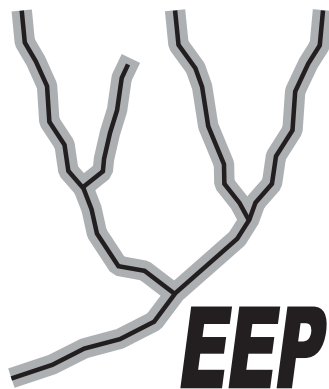# Young Scientists Summer Program 2018

Three Research Projects

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

EEP

Reform of China's marine fisheries management using output control

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Goal

To compare the advantages and disadvantages of input-control and output-control systems in China's fisheries management and to understand the socio-economic and biological impacts of changing the management measures.

Background and motivation

A large proportion of world's fish stocks are overfished. Transitioning to a more sustainable level of fishing would involve significant policy and governance challenges at the global, national, and local levels (World Bank, 2017). Appropriate management measures are necessary for the world fisheries. These range from catch limits to effort limits, which represent so-called output control and input control, respectively. From an economic point of view, the basic reason for government intervention is that, without proper management measures, the individual fisher has insufficient incentives to take into account the effects his fishing activity and catch have on other fishers, on the rest of society, and on the environment. (OECD, 1997). China ranks as the world's leading fishing nation and has the largest fishing fleet and the greatest number of people employed in the fishing sector (Szuwalski *et al.*, 2017). Sustaining its capture fisheries and fishing communities is no small feat and will require a long-run commitment to the health and resilience of marine ecosystems. In response to overfishing and the steady degradation of coastal ecosystems, the Chinese government has introduced a series of management measures to rebuild marine fisheries (Cao *et al.*, 2017). However, most of the measures are input controls including technical measures, for instance, licensing system, vessel buyback program, closed season and area, dual control, minimum mesh size of fishing nets, minimum catch size of fishing targets, fishermen relocation program, zero and minus growth targets, etc.

Recently, the Ministry of Agriculture of the PRC released a series of policy documents related to fisheries management, for example "*The 13th Five-year Plan on Chinese Fishery Development*" and "*Notification on Further Strengthening the Domestic Fishing Boats to Control the Total Amount of Marine Fishery Resources Management*". These new policies and regulations make a definite goal of the Total Allowable Catch (TAC) management, which was introduced in the Chinese Fisheries Law in the year 2000 but with insufficient enforcement. This development shows a kind of paradigm shift in the Chinese fisheries management. Decision makers pay more attention to controlling and reducing the total catch by using the catch limits or output controls. Starting from the year of 2017, the government is setting pilot areas in five provinces (Liaoning, Shandong, Zhejiang, Fujian and Guangdong) to try to use the TAC management in some specific fisheries. My research will focus on how to use the output control management based on the specific features of China's marine fisheries.

Research questions

The socio-economic status of Chinese fishermen

- What are the characteristics of Chinese marine fishermen as a group?
- How the fisheries policies changed the marine fishermen's life?

The fisheries resource status of China's fisheries

- What is the ecosystem like in the past and now? And how it will be like in the future?
- How does the fisheries activity impact the fisheries ecosystem?
- What will happen if the fishing behaviors changed under the shift of fisheries regulations?

Using output control system in fisheries management.

- What are the advantages and disadvantages of input-control and output-control systems when they are used in China's marine fisheries management?
- How can we reform the fisheries management to improve sustainable fishing, and at the same time guarantee the fishermen's livelihood?

Method and work plan

Method

For the first part of this project, I will describe the past and current fisher population. Social survey data have been used to analyze the characteristics of and changes in the fishers' population in terms of demography, mobility, and income. By comparing the historical analysis result, I want to find out how it changed as time goes by. In the second part, I will develop a dynamic model for quantitatively comparing the advantages and disadvantages of input and output controls.

