# Emergence of structured communities through evolutionary dynamics

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HIGHLIGHTS

- Evolutionary dynamics of a community of competing species is considered.
- Our model is capable of generating stable systems with hundreds of interacting species, solving the complexity-stability problem.
- The emerged community has a modular structure.
- Closely related species have large niche overlap but small fitness differences.
- Relevance to many recent works on community structure, competition-relatedness, etc.

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ABSTRACT

Species-rich communities, in which many competing species coexist in a single trophic level, are quite frequent in nature, but pose a formidable theoretical challenge. In particular, it is known that complex competitive systems become unstable and unfeasible when the number of species is large. Recently, many studies have attributed the stability of natural communities to the structure of the interspecific interaction network, yet the nature of such structures and the mechanisms behind them remain open questions. Here we introduce an evolutionary model, based on the generic Lotka–Volterra competitive framework, from which a stable, structured, diverse community emerges spontaneously. The modular structure of the competition matrix reflects the phylogeny of the community, in agreement with the hierarchial taxonomic classification. Closely related species tend to have stronger niche overlap and weaker fitness differences, as opposed to pairs of species from different modules. The competitive-relatedness hypothesis and the idea of emergent neutrality are discussed in the context of this evolutionary model.                                                                          **Q4**

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## 1. Introduction

A long standing puzzle in theoretical ecology regards the coexistence of many competing species in a single community on a confined spatial domain. This phenomenon is ubiquitous in nature, manifesting itself in many systems such as fresh-water plankton (Evelyn Hutchinson, 1961; Stomp et al., 2011), tropical forests (Steege et al., 2013) and coral reefs (Connolly et al., 2014). Although the empirical identification of niches and the quantification of niche differentiation is a very difficult task in high-diversity assemblages, it seems clear that the overlap between niches of different species is substantial, as most of these species extensively utilize a common small set of resources, such as space, nutrients and water.

This, however, makes coexistence problematic, as first noticed by Robert May in his classical 1972 paper May (1972). For a system with random degrees of niche overlap, May showed that the number of coexisting species is quite limited unless the overlaps are extremely small. This problem is known as the complexity–diversity puzzle: a complex system (in our context, many coexisting and strongly competing species) cannot be diverse, since generically there exists a combination of competitor species that will apply strong pressure on a given species and will drive it to extinction. This is a probabilistic effect: for any number of species there exists a set of interaction matricies that allow for coexistence, but the chance of a randomly picked matrix to fulfill this condition decays exponentially with the number of species (see recent discussion in Allesina and Tang, 2012). Even if, by some miracle, the interaction parameters support a high-diversity community, any slight perturbation of the environment will lead to an altered interaction matrix and almost surely a substantial loss of diversity.

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Clearly, an empirically observed collection of trees or plankton species is not a random assemblage but the outcome of a long evolutionary process during which new species appeared and old species became extinct, eventually yielding the current structure of the community. Accordingly, one would like to study an evolutionary model in order to see if, or under what conditions, the evolutionary process may "solve" the complexity–diversity problem, i.e., whether or not a set of interaction matrices supporting coexistence may appear spontaneously from the evolutionary dynamics.

Several evolutionary models have been suggested in an attempt to address the complexity–stability problem. Ginzburg et al. (1988) presented an evolutionary model based on Lotka–Volterra dynamics in conjunction with speciation events. Upon speciation, the interaction of the daughter species are set to be similar to those of the mother species modulo small and random modifications (Akçakaya and Ginzburg, 1991). The model of Ginzburg et al. is conceptually appealing in its assumptions and method yet it resulted in stable coexistence of only a very limited number of species (∼6), too small to account for empirically observed communities. Other approaches, e.g. Tokita and Yasutomi (2003) and Yoshida (2003), were based on a similar evolutionary mechanism however they allowed for mutualistic interactions. The inclusion of mutualistic interactions combined with speciation and extinction events applies a selective pressure towards symbiotic interactions, thereby fostering the coexistence of many species. While these models did exhibit coexistence of a large number of species (tens or more) they cannot account for ecosystems in which there is no or negligible mutualistic interactions. See further consideration in the Discussion section.

Here we propose a modified version of the Ginzburg et al. model, which does succeed in producing a stable community with many (up to hundreds) species. Our modification is motivated by the insight that competitive interactions arise from niche overlap; the necessarily non-perfect niche overlap between a daughter and a mother species inevitably leads to weaker competition between individuals of the mother and daughter species than that of conspecific individuals. This idea is implemented by the addition of a new parameter, $h < 1$, which controls the strength of interaction between mother and daughter species relative to the intraspecific interaction. This seemingly minor change has the effect of increasing the number of coexisting species by over an order of magnitude.

