

Mutualism evolution on heterogeneous landscapes

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Goal

To investigate the evolution and stability of mutualistic interactions based on changing interaction topologies, spatially heterogeneous habitats, asymmetries in partner numbers, and processes of partner fidelity and partner choice.

Background and motivation

Numerous effects sustaining cooperation have been identified since the very first models of cooperation and mutualistic interactions were published. In particular, these early models incorporated mainly static interaction topologies. Such topologies were designed so that a certain member of the population was interacting either within a fixed neighborhood or with the whole population. In contrast, biological experience often shows that individuals can select their interaction partners from an assembly of potential “applicants” (Schwartz & Hoeksema 1998). Once an interaction is established, an individual can also interrupt it again if it is not satisfied with the benefit it thus gains (West et al. 2002). Thus the number and the quality of interactive links of an individual are often expected to change across the population and over time, leading to a dynamic interaction topology. Such dynamism may apply to interactions involving both interspecific and intraspecific cooperation.

Even when mutualistic relationships are obligatory for the participants, a particular interaction with a single partner can thus still be conditional. The larger the supply of potential partners, the easier it is to dispose non-mutualistic partners (cheaters) and seek out better mutualistic partners. This leads to the dynamic formation and loss of contacts between individuals, resulting in a changing composition of interacting groups.

The distinction between partner fidelity (PF) and partner choice (PC) models was first considered by Bull and Rice (1991). PF models focus on the termination of contacts between individuals of two species, while PC models, interpreting the cooperative act as a good offered in a biological marketplace, focus on the initiation of contacts between individuals of two species.

The majority of modeling work in the field of cooperation and mutualistic interactions has incorporated partner fidelity. The same applies to a model of mutualism by Doebeli and Knowlton (1998), which I have previously used to explore the effects of spatial heterogeneity on the evolution and stability of mutualism (Boza and Scheuring 2004). My previous model was based on a fixed interacting neighborhood, so that an individual could only choose its partner from the same location on a grid. Only the intraspecies competition could lead to changes in the interspecific allocation of partners. A spatial game-theoretical model incorporating both partner fidelity and partner choice will extend this earlier work and will serve as a natural next step in understanding mutualism.

The main idea for the summer project is to generalize Axelrod’s well-known Pavlov strategy from game theory, also known as „win stay–lose shift”, to describe part-

ner fidelity in mutualistic interactions. Addressing the so far uninvestigated issue of asymmetry in partner numbers, the formation of mutualistic groups will allow the participation of one or more individuals from one of the two mutualistic species, with the other species being referred to as the host. Incorporating partner choice, such groups will be established based on the initial offer from applicants. Incorporating partner fidelity, the maintenance of these groups will depend on the level of satisfaction with the benefits participants are receiving. To explore the implications of spatial structure, we will focus on systems with limited dispersal. Plant-mycorrhizal (Hoeksema and Kummel 2003) and plant-rhizobium (Simms and Taylor 2002) interactions are the most important natural systems motivating the design of our model.

Research questions

The main purpose of this project is to study the evolution and stability of mutually beneficial interactions based on dynamically changing interaction topologies. We will examine the optional mix of partner fidelity and partner choice processes.

Our specific research questions are as follows:

- What are the effects of different acceptance and rejection levels of the host in choosing adequate partners? Are these mechanisms enough to filter out cheaters?
- Is there an interaction between the processes and traits describing partner choice and partner fidelity? What happens when both processes are instead characterized by a single fixed parameter, or a single evolving trait, describing an individual's satisfaction level?
- Will the interaction of one host with several symbiotic partners (instead of one host with a single symbiotic partner) help or hinder the evolution of mutualistic interactions? What are the evolutionary consequences of allocating to each host several nodules, within each of which mutualistic interactions with a group of symbiotic partners are occurring?
- What are the implications of different search ranges of the host for the stability of mutualism? What is the evolutionarily optimal search range? Are larger search ranging helping to find more adequate partners, or do they only give more opportunity for cheaters to spread?

Methods and work plan

The environment in which the hosts reproduce and compete is represented by a lattice consisting of $L \times L$ sites with periodic boundary conditions. Each host has n nodules harboring m symbionts each.

Traits of the host

The host is characterized by its search range (s), acceptance level (α), and rejection level (δ). In addition, we use a linear reaction norm for determining the investment of a host individual in dependence of the payoff it has received from the symbionts, with a given intercept (a_H) and slope (b_H). The search range is the spatial radius of the neighborhood in which the host searches for new symbiotic partners. The acceptance level is the initial offer of the symbiont above which the host accepts the partner with more than 50% probability. The rejection level is the benefit obtained from the mutualistic interaction below which the interaction is broken more than 50% probability.

Traits of the symbiont

Also for the symbionts, we use a linear reaction norm for determining the investment of a symbiont individual in dependence of the payoff it has received from the host, with a given intercept (a_s) and slope (b_s).

Population dynamics of the host

Each site in the lattice is occupied by a host. Hosts are picked for update randomly. The population dynamics is governed by one of three alternative update rules to be considered (see below). On occasion of an update of the host, it is replaced by an offspring of a host from its neighborhood (by default we will use the von Neumann neighborhood, consisting of the focal individual and its four closest neighbors).

With the *proportional update rule*, the chance of host j to get to occupy the focal site is proportional to its payoff in relation the payoff of the others $P_j / \sum_{i=1}^m P_i$ (see below for how to calculate payoffs). Here, also the offspring of the focal individual can be the winner of the competition. We will also consider a *death-birth update rule*. This is similar to the proportional update rule, but here the focal individual itself cannot reproduce. With the *pairwise update rule*, reproduction to the focal site is determined by the difference in the payoffs between the focal individual and one of its neighbors. The higher the neighbor's payoff, the higher is its chance to reproduce to the focal site. In all three cases, the new individual inherits its parent's trait. In addition, mutations occur with a certain small probability independently in all five phenotypes (S , δ , α , a , and b).