To predict the impacts of changing the management system, we have developed a coupled biological-socio-economic model. First, an Ecopath with Ecosim (EwE) model has been devised to simulate the northern South China Sea (NSCS) ecosystem. Catchability, describing efficiency of fishing gears in capturing different ecosystem components, has been estimated using the EwE-predicted biomass together with effort and catch data. Next, different management scenarios (i.e., input and output control) will be applied to predict their impacts on the ecosystem and the fishers' life.

Data

For the different parts of my research, I will use different types of data and methods. In the first part, I will use the national level data to see the general issues of Chinese fishermen. I will use the database from the China Health and Nutrition Survey (CHNS) which is based on a national wide questionnaire survey. The sample we will use is to select the fishermen's households from the total households samples. In the second part, I will use data on biological characteristics, fishing effort and catch in the northern of South China Sea (NSCS) as a case study. The biological data are from marine fisheries resource survey in the NSCS, together with data from literature, including published ecosystem models (William Cheung, 2000; Chen and Qiu 2010), national statistical yearbooks, and the FishBase. The data of fishing effort are estimated from the fishing vessel data available from Global Fishing Watch (Kroodsma *et al.*, 2018). The catch data are obtained from the Sea Around Us database (Pauly and Zeller, 2015).

Work plan

I plan to work on this project in the following steps.

- Analyze the fishermen data and compare the results
- Estimate the catchability of species in the NSCS by different fishing gears
- Simulate the input and output control management scenarios
- Compare the advantages and disadvantages of input and output controls
- Write the draft of two manuscripts for publication

Relevance and link to EEP's research plan

This project is related to EEP's interest in integrated assessment of fisheries, focusing on developing tools that integrate the biological, social, and economic aspects of fisheries. This project will contribute towards development of improved fisheries management to reach sustainable fisheries in China.

Expected output and publications

The result of this research is part of my thesis and intended for publication as two coauthored articles in international journals.

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Fruit harvesting: A potential threat to plant-frugivore systems and frugivore-driven evolution of fruit size

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Goal

To investigate the effects of fruit harvesting on the ecological dynamics of plant-frugivore mutualistic interactions, and on the frugivore-driven evolution of fruit size.

Background and motivation

Frugivore species that feed on plant fruits play a central role for plant communities by providing seed dispersal services (Howe 1984, Keenan *et al.* 1997, Herrera 1989 & 2002, Bascompte & Jordano 2007, Jordano *et al.* 2011). The loss of frugivore species may alter the abundances of economically and socially important plants (Egerer *et al.* 2018), and gradually lead to extinctions of plant species (Caughlin *et al.* 2015, Perez-Mendez *et al.* 2015). Frugivores gain nutritious food from fruit consumptions while dispersing the seeds encapsulated in the fruit pulps. The plant-frugivore interactions benefit both partners and strongly affect plant persistence and spatial distributions (Mohammed *et al.* 2018). However, such mutualistic interactions between plants and their frugivores are now increasingly being disturbed and threatened by anthropogenic activities (Markl *et al.* 2012). Anthropogenic threats have left, over long period of times, negative impacts on global diversity, ecosystem services and significantly shaped our present conditions (Mishra *et al.* 2004, Hunter 2007, McConkey *et al.* 2011, Diaz *et al.* 2016).

