How Clustering Promotes Biodiversity: A Solution to the Plankton Paradox

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It is known that a species-saturated ecological community driven by competitive Lotka-Volterra equations, following a path of competitive exclusion, lingers in a long-term state with species congregated in niche space into well-separated clusters. Characterizing the topology of the niche structure of this state as a hierarchical one, we put forward a generalization of the Lotka-Volterra multi-resource competition model, which recognizes this topology at the basis of its own network structure of interrelated differential equations. This kind of generalization substantially reduces the competitive constraints on species coexistence, offering promising potential for a conceptual resolution of the plankton paradox.

The plankton paradox, a term coined by Hutchinson[1] in 1961, refers to the enormous diversity of phytoplankton species observed virtually in all aquatic ecosystems, while a straightforward understanding of the principle of competitive exclusion[2,3], the core tenet of theoretical ecology, teaches that in competitive equilibrium a number of species competing for fewer number of resources cannot coexist. Indeed, the aquatic environment is seemingly too homogeneous to allow different species of phytoplankton, competing for light and, in order of magnitude, a dozen mineral resources, to be settled in different compartments in niche space, unless the principle of "one niche – one species" is violated. Hutchinson[1] saw the solution to the problem in that varying environmental conditions prevent the formation of competitive equilibrium in a phytoplankton community, thereby suspending the extrusion of less adapted species. Another reason for suspending competitive exclusion was hypothesized[4,5] to be the internal chaotic dynamics in multispecies competitive communities. Over the past six decades, other solutions to the problem have been discussed in the literature[6], with an equally remarkable diversity of proposed mechanisms. While most allow the coexistence of a few more competitors in addition to what is allowed by competitive exclusion, only a few highly idealized theories allow for the coexistence of hundreds of species limited by a small number of resources. In the absence of a generally accepted solution to the problem, we outline here another conceptual solution that, however, fits well within the framework of competitive exclusion, rather than specifying how species-rich communities can defer the competitive exclusion.

At the first step of our reasoning, we recall the so-called May instability[7]. Somewhat folkloric, somewhat under the authorship of Elton[8], MacArthur[9] and others, the dominant view was that the stability of an ecosystem positively correlates with its biodiversity and complexity. However, in the early 1970s, May[10] sharply challenged this opinion, from a cybernetic perspective showing exactly the opposite. May himself, referring to Gardner and Ashby's[11] computations, saw a solution to the problem his analysis posed in the block structure[12] of the community-matrix of an ecosystem.

More recent numerical simulations of the dynamics of the species-reach Lotka-Volterra community with interspecific competition quantified by niches overlap have indeed shown a lumpy distribution of species along a niche axis[13], which actually confirms May's rather general surmise in a particular embodiment. We hypothesize that this is the case with phytoplankton communities, the more so because there are empirical evidences[14,15,16] to support this.

The following question guides our further reflection. Should we think of this phenomenon of grouping of species in niche space as something transient and purely quantitative along the path of competitive exclusion? With a positive answer, one may trace the dynamics of the community to the state of bankruptcy of individual clusters to single species. Not what we seek. Otherwise, we ought to take this state for granted, by and large, without regard to the mechanisms that brought the system to this state, whether they involve May's instability[12], competitive exclusion[17], or evolutionary assemblage of a community[18], but accepting the modular assemblage of species in niche space into clusters as a principal internal determinant of subsequent community dynamics. Namely, the niche structure of the community under consideration shows a clear tendency towards a new topological order. Meanwhile, Lotka-Volterra dynamics by itself cannot provide this topological transition, but only signals about it. And seeing behind the dynamics of the community a transition to a qualitatively new topological state, not potential, but actual, and taking into account the obvious fact that the structural topology of a community is not its quantitative, but qualitative attribute, we have to encode it into the governing equations of the system from the outset. To implement this program, we put forward the key assumption of the study that clarifies our understanding of the topology we are talking about. That is, interspecific competition plies between species from different clusters can be woven together into competitive ropes stretched between clusters as holistic ecological units, hereinafter referred to as cliques (Fig. 1). Some justification for this assumption can be found in the concept of ecological species[19] as follows. In the case under consideration, the fragmentation of niche space has to be thought of as a sequential hierarchical process, not in the course of time, but along the path of reasoning. The coarse-grained level of fragmentation demarcates compartments in niche space for the quartering of cliques, comprising ecologically related species whose ecological traits are indistinguishable at this level of detail between species in the same clique and clearly

distinguishable between species from different cliques, and competing as integral groups with other peer groups for a vital amount of niche space. That is, competition for more favorable coarse-grained fragmentation of niche space is of a group nature, occurring between cliques as integral ecological species. Further fine-grained fragmentation, in turn, occurs in individual niche compartments of ecological species as a result of competition between biological species that make up a given ecological species.

