Coexistence of species in complex ecological communities

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Abstract: We live surrounded by ecosystems made up of a large number of interacting species. In ecological models it is very improbable to obtain the stable coexistence of all these species. To make it possible, we have to consider that ecosystems are only the remaining part of a much larger community after their dynamics has evolved sufficiently. Here we analyze the coexistence of a given number of species that interact randomly according to different prescriptions of current interest.

I. INTRODUCTION

One of the fundamental questions in ecology is in what way different species coexist in a given area and how they are maintained through time. Answering this question will not only help in understanding nature but it will also provide us with tools to predict how will ecosystems respond to the loss of a specie, to human-induced alterations such as fragmentations, or the loss of a especie.

A population model is a dynamic system which aims to predict the temporal evolution of the number of individuals for a set of species. Interactions between populations can have different degrees of intensity and can be beneficial for some species and detrimental for others. Therefore, a totally general population needs an extraordinary complex formulation and in some cases may exceed the scope of current analytical and computational methods.

Lotka and Volterra equations are one of the first population models which has been studied and refined by countless studies [1-8]. This model assumes that the rate of increase or decrease per individual in each population is a linear function of the number of existents. This linearity assumption could be criticized. Though as discussed in [7], it can be shown that non-linear models have the same qualitative behavior as the Lotka-Volterra model for the same ecosystem.

The majority of models that can be solved analytically are of one, two or three interacting populations and only for some specific cases. These are not useful to explain the behavior of large and complex ecosystems. For this reason, we will have to resort to computational methods. As we will see, in Lotka-Volterra model is extremely improbable to obtain the coexistence of all species in a large community. We attempt to predict the number of species we obtain when starting from a community of n species, and let the dynamics evolve.

This report is organized as follows: In section II we introduce Lotka-Volterra equations and we define some fundamental concepts. In section III we analyze an analytical particular case: the prey-predator model. Section IV consists on a statistical approach on the equations using random parameters. Section V aims to model the movement of wild animals in a simple way and to corroborate the previous section results.

II. THE LOTKA-VOLTERRA MODEL

We take the model proposed by Lotka [1] and Volterra [2]. Early models attempted to explain the interaction between two species such as the prey-predator, competitive or mutualism interactions. These simple models have been generalised with the computational improvement in order to describe larger ecosystems. In general, Lotka-Volterra equations for n populations are a set of n coupled ODE's of the form:

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^{n} a_{ij}x_j \right); \quad i = 1, 2, \ldots, n, \quad (1)$$

where $\cdot$ denotes d/dt, $x_i = x_i(t)$ represents the number (or density) of individuals for each specie in a given instant of time, $\{r_i\}$ are the growth or death rates ($r_i > 0$ or $r_i < 0$, respectively) and coefficients $\{a_{ij}\}$ describe interactions between species.

The matrix $A = (a_{ij})$ is called interaction matrix. The off-diagonal coefficients $(a_{ij}, i \neq j)$ are the inter-specific interactions and they represent the effect that j-th specie has on i-th specie. Mutual interaction of individuals of the same specie is described by the diagonal coefficients a_{ii}, called intra-specific interactions. In general, A is not symmetric since the interaction of i on j is not the same as of j on i. If $a_{ij} > 0$, the presence of j specie favors the growth of i. If $a_{ij} < 0$, the presence of j inhibits i. Diagonal elements a_{ii} are taken as zero in the simplest models (where mutual interaction is not considered). When self-interactions are contemplated, self-regulating terms have to be added since any species can only interact in a detrimental way with itself, i.e. $a_{ii} < 0$.

The n-dimensional space, whose axis are the x_i variables, is called phase space. Solutions of Lotka-Volterra equations are trajectories in this space. Note that only those solutions with $x_i \geq 0$ are acceptable considering that $x_i < 0$ implicate a negative number of individuals.

A point x_i^* is a fixed point of the system if

$$x_i^* \left(r_i + \sum_{j=1}^{n} a_{ij}x_j^* \right) = 0; \quad i = 1, 2, \ldots, n. \quad (2)$$