An important example of an anthropogenic disturbance that can potentially expose plant-frugivore systems to risks is fruit harvesting. Fruit harvesting affects plant and frugivore abundances, fruit-consumption rates and global dispersal patterns of seeds (Moegenburg & Levey 2003, Markl *et al.* 2012, Edeline 2016). Harvesting could have both advantages (Kuparinen & Festa-Bianchet 2017) and disadvantages (Law & Salick 2005) for species demography and fitness-related phenotypic traits, depending the on intensity of harvesting (Bauer *et al.* 2013). For example, non-intensive fruit-harvesting can decrease competition-induced mortality when the local dispersal ability of plants is high in the absence of frugivores, while too intensive harvesting increases the mortality of plants. On the other hand, the probability of population persistence decreases when harvesting is intensively increasing, while the population growth rates increase with increasing maximum sustainable harvesting rate (Bauer *et al.* 2013). However, recent studies (Kuparinen & Festa-Bianchet 2017) suggest that harvesting causes reduction in the resilience and recovery ability of the affected population. Additional risks introduced to fleshy-fruited plants are associated with the effectiveness of frugivorous seed-dispersal (Janzen 1970 & 1971, Herrera 2002, Howe & Estabrook 1977), only efficient frugivores could allow plant persistence when the local dispersal ability is low (Mohammed *et al.* 2018). Highly efficient frugivores may mitigate the impact of anthropogenic disturbances on plant demography and dispersal-related traits by successfully dispersing large amount of seeds away from where plants experience huge selective pressures. Recent empirical work by Beckman *et al.* (2018)

confirmed that long-distance dispersal ability (often by efficient frugivores) is positively corre-lated with fast life-history strategies of plants. Thus, the evolution of plant traits is expected to slow down when the local dispersal ability in the neighborhoods of focal plants is high.
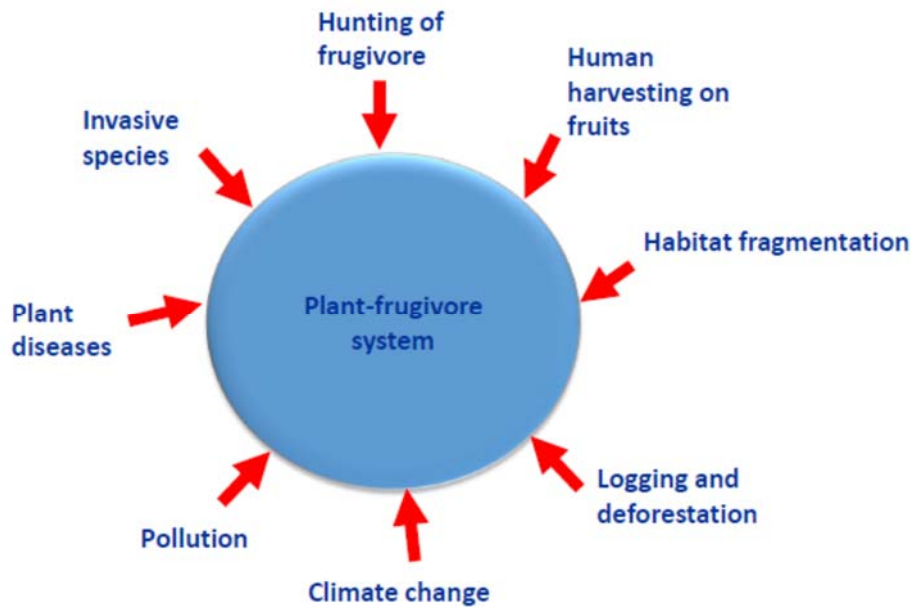

Figure: *Components of anthropogenic threats to plant-frugivore systems.*

Empirical evidences reported that plant-frugivore interactions are major drivers of the evo-lution of plant phenotypic traits (Edeline *et al.* 2007, Lomáscolo *et al.* 2010, Fontúrbel & Medel 2017, Kuparinen & Festa-Bianchet 2017). Frugivore species can thus derive the evolution of fruit traits by expressing their preferences for particular fruits (Wheelwright 1993, Duan *et al.* 2014, Encinas-Viso *et al.* 2014). Fruits with large size and of good quality are often positively correlated with fruit attractiveness to frugivores and frugivore visit frequencies (Howe & Es-tabrook 1977, Schleuning *et al.* 2011). However, fruit size development is usually limited by environmental resources that can be invested by plants for reproduction and therefore fruits can evolve according to such limitations. By considering carbon allocations for fruit production, plants can either invest more carbon to enlarge the fleshy part of the fruits and entice more frugivores or invest substantial amount of carbon to produce more seeds but small fruits. Such plant trade-offs can also influence the evolution of fruit size.

