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, published in the same issue of Nature Communications.

While both approaches agree in identifying the number of species and the average interspecific competition as two key parameters that reduce stuctural stability, they adopt different definitions of structural stability, respectively 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 the volume of parameter space is almost the same for real and random mutualistic networks, but that another measure more related with the maximum perturbation differs between the two kinds of networks. Consistently, we showed that the maximum perturbation is strongly influenced by the fraction of shared mutualistic interactions, which was termed nestedness in previous approaches, and which differs between real and random mutualistic networks.

Our 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 one of the reasons why Grilli *et al.* missed it.

An important difference between Ref. [1] and Ref. [2] is the definition of structural stability. Structural stability was measured 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. We think that this different definition explains the apparent contradiction between Ref. [1] and the works derived from Ref. [2] (see below). 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. Other differences are the analytical framework (an elegant statistical mechanical theory in Ref. [1] and matrix theory in Ref. [2]) and the change of units $B_{ij} = C_{ij}/\sqrt{C_{ii}C_{jj}}$ performed in Ref. [2] to set the analogous of parameter d in Ref. [1] equal to -1.

The two most relevant differences between Ref. [1] and the works derived from Ref. [2] concern the application of these results to mutualistic systems. The approach of Ref. [2] allowed to analytically predict the structural stability of mutualistic model ecosystems [3, 4, 6], defined as the maximum perturbation compatible with coexistence. The analytical and numerical results of Ref. [3, 4] indicate that the structural stability so defined is strongly influenced by the fraction of shared mutualistic links, termed nestedness, which differ between real and random networks. On the contrary, Fig.2 of Ref. [1] shows that the volume of parameter space compatible with feasibility is almost the same for real and random networks. This is because the maximum perturbation depends on the most vulnerable species and it is different from the volume of parameter space compatible with feasibility. 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, 3, 4, 5], differ between random and real networks. 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 observation allows rationalizing many apparently contradictory findings on model mutualistic systems, including those of Ref. [4, 7, 8, 9, 10, 11, 12], and it also reconciles 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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