These points represent equilibrium solutions of Eq. (1). A fixed point is locally stable if, following any sufficiently

small perturbation of the number of individuals, the system returns to the fixed point. The fixed point is globally stable (or attractive) if the system eventually returns to it, starting from any positive initial condition within a finite domain. A fixed point is feasible if $x_i^* > 0$ for every population. For convenience, we collect the coefficients x_i and r_i into the column vectors $\boldsymbol{x}$ and $\boldsymbol{r}$, respectively. From Eq. (2), if a feasible fixed point exists, it is given by the solution of

$$A\boldsymbol{x}^* = -\boldsymbol{r}. \qquad (3)$$

If A is invertible, then

$$\boldsymbol{x}^* = -A^{-1}\boldsymbol{r}. \qquad (4)$$

In order to study the stability of the fixed points it is sufficient to linearize the Lotka-Volterra equations around $\boldsymbol{x}^*$. If we define the right term of Eq. (1) as $F_i(\boldsymbol{x})$ and we consider the definition of fixed point ($\boldsymbol{F}(\boldsymbol{x}^*) = 0$) we can get:

$$\dot{\boldsymbol{x}} = J(\boldsymbol{x}^*)(\boldsymbol{x} - \boldsymbol{x}^*), \qquad (5)$$

where $J(\boldsymbol{x}^*)$ is the Jacobian of $\boldsymbol{F}(\boldsymbol{x})$ evaluated at $\boldsymbol{x}^*$. Hartman-Grobman theorem introduced in [5] states that stability is ensured when all the real parts of the eigenvalues of $J(\boldsymbol{x}^*)$ are strictly negative. If any of them is positive, the fixed point is unstable. If any of the eigenvalues is zero, this theorem does not ensure stability or instability and we would need to apply more complete methods. Note that this criterion tells us nothing about the type of stability.

III. PARTICULAR CASE: PREY-PREDATOR MODEL WITH INTRA-SPECIFIC COMPETITION

Prey-predator model is one of the simplest, but it is also one of the most illustrative. It describes the interaction between two populations, which are prey and predator. We denote them with $x(t)$ and $y(t)$, respectively. This model is one of the few that can be solved analytically. Lotka-Volterra equations in this particular case are:

$$\begin{aligned} \dot{x} &= x\left(r_x - a_{xx}x - a_{xy}y\right), \\ \dot{y} &= y\left(-r_y + a_{yx}x - a_{yy}y\right), \end{aligned} \qquad (6)$$

where r_x is the intrinsic growth rate of the prey population in absence of predators, r_y is the intrinsic death rate of the predator population in absence of preys and a_{ij} the interaction matrix. All constants are defined as positive.

One can find fixed points by solving the system $\dot{x} = \dot{y} = 0$. Solutions are:

$$\begin{aligned} x_1^* &= 0, & y_1^* &= -r_y/a_{yy}, \\ x_2^* &= r_x/a_{xx}, & y_2^* &= 0, \\ x_3^* &= \frac{a_{xy}r_y + r_x a_{yy}}{a_{xy}a_{yx} + a_{xx}a_{yy}}, & y_3^* &= \frac{r_x a_{yx} - r_y a_{xx}}{a_{xy}a_{yx} + a_{xx}a_{yy}}. \end{aligned} \qquad (7)$$

It is obvious that the first solution is not acceptable since it is not found in the first quadrant of the phase plane (2D phase space). Following the analysis made in [5], we can find three different scenarios:

1. $r_x/r_y > a_{xx}/a_{yx}$: In this case, the fixed point (x_3^*, y_3^*) lies in the first quadrant of the phase plane, so it is the feasible fixed point. As you can see in Figure 1 (left), all solutions converge at this point regardless of the initial conditions. Consequently, it is a globally stable fixed point. When steady state is reached, the two species coexist.

2. $r_x/r_y = a_{xx}/a_{yx}$: In this case, the fixed points (x_2^*, y_2^*) and (x_3^*, y_3^*) coincide and are located at the boundary of phase plane, above the x-axis. As shown in Figure 1 (right), all solutions reach the equilibrium with predator extinction for any initial conditions, so it is also a globally attractive point.

3. $r_x/r_y < a_{xx}/a_{yx}$: Now (x_3^*, y_3^*) is located outside the first quadrant so it is not an acceptable solution. Thus, (x_2^*, y_2^*) is the only fixed point and we find a case analogous to 2.
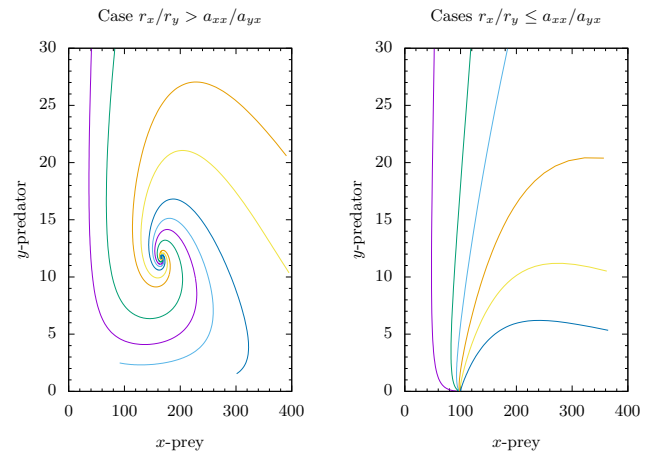

FIG. 1: Population evolution in phase space for a prey-predator model. Trajectories for different initial conditions are shown in different colours. To solve Eq. (6) we have used the 4th-order Runge-Kutta method. Values of the parameters taken in left are: $r_x = 4, a_{xy} = 0.2, r_y = 3, a_{yx} = 0.025, a_{xx} = 0.01, a_{yy} = 0.1$; and right: $r_x = 1, a_{xy} = 0.05, r_y = 3, a_{yx} = 0.03, a_{xx} = 0.01, a_{yy} = 0.1$.

