How Clustering Promotes Biodiversity: A Solution to the Plankton Paradox

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Abstract

From a mathematical perspective, randomly assembled species-rich competitive communities exhibit a high degree of instability, as described by May's stability theorem. This suggests that actual ecological communities should possess a significant level of organization in their competitive network structure, perhaps with a modular topology, to withstand May's instability. It is also 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, thereby competing in a modular manner. Without regard to origin, we characterize the modular network topology of interspecific competition in such a community as a hierarchical one, putting forward a generalized multi-resource multi-species competition model that recognizes this topology at the basis of its own network structure of interrelated governing equations of species dynamics. This kind of generalization substantially reduces the competitive constraints on species coexistence, offering promising potential for a conceptual resolution of the plankton paradox.

Introduction

The plankton paradox, a term coined by Hutchinson (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 (Hardin 1960, Armstrong and McGehee 1980), the core tenet of theoretical ecology, teaches that in competitive equilibrium a number of species competing for a fewer number of resources cannot coexist. Indeed, the aquatic environment is apparently 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. One way out of this difficulty is hinted at in the very

formulation of the principle of competitive exclusion, which oriented Hutchinson (1961) to seek a 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 to be the internal chaotic dynamics in multispecies competitive communities (Huisman and Weissing 1999, Benincà 2008). Over the past six decades, other solutions to the problem and their variations have been discussed in the literature (Roy and Chattopadhyay 2007), 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 universally agreed-upon resolution to the issue, we outline here another conceptual solution that, besides, fits well within the framework of the principle of competitive exclusion, rather than specifying mechanisms that mitigate competitive exclusion in species-rich communities. However, this comes at the expense of rethinking the principle of competitive exclusion to address the question regarding the specific meaning of the term "species" in this context. This issue holds relevance at least due to the multiplicity of species concepts (Aldhebiani 2018), such as biological, morphological, ecological, and phylogenetic concepts, among others. To our knowledge, this matter has never arisen before. However, once formulated, the answer suggests itself – ecological species, which we will promote below with ensuing consequences.

Concept

At the first step of our reasoning, we recall the so-called May instability (Allesina and Tang 2015). Somewhat folkloric, somewhat under the authorship of Elton (1958), MacArthur (1955) 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 (1972) sharply challenged this opinion, from a mathematical perspective showing exactly the opposite. May himself, referring to Gardner and Ashby's (1970) computations, saw a solution to the problem his analysis initiated in the block structure of the community-matrix of an ecosystem (Grilli et al. 2016).

More recent numerical simulations of the dynamics of the species-rich Lotka-Volterra community with interspecific competition quantified by niche overlap have indeed shown a lumpy distribution of species along a niche axis (Scheffer and van Nes 2006), which actually confirms May's rather general surmise in a particular embodiment. We hypothesize that this is

also the case with phytoplankton communities, all the more so because there are empirical evidences to support this (Vergnon et al. 2009). Indeed, drawing on the correlations between morphological properties and functional traits of phytoplankton species (Kruk and Segura 2012), a number of studies (Segura et al. 2011, 2013, Graco-Roza et al. 2021) have suggested that the multimodal pattern observed in species size distribution within phytoplankton communities reflects a clustered arrangement of species along niche gradients.

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, in order to account for the suppression of competitive exclusion at this stage, mechanisms akin to those mentioned at the outset will have to be invoked again, albeit with a more favorable prospect. However, there is another option to untangle the dilemma outlined. Namely, 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 (Grilli et al. 2016), competitive exclusion (Haraldsson and Thébault 2023), or evolutionary assembly of a community (Bonsall et al. 2004), instead accepting the modular arrangement of species in niche space into clusters as a principal internal determinant of subsequent community dynamics.

The general scheme of mathematical models of the dynamics of ecological communities is such that each species of the community is assigned its own dynamic equation from a finite class of equations, say logistic ones, while the interaction between species is modeled by appropriately linking the governing equations corresponding to the interacting species. This way, the network topology of interspecific relationships is mirrored in the network of interrelations among the species governing equations, thereby imposing a predetermined topological constraint on the model. As a consequence, even if the niche structure of the model community shows a clear tendency towards a new topological order, the imposed dynamics by itself cannot provide this topological transition, but rather suggest the possibility of such a change. And seeing behind the dynamics of the community a transition to a qualitatively new topological state, not potential, but actual, we have to restructure the network of interrelations between the governing equations of species, conforming it with the newly emerging niche topology of the community. Below we are going to implement this program for communities with a modular network of interspecific competition.

The intensity of competition among organisms is contingent upon the resemblance of their requirements for shared resources of limited supply. The classification of competitive relationships as either intraspecific or interspecific reflects precisely the qualitative distinction that should exist in these requirements of individuals from the same versus different species. However, following this line of reasoning, we contend that it would also be warranted to make a qualitative distinction between the competition among species within the same cluster and those from different clusters in competitive communities featuring a well-defined modular niche structure. Thus, when dealing with an ecological community comprising species clumpy distributed in niche space, and quantifying competition between species based on the overlap of their ecological niches, the degree to which interspecific competition contrasts within and between clusters largely depends on the degree of modularity of the community niche structure. In the asymptote of high modularity of the community's competitive network, this contrast will obviously acquire a qualitative character, which makes it quite reasonable to accept the same idea even with a moderately high level of modularity of the competitive network.

However, the subclassification of interspecific competition as either intra-cluster or inter-cluster competition at this stage of the reasoning holds only nominal significance. To give it practical meaning, we will invoke the concept of ecological species (Andersson 1990), seeing it as the most appropriate notion for characterizing the species clusters we are talking about. Indeed, clusters comprise species with closely adjacent and significantly overlapping realized niches, which, by the same token, are greatly narrowed due to intense competition within the clusters. All of this clearly suggests that the fundamental niches of species within individual clusters significantly coincide, which, in turn, is nothing else than the criterion of an ecological species.