Harvesting is recognized to influence the life-history adaptive traits in fish populations (Landi *et al.* 2015). However, the impact of harvesting-induced selection on the frugivore-driven evolution of fruit traits remains an open question. We will develop a spatially explicit individual-based model to investigate the response of plant-frugivore interactions to fruit har-vesting and the effects of harvesting-induced selective pressures on the frugivore-driven evo-lution of fruit size.

Research questions

By developing an individual-based model of plant-frugivore-human interactions, we will at-tempt to answer the following questions:

- What are the effects of fruit harvesting on the ecological dynamics of plant-frugivore systems?
- What are the effects of frugivores preferences on the evolution of fruit size?

- What are the effects of fruit harvesting on the frugivore-driven evolution of fruit size?

Method and model structure

Individual-based model of plant-frugivore-human interactions

We develop a spatially explicit individual-based model of plant-frugivore mutualistic interactions through seed dispersal to investigate the effects of anthropogenic disturbances on plant and animal densities and the frugivore- and harvesting-driven evolution of fruit sizes. We first consider a finite regular lattice where each seed is either dispersed locally by parental plants in their neighborhoods or anywhere in the lattice by frugivorous animals (Harada & Iwasa 1994, Mohammed *et al.* 2018). Each lattice site is either occupied by an individual plant or empty (see Fig. 1). Plants reproduce seeds at rate r and naturally die at rate P_d. Without frugivores, plants can only disperse seeds in their neighborhoods with certain probabilities or die naturally. By considering frugivorous seed-dispersal, we divide seeds into two groups: seeds eaten by animals and dispersed globally in the lattice and seeds dispersed naturally by parental plants in their neighborhoods. For simplicity, we assume that each fruit contains a single seed in it. Animals are assumed to have both a random special distribution and foraging behavior and an individual frugivore encounters a seed with attack probability a. The attack rate of all individual frugivores per seed per unit time is given by aA, where A is the animal density. By using Holling Type-II functional response, the frugivores attack rate per seed is given by $c = \frac{aA}{1 + h_t rP}$, where h_t is the handling time (time frugivores spend to consume fruits) and P is the plant density. We later assume that the attack rate a is not merely constant and depends on frugivore preferences for particular fruit sizes. The frugivore attack probability is crucial in determining the abundance of frugivore species.

Let s to be the intrinsic rate at which non-eaten seeds are dispersed naturally by focal plants in their neighborhoods and that c is the rate at which seeds are eaten by frugivores. The proportion of seeds that are naturally dispersed by plants is $\frac{s}{c+s}$ and the proportion of seeds that are dispersed by frugivores is $\frac{c}{c+s}$. Before seeds being successfully dispersed, the eaten seeds will experience some risk while passing through the digestive system of frugivores and thus the proportion of seeds that will be dispersed globally by frugivores is $\mu \frac{c}{c+s}$, where μ measures the frugivore dispersal efficiency (conversely, $(1 - \mu)$ measures the dispersal cost). However, both locally and globally dispersed seeds must fall in empty lattice sites before germination. The probability of finding an empty local site is given by $(1 - \frac{p}{z})$, where z is the number of neighboring sites of a focal plant and p is the number of occupied sites of z. In addition to the natural dispersal ability of plants, the parameter z also measures the number of sites that could potentially affect the growth of a focal plant if they are occupied (Harada & Iwasa 1994). Likewise, The probability of finding an empty global site is given by $(1 - \frac{P}{N})$, where N is the number of lattice sites that can be occupied by plants and P is the number of occupied sites of N at time t. Finally, dispersed seeds that successfully land in empty lattice sites will germinate with probability g.

