

# Alternative steady states in ecological networks

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In many natural situations one observes a local system with many competing species which is coupled by weak immigration to a regional species pool. The dynamics of such a system is dominated by its stable and uninvadable (SU) states. When the competition matrix is random, the number of SUs depends on the average value and variance of its entries. Here we consider the problem in the limit of weak competition and large variance. Using a yes/no interaction model, we show that the number of SUs corresponds to the number of maximum cliques in an Erdős-Rényi network. The number of SUs grows exponentially with the number of species in this limit, unless the network is completely asymmetric. In the asymmetric limit the number of SUs is  $\mathcal{O}(1)$ . Numerical simulations suggest that these results are valid for models with a continuous distribution of competition terms.

## I. INTRODUCTION

The richness of ecological communities poses a prolonged theoretical challenge. Focusing on guilds of many species competing for a common resource (and neglecting, for the moment, processes like predation or mutualism) the main problems are two. First, the competitive exclusion principle [1, 2] suggests that the result of competition for a single limiting resource is the extinction of all except the fittest species, and that in the presence of a few limiting resources the equilibrium number of species is smaller than or equal to the number of resources [3]. Second, even if the number of limiting resources is large, May [4] pointed out that if the niche overlap between species is substantial the chance of a system of  $N$  species to admit a stable equilibrium decreases exponentially with  $N$ . May's result is based on the spectral properties of random stability matrices. Practically, it implies that to achieve a stable coexistence of more than 6-8 species one has to fine-tune the competition parameters in an unrealistic manner.

However, in many situations the (inter- and intra-) specific dynamics takes place on local patches, which are coupled by migration to each other or to a regional pool. Accordingly, many ecological models are focused on the dynamics of a local patch, putting aside the global stability problem. A *mainland-island* model [5, 6] is the simplest scenario considered in this context: a set of local populations of different species compete with each other and the island is exposed to weak migration from a static pool of  $N$  species on the mainland. The structure of the community on the island reflects a balance between local extinctions and colonization by immigrants from the mainland. Extinctions may be either deterministic, due to the pressure that a species suffers from its competitors (or from the local environment), or stochastic, caused by the random nature of the birth-death process [7, 8] possibly superimposed on the effect of environmental variations [9, 10].

In a recent work [11], Kessler and Shnerb suggested a classification of the qualitative features of the community on the island. Four different “phases” were identified.

**I. Full coexistence:** If the interspecific competition

is weak (say, if different species use essentially different resources) any species in the mainland may invade the island and establish a finite population, so all  $N$  species are present on the island. Local extinctions still occur but if the local populations in steady state are large, these events are rare and transient. Technically speaking, the deterministic (i.e., noise-free) model allows for a stable fixed point with all the  $N$  species coexisting.

**II. Partial coexistence:** As the competition among species grows, the species' abundances decay as they feel more pressure from other species. Since the competition matrix is heterogenous, some species feel more pressure than others, and the deterministic model for sufficiently strong competition eventually allows for a stable fixed point for only a finite subset containing  $S$  of the  $N$  species. The other  $N - S$  species on the mainland cannot invade the island, i.e., their growth rate at low densities on the island is negative.

**III. Disordered:** When the competition increases even further, *and the competition matrix is not symmetric* (meaning that while species 1 puts a lot of pressure on some species 2, that species 2 puts less pressure on species 1), the system may not have an attractive fixed point at all or, even if it has one, its basin of attraction will be very narrow. In the presence of noise, the system fails to converge to an equilibrium state and instead it shows intermittent behavior with many long excursions that reflect high-dimensional chaotic/periodic trajectories.

**IV. Alternative steady states:** Finally, when the competition terms are large, there will be a number of different subsets of the  $N$  species which are both stable and uninvadable. For example, if the interspecific competition is extremely large and the island is colonized by a single species, all other mainland species cannot invade, so one needs to wait for a rare stochastic extinction in order to see species turnover. If the competition is not so strong, subsets of more than one species play the same role: species within the subset interact only weakly so they may

live happily together, but other species cannot invade.

The aim of this paper is to discuss this last phase, which is characterized by strong competition and alternative steady states. The immediate motivation for this discussion comes from a recent paper by Fisher and Mehta [12], who suggested that in this phase the dynamics of the island exhibits a glass transition: with weak noise/immigration the system is trapped for most of the time in one of the SUs, while when stochastic effects are strong it behaves like a “liquid” and its dynamics is closer to the disordered phase discussed above. In [12], a version of the symmetric competition model with strong interaction was mapped into a well-known physical model for glassy behavior, the random energy model [13].

Technically, the appearance of a glass transition in the random energy model is related to the exponential increase of the number of local minima with the system size (here, the number of mainland species,  $N$ ). When both the energy and the entropy increase linearly with the system size, a glass transition appears at finite temperature (level of noise). Therefore, it is natural to investigate the scaling of the number of SUs on an island with the number of species. In fact, this problem has been considered by ecologists for many years [14, 15].

Recently, we have studied this problem and derived a few exact results [16]. Using a version of the model we call the Binomial model, we have mapped the problem of counting SUs to that of finding the number of maximal cliques in a random network. We showed that in a particular parameter regime the number of SUs is *not* exponential; it goes like  $N^{\ln(N)}$  for symmetric networks, and like  $N/\ln^{3/2}(N)$  for (fully) asymmetric networks. The random network considered in [16] is “dense”: every pair of species interact with a fixed probability  $p$ , so the number of edges per node scales with the number of nodes (the Gilbert model of random graphs).

Here, we analyze the very same model in a different parameter regime, which includes the case where the competition is weak and the heterogeneity is strong (this is the case considered in [12] and [17], see discussion). The corresponding random graph in our yes/no model is described by an Erdős-Rényi model where the chance of every pair of species to compete scales like  $1/N$ , so every species has, on average, a fixed ( $N$  independent) number of enemies. We will show that in this regime the number of SUs indeed increases exponentially with  $N$ , if the system is not fully asymmetric. On the other hand, for the asymmetric system (see the definitions below) the number of SUs in this regime is of order one. We also show how to make a connection between this Erdős-Rényi regime and the results obtained for strong competition in [16], and provide some intuitive arguments.

This paper is organized as follows. In the next section we summarize the results of [16]; we present the generalized competitive Lotka-Volterra model (GCLV) and our simplified, Binomial model, and show how to map SUs to

maximal cliques, arriving at the formula of Bollobás and Erdős [18]. In the next three sections we present our main result, the number of SUs, as calculated from this formula, for the symmetric, the asymmetric and the mixed case. We also present numerical computations showing that the results of the Binomial model describe the qualitative behavior of the more realistic Gamma model. Finally we discuss the works of Refs. [12] and [17] and the relevance of the results presented herein and in these papers to realistic ecological networks.