The resulting model evades the theorem of May by generating a nonrandom structure for the matrix of interaction strengths. One simple way to verify this claim is by studying the community structure with a randomly shuffled version of the interaction matrix. Indeed, we find that the random shuffled system leads to the extinction of large numbers of species, reducing the system to a few coexisting survivors.

Another way of investigating the structure is via the use of standard "modularity maximization" algorithms that are designed to detect modular structure in matrices. Running an algorithm of this type (Blondel et.al, 2008), we find that it succeeds in identifying a significant degree of modularity.

We can do better however since we have access to the phylogenetic history of the species in the simulation. Using the phylogenetic distance matrix and a phylogeny reconstruction algorithm to reorder the species, a unique hierarchical structure of the interaction matrix is revealed. In this structure, which arises spontaneously via the evolutionary process, the interaction matrix can be partitioned into subcommunities such that the interaction strength between two species within the same subcommunity is high while the interaction between two species from different subcommunities is low. It is moreover seen that the species within a subcommunity are phylogenitically closely related while species in two different sub communities are only distantly related.

In the following section we describe our model and equations in detail. In Section 3 we present our results and in the last section we discuss our main findings and describe several future research directions.

## 2. Materials and methods

Our results emerge from simulations of the generalized competitive Lotka–Volterra model, where speciation and extinction events are allowed to change the number of species, generating an evolutionary process. Denoting the (instantaneous) number of species in the community by $Q$, the dynamics satisfies

$$\dot{n}_i = \alpha n_i \left(1 - \frac{n_i}{K}\right) - \frac{n_i}{K} \sum_{j=1}^{Q} C_{i,j} n_j, \tag{2.1}$$

where $n_i$ is the abundance of species $i$, $\alpha$ is the linear growth rate (assumed for simplicity to be species-independent), $K$ is the carrying capacity and $C_{i,j}$ is the competition matrix.

Formally, even when a species is under strong competitive pressure and its abundance decays, the dynamics described by the deterministic (2.1) leads to decay of its abundance to infinitesimal values but it can never reach zero. This property of (2.1) is a disadvantage, since species may recover from a long period of diminishing abundance when the community structure changes during evolution, while in the real world species that undergo extinction are out of the game for good. To allow for extinction we define a threshold value $n_0$, below which a species is removed forever and the corresponding row and column of the matrix $C_{i,j}$ are deleted.

Speciation events, on the other hand, involve the addition of a species to the dynamics described by (2.1). To model speciation, an existing species is chosen at random (with a probability proportional to its population size) to be the "mother" species, and its population is reduced by 5%; the individuals belonging to this 5% fraction are declared as a new, "daughter" species, that inherits most of the features of the mother species up to small modifications as described below. This implies that closely related species play a similar role in the dynamics (2.1), reflecting the similarity of their biological functions.

We illustrate this speciation process via the example of two species becoming three due to the speciation of species 1. Denoting the daughter species by the label 3, the change in the interaction matrix $C_{i,j}$ is given by

$$\begin{pmatrix} 0 & C_{1,2} \\ C_{2,1} & 0 \end{pmatrix} \Rightarrow \begin{pmatrix} 0 & C_{1,2} & h(1-\gamma)+\gamma\epsilon_1 \\ C_{2,1} & 0 & C_{2,1}(1-\gamma)+\gamma\epsilon_2 \\ h(1-\gamma)+\gamma\epsilon_3 & C_{1,2}(1-\gamma)+\gamma\epsilon_4 & 0 \end{pmatrix} \tag{2.2}$$

Our model distinguishes between the competition of the daughter species with its mother and its competition with all other species. For any species other than the mother, the daughter inherits the competition terms of its mother with small, random modifications. In particular, if $C_{\text{mother},j}$ is the interaction of the mother with species $j$, $C_{\text{daughter},j} = C_{\text{mother},j}(1-\gamma)+\gamma\epsilon$, where $\gamma \ll 1$ and $\epsilon$ is a random variable drawn from a gamma distribution with mean 1 and variance 1. In Eq. (2.2) we numbered the $\epsilon$'s to emphasize that each of them is chosen independently from the same distribution. The competition matrix terms for $C_{j,\text{daughter}}$ are obtained using the same procedure.

The mother–daughter interaction terms are subject to different rules. As explained, the mother and the daughter are usually similar in their biological functions, however some degree of niche separation appears to be a condition for successful speciation. Accordingly, we set $C_{\text{mother},\text{daughter}} = h(1-\gamma)+\gamma\epsilon$, where the