of their children. The status s determines the amount of wealth $W(s)$ parents can distribute to their children. Given their wealth, parents will decide to have many children if their endowment target e is small, while they decide to have only a few children if their endowment target is large. The strategy space is defined by a set of functions which map the status s of a parent to their endowment target e for their children. The state of the population at generation t in regard to these characteristics is described by the bivariate probability density $f_t(s, e)$, for which we assume the following intergenerational dynamics,

$$f_{t+1}(s, e) = \int_0^1 \int_0^1 S(s|s_p, e_p, f_t) f_t(s_p, e_p) \int_0^1 \int_0^1 E(e|s, e_p, s_m, e_m, f_t) f_t(s_m, e_m) ds_m de_m ds_p de_p,$$

where $S(s|s_p, e_p, f_t)$ describes the transmission of socio-economic status and denotes the probability density that a child has socio-economic status s whose parents have socio-economic

status s_p and an endowment target e_p in a population composed according to f_t , while $E(e|s, e_p, s_m, e_m, f_t)$ describes the transmission of the endowment target and denotes the probability density that a child adopts the endowment target e when having socio-economic status s , parents with an endowment target e_p , and a role model characterized by (s_m, e_m) , in a population composed according to f_t .

For status transmission we make the following assumptions:

- Parents have an expected number $n(s_p, e_p) = W(s_p)/e_p$ of children, where $0 \leq W(s_p) \leq 1$ denotes the total wealth parents can endow to their children, scaled to a maximum of 1 without loss of generality.
- Wealth increases with the parents' socio-economic status s_p , $W'(s_p) > 0$.
- A child's socio-economic status s is normally distributed about the rank $r(e_p, f_t)$ of the child's endowment e_p .
- The standard deviation $D(s_p) \geq 0$ of this variation decreases with the parents' socio-economic status s_p , $D'(s_p) < 0$.

Status transmission can be expressed by

$$S(s|s_p, e_p, f_t) = \frac{1}{Z_S(s_p, e_p, f_t)} N(s|r(e_p, f_t), D(s_p))$$

where $N(s|m, d)$ denotes the probability density of the normal distribution of s with mean m and standard deviation d and $Z_S(s_p, e_p, f_t)$ is a normalizing constant so that $\int_0^1 S(s|s_p, e_p, f_t) ds = 1$. The endowment rank $r(e_p, f_t)$ is given by

$$r(e_p, f_t) = \frac{1}{Z_r(f_t)} \int_0^{e_p} \int_0^1 n(s, e) f_t(s, e) ds de$$

with a normalizing constant $Z_r(f_t) = \int_0^1 \int_0^1 n(s, e) f_t(s, e) ds de$, i.e., $r(1, f_t) = 1$.

For target endowment transmission we further assume that

- The endowment target a child adopts comes from its parents with probability $0 \leq v \leq 1$ and otherwise from a role model.
- Role models are chosen according to an imitation kernel, $i(s, s_m, f_t)$. The imitation kernel regulates the transmission of the target endowment by determining how children choose their role models and the probability that they imitate this role model given the socio-economic status of the child s , the socio-economic status of the role model s_m . The imitation kernel is given by the product of a normal distribution and a Fermi function

$$i(s, s_m, f_t) = \frac{1}{Z_i(s, f_t)} \frac{N(s_m|s, 1/a)}{1 + \exp(-w(s_m - s))}$$

with normalizing constant $Z_i(s, f_t)$ so that $\int_0^1 \int_0^1 i(s, s_m, f_t) f_t(s_m, e_m) ds_m de_m = 1$.

The parameter $a \geq 0$ determines the assortativity of imitation with regard to socio-economic status and the parameter $w \geq 0$ determines the importance of positive status difference for imitating the role model's strategy.

Target endowment transmission can be expressed by

$$E(e|s, e_p, s_m, e_m, f_t) = v\delta(e - e_p) + (1 - v)i(s, s_m, f_t)\delta(e - e_m),$$

where δ denotes the Dirac delta function. The model's parameters are thus given by v , a , w , and the functions W and D .