## II. THE MODEL

To get oriented, we start with a system of two competing species without noise and immigration. The GCLV reads

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 - x_1(x_1 + \tilde{c}_{1,2}x_2) \\ \frac{dx_2}{dt} &= x_2 - x_2(x_2 + \tilde{c}_{2,1}x_1),\end{aligned}\tag{1}$$

where  $x_i$  is the abundance of each of the species. This system is characterized by the competition matrix

$$\begin{pmatrix} 0 & \tilde{c}_{1,2} \\ \tilde{c}_{2,1} & 0 \end{pmatrix}.$$

where the intraspecific density dependence (a decrease in the growth rate with abundance, manifested in the diagonal term) was taken to be one and is not part of the matrix. The stress put upon species 1 by species 2 is  $\tilde{c}_{1,2}$  and the stress put upon 2 by 1 is  $\tilde{c}_{2,1}$ .  $\rho \equiv \tilde{c}_{1,2} + \tilde{c}_{2,1}$  is a rough measure for the niche overlap, or total strength of competition in the system.  $\kappa \equiv \tilde{c}_{1,2} - \tilde{c}_{2,1}$  measures the heterogeneity of the competition matrix, i.e., it tells us how much the species differ from each other in their response to an increase in the density of a competitor. We consider a model as *symmetric* if  $\tilde{c}_{i,j} = \tilde{c}_{j,i}$  for any pair of species, and as *asymmetric* if there is no correlation between  $\tilde{c}_{i,j}$  and  $\tilde{c}_{j,i}$ .

A steady solution for (1) in which both  $x_1$  and  $x_2$  are non-negative is called a feasible solution (we cannot allow negative densities). If both densities are positive and the solution is stable, we called it a coexistence solution. Such a solution for (1) exists as long as  $\rho < 2 - |\kappa|$ , meaning that, for a given level of niche overlap  $\rho$ , the system becomes less stable as the heterogeneity grows. This basic logic holds also in more diverse systems.

For a system of many competing species the GCLV is:

$$\frac{dx_i}{dt} = x_i - x_i^2 - \sum_{j \neq i} \tilde{c}_{i,j} x_i x_j.\tag{2}$$

The mean of the terms of the competition matrix,

$$C \equiv \frac{1}{N(N-1)} \sum_{i,j} \tilde{c}_{i,j},$$

reflects the overall strength of the competition in the system. The variance of these entries,  $\tilde{\sigma}^2$ , is the simplest measure for its heterogeneity. To emphasize these properties we will factor out the average from the competition matrix, so the GCLV takes the form,

$$\frac{dx_i}{dt} = x_i - x_i \left( x_i + C \sum_{j \neq i}^N c_{i,j} x_j \right), \quad (3)$$

where  $\bar{c}_{i,j} = 1$ .

May's analysis [4] of the complexity-stability problem is based on the observation that a linear stability analysis of a feasible solution of (3) yields an  $N \times N$  random matrix with properties that are similar to those of the interaction matrix, including the intraspecific diagonal terms. For such a state to be stable all the eigenvalues of this matrix should be negative. However, a random matrix with  $(-1)$  on the diagonal and off diagonal terms with mean zero and variance  $C^2 \tilde{\sigma}^2$  has its eigenvalues between  $-1 + C\tilde{\sigma}\sqrt{N}$  and  $-1 - C\tilde{\sigma}\sqrt{N}$ , so a feasible solution for (3) is almost surely unstable when  $N$ , the number of species, is above  $N_c = 1/(C\tilde{\sigma})^2$ . The applicability of this argument to purely competitive systems requires some more discussion, since the main problem in these systems is to ensure feasibility [11, 19], but the main insight turns out to be valid here as well.

In this paper, as in [16], we are interested in the features of the system way above this ‘‘May limit’’, i.e., when  $N \gg N_c$  and the system supports alternative steady states. What we would like to know is how many stable and uninvadable (SU) subsets of the  $N$  species exist, i.e., how many  $\mathcal{S}$ -subsets of the  $N$  species satisfy the following two conditions:

1. *Stability and feasibility:* Eq. (3), when limited to a specific size  $S$  subset,  $\mathcal{S}$ , yields a time independent solution for which  $\bar{x}_i > 0$  for all of the species in  $\mathcal{S}$ , where  $\bar{x}_i$  is the equilibrium density of the  $i$ -th species in the subcommunity.
2. *Uninvadability:* Eq. (3), when applied to all absent  $N - S$  species and linearized around the fixed point  $x_i = \bar{x}_i$  for  $i \in \mathcal{S}$  and  $x_i = 0$  for  $i \notin \mathcal{S}$ , yields negative growth rates  $\dot{x}_i/x_i$  for all  $i \notin \mathcal{S}$ .

We are interested in the SU enumeration problem for a random matrix, so we would like to draw the  $c_{i,j}$ s from a uniform, positive semi-definite, distribution with a mean one and a given variance [11, 12]. For our numerics we have used the Gamma distribution for this purpose, and denote this as the Gamma model. A  $c_{i,j}$  matrix (for simplicity the examples are given for the symmetric case) may look like,

$$\begin{pmatrix} 0 & 0.95 & 1.63 & 0.96 \\ 0.95 & 0 & 0.48 & 0.97 \\ 1.63 & 0.48 & 0 & 1.12 \\ 0.96 & 0.97 & 1.12 & 0 \end{pmatrix}.$$

To map this problem to the maximum clique problem, we treat an alternative model, the Binomial (yes/no) model, where all the elements of the  $c_{i,j}$  matrix (in the asymmetric case; the pair  $c_{i,j} = c_{j,i}$  in the symmetric case) either are strictly zero (with probability  $p$ ) or (with probability  $1 - p$ ) are equal to a finite constant  $C \cdot A$ , so the interaction matrix  $\tilde{c}_{i,j}$  takes the form, say,

$$C \begin{pmatrix} 0 & A & 0 & A \\ A & 0 & 0 & A \\ 0 & 0 & 0 & 0 \\ A & A & 0 & 0 \end{pmatrix}.$$

The Gamma and the Binomial model have the same competition strength,  $C$ , if

$$A = \frac{1}{1 - p}. \quad (4)$$

The variance of the matrix elements of the Binomial model is given by,

$$\tilde{\sigma}^2 = C^2 \frac{p}{1 - p}. \quad (5)$$

For the symmetric model, if  $C$  is large enough, each pair of species  $i$  and  $j$  is either non-interfering,  $\tilde{c}_{j,i} = \tilde{c}_{i,j} = 0$ , or mutually exclusive. Accordingly, as explained in [16], the SU problem has a geometrical interpretation. For a graph in which each node represent a species and each pair of non-interfering species is connected by an edge, a stable state corresponds to a subset  $\mathcal{S}$  of nodes such that the induced subgraph is complete. For this stable state to be uninvadable any vertex that is not a part of the clique is required to have at least one mutually exclusive species in the clique, i.e., that the clique is maximal such that it cannot be extended by including any other connected vertex. Accordingly, for large enough  $C$  the number of SUs is equal to the number of maximal cliques of the corresponding graph.