Figure 2 shows the temporal dependence of the number of individuals for each specie. A variation of the population is observed over time until its equilibrium state is reached.

IV. RANDOM INTERACTIONS

In this section we study the behavior of ecological models in which the parameters are randomly drawn from fixed distributions. From a biological point of view, this means that species have not had time to evolve or adapt.
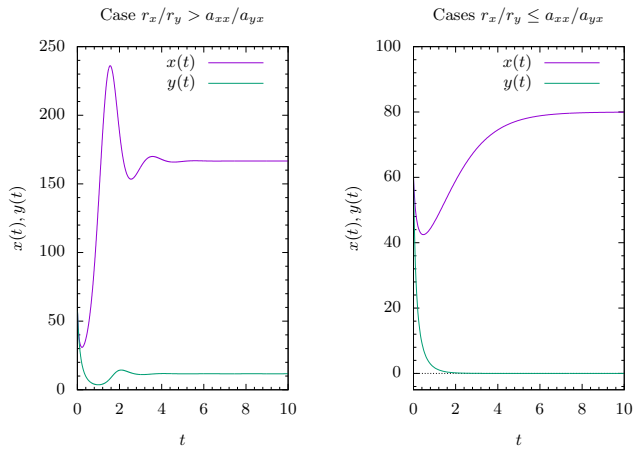
FIG. 2: Dependence of population over time for each specie. Values of the parameters are the same as those in Figure 1.

On the one hand, we will focus to study the interactions between species and not on the intra-specific parameters. On the other hand, we will study the effect of r_i and a_{ii} also randomly distributed, which is a more relativistic case. The system of study in this section will be 4-dimensional, made of four interacting species.

In order to carry out the following analysis, computational tools have been used. The program consists on finding the fixed points solving Eq. (2) for a given A. We have used the multidimensional Newton-Raphson method. It also computes the Jacobian matrix for each numerical solution found and returns its eigenvalues. Once stable fixed points are obtained, it sorts them according to the number of coexisting species (nonzero elements of $\boldsymbol{x^*}$). To make the statistics possible, we have repeated this process 1000 times with different A.

A.   Random inter-specific interactions

From now, we consider that all species have a positive growth rate and negative logistical term. For simplicity, we take $r_i = -a_{ii} = 1$. We sample the inter-specific interactions $(a_{ij}, i \neq j)$ from a distribution that is symmetric around zero. For example, we could draw them from a Normal distribution with zero mean.

Figure 3 shows the probability of obtaining a stable solution and a certain number of coexisting species hinging on the deviation of the Normal distribution, $P_s(\sigma)$ and $P_s^i(\sigma)$, respectively. Deviation is closely related to the probability of obtaining a zero element of the interaction matrix. The higher the σ value, the lower the probability of a parameter being zero ($a_{ij} = 0 + \delta x$), and the greater the absolute values of a_{ij} are (more influence of one population over another).

We can see that the probability of obtaining a stable solution (P_s), decreases for high values of σ (see Figure 3 (a)). In order to explain this behavior, we will take advantage of the work done by May [3]. May's theorem

deals with an interaction matrix in which the diagonal is $a_{ii} = -d$ and the off-diagonal coefficients are drawn from a Normal distribution $N(\mu = 0, \sigma)$ with probability C and zero otherwise. For large n, May proved that the probability of stability is close to zero whenever the "complexity" $K \equiv \sigma\sqrt{nC} > d$. For our particular case: $n = 4$, $C = 1$ and $d = 1$, so the fact that n is large is not satisfied. However, there is approximately good agreement with our results. May's stability criterion gives a stability transition in $\sigma = d/\sqrt{nC} = 0.5$. As we can see in Figure 3 (a), $\sigma = 0.5$ corresponds to the value in which the probability goes from being 100% to a lower value. If n is large enough, the width of the transition from high to low probability of stability would be zero and the decrease of stability would be very abrupt. As a consequence of working with finite and small values of n, such as $n = 4$, we observe a gradual and slow drop of stability.
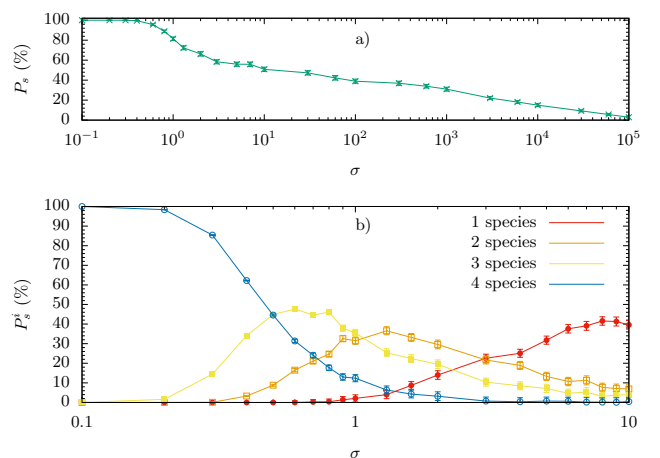

