Evolutionary community assembly with size-structured populations

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Goal

To develop a continuously size-structured population model with two evolving traits describing body size at maturation and ecological niche, to explore conditions under which species can diversify in these traits, and to examine the resultant multi-species communities.

Background and motivation

To date, two categories of evolutionary food web models with explicit population dynamics have been investigated. The first comprises physiologically unstructured population models in which individuals are characterized by one or more evolving traits, while the other comprises continuously size-structured population models in which individuals are characterized by size at maturation as the single evolving trait. While these two modeling frameworks already reach a relatively high degree of evolutionary and ecological realism, they still have important limitations.

On the one hand, species in unstructured population models are usually represented by aggregate variables such as total abundance, density, or biomass. When these models describe predation, food intake causes an immediate increase in abundance or biomass that, again immedeiately, contributes to reproduction. In reality, these effects are delayed through gradual growth and through the need for individuals to mature before being able to reproduce.

On the other hand, in continuously size-structured population models (Andersen & Beyer 2006; Pedersen et al. 2009), species are characterized only by their size at maturation, which is assumed to be proportional to their maximally attainable body size. Here, size at maturation is assumed to be the most important determinant of a species' ecological niche. In comparison with unstructured population models, these models are more realistic by describing continuous size structure. However, a major limitation of these models is that they are unable to explain the coexistence of species with comparable sizes at maturation.

An intermediate approach is to divide populations into several discrete stages, such as juveniles and adults, and then to describe transitions between such stages. In this context, delay differential equations help taking into account the time required for transistions between stages. However, the introduction of discrete stages is a rather drastic simplification of life histories. It is therefore desirable to model gradual changes in individual physiology and life history. Here gradual changes in body size are key, since body size has implications beyond determining an individual's trophic position, because of its significant role in determining the type and strength of ecological processes occurring within a community. Additionally, most life-history processes – including food diet selection, foraging-behavior, growth, maturation, reproduction, mortality etc. – are well described as functions of body size (Peters 1983; Ebenman & Persson 1988; Brown et al. 2004).

In continuously size-structured population models, it is then further desirable to involve more than one niche trait. In order to distinguish among species with approximately the same body size, Roy et al. (2008) introduced an evolving trait describing an individual's ecological niche in addition to one describing its asymptotic size. This extends previous work by Brännström et al. (preprint) and Loeuille & Loreau (2005), which investigates how evolution of a body-size trait can lead to diverse food webs. Roy et al. (2008) found that the evolving communities do not generally reach an evolutionarily stable state, but evolution instead proceeds in complex non-equilibrium patterns of diversification and extinction. This contrasts sharply with results found for food webs evolving in terms of a single trait, which normally reach an evolutionarily stable endpoint.

To better understand evolutionary community dynamics with diversification and extinction, I will synthesize and extend the two categories of models described above, by developing and investigating a continuously size-structured population model with two evolving traits, with the first one describing an individual's ecological niche and the second one describing its size at maturation.

Research questions

The main questions to be addressed in this project concern the evolutionary dynamics of community assembly of continuously size-structured populations with a body-size trait and a niche trait. In particular, three questions will be examined:

- What conditions enable diversification of a single-species to a multi-speices community?
- What is the eventual outcome of such diversifying evolution?
- What relationship, if any, exists between the initial and final diversification?

If time allows, I will also explore the influence of continuous size structure on the evolution of a community's maximum trophic level.

Methods and work plan

To investigate these questions, I will first develop and implement a continuously size-structured population model in which each species is characterized by its size at maturation and its niche trait.

I will assume that large individuals consume smaller ones, if their niche traits are in the vicinity of that of the predators, and that species with similar body sizes interact through interference competition. The dynamic behavior of species abundances is governed by the growth rate, the fecundity rate, as well as by the mortality rates caused by starvation, predation, and interference competition.

The growth rate, fecundity rate, and the rate of starvation mortality are determined by the energy derived from food intake. This energy will first be used for metabolism and then for reproduction. Additional mortality results from trophic interactions among species, i.e., from the predation by larger individuals on smaller individuals (including those of their own species, through cannibalism), and from interference competition. Finally, we assume that there is one primary resource (such as zooplankton) that is subject to logistic growth and that is normally distributed along the niche-trait axis.

With these assumptions, population dynamics are governed by the following partial differential equation of transport type,

$$\frac{\partial}{\partial t}N_i(t,m)+\frac{\partial}{\partial m}(g_i(m\sum_j a_{ij}N_j(t,m)N_i(t,m))=-\mu_i(m\sum_j b_{ij}N_j(t,m))N_i(t,m),$$

where the sums are taken over all extant species. The boundary condition describes recruitment,

$$R_i(t)=g_i(m_0,\sum_j a_{ij}N_j(t,m_0))N_i(t,m_0))N_i(t,m_0),$$

where N_i is the density of species i $(i=1...N)$. The latter equation means that the total reproduction rate R_i equals to the total growth rate g_iN_i of new recruits with body size m_0. The growth rate g_i is given

g_i = food intake – metabolism – reproduction.

The mortality rate μ_i comprises the losses from starvation, predation, and interference competition.

The coefficients a_{ij} and b_{ij} are obtained as functions of the niche–trait value and of the size at maturation of species i and j.

The gradual evolutionary dynamics of these traits in each species will be described by the canonical equation of adaptive dynamics (Dieckmann and Law 1996). Extinctions occur when a species' density falls below a given low threshold value without rebounding. Diversification through evolutionary branching may take place at evolutionarily singular strategies, where the gradient of a species fitness landscape vanishes. The emergence of a new species is reflected by adding an additional partial differential equation for its population dynamics and two additional differential equations for its evolutionary dynamics.

The model will be implemented and studied in Matlab.

Relevance and link to EEP's research plan

The project seeks to establish insights into the ecological diversification of continuously size-structured populations involving a body-size trait and a niche trait. This extends ongoing research on the evolution and assembly of food webs in the EEP project on *Evolving Biodiversity* and advances our understanding of the mechanisms and processes underlying biodiversity changes in nature.

Expected output and publications

The work is expected to result in one or more coauthored publications in international scientific journals.

References

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