In [16] we showed that, as long as  $p$  is  $\mathcal{O}(1)$ , the growth of the number of maximal cliques,  $SU(N)$  with  $N$  is *not* exponential, and in fact for a symmetric system it grows as

$$SU(N) \sim N^{\zeta(p) \ln(N)}, \quad (6)$$

where  $\zeta(p) = 1/[2 \ln(1/p)]$ . Clearly, the expression (6) must fail when the value of  $p$  is close to one, since  $p \rightarrow 1$  implies  $\ln(1/p) \rightarrow 0$  and  $SU(N) \rightarrow \infty$ . On the other hand when  $p = 1$  we reach an extreme stabilization and the system has only one stable uninvadable state,  $SU(N) = 1$ . In order to clarify the behavior of the system in this limit, in the next three sections we will find a formula for  $SU(N)$  in the limit  $N \rightarrow \infty$ , where  $p = 1 - \alpha/N$  and  $\alpha = \mathcal{O}(1)$ . In this limit the number of ‘‘enemies’’ for every species is  $N$  independent, so the corresponding graph is of Erdős-Rényi type.

As in [16], the study presented here is limited to values of  $C$  such that only sets of noninteracting species may live

together on the island. However, the critical value of  $C$ , above which the clique picture is valid, was found in [16] to be  $1 - p = \alpha/N$ . Therefore, the results below are relevant for any finite positive value of  $C$  as  $N$  goes to infinity.

### III. THE SYMMETRIC CASE

In this section we consider the symmetric version of the binomial model. Every pair of species is noninterfering ( $c_{i,j} = c_{j,i} = 0$ ) with probability  $p$  and have symmetric competition ( $c_{i,j} = c_{j,i} = A$ ) with probability  $1 - p$ . We assume that  $C$  is large such that no pair of competing species is allowed on the island (if they are interacting, then they are mutually exclusive), and a species cannot invade the island in the presence of one of its competitors. Accordingly, each maximal clique of the network is a stable and uninvadable state.

To get the basic intuition for the results we derive in this section, let us consider the case  $p = 1$ , i.e., all species are noninteracting. Clearly, in this case there is only one maximal clique - the one with all the  $N$  species.

Now let us break the link between, say, species 1 and 2, so  $c_{1,2} = c_{2,1} = A$ . The number of maximal cliques is now two: species 1 and all the species 3.. $N$  and the set

2.. $N$ . Breaking the next link (without loss of generality, between 3 and 4) doubles the number of maximal cliques and so on. Hence, the number of maximal cliques grows exponentially as  $p$  decreases, until we start to break more than one link per node. Since there are  $\mathcal{O}(N^2)$  links in the system, this will happen when the number of broken links is  $\mathcal{O}(N)$ . Accordingly, one expects that, when the deviation of  $p$  from one is  $\mathcal{O}(1/N)$ , the number of SUs will be exponentially large in  $N$ .

Bollobás & Erdős [18] showed that the number of maximal cliques of size  $S$  in a random graph of  $N$  nodes is given by

$$SU(N, S) = \binom{N}{S} p^{S(S-1)/2} (1 - p^S)^{N-S}. \quad (7)$$

In [16], we performed the sum over  $S$ , giving the behavior of  $SU(N)$ , Eq. (6), when  $p$  is not too close to unity.

Now let us find the leading asymptotic behavior of the sum (7) when  $1 - p$  is small, of order  $\mathcal{O}(1/N)$ . More precisely, we define

$$p \equiv 1 - \frac{\alpha}{N}, \quad S \equiv N\beta, \quad (8)$$

where  $\alpha$  and  $\beta$  are both  $\mathcal{O}(1)$ . With these definitions, (7) reads

$$SU(N, \beta) = \binom{N}{N\beta} \left(1 - \frac{\alpha}{N}\right)^{N\beta(N\beta-1)/2} \left(1 - \left(1 - \frac{\alpha}{N}\right)^{N\beta}\right)^{N-N\beta}. \quad (9)$$

In the large  $N$  limit, the expression (9) may be written as,

$$SU(N, \beta) \approx \binom{N}{N\beta} e^{-N\alpha\beta^2/2} e^{N(1-\beta)\ln(1-e^{-\alpha\beta})} \quad (10)$$

For  $\beta \sim \mathcal{O}(1)$ , both  $N\beta$  and  $N(1-\beta)$  are large. Hence we can approximate the combinatorial factor using Stirling's formula, giving

$$\binom{N}{N\beta} \approx \frac{e^{-N[(1-\beta)\ln(1-\beta) - \beta\ln(\beta)]}}{\sqrt{2\pi N\beta(1-\beta)}}. \quad (11)$$

Accordingly,

$$SU(N, \beta) \approx \frac{e^{NF(\beta)}}{\sqrt{2\pi N\beta(1-\beta)}}, \quad (12)$$

where

$$F(\beta) = -(1-\beta)\ln(1-\beta) - \beta\ln(\beta) - \frac{\alpha\beta^2}{2} + (1-\beta)\ln(1-e^{-\alpha\beta}). \quad (13)$$

The total number of SUs is the sum over  $S$  of  $SU(N, S)$ , which translates to an integral over  $\beta$  of (12). This integral may be approximated via Laplace's method, as  $F(\beta)$  has a maximum in the range  $0 < \beta < 1$ . We denote the location of this maximum by  $\beta_0$ , which depends on  $\alpha$  and satisfies

$$F'(\beta_0) = -\alpha\beta_0 + \frac{\alpha(1-\beta_0)}{e^{\alpha\beta_0} - 1} + \ln(1-\beta_0) - \ln(\beta_0) - \ln(1-e^{-\alpha\beta_0}) = 0. \quad (14)$$

The graph of  $\beta_0(\alpha)$  is depicted in Fig. 1. Then, the total number of SUs,  $SU(N)$ , is given to leading order by

$$SU(N) \equiv N \int_0^1 SU(N, \beta) d\beta = \frac{e^{NF(\beta_0)}}{N\sqrt{|F''(\beta_0)|}\beta_0(1-\beta_0)}, \quad (15)$$

so that indeed the number of SUs increases exponentially with  $N$  in this parameter range.

Here we focus only on the controlling factor,  $F(\beta_0)$ . For general  $\alpha$ , this needs to be computed numerically, with the results shown in Fig. 2. We see that  $F(\beta_0)$  rises from 0 at  $\alpha = 0$ , reaches a maximum and then decreases

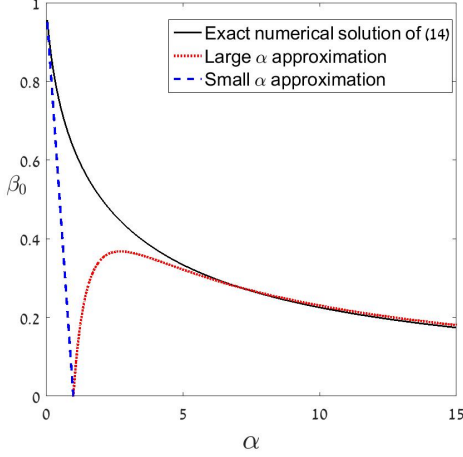


FIG. 1. Solutions for Eq. (14). The full, black line is the exact numerical solution, the dashed blue is  $1 - \alpha$  and the dotted red line depicts  $\ln(\alpha)/\alpha$ .

slowly for large  $\alpha$ . The behavior at large and small  $\alpha$  is accessible to analysis. For small  $\alpha$ , we see from Fig. 1 that  $\beta_0$  is close to unity and thus to leading order in  $\alpha$ ,  $1 - \beta$  we have

$$F'(\beta_0) \approx \ln(1 - \beta_0) - \ln \alpha \quad (16)$$

so that  $\beta \approx 1 - \alpha$  and  $F(\beta_0) \approx \alpha/2$ . For large  $\alpha$ , since  $\beta_0$  is small but  $\alpha\beta_0$  is large, the dominant balance of terms is

$$-\alpha\beta_0 + \frac{\alpha}{e^{\alpha\beta_0} - 1} \approx \ln(\beta_0). \quad (17)$$