Extensions

- Dynamic programming could be used as a tool to determine individual decision making.
- In the model described above, we make the assumption that the cultural transmission of strategies is according to social status. We instead could consider the evolution of a trait which regulates the transmission of a strategy. In doing so, we might provide both an ultimate and proximate explanation for the fertility transmission.
- In the model above it is also assumed that the wealth of an individual is divided equally amongst its children. Instead, a second decision for the individual can be introduced where the parent must decide how to allocate its wealth amongst its children. This allows a range of strategies to be considered: from giving all wealth to one child; the equal division of wealth between all or some children; the unequal division of wealth amongst all or some children.

Work plan

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

- Gain familiarity with model structure, coding, and execution.
- Determine the exact nature of the functions $W(s)$ and $D(s)$ to mimic realistic life history traits of parents in post-transition societies using appropriate literature.
- Explore the effect of model parameters v , a , w , and the functions W and D .
- Summarize main results in a manuscript draft.
- Formulate a conjecture on the ultimate reasons why role models with high socio-economic status are frequently imitated despite their low fertility.
- If time permits, include the extensions described above in the model.

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.

Expected output and publications

The work from this project is expected to result in a publication as a coauthored article in an international journal and form a chapter in my PhD thesis.

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Trait-based modeling of forest-biodiversity dynamics in India

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Goal

To develop a trait-specific ecological model for studying the community structure of Moist Bhabar Doon Sal (*Shorea robusta*) forests in Terai central province, situated between the Ganges River and the Shiwalik hills in the lower Himalaya.

Background and motivation

Until very recently, up to the 1950s, forests covered almost 75% (Joshi, 2002) of the subtropical lowlands in the Terai region of India. However, exploitation of these forests for both commercial and subsistence purposes reduced the forested area to less than 50% of the total land area in Terai by 1988 (Webb and Sah, 2003). The heavy human impacts in this region has left the remaining forest degraded and fragmented, posing threats to biodiversity conservation and local livelihoods. Climate change is also disturbing these forests. The increase in global surface temperature over the 20th century has already changed the composition of forest plant communities around the world (Walther, 2003), with both regional and global warming causing alterations in species-distribution patterns (Colwell *et al.*, 2008) and their demographic dynamics.

Forest ecosystems can be described through three key attributes: structure, composition, and function (Noss, 1990; Franklin, 1988). These attributes change in response to climate, topography, and disturbances—human induced and natural. The above-mentioned factors along with forest succession are also responsible for both local (within stand) and landscape-level variation in forest attributes, thereby producing spatial heterogeneity (Mandal and Joshi, 2014). Many species-distribution models have been developed to study the impact of climate change and human disturbances on species distributions (Guisan and Thuiller, 2005). These models commonly utilize associations between environmental variables and known species' occurrence records to identify environmental conditions within which a population can be maintained in any spatial and temporal domain. However, the debate concerning the strengths and limitations of species-distribution models and potential areas for their improvement ranges from the incorporation of land-cover variables and biotic interactions to functional traits (Clark *et al.*, 2011). More detailed forms of data, becoming available on the life histories of many taxa, can significantly improve biodiversity projections.

To develop a better understanding of the role of ecological niches in structuring forest communities and for species coexistence, it is necessary to secure knowledge on how life-history strategies of different species differ in terms of functional traits. For this, it is important to know how physiological traits of tree species combine to define vital rates and responses to resource availability, environmental changes, and disturbances regimes and how the different life-history strategies drives forest dynamics and species coexistence. In the past, studies have been undertaken to study the impacts of human-induced disturbances and the effects of climate change on forest communities through species-distribution models. However, relatively few studies have considered the role of functional traits in defining species ranges and forest structure, in particular from the theory side. An important exception is a recent comprehensive framework for studying trait-, size- and patch-structured met populations of plants by Falster *et al.* (2011),

which can be used to study how forests respond on both demographic and evolutionary time-scales to anthropogenic and climatic impacts. Among other factors, the model encompasses probabilistic disturbances and competition for light.