With the above considerations, we are now ready to introduce the main assumption of the study, designed to demonstrate our comprehension of the network topology of competitive relationships in competitive ecological communities with a clumpy arrangement of species in niche space. Namely, species within individual clusters compete in a general manner, while inter-cluster competition of species proceeds as competition between ecological species acting as holistic ecological units and represented by these very clusters. This assumption outlines a certain hierarchical topology for modular competitive networks (Fig. 1).

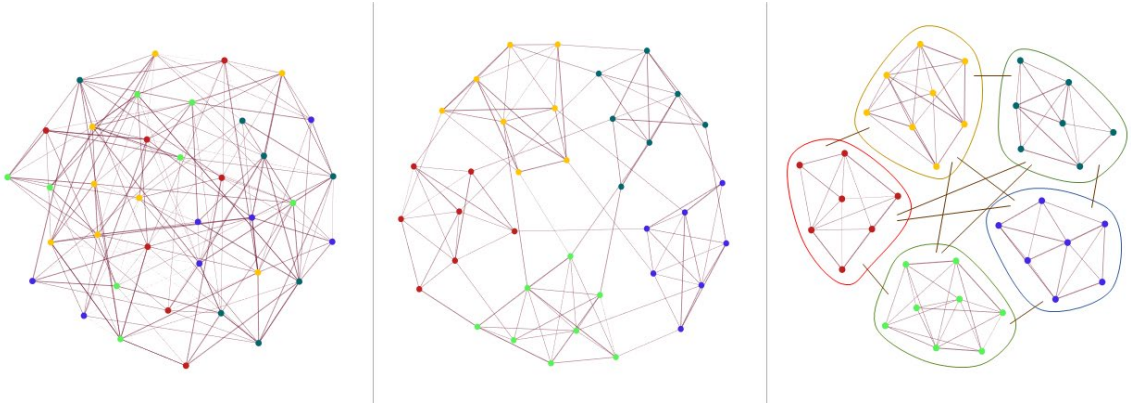

Figure 1. Network structure of a community with a general (random) distribution of competitive relationships between species (left panel); with a clear cluster aggregation of species, when species compete more intensely within clusters and less intensely between clusters(middle panel); with a hierarchical topology of competitive links, 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 – ecological species (right panel).

It is important to acknowledge that this assumption is somewhat conceptual in nature, and as such, its validation should be based on empirical evaluation of the ensuing consequences, rather than on logical reasoning derived from established frameworks.

Overall, the following picture emerges. In the case under consideration, interspecific competition and the resulting fragmentation of niche space have 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 clusters, comprising ecologically related biological species whose ecological traits are indistinguishable at this level of detail between species in the same cluster and clearly distinguishable between species from different clusters, and competing as integral groups – ecological species – with other peer groups for a vital amount of niche space. Further fine-grained fragmentation, in turn, occurs in individual niche compartments of ecospecies as a result of competition between biological species that make up a given ecospecies.

Mathematical clarification

To further clarify the above from a mathematical perspective, we define a hierarchical extension of the Lotka-Volterra type multi-resource competition model, drawing upon the model and its analysis presented in the classical paper by Levin (1970), which has significantly shaped our current comprehension of competitive exclusion in multi-resource multi-species communities. That is,

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

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

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

Here $N_{i,j}$ stands for the abundance of the jth of n_i species in the ith cluster, 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 cluster to cluster and at the level of inter-cluster competition. As for M_i, it is intended to denote the effective abundance of the ith of m clusters of the community, or simply the weighted sum of the abundances of all species in a given cluster, 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.

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 (Levin 1970, Armstrong and McGehee 1980). Thus, the system of equations (1), as well as each subsystem of the system (2) obtained by fixing the cluster index i, from a mathematical point of view repeats that system, as it has been designed consciously. Therefore, abiding by the analysis of Levin (1970), 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-cluster competition and $z_{i,q}$, representing k_i limiting factors for interspecific competition within the ith cluster, the system (1) and (2) takes the following form:

$$\frac{dM_i}{dt} = M_i F_i(Z_1, \dots, Z_K), \tag{3}$$

$$\frac{dN_{i,j}}{dt} = N_{i,j} f_{i,j}\left(z_{i,1}, \dots, z_{i,k_i}\right), \tag{4}$$

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

Reproducing further the analysis of Levin (1970) separately for the system (3), we will reach the same conclusion as there, which can be paraphrased in a common manner as follows: the state of competitive equilibrium of the community, cyclic or static, can accommodate no greater number of clusters of species than the number of limiting factors at this level: $m \leq K$. As for the system of equations (4), for a fixed cluster index i, it controls the interconnected dynamics of species within this cluster, but with one additional condition linearly relating the abundances of species in a given cluster to the effective size of the cluster emanating from (3). However, it is quite obvious that this extra clause cannot in any way mitigate the just-mentioned constraint on the maximum number of species in equilibrium implied by the system (4) without this extra clause: $n_i \leq k_i$, but perhaps tighten it. Overall, we conclude that the equilibrium of the model under consideration can harbor in total 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-cluster competition and in each cluster, 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 of the principle of competitive exclusion (Armstrong and McGehee 1980, Levin 1970, MacArthur and Levins 1964, Rescigno and Richardson 1965) and seems to be a relevant open question.

Concluding remarks

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 (Huisman and Weissing 1999, Benincà 2008) or variable external conditions (Hutchinson 1961), but

rather can incorporate them into itself with great harmony, leading to a more sustainable solution to the problem.

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