

NEWS AND COMMENTARY

Evolutionary studies

Evolution within food webs: the possible and the actual

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Why is not everything possible? Why are only a few biological structures, from molecules to ecosystems, actual among all the combinatorial possibilities? Jacob (1982) stated that complex objects are produced by evolutionary processes involving two factors: the constraints that specify the rules of the game and define what is possible and the historical circumstances that determine the actual course of events and control the actual interactions between the systems. Constraints plus history thus equals reality. Ecosystems can be mapped as networks of interactions among individuals, via feeding interactions resulting in food webs for example, where well-defined, non-random topological properties can be observed across a range of habitat types (Montoya *et al.*, 2006). The question is why we observe these patterns and not others that are possible. Bell (2007) offers a promising avenue to solve this question by introducing a new food web model that incorporates evolution of individuals and their trophic interactions.

Most current food web models have a serious limitation—they do not consider evolution, so species composition and the patterns of connectivity among them usually do not change over time (McKane and Drossel, 2005). Although great strides have been made in understanding the evolution and ecology of two-species interactions (Ehrlich and Raven, 1964), little is known about evolution in a broader community and ecosystem context (Whitman *et al.*, 2006). The model of Bell introduces evolution at the individual level, so that mutations may result in offspring that differ from their parents. The rules of engagement between a resource and a consumer are based on their diet complementarity, which varies according to tunable mutation rates. The model also accounts for species invasion in ecological time from a pool of species and, therefore, the fundamental process of species migration is considered.

By tuning mutation rates and the complexity and variability of species

genotypes, a series of *in silico* food webs are generated, resembling real food webs from different habitat types. More importantly, two types of evolutionary stable interaction networks are observed. First, simple webs assembled from small species pools that show a very low species turnover over time. Simple webs therefore maintain both their topological features, such as the connectance of the network, and the degree of specialization of species constant over time and also their species composition. Second, complex webs assembled from large species pools that keep their topology constant, but species composition changes over time. Complex webs are thus topologically stable but highly unstable in terms of their constituent species. This suggests a very interesting and potentially testable prediction, which can be illustrated with an extreme example.

Consider a tropical rainforest as an ecosystem assembled from a large species pool and a desert as one assembled from a small species pool. While the architecture of the network of trophic interactions of both will remain constant over evolutionary time, a rainforest will show a much larger species turnover than the desert. Comparing current food webs with their corresponding paleo-food webs is an extremely interesting but daunting perspective. While species do fossilize, their trophic interactions do not. It is therefore possible to analyze species turnover over time, but not the predicted stability of the architecture of species interactions.

This result introduces two fundamental questions within ecology and evolution: why species turnover faster in highly diverse systems and why food web topology is constant over evolutionary time. A possible answer to the first question is that speciation rates are higher in more diverse systems. In our example, speciation should be faster in the tropics than in the desert. That also intuitively explains why the tropics harbor greater number of species than deserts and therefore contain larger species pools. However, recent studies challenge common wisdom. The time to

divergence of sister species—pairs of species in which each is the other's closest relative—of birds and mammals is longer in the tropics compared with higher latitudes (Weir and Schluter, 2007). The answer is not straightforward, and further tests are needed in other taxa.

The second question, that is the invariability of trophic structure through time, may suggest some kind of higher-level optimization, as if evolution would maximize productivity, both in terms of resource and consumer biomass. Many theoretical and experimental studies show how food web structure regulates the dynamics of species populations and, ultimately, the stability of the whole community (de Ruiter *et al.*, 2005). So we could think that either productivity or stability is maximized through evolution. This may result from a particular configuration of species interactions within the ecological network. The results of Bell contradict any optimization process at high levels of organization. The food webs that persist over time do not show higher productivity, stability or any other community property than those food webs that do not persist. The contrary appears to be the case for stability. For example, for any predator–prey interaction, selection will favor more effective predators—those genotypes with stronger interactions—as they have a larger effect on prey population than weak interactors. Strong interactions between species usually mean unstable species dynamics, that is non-equilibrium population densities, that usually leads to species extinction. Such instability can be compensated by high species turnovers of both prey and predators, but no optimization can be alleged.

Models of ecological networks should contemplate species turnover at both ecological scales, through species invasion, and evolutionary scales, through speciation. Evolution is a very slow process compared to the way species move in and out of communities through invasion and extinction (Lockwood *et al.*, 1997). However, in both cases, the way to maintain high levels of diversity and realistic food web topologies is through fast species turnover. This suggests that complex ecological communities are in a state of 'self-organized instability' (Sole and Bascompte, 2006), where the architecture of a network of interactions is the key and is more constant over time than the identity of interacting species. The growing literature on other types of

interaction networks, mutualistic, for example, begets the question of whether these predictions will hold. What we actually observe is a small fraction of what is possible. Differences between the possible and the actual are larger for network-level properties than for species composition *per se*. While the spectrum of possible network architectures is larger than that of species combination, the spectrum of actual architectures of interaction networks is much smaller than actual species combinations within a fixed architecture. Biodiversity changes continuously, but the architecture of biodiversity remains. Will this remain even under current extinction scenarios?

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