In this research project, I aim to predict the variability of functional traits in Moist Bhabar Doon Sal (*Shorea robusta*) forests in Tarai central province, situated between the Ganges River and the Shiwaliks Hills in the lower Himalaya. In a first step, I will aim to reproduce the variability within a site. This investigation will then be extended across a larger geographical area and the predictions will be compared with empirical data. The core of my research effort will be devoted to parameterizing and calibrating the PLANT model (Falster, 2016) to match empirical observations from Indian forests. Time permitting, I will then use the calibrated model to predict the impacts of climate change and global warming on these Indian forests.

Research questions

I will address the following questions:

- How to parameterize the physiological model to study the dynamics and functioning of Sal forest ecosystem?
- How to fit the PLANT model to match the variation in functional traits at selected local sites for the Sal forest ecosystem?
- How to extend the results across larger geographical regions?

Methods and work plan

An ecological model for trait-specific parameters will be set up during my project work. The model will be calibrated and parameterized to deduce the significance of traits in determining the composition of the Sal forest ecosystem.

Physiological model

The PLANT model will be used for modeling the growth, reproduction, and mortality of plant species using physiological parameters, light environment, etc. The model will be set up according to vegetation-type parameters and environmental conditions. Some of the key components of the model are (i) growth driven by carbon assimilation and light interception, (ii) fecundity calculated from reproductive investment and mass per seed, and (iii) an exponential increase in mortality with declining carbon income per leaf area (Falster *et al.* 2011).

One of the parameters that can be calculated through the physiological model include average rate of photosynthesis across the plant which can be given as

$$\bar{p}(x, H, E_{x,a}) = \int_0^H p(x, z, E_{x,a})q(z, H)dz,$$

in which H is the height of the plant, $E_{x,a}$ is the vertical profile of shading in a patch of age a , $p(x, z, E_{x,a})$ is the gross rate of photosynthesis per unit leaf area within the canopy of plants with traits x at light level $E(z)$, z being the height within canopy and $q(z, H)$ is the vertical distribution of leaf area with respect to height z .

Demographic dynamics

A metapopulation consists of many patches of different sizes and different ages. A patch at any age a is described by a size-density distribution $N(H|x, a)$ of plants with traits x and height H .

For large patches, the dynamics of N can be modelled deterministically via the following partial differential equations (Roos *et al.*, 1997)

$$\frac{\partial}{\partial a} N(H|x, a) = -d(x, H, E_{x,a}) N(H|x, a) - \frac{\partial}{\partial H} [g(x, H, E_{x,a}) N(H|x, a)],$$

where, $g(x, H, E_{x,a})$ is the height growth rate and $d(x, H, E_{x,a})$ is the mortality rate.

Adaptive dynamics

An evolving forest population consists of reproducing individuals, in which the seeds carries the genetic information of the trees. New types are also added to the community via mutations or immigration (dispersal). Dispersal plays an important role in the metapopulation dynamics. Natural selection emerges if mutants reproduce at different rates and compete for limiting resources. Writing $p(a)$ for the frequency-density of patches of age a in the landscape, we assume that a dispersing seed with trait x' has the infinitesimal probability $p(a)da$ of landing in a patch of age a . The basic reproduction ratio for a dispersing seed with traits x' thus can be given by

$$R(x', x) = \int_0^{\infty} p(a) \tilde{R}(x', E_{x,a}) da.$$

Here, $\tilde{R}(x', E_{x,a})$ describes the expected number of dispersing seeds with traits x' produced by each dispersing seed with traits x' arriving in a patch of age a .

Data availability

Data on plant physiological traits has been obtained from field studies as well as literature searches. The rest of the parameters will be set to the representative values given by Falster *et al.* (2011) and will be considered as global parameters. The parameters for which data is available at a regional level (mostly through literature) will be considered as regional parameters. The parameters on which data has been generated from the field will be considered as local parameters. In presenting the data availability in more detail, it is helpful to distinguish between two primary areas: plant physiology and plant demography.