We can exactly solve this equation using an auxiliary variable  $r$ ,  $\alpha \equiv r^r \ln r$ , in terms of which  $\beta_0 = r^{1-r}$ , as can be directly verified by substituting into the equation. This implicit approximate solution is correct to order  $1/\alpha^2$  for large  $\alpha$ . If we try to produce an explicit solution from this, we run into correction terms like  $\log(\log(\alpha))$  and the convergence is super-slow. Nevertheless, a simple rough approximation is

$$\beta_0 \approx \frac{\ln \alpha}{\alpha}, \quad (18)$$

up to corrections of  $\ln(\ln r)/\alpha$ , which is correct to better than 6% for  $\alpha > 10$ . We can now approximate  $F(\beta_0)$  for large  $\alpha$ , where the  $\alpha\beta_0^2/2$  term is dominant, and so

$$F(\beta_0) \approx \frac{r^{2-r} \ln r}{2} \approx \frac{\ln^2 \alpha}{2\alpha} \quad (19)$$

Our result connects directly with our previous result, Eq. (6), when  $\alpha$  is  $\mathcal{O}(N)$  and  $1 - p$  is  $\mathcal{O}(1)$ . Remember the relation between  $p$  and  $\alpha$ , as  $\alpha$  becomes large,  $p$  moves away from the region close to unity, and so

$$\ln SU(N) \approx \frac{\ln^2 N(1-p)}{2(1-p)} \approx \frac{\ln^2 N}{2 \ln(1/p)} \quad (20)$$

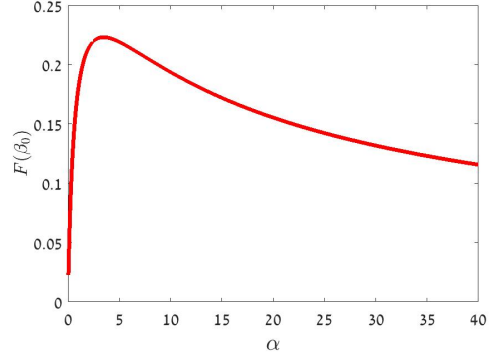


FIG. 2.  $F(\beta_0(\alpha))$ , or  $\ln(SU)/N$ , vs.  $\alpha$  for  $0 < \alpha < 40$ . The number of SUs grows exponentially with  $N$ , where the coefficient of the exponent is between 0 and 0.25.

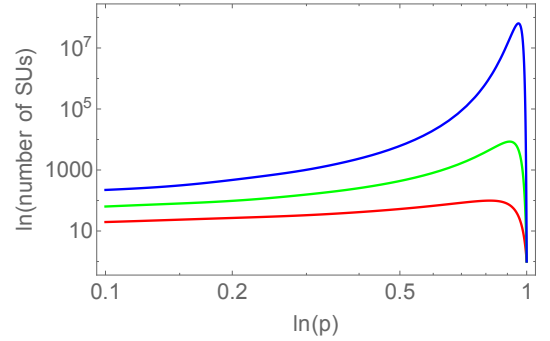


FIG. 3.  $\ln(SU)$  vs.  $\ln(p)$ , as obtained from a numerical summation of the Bollobás-Erdős formula for the symmetric case, for  $N = 20$  (red)  $N = 40$  (green) and  $N = 80$  (blue). The growth of the number of SUs with  $N$  becomes exponential when  $1 - p$  is  $\mathcal{O}(1/N)$ , as expected. When  $1 - p$  is  $\mathcal{O}(1/N^2)$ , there is a drop towards one SU with all the  $N$  species. In this regime the number of SUs is independent of  $N$ .

as expected.

In the opposite limit, when  $\alpha$  is very small, say,  $\alpha = \gamma/N$  (so  $p = 1 - \gamma/N^2$ ),  $\beta_0 = 1 - \alpha$ , and the exponential term of (15),  $\exp(\gamma/2)$ , is unity at  $\gamma = 0$  and grows exponentially with  $\gamma$ , as discussed above.

These three regimes are depicted in Figure 3. As opposed to the case where  $1 - p$  is  $\mathcal{O}(1)$  (or  $\alpha$  is  $\mathcal{O}(N)$ ) considered in [16], where the growth is of  $N^{\ln N}$  type, when  $\alpha$  is  $\mathcal{O}(1)$  the growth is exponential while if  $\alpha$  is  $\mathcal{O}(1/N)$  the number of SUs is close to one. In figure 4 we show that the same qualitative behavior is observed in the corresponding symmetric Gamma model [16].

#### IV. THE ASYMMETRIC NETWORK

Unlike the symmetric case where  $c_{i,j} = c_{j,i}$ , in an asymmetric system  $c_{i,j}$  and  $c_{j,i}$  are drawn independently from a given distribution. In this section we consider the Binomial model in this case.

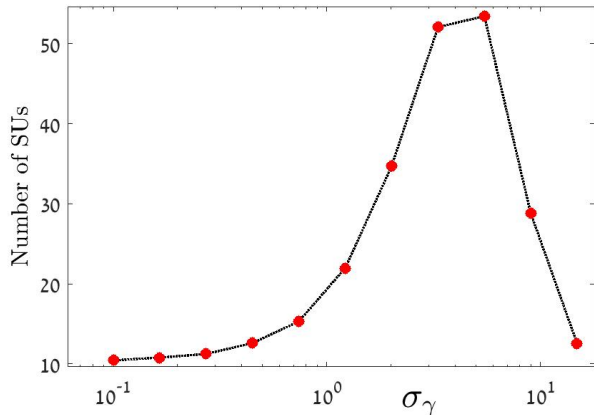


FIG. 4. Number of SUs (averaged over 500 samples) vs.  $\sigma_\gamma$  as obtained from an exact enumeration of all the stable and uninvadable combinations of species in the Gamma model for  $N = 20$ . Red points are actual results, each obtained from examination for stability and uninvadability of all the  $2^{20}$  combinations of species, the dashed line is just to guide the eye. The Gamma model is described by Eq. (3) with  $C = 1$  and where each pair of numbers  $c_{i,j} = c_{j,i}$  is picked independently from a Gamma distribution with mean one and standard deviation  $\sigma_\gamma$ . While the number of SUs is smaller than their number in the corresponding Binomial model (we have suggested in [16] that the Binomial model yields an upper bound for the Gamma) we still observe the growth in the number of SUs when  $\sigma_\gamma \sim \sqrt{N}$  (around 4-5), then it drops towards the full coexistence phase.

The strong competition phase of the asymmetric Binomial interaction model allows for *three* types of relationships between species  $i$  and  $j$ . As in the symmetric case, it may happen that  $c_{i,j} = c_{j,i} = 0$ , so the species are non-interfering, and  $c_{i,j} = c_{j,i} = A$ , meaning that for large enough  $A$  the two species are mutually exclusive. The asymmetry allows for a third, *dominance*, relationship at large  $A$ : if  $c_{i,j} = A$ ,  $c_{j,i} = 0$ , species  $i$  may invade  $j$  but the opposite process is forbidden. Accordingly,  $j$  may be a member of a maximal clique only if another species in this clique is uninvadable by  $i$ .

