## Phenotype-based evolution of complex food webs

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Explaining the relation between structure and dynamic of food webs remains one of the most daunting challenges in ecological theory. The trophic structure is a fundamental property of ecological communities that relates their diversity to productivity and stability. Understanding the generic properties of food webs requires insight in the way these networks are assembled. Although ecological communities are often augmented by invasion rather than adaptive speciation, the diversity in an ecological network can ultimately only be explained from an evolutionary perspective. Recently, several aggrerate population models for the evolution of food webs have been proposed. Here, we present an individual-based model in which we show the evolutionary emergence of complex trophic networks from the bottom-up.

We use a spatial individual-based model with a nonlinear mapping between genotype and phenotype. An individual is specified by a genotype that determines its phenotype in a redundant ("many-to-one") and epistatic ("one-to-many") fashion. All behavioral/ecological properties of the individual (e.g. reproduction/mortality rate, auto/heterotrophy, prey preference, etc.) are derived from specific aspects of the phenotype, such that trade-offs in ecological function are inherently introduced. Autotrophs only consume abiotic resources, while heterotrophs can consume individuals in their spatial neighborhood. The outcome of the consumption interactions depends on prey preference and the distance between both phenotypes. Mortality and (asexual) reproduction are based on energy that decreases linearly, and is increased by consumption. Mutations occur by substitutions in the genotype with a low probability per locus.

The system is inoculated with a single genotype coding for a random autotroph. After the appearance of heterotrophs, coevolution between auto- and heterotrophs causes phenotypic diversification. The number of species (i.e. individuals with same phenotype) varies around 40-60 for the given system size (+/- 75000 individuals), of which approximately half are heterotrophs. The evolved species show a large variation in life history and consumption patterns, balancing various trade-offs. The structure and composition of the network can continually change, although evolutionary stability increases over time. We assess the ecological stability of the evolved food webs by canceling mutation. After a partial collapse, the truncated food web (with typically 10-15 species) persists over an indefinitely long period, during which it shows chaotic population dynamics.

We demonstrate the evolutionary emergence of ecological stable food webs in an individual-based model. The genotype-phenotype mapping provides efficiency and robustness in the exploration of phenotype space, while spatial interactions stabilizes population dynamics and preserves diversity. By encapsulating the ecological properties and their trade-offs in the phenotypes, rather than defining them as global state variables, allows for the niche differentiation by which food webs are assembled.