We now introduce the effect of anthropogenic disturbances (particularly, fruit harvesting) to the plant-frugivore system by assuming that some fruits are being harvested at rate h. The proportion of seeds that are dispersed locally will then become $\frac{s}{h+c+s}$ and the proportion of seeds that are dispersed globally by frugivores will become $\mu \frac{c}{h+c+s}$ and the proportion of seeds that are harvested is $\frac{h}{h+c+s}$. Now, birth of a new individual plant takes place in two ways: birth due to local dispersal of seeds by plants in their neighborhoods and birth due to global dispersal

of seeds by frugivores. We summarize the birth-death processes of frugivores and their host plants as the followings. Birth of a new individual plant takes place in two ways: birth due to local dispersal by plants in their neighborhoods and birth due global dispersal by frugivores. Death of a plant takes place in two ways: natural death and harvesting-induced mortality of plants. Birth of a new individual frugivore occurs due to fruit consumption by frugivores while death of an individual frugivore occurs naturally. All these six birth-death events of plants and frugivores occur at random in our model.

Frugivore-driven evolution of fruit size

By allowing evolution for fruit size, we characterize the fruit size by the amount of carbon invested by plants to develop the fleshy part of the fruit. We then allow the evolution of fruit size to be driven by frugivore preferences for particular fruit sizes (Buckley *et al.* 2006, Encinas-Viso *et al.* 2014) under selective pressures of fruit harvesting. Plants can invest carbon to produce more seeds but small fruit size or produce large fruits but small number of seeds. However, we here assume that the seed size in each fruit produced by all plants is the same and constant. Let c_p to be the carbon rate invested plants to reproduce, C_s is the amount of carbon invested by a plant for reproducing seeds and C_f is the amount of carbon invested by a plant for reproducing the fleshy part of the fruit. Since we are here interested in the frugivore-driven evolution of fruit size and assuming that the seed size is constant then C_s and C_f varies. Now, the trait-dependent fruit production rate is given by $r = \frac{c_p}{C_s + C_f}$. All fruits produced by a single plant will have the same trait value. Therefore, an individual frugivore searches for a particular plant with a particular fruit size and attack with trait-dependent attack rate $an \frac{C_{f,i}^{\alpha}}{C_{f,1}^{\alpha} + C_{f,2}^{\alpha} + \cdots + C_{f,n}^{\alpha}}$, instead of the rate a at which an individual plants is attacked randomly without any preference. Where n indexes the number of plants, $\alpha > 0$ describes frugivore preferences (no preferences when $\alpha = 0$) for particular fruit sizes and $i = 1,2,\dots,n$ indexes the target fruit to be attacked by an individual frugivore (for alternative approach, see Ryabov et al. 2015). Together with frugivores preferences selection, the evolution of fruit size is driven by small and rare mutations randomly appear in new born fruits.

Work plan

We split the work into the following parts:

- Develop an individual-based model of plant-frugivore mutualistic interactions
- Investigate the effects of fruit harvesting on the eco-evolutionary dynamic of plant-frugivore systems
- Apply approximation techniques to facilitate the analysis of the model
- Analyze the model and interpret the results

Further extensions

We can extend this work to study the coevolution of animal traits (e.g., gape or mouth size) and incorporate the effects of habitat disturbances and fragmentations to the plant-frugivore system and investigate how this can influence the evolution of seed dispersal and the spatial distribution of plants.

Relevance and link to EEP's research plan

This project will improve our understanding of the impact of anthropogenic disturbances on plant-frugivore dynamics, and on the evolution of fruit sizes. This project can thus be linked with IIASA's policy-oriented mission on biodiversity and food security. The proposed research project is directly linked with EEP's ongoing research on adaptive dynamics and plant biodiversity.

Expected output and publications

The expected results of this project will be a coauthored publication in peer-reviewed international journal.

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Evolutionary rescue in changing environments

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Goal

To further our understanding of how natural populations can avoid extinction due to environmental change via evolutionary rescue using an integrative modeling framework.