In the asymmetric Binomial model, we define  $\tilde{p}$  to be the chance that a **single entry** of the interaction matrix is zero. The heuristic argument presented at the beginning of the last section yields a completely different answer in this case. Starting from  $\tilde{p} = 1$  and breaking one link (say, between 1 and 2), implies that 1 can invade 2 but 2 cannot invade 1, so the number of maximum cliques remains one. This will be the case until we hit both links between two specific species, and again this will happen only when  $1 - \tilde{p}$  is  $\mathcal{O}(N)$ . Accordingly, at the asymmetric case we expect that the number of SUs for  $p$  close to one will be  $\mathcal{O}(1)$ .

By extending this argument, one can develop some intuition for the generic case which is neither symmetric nor asymmetric. In general one may expect that the

stress species 1 suffers from 2 is not exactly the same as the stress species 2 suffers from 1, but that they are related to each other. For example, if there is some niche overlap between species 1 and 2, but the niche of 1 is wider than the niche of 2, one expects  $c_{1,2} < c_{2,1}$ , but their values are correlated.

Naively, one may guess that symmetry is a “fragile” property, so any deviation from perfect symmetry will send the system to the equivalence class of the asymmetric model. However, our above argument indicates that the opposite is true. As long as the system allows for a finite fraction of symmetric links, the breaking of each of them doubles the number of maximal cliques when the system is very close to its complete graph limit. Accordingly, as long as there is *some* symmetry in the problem ( $c_{i,j}$  is positively correlated with  $c_{j,i}$ ) one should expect an exponentially large number of SUs when  $\alpha$  is  $\mathcal{O}(1)$ , although the coefficient of  $N$  in the exponent falls along with the degree of correlation. As we shall see below (see next section), the result in the purely asymmetric case reflects a “miraculous” cancelation of terms, so the properties of the purely asymmetric case are those who turn out to be fragile.

In Ref. [16], we extended the Bollobás-Erdős formula to the asymmetric case, showing that the number of SUs satisfies,

$$SU(N, S) = \binom{N}{S} \tilde{p}^{S(S-1)} (1 - \tilde{p}^S)^{N-S}. \quad (21)$$

Interestingly, the only difference between (21) and (7) is the factor of 2 in the second term, reflecting the fact that for a collection of  $S$  species to be noninterfering one needs all the  $S(S-1)/2$   $c_{i,j}$ s to be zero in the symmetric case, while in the asymmetric case  $c_{i,j}$  and  $c_{j,i}$  are picked at random so the number of independent links is doubled. As we shall see, this innocent looking modification has highly nontrivial consequences.

Implementing the method used for the symmetric case, one finds,

$$SU(N, S) = \frac{e^{NF_{as}(\beta)}}{\sqrt{2\pi N}}, \quad (22)$$

where,

$$F_{as}(\beta) = -(1 - \beta) \ln(1 - \beta) - \beta \ln(\beta) - \alpha \beta^2 + (1 - \beta) \ln(1 - e^{-\alpha \beta}). \quad (23)$$

As before, this pair of formulas appear to suggest that, as long as both  $\alpha$  and  $\beta$  are  $\mathcal{O}(1)$ , the number of SUs is exponential in  $N$ . However, we shall see that in this case  $F_{as}(\beta_0) = 0$  and the actual large- $N$  asymptotic turns out to be non-exponential.

The equation for  $\beta_0$  now reads

$$F'_{as}(\beta_0) = -2\alpha\beta_0 - \frac{\alpha(-1 + \beta_0)}{-1 + e^{\alpha\beta_0}} + \ln(1 - \beta_0) - \ln(\beta_0) - \ln(1 - e^{-\alpha\beta_0}) = 0. \quad (24)$$

Surprisingly, one can find an *exact* solution to this equation,

$$\beta_0 = \frac{W(\alpha)}{\alpha}, \quad (25)$$

where  $W$  is the Lambert  $W$  function, defined by  $W(x)\exp[W(x)] = x$ . Plugging this into  $F$ , we find that  $F_{as}(\beta_0)$  *vanishes identically*. This implies that the first contribution from the Laplace integral is  $\mathcal{O}(1)$  (instead of being exponential in  $N$ ) so we should repeat the exercise from its starting point, keeping all the  $\mathcal{O}(1)$  terms (omitting only  $\mathcal{O}(1/N)$  and other small terms).  $F_{as}$  in the controlling factor of (22) then takes the form,

$$F_{as} = -(1 - \beta + \frac{1}{2N}) \ln(1 - \beta) - (\beta + \frac{1}{2N}) \ln(\beta) - \alpha\beta^2 + \frac{\alpha\beta}{N} - \frac{\alpha^2\beta^2}{2N} + (1 - \beta) \ln(1 - e^{-\alpha\beta - \frac{\beta\alpha^2}{2N}}). \quad (26)$$

To continue, let us write  $F_{as}$  as,

$$F_{as} = F_{as}^{(0)} + \frac{F_{as}^{(1)}}{N} \quad (27)$$

where  $F_{as}^{(0)}$  is given in (23) and

$$F_{as}^{(1)} = \frac{\alpha^2\beta^2}{2} + \frac{\alpha^2\beta^2}{2(e^{\alpha\beta} - 1)} - \frac{\alpha^2\beta}{2(e^{\alpha\beta} - 1)} - \alpha\beta + \frac{1}{2} \log(1 - \beta) + \frac{\log(\beta)}{2}. \quad (28)$$

Evidently, the main contribution in the large  $N$  limit still comes from  $\beta_0$  given in (25) and,

$$e^{F_{as}^{(1)}(\beta_0)} = \frac{1}{2} \left( \log \left( 1 - \frac{W(\alpha)}{\alpha} \right) - 3W(\alpha) \right), \quad (29)$$

meaning that there is no exponential growth of the number of maximal cliques with  $N$ .

Now we can implement the Laplace integral scheme to (22) (the sum over  $S$  is converted to an integral over  $Nd\beta$ ) to obtain,

$$SU(N) = N \int_0^1 d\beta \frac{e^{NF_{as}(\beta)}}{\sqrt{2\pi N}} = \frac{N}{\sqrt{2\pi}} e^{F_{as}^{(1)}(\beta_0)} \int_{-\infty}^{\infty} e^{-N|(F_{as}^{(0)})''|_{\beta_0}(\beta - \beta_0)^2} = \frac{e^{F_{as}^{(1)}(\beta_0)}}{\sqrt{2|(F_{as}^{(0)})''|}}, \quad (30)$$

so

$$SU(N) = \frac{\alpha}{W(\alpha) + W^2(\alpha)} \quad (31)$$

In the limit where  $\alpha$  is  $\mathcal{O}(N)$  considered in [16] the width of the Gaussian in the integration of (30) is  $1/N$ , meaning that only a single large term in the sum of  $SU(N, S)$  over  $S$  contributes (see Fig. 5). In such a case there is no contribution from the integration around the maximum, and the number of cliques is

$$SU(N) \sim \frac{e^{F_{as}^{(1)}(\beta_0)}}{\sqrt{2\pi N}} \sim \frac{N}{\ln^{3/2}(N)} \quad (32)$$

as shown in [16].