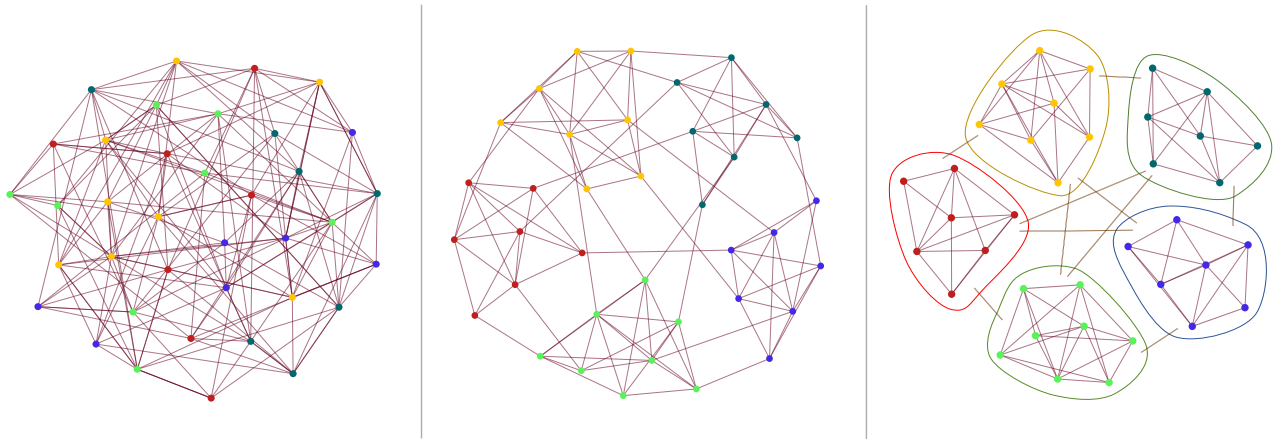

Figure 1. | Network structure of a community with a general (random) distribution of competitive relationships between species (left panel); with a clear cluster aggregation of species (middle panel), when species compete more intensely within clusters and less intensely between clusters; with a hierarchical topology of competitive links (right panel), when species compete in a general manner in clusters, while inter-cluster species competition proceeds as inter-cluster competition with species being amalgamated in holistic groups – cliques.

To bring some math to the above, let's define a hierarchical generalization of the Lotka-Volterra multi-resource competition model[20,21] as follows:

$$\frac{dM_i}{dt} = M_i F_i(M_1, \dots, M_m; R_1, \dots, R_s), \tag{1}$$

$$\frac{dN_{i,j}}{dt} = N_{i,j} f_{i,j}\left(N_{i,1}, \dots, N_{i,n_i}; R_1, \dots, R_s\right), \tag{2}$$

$$i = 1, \dots, m, \quad j = 1, \dots, n_i$$

Here $N_{i,j}$ stands for the abundance of the jth of n_i species in the ith clique, and the variables (parameters) $R_1, \dots, R_s$ bring into play the overall set of resources (factors) shared at both levels of competition, although, in general, the actual subset of shared resources may vary widely from clique to clique and at the level of inter-clique competition. As for M_i, it is intended to denote the effective abundance of the ith of m cliques of the community, or simply the weighted sum of the abundances of all species in a given clique, with coefficients reflecting the relative per capita capacities of species to exploit shared resources.

With the provisos above, the model (1) and (2) constitutes a system of interrelated differential equations with a hierarchical topology of the network of connections between them, which is what fundamentally distinguishes it from the archetypal one[20].

Refraining from delving into the mathematical analysis of the model defined by equations (1) and (2), we only mention one feature of it, which is directly related to the plankton paradox and the principle of competitive exclusion and can be deduced by analogy with the long-known properties of the modified Lotka-Volterra multi-resource competition model[20,3]. Thus, the system of equations (1), as well as each subsystem of the system (2) obtained by fixing the clique index i, from a mathematical point of view repeats that system, as it has been designed consciously. Therefore, abiding by the analysis of Ref.[20], we have to move from shared resources to limiting factors as a minimal complete set of independent arguments for the functions F_i and $f_{i,j}$, with no smaller collection of variables being sufficient to serve this purpose:

$$Z_p = Z_p(M_1, \dots, M_m; R_1, \dots, R_s), \qquad p = 1, \dots, K,$$
$$z_{i,q} = z_{i,q}\left(N_{i,1}, \dots, N_{i,n_i}; R_1, \dots, R_s\right), \qquad q = 1, \dots, k_i.$$

With these variables Z_p, representing K limiting factors at the level of inter-clique competition and $z_{i,q}$, representing k_i limiting factors for interspecies competition in the ith clique, the system (1) and (2) takes the following form:

$$\frac{dM_i}{dt} = M_i F_i(Z_1, \dots, Z_K), \tag{3}$$
$$\frac{dN_{i,j}}{dt} = N_{i,j} f_{i,j}\left(z_{i,1}, \dots, z_{i,k_i}\right), \tag{4}$$
$$i = 1, \dots, m, \quad j = 1, \dots, n_i$$

Further, reproducing the analysis of the work[20] separately for the system (3) and separately for the system (4) with a fixed clique index i, we will come to the same conclusion as there, which can be somewhat loosely paraphrased in a common manner as follows: the state of competitive equilibrium of the community, cyclic or static, can accommodate no greater number of cliques of species than the number of limiting factors: $m \leq K$; and the same for species in each clique: $n_i \leq k_i$. To summarize, we conclude that the equilibrium of the model under consideration can harbor at most as many species as $n_{max} = \sum_{i=1}^{K} k_i$. In the simplest situation, when the number of limiting factors is the same at the level of inter-clique competition and in each clique, the competitive exclusion constraint boils down to $n \leq k^2$. Given a dozen limiting factors and hundreds of phytoplankton species, this is quite enough to conceptually resolve the plankton paradox.

The above consideration does not address the question of the achievability of the limit imposed on the maximum number of species in an equilibrium community. However, it should be noted that this issue has been largely silent in other theoretical studies[3,20,21,22] of the principle of competitive exclusion and seems to us to be a relevant open question.

In conclusion, we would like to emphasize that the main thesis of the above concerns not the equations with which we have embodied the main message of this work, but the hierarchical network structure of competitive connections that we attribute in particular to phytoplankton communities. In this respect, the proposed hierarchical structure can be used to explore other modular network systems with different governing equations, as well as with richer levels of hierarchy. In the context of the plankton paradox itself, we also note that the above resolution does not in any way contradict most previously studied approaches to solving this problem, such as those associated with intrinsic dynamic chaos in phytoplankton communities[4,5] or variable external conditions[1], but rather can incorporate them into itself with great harmony, leading to a more sustainable solution to the problem.

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