The architecture of mutualistic networks does influence structural stability.
Version 1

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Abstract We discuss similarities and differences between a recent approach to the computation of the structural stability of ecological systems (Grilli et al., Nat Commun 2017, 8:14389) and a previous one based on the effective competition (Bastolla et al. J. Theor. Biol. 2005 235:521) and the works derived from it, including Pascual-García and Bastolla (Nat Commun 2017, 8:14326). Both approaches agree in identifying the number of species and the average interspecific competition as two key parameters that reduce the stuctural stability of purely competitive systems. Nevertheless, their results differ when they are applied to mutualistic systems. Grilli et al. show that the structural stability is almost the same for real and random mutualistic networks, whereas our work shows that it is strongly influenced by the ecological overlap (also termed nestedness), which is significantly different between the two kinds of networks.

This apparent discepancy stems from two differences. Firstly, structural stability is differently defined as the volume of parameter space compatible with feasible equilibria on one hand, and as the maximum perturbation compatible with coexistence of all species, on the other hand. Grilli et al. show that a measure more related with the maximum perturbation differs between real and random mutualistic networks, which reconciles our findings. Second, and more important, Grilli et al. treat mutualistic systems in the same way as purely competitive systems, analyzing their full interaction matrix, whereas we analyze the effective competition matrix of groups of species that interact through direct competition. The fact that all intra-group interactions are negative allow us to apply the Perron-Frobenius theorem, and to interpret the main eigenvector of the effective competition matrix, whose elements are all positive, as the equilibrium abundances that maximize the structural stability. The effective competition involves also indirect interactions through shared and non-shared mutualistic links, and in this way it depends on the ecological overlap.

The effective competition approach also allows to show that the effect of mutualism of increasing or reducing the structural stability critically depends on the direct competition between species of the same group. Finally, we recall the importance of modelling the saturation of mutualistic benefits, otherwise models of mutualism such as those of Grilli et al. are dynamically stable only for interaction strengths that decrease with the number of species. The effective competition framework allows for analytically dealing with the stability of models with saturating mutualism.

We would like to drive the attention of the authors and readers of the paper recently published by Grilli *et al.* in Nature Communications [1] to the analogies and differences between its main conclusions (Eq.2 in Reference [1]) and those of J. Theor. Biol. 2005 [2] and subsequent works, including Ref. [3], which was published in the same issue of Nature Communications.

In Ref. [2] it was shown that the structural stability of a competitive system is a decreasing function of the number of species and the effective competition parameter ρ, which is essentially the same as the ratio between the average interspecific and intraspecific interactions, E_1/d in Eq. 2 in Ref. [1]. Thus, the two approaches identify the same two main determinants of structural stability. Reference [2] inspired the analysis of the structural stability of mutualistic systems presented in Ref. [4, 5, 6] but it was cited in Ref. [6] only in the Supporting Information, which may be the reason why Grilli *et al.* missed it.

Nevertheless, when the two frameworks are applied to mutualistic systems, their results appear to be in contradiction. Whereas Fig.2 of Ref [1]. shows that the volume of parameter space compatible with feasibility is almost the same for real and random mutualistic networks, the approach of Ref. [2] shows, both analytically and numerically, that the structural stability of mutualistic model ecosystems strongly depends on the ecological overlap (also called nestedness), which differs between real and random networks [2, 4, 5, 6]. We think that this apparent discrepancy stems from two main differences. Firstly, structural stability was defined in Ref. [2] as the maximum perturbation compatible with the coexistence of all species, more related to the directional perturbation depicted in Fig.3 of Ref. [1] than to the volume of parameter space depicted in its Fig.2. In our opinion, despite the universality of the volume of phase space is a remarkable result, the maximum perturbation compatible with coexistence is more relevant for the species coexistence problem, with which it is directly related. Indeed, our result is consistent with Fig.3 of Ref. [1], which shows that the directional perturbations of mutualistic systems, related with the measure of structural stability adopted in Ref. [2, 4, 5], differ between random and real networks.

Another difference, perhaps even more important, between Ref. [1] and Ref. [2] concerns systems that are not purely competitive, i.e. not all the elements of the species interaction matrix are negative. The works derived from Ref. [2] ([4, 5, 6]) consider two or more groups of species, such that their within-group interactions are competitive and between-group interactions are mutualistic or predatory. The fact that all intra-group interactions are negative is crucial for applying the Perron-Frobenius theorem, which guarantees that the main eigenvector of the intra-group interaction matrix has only positive components that are interpreted as the equilibrium abundances that maximize the structural stability (in suitable units). More precisely, for such bipartite systems we describe the fixed point equations in terms of the effective competition matrix between species in the same groups that results from the sum of their direct competition plus their indirect interactions through species in the other group. Therefore, the effective competition is strongly influenced by the fraction of shared links, i.e. the ecological overlap, which was called nestedness in previous papers [4, 5, 6], and ρ (or equivalently E_1/d) is computed only from the intra-group effective competition matrix. In contrast, in Ref. [1] bipartite systems are treated in the same way as purely competitive systems, computing ρ (E_1/d) for the full interaction matrix with both positive and negative elements. We conclude from this analysis that species coexistence does depend on the architecture of mutualistic networks, in particular on its ecological overlap, despite some measures of structural stability may depend only on the average connectance.

Furthermore, Ref. [3] shows that mutualistic interactions reduce the effective competition parameter, and thereby increase structural stability and enhance species coexistence, only when the direct interspecific competition between species of the same group is weak, while the contrary holds for predatory interactions. This result stems from the computation of the indirect interactions. Shared mutualistic links yield a positive contribution that decrease the effective competition, while pairs of species that form non-shared links yield a negative contribution proportional to the direct competition between the two species. The existence of a critical competition strength allows rationalizing many apparently contradictory findings on model mutualistic systems, including those of Ref. [4, 7, 8, 9, 10, 11, 12]. The results of Ref. [3] also reconcile the two seminal points of view on the complexity-stability relationship of Robert MacArthur [13] and Robert May [14], the first one more based on what we call the propagation of perturbations and the second one more based on dynamical stability.

Additionally, positive definiteness of the interaction matrix, which is a sufficient condition for global stability [15], implies the inequality $\rho > -1/(S-1)$ (or $E1/d > -1/S$ in Ref. [1]). This inequality or equivalent arguments were often used to claim that the mutualistic interaction strengths must decrease with the number of species [16, 17], but they were also interpreted as evidence that models of mutualism must include the saturation of mutualistic benefits [18]. Several authors, among which ourselves, argued that it is important to consider mutualistic systems with saturating interactions. When this is done, as in Ref. [4, 5, 3, 6, 18], mutualistic systems with saturating interactions are globally stable even for strong interactions, and the analytical treatment is almost as simple as

for the linear case. In fact, we have shown recently [19] that the global stability of saturating mutualistic systems is governed by the same effective competition parameter ρ that influences structural stability, with the dynamical equations suitably linearized close to the equilibrium point.

Finally, there are important challenges still to be met, such as the experimental determination of parameters such as competition coefficients, mutualistic benefits, and abundances suitable to be incorporated in ecological models.

We hope that this comment contributes to clarifying the similarities and differences between the two analytical approaches and the interpretations derived from them, and can strengthen their synergy.

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