The behavior of the number of SUs in different regimes of the Binomial model is depicted in Figure 5, and the results of the corresponding Gamma model are shown in Figure 6.

## V. A GENERIC NETWORK: MIXED CASE

In this section we consider the generic scenario that interpolates between the fully symmetric and the fully

asymmetric one. To do that, we use the “four corner” distribution used in the supplementary information section of [20]. The yes/no interaction matrix is generated using the following procedure: For each pair  $\{i, j\}$  with  $i < j$ ,  $c_{i,j}$  is picked first and takes the value zero with probability  $p$  and the value one with probability  $1 - p$ . Then, with probability  $1 - \eta$ ,  $c_{j,i}$  is set to be equal to  $c_{i,j}$  and with probability  $\eta$ ,  $c_{j,i}$  is chosen at random (again it is zero with probability  $p$  and otherwise unity). Therefore,  $\eta$  sets the amount of symmetry in the problem,  $\eta = 0$  is the fully symmetric case and  $\eta = 1$  is the fully asymmetric case. In the asymmetric case,  $p$  has the same meaning as  $\tilde{p}$  of the last section. The chance that a given pair of species is noninteracting is  $p_{00} = p - \eta p + \eta p^2$ , and it reduces to  $p$  in the symmetric case and to  $p^2$  in the asymmetric one.

Since we did not consider the general model in [16], we have added here an appendix in which the results for  $1 - p$  of  $\mathcal{O}(1)$  are considered. In what follows we discuss the case of interest here, i.e., where  $1 - p$  scales like  $1/N$ .

The general formula for the number of maximal cliques is now

$$SU(N, S) = \binom{N}{S} p_{00}^{S(S-1)/2} (1 - p^S)^{N-S}, \quad (33)$$

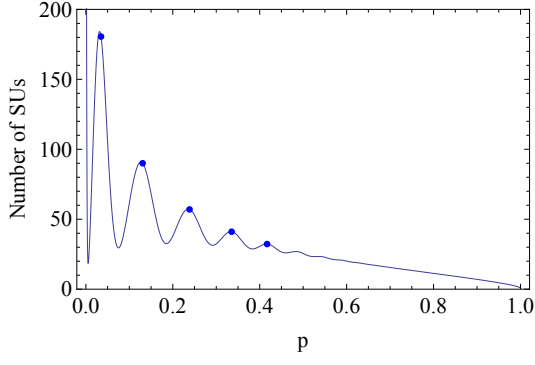


FIG. 5.  $\ln(SU)$  vs.  $p$ , as obtained from a numerical summation of the Bollobás-Erdős formula for the asymmetric case, for  $N = 1000$ . In general the number of SUs decays with  $p$ , with no exponential peak close to the fully connected limit. This general trend is superimposed on oscillations in the region where  $p$  is  $\mathcal{O}(1)$ , since in this regime there is only one integer value of maximal clique sizes that dominate the sum, as explained in the text. To demonstrate that, thick points were added to mark the  $p$  values for which  $S = \beta_0 N$  is 2, 3, 4, 5 and 6.

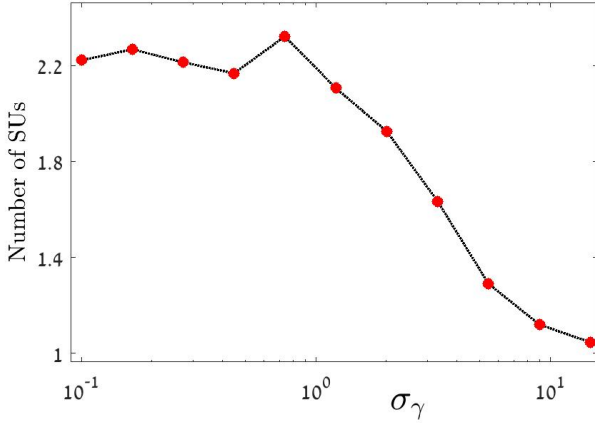


FIG. 6. Number of SUs (averaged over 500 samples) vs.  $\sigma_\gamma$  as obtained from an exact enumeration of all the stable and uninvadable combinations of species in the asymmetric Gamma model for  $N = 20$ . Red points are actual results, each obtained from examination for stability and uninvasability of all the  $2^{20}$  combinations of species, the dashed black line is just to guide the eye. The asymmetric Gamma model is described by Eq. (3) with  $C = 1$  and where each  $c_{i,j}$  is picked independently from a Gamma distribution with mean one and standard deviation  $\sigma_\gamma$ .

since it requires no interaction between all  $S(S-1)/2$  pairs inside the clique and having at least one enemy within the clique for all the  $N-S$  species on the mainland.

For  $p$  near 1, the relevant quantities take the form,

$$p = 1 - \alpha/N; \quad p_{00} = 1 - \alpha_0/N; \quad \beta = S/N \quad (34)$$

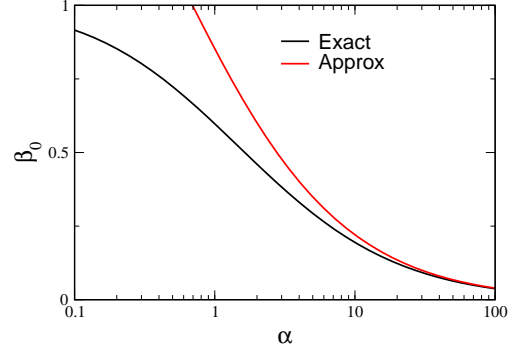


FIG. 7. The scaled most common clique size,  $\beta_0$ , as a function of  $\alpha$  (the scaled value of  $p$ ), for  $\eta = 0.5$ .

where  $\alpha_0 = \alpha(1 + \eta)$ .

Then (in parallel with the discussion that leads to (13) above)  $\ln SU(N, S) \approx NF(\alpha, \beta)$  where

$$F(\alpha, \beta) = -\beta \ln(\beta) - (1-\beta) \ln(1-\beta) - \frac{\beta^2 \alpha_0}{2} + (1-\beta) \ln(1-e^{-\alpha\beta}). \quad (35)$$

The equation for the maximum,  $\beta_0$  is

$$-\ln(\beta_0) + \ln(1-\beta_0) - \alpha_0 \beta_0 + \frac{\alpha(1-\beta_0)}{e^{\alpha\beta_0} - 1} - \ln(1-e^{-\alpha\beta_0}) = 0. \quad (36)$$

The small  $\alpha$  behavior is as before,  $\beta_0 \approx 1 - \alpha$ , independent of  $\eta$ . For large  $\alpha$ ,  $\beta_0 \ll 1$ ,  $\alpha\beta_0 \gg 1$ , we can rewrite the approximate equation in a way that emphasizes the quantity  $\alpha_0 - \alpha$ , that vanishes in the symmetric limit  $\eta = 0$  but is finite otherwise,

$$\begin{aligned} & -\ln(\beta_0) - \alpha_0 \beta_0 + \alpha e^{-\alpha\beta_0} \\ & = \ln(\alpha e^{-\alpha\beta_0}) - (\alpha_0 - \alpha)\beta_0 - \ln(\alpha\beta_0) + \alpha e^{-\alpha\beta_0} = 0. \end{aligned} \quad (37)$$

The first term is negligible, so we have the approximate equation

$$(\alpha - \alpha_0)\beta_0 - \ln(\alpha\beta_0) + \alpha e^{-\alpha\beta_0} = 0 \quad (38)$$

If  $\alpha \neq \alpha_0$ , the  $\ln(\alpha\beta_0)$  term is also negligible and we get

$$\beta_0 = \frac{1}{\alpha} W\left(\frac{\alpha}{\eta}\right) \quad (39)$$

Figure 7 demonstrates the quality of this approximation, by comparing the exact value of  $\beta_0$  with the prediction of (39). One observes that the approximation becomes very good as  $N$  increases.