Plant physiology: The data on plant physiology will be used to estimate parameters related to plant construction, like wood density, leaf area per sapwood area, and parameters related to plant production, like leaf photosynthesis per area, baseline rate of leaf turnover, etc. Out of a total of eighteen parameters, data on leaf area per sapwood area, bark area to sapwood area, leaf photosynthesis per area, biomass, yield, baseline rate of leaf turnover, height-leaf area scaling, turnover rate of bark and fine roots has been collected through field studies and literature. The data will be used for calibration and validation of the results on plant growth rates omitted by physiological model.

Plant demography: The data on plant demography will be used to estimate parameters related to plant mortality, such as survival probability during dispersal, growth dependent mortality, etc., and parameters related to plant fecundity, such as accessory cost per seed, seed mass, etc. A total of nine demographic parameters will be estimated, out of which, data on seed mass, survival probability during dispersal, growth-independent mortality, and growth-dependent mortality has been obtained from literature. The available demographic data will also be used to corroborate results obtained from the model, for example by comparing realized fecundity and mortality rates.

Work plan

- Parameterization of the physiological model for the Sal forest ecosystem on the basis of source of data, i.e., global, regional or local (on site).
- Gaining knowledge of the model structure, coding, and execution by replications and selective findings.
- Corroborating the model by comparing the results obtained from the plant physiological model and demographic model for different functional traits and demographic parameters with the empirical data mentioned in the data-availability section.
- Projecting final results on landscape level by running the model for different vegetation types and for different sub-climatic zones present.

Relevance and link to EEP's research plan

The project is expected to contribute to EEP's research project *Eco-evolutionary Vegetation Modeling and Management* by developing a trait-based physiological growth model incorporating relevant trade-offs based on known empirical patterns for the Indian Sal forest ecosystem.

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Plasticity and evolution of species in a changing climate

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Goal

To understand how function-valued traits (e.g. reproductive timing) evolve under fluctuating environmental conditions and to make projections forward for populations facing threats from climate change.

Background and motivation

For many species their seasonal timing of life history events, or phenology, is important for both ecological and evolutionary dynamics (Forrest and Miller-Rushing, 2010). While it is well established that the phenological timing of many species has advanced in response to climate change, it remains unclear if these responses suffice for population persistence (Merilä and Hendry, 2014). For example, the reproductive timing is often restricted to certain parts of the year. This timing depends on factors like snowfall, food availability, and predation pressures, which not only change from year to year, but may also follow trends caused by climate change (Reed *et al.*, 2011). In turn, organisms will have different levels of fitness depending on when they reproduce, allowing natural selection to act.

Two processes may help species in response to climate change. First, phenotypic plasticity allows an organism to modify its trait depending on the environment (Merilä and Hendry, 2014). In the context of reproductive timing, an organism could adjust its timing depending on the environmental conditions of that particular year. The ability of plasticity to help organisms cope with environmental change depends on costs of plasticity, reliability of cues, and the fitness effects gained by being plastic (Reed *et al.*, 2011, Chevin *et al.*, 2010). Besides plasticity, a population may also genetically adapt to changing environmental conditions (Merilä and Hendry, 2014). Here the speed of genetic change (as determined by mutation rate, population size, generation time) compared to the speed of environmental change will determine if a population will persist.

There have been several recent modeling and empirical studies focused on seasonal reproductive timing, especially in the context of climate change (Merilä and Hendry, 2014). Empirically, studies on birds and small mammals provide strong evidence of advances in reproductive timing driven by climate change (Merilä and Hendry, 2014). However, it is unclear how much of these changes are driven by plastic or genetic responses, if the responses are adaptive, and if the responses are adequate or rapid enough (Merilä and Hendry, 2014). Most of this empirical literature has been disconnected from theoretical models of phenotypic changes driven by environment change.

From a modeling perspective, two approaches have examined seasonal reproduction: quantitative genetics and game theory. Quantitative genetics focuses on more realistic genetic mechanisms and ignores ecological factors like frequency-dependence models (Chevin *et al.*, 2010). Conversely, game theory, and more specifically adaptive dynamics, sacrifices genetic aspects for increased ecological realism (Johansson and Jonzén, 2012). It is possible to find the optimal

timing of reproduction with timing defined as a scalar trait. A more biologically realistic approach would be to model reproductive timing as a function-valued trait. In this scenario, the optimal strategy would be a curve instead of a scalar value; therefore, reproductive output could be distributed over the course of an entire season (Dieckmann *et al.*, 2006, Parvinen *et al.*, 2006).