Background and motivation

Evolution can rescue species facing population decline and extinction due to natural or anthropogenic environmental change (Gonzalez *et al*. 2013, Carlson *et al*. 2014). The potential for evolutionary rescue to prevent species extinction is of both pure and applied interest, as it could provide additional tools for managing ecological systems. Evolutionary rescue occurs when a genetic adaptation allows a population to recover from population decline that would otherwise lead to extinction (Gonzalez *et al*. 2013). Theory suggests that evolutionary rescue cannot help all populations amidst rapid environmental change, so defining the limits of evolutionary rescue is a priority for conservation biology. Theory surrounding evolutionary rescue has emphasized the importance of factors including temporal and spatial environmental heterogeneity, gene flow, and ecological interactions on their own, but unlike in simple models that treat these variables exclusively, in a natural system these factors all play a role in concert.

In order to determine the relevant integrative variables in the current model, we first review the factors that previous studies have shown are important, largely in isolation. When modeling populations we must have an understanding of the local demographic rates such as birth, death, and dispersal, as well as the parameters that affect them such as spatial and temporal environmental heterogeneity, and local adaptation. These factors will ultimately determine the potential persistence of populations (Chesson 2000). The interplay between ecological and evolutionary components are especially relevant, as the quickening rates of anthropogenic environmental change are fueling contemporary evolution, or evolution that occurs over humanly observable time scales (Kinnison & Hairston 2007). Model frameworks have recently begun to be used to make short-term predictions regarding eco-evolutionary dynamics in response to climate change, and by incorporating theory regarding local adaptation and spatial dynamics, have the potential to lend insight into what may allow populations to undergo evolutionary rescue. The ability for species to evolve is likely tightly linked not only to their environment and the ability to disperse, but also to how we model their genetic architecture. To date, most models investigating evolutionary rescue use unrealistic genetic functions, for example utilizing improbable mutation rates. Few models addressing evolutionary rescue are genetically explicit, although studies have shown that the genetic architecture can have major effects on the adaptability of species (Schiffers *et al*. 2013).

In natural landscapes there is environmental heterogeneity, and species may exist in multiple populations connected by dispersal. In theory, dispersal between subpopulations can aid evolutionary rescue by increasing population size when low and providing a source of novel genotypic variation. However, movement and gene flow between subpopulations can also lead to reduced fitness by constraining local adaptation (Schiffers *et al*. 2013). These interactions between local adaptation and dispersal play an important role in evolutionary rescue (Gonzalez

et al. 2013). Previous work typically represents environmental heterogeneity utilizing simple spatial structures such as discrete metapopulations, but the importance of more complex spatial set ups for a population's evolutionary capacity have been shown (Haller *et al*. 2013), encouraging the incorporation of different kinds of heterogeneity in future models addressing evolutionary rescue.

Single species models have been useful in investigating spatial aspects of population dynamics, but ignore species interactions. These interactions likely play an important role in evolutionary rescue, although this role is poorly understood (Urban 2011, Gonzalez 2013). The potential for a population to adapt to a changing environment relates to the strength of selection that it experiences. Previous studies show that competition has the ability to aid in evolutionary rescue when it increases the strength of selection, thereby increasing the potential for evolution. Competition can also hinder the potential for evolutionary rescue, as when it results in negative density dependence, reducing the population size. Intraspecific competition can increase, decrease or have no effect on the strength of selection, depending on the shape of the competition curve (Osmond & de Mazancourt 2012). Furthermore, interspecific competition can also change the direction of selection, in some cases even causing a population to evolve in the opposite direction of the selection for carrying capacity size (Osmond & de Mazancourt 2012). The complexities associated with intraspecific and interspecific competition provide an array of ecologically relevant cases to investigate when considering a population, or communities' propensity for evolutionary rescue.

In multi-species models with an environmental gradient, range limits correspond to the realized niche of each species, where population growth is negative at some point along the gradient. With a shifting spatial gradient, commonly used in models of species' responses to climate change (Polechová *et al*. 2009), the potential of the establishment of beneficial mutations depends on the spatial gradient, and how that gradient changes through time. Typically the environmental gradient has been modeled as continuous and linear, although the type of environmental gradient has been shown to be important when considering evolvability. The linearity of the gradient, as well as the patchiness have both been show to alter adaptation to different environments (Haller *et al*. 2013).