Although the derivation of (39) from (38) is incorrect in the fully symmetric limit  $\alpha_0 = \alpha$ , the result for  $\beta_0$  is very similar to the form (18), and in fact yields very similar numbers for  $\alpha > 20$ . This suggests that our treatment, although conditioned on  $\alpha_0 \neq \alpha$ , is in fact valid at any



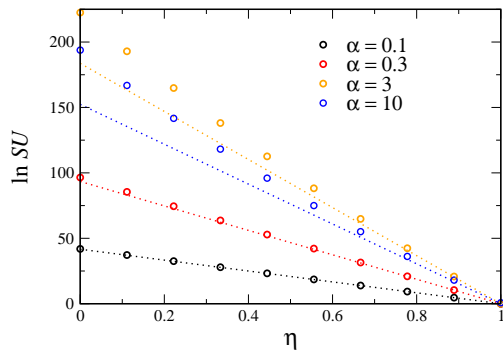


FIG. 8. The natural logarithm of the number of SUs as a function of  $\eta$ , for various  $\alpha$ , with  $N = 1000$ . The linear approximation (40) (dashed lines) is valid close to  $\eta = 1$  for large  $\alpha$ s, but over almost all the region for small  $\alpha$ s.

finite vicinity of the symmetric point, in agreement with the results presented in the following.

Close to the *asymmetric* point, i.e., when  $\eta$  is close to one, we can plug the result for  $\beta_0$  into the expression for the overall number of SUs to obtain,

$$\ln SU(N, S_0, \eta) \approx N(1 - \eta) \frac{W^2(\alpha)}{2\alpha}. \quad (40)$$

This implies that, as long as  $\eta \neq 1$ , the number of maximal cliques grows exponentially in  $N$ , and that the slope of this exponent vanishes linearly close to the fully asymmetric point. The slope increases with  $\alpha$  for small  $\alpha$ , reaches a maximum of  $0.37N$  at  $\alpha \approx 2.7$ .

In Figure 8 the behavior of this slope (for fixed  $N$ ) is shown, as a function of  $\eta$ , for a few values of  $\alpha$ . It turns out that the linear behavior for small values of  $\alpha$  extends almost over all the region between  $\eta = 0$  and  $\eta = 1$ , and even for large values of  $\alpha$  the deviation is not large (of course the actual number of cliques, which is the exponential of these numbers, is more sensitive to these corrections).

Interestingly, the same qualitative behavior - a decrease in the number of point attractors as the level of symmetry decreases - was observed numerically for a neural network model with varying levels of asymmetry of synapse connections [21] (see also [22] for application of the same technique to ecological systems). In neural networks the number of different point attractors determines the memory capacity of the system. An understanding of the relationships between our yes/no model and more complicated models of neural dynamics may, perhaps, help in understanding the factors that govern this important feature.

Most importantly, we have shown here that the number of SUs grows exponentially with  $N$  everywhere except at the fully asymmetric point  $\eta = 1$ , as suggested by the

heuristic argument at the beginning of section IV.

## VI. DISCUSSION

In this paper we have studied the number of stable and uninvadable states in an ecological network. We assumed a local community which is coupled to a regional species pool. In the local community the particular level of competition between any given pair of species was drawn at random.

Many empirical ecological networks (in particular food webs [23] and networks with mutualistic interactions [24]) were shown to admit a nontrivial structure (such as modularity or nestedness) so their description as completely random networks is problematic. Still, we believe that the analysis presented here is relevant to various aspects of the general problem. First, there are less evidence, as far as we know, for a general structure in systems of competing species (see, e.g., [25]). Second, even if the mainland interactions are structured, there is no a priori reason to assume that this is the case on the island. A third point (which is complementary to the second) is that, when the interactions are inferred from empirical studies of local communities, one would like to understand what aspects of these interactions are the result of the restriction of a regional system with a (possibly) different structure to its SUs.

The symmetric model considered here is characterized by three parameters: the number of species in the regional pool  $N$ , the mean value of the off-diagonal entries of the competition matrix  $C$  and the parameter that reflects the heterogeneity of the competition terms,  $\tilde{\sigma}^2$ . In the Binomial model (see Eq. 5 above)  $\tilde{\sigma}^2 = C^2 p / (1 - p)$ , so in the limit when  $p = 1 - \alpha/N$ ,

$$\tilde{\sigma}^2 \sim \frac{C^2 N}{\alpha}.$$

In the works of Mehta and Fisher [12] and Bunin [17] the average value of an (off diagonal) interaction matrix term and the variance of these terms both are taken to be of order  $1/N$ . This parameter regime is right on the border of the regime defined by May's stability criteria mentioned above. Translating this to the notations of our paper, one has  $C \sim \mu/N$ , say (when  $\mu$  is  $\mathcal{O}(1)$ ), hence  $\tilde{\sigma}^2 = \mu^2 / N\alpha$ . Thus, the regime of parameters covered by the  $p = 1 - \alpha/N$  limit of the Binomial model (with  $\alpha$  order one) includes the regime considered in [12, 17] as a special case.

The main outcome of the analysis presented here and in [16] is that the number of SUs grows exponentially with  $N$  if  $\alpha$  is  $\mathcal{O}(1)$ , and the matrix is not purely asymmetric. If  $p$  is order one, or in the case of an asymmetric competition terms, the growth is subexponential, ranging from  $N^{\ln(N)}$  dependency to sublinear growth. This implies that, as long as an exponential number of SUs is required for a glass transition (as suggested by the analogy with the random energy model presented in [12]),

such a transition occurs only in the regime of very weak competition and very large systems.

When ecologists consider high-diversity assemblages and try to understand the forces that shape their structure, they usually have in mind systems such as tropical trees [26], coral reef [27] or plankton [28]. In these cases, the level of niche overlap between species is evidently quite high, as all these species use the same set of a few key resources, more or less in the same manner. Accordingly, one should expect these systems to be in the regime where the interaction terms of the competition matrix are  $\mathcal{O}(1)$  (see, e.g. the recent study [29]), where the number of species in an SU scales logarithmically with  $N$  [16], the number of SUs is subexponential, and there is no glass transition.