I will model reproductive timing as a function-valued trait. However, I will also include environmental variability into the model. In turn, the function for reproductive output could vary from year to year, depending on environmental conditions. Therefore, there is phenotypic plasticity within the course of a given season and between years. I will apply this model to two well-studied populations of small mammals: the Yukon red squirrel and the Collared pika (Williams *et al.*, 2014, Franken and Hik, 2004). Both of these populations have seen recent declines with climate change as a potential driver.

Research questions

I will use a simple population model where reproductive timing can evolve and is given as a function-valued trait. I will examine how evolution of the trait occurs in a variable environment to address the following five questions:

- What is the optimal timing of reproduction (as a function-valued trait) for organisms facing various selection pressures?
- How does the framework of function-valued dynamics generalize to situations with fluctuating environmental conditions?
- How do predictions from theoretical models compare to field data?
- Under which scenarios will genetic evolution or phenotypic plasticity be adequate for organisms to keep up with climate change?
- When does phenotypic plasticity mask the effects of climate change?

Methods and work plan

Model overview

Below I outline the general model to study the evolution of reproductive timing. I explicitly model the environmental conditions ($E(t)$), adult abundance ($A(t)$), juvenile abundance ($J(t, \tau)$), adult body condition ($B_A(t)$), juvenile body condition ($B_J(t, \tau)$), and the resource level ($R(t)$). Importantly, here t is the time within a season and τ is the time a juvenile is born, allowing there to be many juvenile cohorts during a season. In general, the model can be thought of in three main stages: within season dynamics, birth process, and between season dynamics. The model is deterministic except for the between season environment initial condition. We study the evolution of $s(t, E(t))$, the adult contribution (time or energy) to reproduction at any given time.

General model

Within season dynamics

$$\begin{aligned}
\text{Environment:} \quad & \frac{d}{dt}E(t) &= & h(E(t)), \\
\text{Adult abundance:} \quad & \frac{d}{dt}A(t) &= & -A(t)u_A(A(t)), \\
\text{Juvenile abundance:} \quad & \frac{d}{dt}J(t, \tau) &= & -J(t, \tau)u_J(E(t), \hat{J}(t)), \\
\text{Adult body condition:} \quad & \frac{d}{dt}B_A(t) &= & f_A(c_A(R(t)), B_A(t)) - \delta(B_A(t), s(t, E(t))) \\
& & & -g_A(B_A(t)), \\
\text{Juvenile body condition:} \quad & \frac{d}{dt}B_J(t, \tau) &= & f_J(c_J(R(t)), B_J(t, \tau)) - g_J(B_J(t, \tau)), \\
\text{Resource level:} \quad & \frac{d}{dt}R(t) &= & k(R(t)) - A(t)c_A(R(t)) - \hat{J}(t)c_J(R(t))
\end{aligned}$$

Here $E(t)$ changes deterministically through the season. Both $A(t)$ and $J(t, \tau)$ decrease during the course of the season according to mortality rates u_A and u_J , respectively. Changes in adult body condition $B_A(t)$ are dependent on resource acquisition f_A , the cost of reproduction δ , and the decay of their body condition g_A . Juvenile body condition $B_J(t, \tau)$ is similar to adults with a corresponding f_J and g_A , but no cost of reproduction. Lastly, the resource level has some growth k and is consumed by adults and juveniles at rates c_A and c_J , respectively. Here the total juvenile abundance summed across all cohorts τ at time t is $\hat{J}(t) = \int_0^t J(t, \tau) d\tau$.