Population dynamics of the symbiont

Symbionts are considered to reproduce constantly and create a symbiont pool at their site. The densities of free-living symbiont phenotypes will be assumed either to be proportional to the payoffs of symbiont phenotypes within nodules, or they will be subject to a logistic death rate in combination with birth rates that are proportional to the payoffs of symbiont phenotypes within nodules. In the second case, symbionts can reproduce in the soil outside of nodules, as well as inside a nodule. However, the symbionts' reproduction rate in a nodule is much higher, because of the benefits of the mutualistic interaction.

Symbiont can enter an interaction with a host (1) when the host has newly reproduced to the site or (2) after the host has rejected one of its nodules (see below). Again, new symbiont individuals (entering a newly formed nodule) inherit the traits of their parent, potentially with mutations.

Mutualistic interaction

According to their phenotype, a host invests to nodule i the amount $I_{H_i} = a_H + b_H P_{H_i}$, where P_{H_i} denotes the payoff gained from nodule i the previous round. In the first round of an interaction, we always have $P_{H_i} = 0$. A symbiont j in nodule i invests $I_{S_{i,j}} = a_{S_{i,j}} + b_{S_{i,j}} P_{S_{i,j}}$, where $P_{S_{i,j}}$ denotes the payoff gained from the host in the previous round. The symbionts' investments are pooled for a given nodule, so that the host receives an average investment of $I_{S_i} = \frac{1}{m} \sum_{j=1}^m I_{S_{i,j}}$ from nodule i . Symbionts either get the full benefit of the host's investment, or share it equally.

The investments of symbionts and hosts imply a cost for the investor ($C(I_{receiver})$) and a benefit for the receiver ($B(I_{investor})$). The cost is a linear function of the investment, $C(I_{receiver}) = C_0 \cdot I_{receiver}$, while the benefit is a saturating function of the investment, $B(I_{investor}) = B_0 \cdot (1 - \exp(-B_1 \cdot I_{investor}))$. C_0 , B_0 , and B_1 are parameters of the model that

can be different between the hosts and the symbionts or can be considered identical for both species. Thus, the payoffs gained in one round of the potentially mutualistic interaction between the host and its symbiont are as follows:

$$P_{H_i,t} = B(I_{S_{i,t}}) - C(I_{H_i,t}) = B_0[1 - \exp(-B_1 \cdot \frac{1}{m} \sum_{j=1}^m (a_{S_{i,j}} + b_{S_{i,j}} P_{S_{i,j},t-1}))] - C_0(a_{H_i} + b_{H_i} P_{H_i,t-1}),$$

$$P_{S_{i,j},t} = B(I_{H_i,t}) - C(I_{S_{i,j},t}) = B_0[1 - \exp(-B_1 \cdot (a_{H_i} + b_{H_i} P_{H_i,t-1}))] - C_0(a_{S_{i,j}} + b_{S_{i,j}} P_{S_{i,j},t-1}).$$

In order to include the effect of b in partner choice, two rounds of interaction take place right at the (potential) beginning of a new mutualistic relationship. Further (single) rounds of interaction occur until the rejection of a nodule or until the death of the host.

During one interaction step of the model, a host and one of its nodules are chosen randomly and updated. Payoffs are calculated, and the host can choose to reject the nodule based on its rejection level and the payoff gained from the interaction. The probability of rejection is $[1 + \exp((\delta - P_{H_i,t}) / \kappa_R)]^{-1}$, where κ_R is the slope of this function at its inflection point and measures how imperfectly the host perceives the payoff obtained from the symbionts. Interaction steps as described here are repeated a fixed number of times ($k \cdot L \cdot L \cdot n$, where $k > 1$ is a parameter; the rest of this product equals the number of nodules in the model).

Choosing new symbionts

A new host or a host with an empty nodule (resulting from rejection) develops a new nodule and chooses new symbionts. Symbionts present themselves to the host as long as there is an empty slot in the nodule (i.e., as long as the number of symbionts in the nodule is less than m). Only symbionts available within the search range of the focal host are considered. A symbiont is accepted based on its initial offer (a_s) and the acceptance level of the host. The probability of accepting the symbiont is $[1 + \exp((\alpha - P_{S_{i,j},2}) / \kappa_A)]^{-1}$, where κ_A is the slope of this function at its inflection point and measures how imperfectly the host perceives the initial offer of a symbiont.

Work plan

We will increase the complexity of the model gradually. The first version will model one-to-one interactions ($m = 1$ and $n = 1$). This is a direct extension of the Doebeli & Knowlton (1998) model to include partner choice and partner fidelity. Then we allow more symbionts per nodule, while keeping the number of nodules equal to 1. Finally, both parameters (n and m) will be set to exceed 1. The search range of hosts (s) is initially set to 1, i.e., hosts search for symbionts only in their immediate vicinity. Later on, we will increase this search range and also allow it to evolve.

Relevance and link to EEP's research plan

Pairwise cooperative interactions have been a subject of EEP research already for a long time. As this model focuses on pairwise cooperative interactions between individuals from different species, involving complex and dynamic interaction topologies, it will extend this previous research toward the investigation of real-life interaction network models and hopefully shed light on new effects that help maintaining cooperation.

Expected output and publications

We envisage at least one coauthored publication coming out of this summer project. The formulation of the problem is general, and we could eventually investigate other, related questions, which could result in further publications in the future.

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