To the best of our understanding, the parameter regime considered in [12, 17] and here corresponds to a completely different scenario. This is the case of a community with many species but with strong niche partitioning (say, many bird species with different beak size, eating different kinds of food) that still have weak competition between species (due to some overlap in the type of food they are eating, weak nest site competition or due to predation by a common predator). Most ecologists feel that the coexistence of many different species in such a scenario needs no explanation (since the main issue they consider is the competitive exclusion principle) but in fact there is still a theoretical problem, namely

May's complexity-diversity relationship, meaning that even a community with very weak interactions will collapse when the number of species is large. Here we have shown that in this case one should expect to see a local community with  $\mathcal{O}(N)$  species ( $\beta_0$  is order one), and possibly some kind of a glass transition. The relevance of this theoretical framework to empirical systems appears to be an open problem.

### Appendix: The general symmetry model in the non-exponential regime

For the sake of completeness, we consider here the general symmetry case, as defined in section V above, for the case where  $1 - p$  is  $\mathcal{O}(1)$ . The symmetric and the asymmetric limits of the model were presented and solved in [16], here we consider the model with general symmetry. As defined above (section V), the parameter that controls the symmetry properties is  $\eta$ , where  $\eta = 0$  is the symmetric case and  $\eta = 1$  the asymmetric one.

The formula for the number of maximal cliques was presented above (Eq. 33),

$$SU(N, S) = \binom{N}{S} p_{00}^{S(S-1)/2} (1 - p^S)^{N-S}, \quad (\text{A.1})$$

and for large  $N$ , general  $p$ ,  $1 \ll S \ll N$  we can write,

$$\ln SU(N, S) \approx S \ln N - (S + 1/2) \ln S - \frac{S^2}{2} \ln(1/p_{00}) - (N - S)e^{-S \ln(1/p)}. \quad (\text{A.2})$$

Unlike our treatment in section V, here we assume that  $p$  is not too close to unity, so we define two new quantities,  $\hat{\alpha} = \ln(1/p)$  and  $\hat{\alpha}_0 = \ln(1/p_{00})$  (both these constants are independent of the system size, i.e., they do not scale with  $N$ , in contrast with  $\alpha$  and  $\alpha_0$  in the main parts of this paper). Taking the derivative of  $\ln SU(N, S)$  with respect to  $S$ , we get the equation for  $S_0$ , which is the most likely number of species in a stable and uninvadable local community:

$$-\ln S_0 + \ln N - \hat{\alpha}_0 S_0 + e^{-S_0 \hat{\alpha}} + (N - S_0) \hat{\alpha} e^{-S_0 \hat{\alpha}} = 0. \quad (\text{A.3})$$

As above, we would like to express this equation in a way that emphasizes the level of asymmetry in the system, so (A.3) is rewritten as,

$$-\ln S_0 + \ln(N e^{-\hat{\alpha} S_0}) - (\hat{\alpha}_0 - \hat{\alpha}) S_0 + e^{-S_0 \hat{\alpha}} + (N - S_0) \hat{\alpha} e^{-S_0 \hat{\alpha}} = 0. \quad (\text{A.4})$$

The first term in (A.4) is small (obviously much smaller than the last term) and can be dropped, as well as the

$-S_0$  in the  $(N - S_0)$  factor in the last term, giving

$$\ln S_0 + S_0(\hat{\alpha}_0 - \alpha) = N \hat{\alpha} e^{-S_0 \hat{\alpha}} \quad (\text{A.5})$$

At  $\eta = 0$ , the symmetric case,  $\hat{\alpha}_0 = \hat{\alpha}$  and we have to keep the  $\ln S_0$  term. Otherwise, we can drop it as being much smaller than  $S$ , and using the Lambert W function,  $W(x) \exp[W(x)] = x$ , this gives us (for any  $\eta \neq 0$ ),

$$S_0 = \frac{1}{\hat{\alpha}} W\left(\frac{N \hat{\alpha}^2}{\hat{\alpha}_0 - \hat{\alpha}}\right), \quad (\text{A.6})$$

which has the large  $N$  asymptotics

$$S_0 \approx \frac{\ln N}{\hat{\alpha}}. \quad (\text{A.7})$$

Fig. 9 demonstrates the quality of this approximation, by comparing the exact results and the simple expression (A.7). Even for  $N = 100$  the approximation works very well, breaking down only near  $p = 1$ , where the assumption that the  $\hat{\alpha}$ s have no  $N$  dependence breaks down.

Substituting (A.7) into (A.2) we get,

$$\ln SU(N, S_0) \approx \frac{\ln^2 N}{\hat{\alpha}} \left[ 1 - \frac{\hat{\alpha}_0}{2\hat{\alpha}} \right]. \quad (\text{A.8})$$

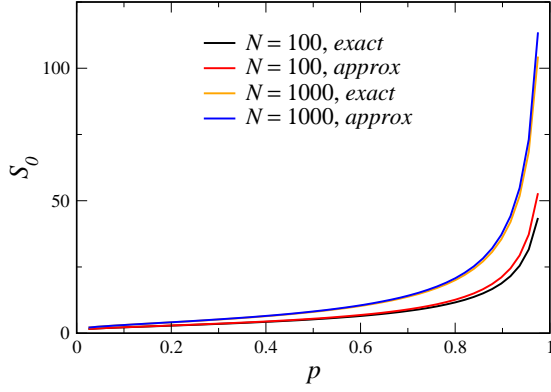


FIG. 9. The most common clique size,  $S_0$ , as a function of  $p$ , for  $\eta = 0.5$ . Exact results are compared with the approximation (A.7) for  $N = 100$ ,  $N = 1000$ .

This result is very interesting. Although we have limited our calculation to all values of  $\eta$  except the symmetric case  $\eta = 0$  [see the discussion that follows (A.4)], the result that the number of cliques grows asymptotically like  $N^{\ln N}$ , shows the same dependency on  $N$  as the result obtained in [16] for the *symmetric* case. The only point at which this general dependency breaks down is the fully asymmetric scenario  $\eta = 1$ , where  $\hat{\alpha}_0 = 2 \ln(1/p) = 2\hat{\alpha}$  and the numerical factor that multiplies  $\ln^2(N)$  vanishes. This supports our general conclusion, i.e., that the symmetric result is generic and the only exception is the purely asymmetric case.

Of particular interest is the behavior near the totally asymmetric case. Here, since the solution for  $S_0$  is

$$S_0(N, p, \eta) = \frac{W(N\hat{\alpha})}{\hat{\alpha}}, \quad (\text{A.9})$$

we have that

$$\ln SU(N, S_0, \eta) \approx \ln SU(N, S_0(\eta = 1), 1) - (1 - \eta) \left[ \frac{\partial \ln SU}{\partial S} \frac{\partial S_0}{\partial \eta} - \frac{1}{2} S_0^2(\eta = 1) \frac{\partial \hat{\alpha}}{\partial \eta} \right]. \quad (\text{A.10})$$

However, the derivative with respect to  $S$  vanishes since it is an extremal point, and the first term vanishes to leading order in  $N$ , so the exponent grows linearly with the distance from the fully asymmetric point,

$$\ln SU(N, S_0, \eta) \approx (1 - \eta) \frac{(1 - p)W^2(N\hat{\alpha})}{2p\hat{\alpha}^2}. \quad (\text{A.11})$$

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