Theory surrounding evolutionary rescue has emphasized the importance of factors including temporal and spatial environmental heterogeneity, gene flow, and ecological interactions on their own, but unlike in simple models that treat these variables exclusively, in a natural system these factors all play a role in concert. We will develop a stochastic individual based model to examine the interactive effects of the movement of individuals along a temporally changing spatial gradient and species interactions on evolutionary rescue. Investigating these joint influences on evolutionary rescue will aid in defining which key factors, alone or in concert, limit adaptation to a changing environment, bringing scientists closer to predicting populations' propensity for evolutionary rescue in the wild.

Research questions

How does the interplay between the following factors affect a population's propensity for evolutionary rescue?

- Environmental gradient
  - Linearity of gradient
  - Patchiness of landscape

- Competition
  - Interspecific
  - Intraspecific
- Reproduction
  - Sexual or Asexual
- Dispersal
  - Rate and frequency

Methods and work plan

Theory surrounding evolutionary rescue has emphasized the importance of factors including temporal and spatial environmental heterogeneity, gene flow, and ecological interactions on their own, but unlike in simple models that treat these variables exclusively, in a natural system these factors all play a role in concert. We will develop a stochastic individual based model to examine the interactive effects of the movement of individuals along a temporally changing spatial gradient and species interactions on evolutionary rescue. Investigating these joint influences on evolutionary rescue will aid in defining which key factors, alone or in concert, limit adaptation to a changing environment, bringing scientists closer to predicting populations' propensity for evolutionary rescue in the wild.

Model Overview

We will incorporate an explicit environmental grid upon which individuals move, allowing for us to test the role of different types of environmental heterogeneity. As in Haller *et al*. (2013) we will vary the linearity and patchiness of the environmental gradient. Furthermore we will vary the magnitude of the environmental change, to observe evolutionary rescue directly.

When an individual gives birth, their mate will be chosen randomly weighted by proximity to the individual giving birth. We will then utilize two treatments of linkage between the adaptive loci as in Schiffers *et al*. (2013). The genome is composed of either one, or several pairs of chromosomes and gametes are composed by duplicating parental chromosomes. Alleles will have a mutation probability and mutational effect.

Dispersal will occur in this model at the same time as a birth. When an individual gives birth, the placement of their offspring on the grid will be determined by a dispersal kernel. We can vary the shape of this kernel to investigate the role of dispersal in extinction risk. Furthermore, we can vary whether or not dispersal is determined by the environment. For example, either an individual can disperse to any area with a distance from their parent weighted by the dispersal kernel, and its fitness would be determined by that environment in which it lands, or an individual can preferentially disperse to good environments.

In order to investigate individual interactions we will incorporate both interspecific and intraspecific competition as described by Osmond and de Mazancourt (2012). For within species competition, the spatial proximity and trait similarity will determine competitive effect. The intensity of competition between species will be determined by the overlap of their niche curve. This is determined by how each species fitness is related to their environment, or their respective niche. The more overlap, the more strongly they compete with each other.

Work plan

There are three steps that will be carried out sequentially:

- Formulate model
- Test permutations/run simulations
- Draft a manuscript for publication

Relevance and link to EEP's research plan

The potential of understanding the determinants of evolutionary rescue from extinction due to climate change and habitat loss is of increasing utility, having clear implications for land management and policy. We will develop transferrable theory to understand the role of ecology and evolution in persistence time. The ability to utilize data and create an applied framework addressing my research questions will strengthen scientist's ability to understand the mechanisms underlying evolutionary rescue.

Expected output and publications

The results of this work will be a chapter of my PhD dissertation, and will be included in a coauthored publication in a scientific journal.

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