The evolution of food-web diversity based on body size and niche traits

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Goal

To explore conditions under which long-term phenotypic evolution of body size and of a trait representing the continuum of alternative ecological niches leads to the emergence of diverse food webs with several trophic levels.

Background and motivation

The concept of ecological niche, which characterizes the function of an organism within an ecosystem, is of fundamental importance in ecology. It is also closely linked to the coexistence of species through the principle of competitive exclusion: this cornerstone of population ecology states that two species cannot coexist if they compete for common resources within a single niche. An important question in ecology is thus to understand how similar two ecological niches can be while still allowing species to coexist.

MacArthur and Levins (1967) first approached this question quantitatively, and their pioneering study has been followed by several others (see, e.g., Meszéna et al. 2006). These studies consider the possibility of packing given species within an abstract niche space, and thus cannot explain how different species coexist when allowed to evolve freely. In fact, as observed by Abrams (1983), evolutionarily realized differences are likely to be much larger than what one would predict from considering species packing alone.

Several physiological and biological traits that may be important determinants of a species' ecological niche have been identified; foremost among these is body size. However, only a few attempts have been made to date to theoretically explore how evolution of such traits may lead to diverse food webs. An exception is a recent study by Brännström et al. (in preparation; see also Loeuille and Loreau 2005) that introduces an evolutionary food web model based on considering the body size of individual species as their evolving trait. Although this model is capable of producing food webs with three to four trophic levels, the resulting food webs always exhibit a certain regularity, with typically equal spacing in body size on a logarithmic scale. Thus, this model cannot yet explain the coexistence of ecologically different species with approximately the same body size.

To overcome this limitation, one can incorporate, in addition to body size, an evolving "niche trait" to distinguish, in a simplified manner, the continuum of possible ecological roles species with the same body size can assume. The ability of a predator to forage on a prey, as well as the interference competition between species, would then be determined both by relative difference in body size and by distance in niche space.

Research questions

The key questions that will be addressed in this project concern the evolutionary dynamics of food web models under the combined effect of a body-size trait and a niche trait. More specifically, we will examine

1. How the niche trait, when combined with the body-size trait, contributes to adaptive radiations between ecologically different species, and
2. How the diversity of a food web is created and maintained in such a setting.

In particular, we will explore how evolved diversity depends on the dimension of the niche trait.

Methods and work plan

The evolutionary food web model we will investigate characterizes a species entirely through its trait value(s). These determine the intrinsic mortality rate, but also intraspecific and interspecific interaction coefficients that represent exploitation and interference competition. Mathematically, this is described by mappings from trait value(s) to interaction coefficients.

In particular, we will consider the intrinsic mortality rate $m(x)$ of a species with body size x, the rate $a(x,y)$ at which a species with body size x exploits a species with body size y, and the mortality rate $c(x,y)$ arising from interference competition between a species with body size x and one with body size y. A niche trait can then be represented by a point in one- or two-dimensional Euclidean space: it affects the strength of interactions such that when two species have niche traits far apart they do not interact. Mathematically, this can be described by $f(|n_1 – n_2|)a(x,y)$ and $f(|n_1 – n_2|)c(x,y)$, where f is a declining but positive function and n_1 and n_2 are the niche traits of species 1 and 2, respectively, using Gaussian functions for $a(x,y)$ and $c(x,y)$ (Brännström et al., in preparation).

Once the mapping from traits to intrinsic mortality and to the two interaction coefficients has been defined, we will employ adaptive dynamics techniques to investigate how these trait values change under gradual evolution. Three processes are of interest here: gradual evolution, extinction, and evolutionary branching (with the latter implying speciation, or adaptive radiation, in asexual organisms). Gradual evolution is described by the canonical equation of adaptive dynamics (Dieckmann and Law 1996). Extinctions can be detected by checking when the density of a species falls below a prescribed threshold. Detecting evolutionary branching requires careful geometric consideration, but, once detected, we can introduce a new species simply by adding an additional equation for describing the evolutionary emergence of the new species in the vicinity of the branching point.

By relying on these simplified descriptions, the evolutionary process in our approach will be analyzed under the assumption of small mutational steps. Adopting the canonical equation of adaptive dynamics in the case with one-dimensional niche trait values, we will have three equations for each species, one Lotka-Volterra equation describing the species' density and two canonical equations describing gradual evolution of its body size and niche trait. When the density of a species drops below a certain threshold, the equations representing the corresponding species will be removed. Near evolutionary branching points, we will introduce a new species with similar trait values so that it may diverge from its ancestor. Although criteria for evolutionary branching get more complex in higher-dimensional trait spaces, the above description is readily extended to niche traits with two or more dimensions. Along with analytical techniques, we will employ suitable numerical simulations using either MATLAB or C/C++.

Relevance and link to EEP's research plan

Exploration of food web evolution based on body size is one of the ongoing topics of research of in the EEP Program. The insights expected from this summer project will be valuable for understanding evolving biodiversity, and will potentially also be applicable to evolutionary fisheries management.

Expected output and publications

We expect that the project will result in one or more coauthored publications in peer-reviewed international scientific journals.

References

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