Birth event

$$\begin{aligned}
\text{Births of juveniles:} \quad & J(\tau, \tau) &= & A(\tau)\alpha(s(\tau, E(\tau))), \\
\text{Juvenile body condition at birth:} \quad & B_J(\tau, \tau) &= & B_J^{ini}(B_A(\tau))
\end{aligned}$$

The birth of new juveniles occurs during the reproductive season with a new cohort of juvenile at time τ . The number of juveniles is the number of adults at time τ multiplied by the per capita reproductive output α , which is governed by the reproductive strategy s . The juvenile body condition $B_J(\tau, \tau)$ at birth can be dependent of the mother's body condition, thus maternal effects are allowed.

Between season dynamics

$$\begin{aligned}
\text{Environment initial condition:} \quad & E(0) &\sim & \text{random variable,} \\
\text{Adult abundance initial condition:} \quad & A_{n+1}(0) &= & l_A(B_A(1), A_n(1)) \\
& & & + \int_0^1 l_J(B_J(1, \tau), J_n(1, \tau)) d\tau, \\
\text{Juvenile abundance initial condition:} \quad & J_{n+1}(0) &= & 0, \\
\text{Adult body condition initial condition:} \quad & B_A(0) &= & B_A^{ini}, \\
\text{Resource initial condition:} \quad & R(0) &= & R^{ini}
\end{aligned}$$

After the reproductive season, adults and juveniles have to try and survive winter until the next reproductive season. We assume that juveniles go through maturation and survive to become adults or die during winter. Therefore, at the start of the next season, there will be zero juveniles. The initial abundance of adults is the number of adults who survive winter, which is dependent

on their body condition, and the number of juveniles that survive and mature, which is dependent on their body condition. The initial value of environment is determined by a random variable.

Numerical approach

To solve for evolutionary singular strategies, $s^*(t, E(t))$, optimal control theory can be used (Parvinen *et al.*, 2013), as opposed to variational calculus (Parvinen *et al.*, 2006). Optimal control theory is useful in situations where the specific strategy used $s(t, E(t))$ affects processes described by differential equations ($\mathbf{y}(a)$), which can then feedback to affect invader fitness (Parvinen *et al.*, 2013). I will numerically evaluate the models in Matlab, as analytical techniques will be inadequate for the full model. Simplifications can be made to the model to allow for some analytical solutions.

Data availability

I will use data collected on several small mammal species in North America. Two longterm datasets of small mammals are appropriate for our modeling framework. First, Yukon red squirrels (*Tamiasciurus hudsonicus*) have been studied continuously since 1991. Reproductive timing and success, in addition to environmental conditions, were all recorded (Williams *et al.*, 2014). And second, collared pikas (*Ochotona collaris*), also in the Yukon, were monitored from 1995 to at least 2002 (Franken and Hik, 2004). In both populations, dynamics are driven by stochastic environmental variables and competition for territories. I will apply my proposed modeling framework to both of these populations and determine evolutionary singular strategies for reproductive output given environmental fluctuations. Unfortunately, there is not detailed enough data to quantitatively parameterize every function in my model. I can use the model to make predictions about how these populations may deal with the threat of climate change.

Work plan

There are three main steps involved in this research project, each of which will take approximately one month. First, I will determine a final modeling framework to use and learn how to use optimal control theory to find singular strategies. Next, I will address the specific aims of this project more in depth. Lastly, I will interpret and write-up the results of my findings.

Relevance and link to EEP's research plan

This project is directly in line with the Evolution and Ecology Program's (EEP) current work on eco-evolutionary dynamics and the development of adaptive dynamics. One of the most important recent developments in adaptive dynamics is the study of function-valued traits, as these are often more biologically realistic (Parvinen *et al.*, 2013). Importantly, I will try to connect function-valued traits to scenarios with fluctuating environmental conditions. In addition, EEP tries to build bridges between fundamental and policy-orientated science. The timing of reproduction and development of applications of function-valued adaptive dynamics are both interesting scientific questions. These questions are also important for policy as global climate change is thought to have an effect on many organisms, because of changes to phenological timing (Forrest and Miller-Rushing, 2010).

Expected output and publications

The results of this work will be submitted to a peer-reviewed scientific journal. I will also use this project as a piece of my PhD dissertation. In addition, I will deliver oral presentations on this work and maintain a webpage with project updates.

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