FIG. 3: (a) Probability of obtaining a stable solution depending on the deviation of the Normal distribution. (b) Probability of obtaining one, two, three or four coexisting species in terms of σ. In this graphic only a_{ij} is randomly distributed.

As we can see in Figure 3 (b), the number of coexisting species is also directly related to σ. For $\sigma \leq 0.2$, system tends to decorrelate and behaves like four uncoupled subsystems of one single specie, which are stable by construction since $x_i^* = -r_i/a_{ii} = 1$ and then $J(\boldsymbol{x^*})$ is a diagonal matrix with all the terms equal to -1, so the probability of obtaining four coexisting species is the maximum. To explain the behavior for $\sigma > 0.2$ we will base on the results obtained in section III, where we saw that when there are more than one possible fixed points (with $x_i^* \geq 0$), the stable solution is the one with maximum number of coexisting species. The same holds for systems with larger dimensionality: as σ increases, the probability that solutions of Eq. (2) have one element $x_i^* < 0$ increases, so the probability that the feasible fixed point is acceptable decreases with σ. Also, the probability of obtaining three coexisting species increases. For higher σ, the same happens for the coexistence of three and two species, as well as for two and one. When one starts to go down, the other one grows.

B. Adding random intra-specific parameters

Now we introduce r_i and a_{ii} also randomly distributed. We set a_{ii} by summing a mean-zero symmetric random variable and a constant $d_i < 0$. Note that d_i is the mean of the a_{ii} distribution. We sample a_{ij} and r_i as in the previous section with $N(\mu = 0, \sigma)$.

Figure 4 shows the same type of representation as Figure 3 but for these generalized parameters. As before, we observe that for greater values of σ the probability of obtaining a stable solution becomes smaller (see Figure 4 (a)). However, the dependence on the coexisting species changes radically (see Figure 4 (b)). Doing the same procedure with a_{ii} constant for all i (i.e. $a_{ii} = d_i = -d$), no appreciable changes are observed in the results. For this reason, the changes that we have obtained regarding the previous section are solely due to r_i sampling. We have considered $d = 1$ and we have kept d_i of the order of -1 for all i. Note that May's stability criterion remains acceptable using $|d_i| \sim d = 1$, since the stability transition continues at $\sigma = |d_i|/\sqrt{nC} = 0.5$.

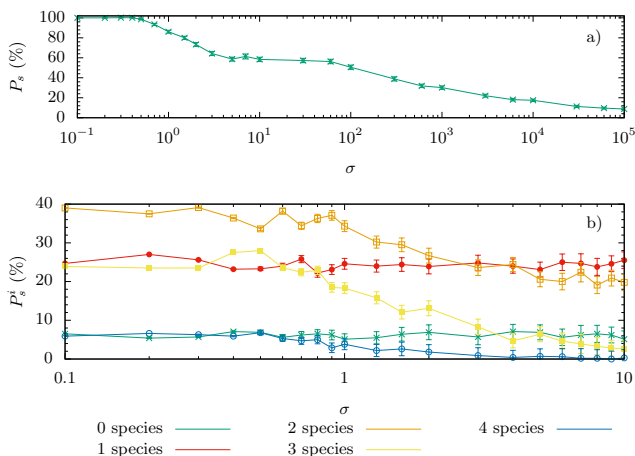| 0 species | 2 species | 4 species |
| 1 species | 3 species | |

FIG. 4: (a) Probability of obtaining a stable solution depending on the deviation of the Normal distribution. (b) Probability of obtaining one, two, three or four coexisting species in terms of σ. In this graphic r_i, a_{ij} and a_{ii} are all randomly distributed.

We call $P(k|n)$ the probability of observing k species stably coexisting when we start with a pool of n interacting populations and let the dynamics evolve. When interactions between species are not contemplated ($\sigma \approx 0$), the probability that Eq. (4) has n positive entries is $P(n|n) = \prod_{i=1}^{n} p_i$, where p_i is the probability of $r_i > 0$. Since the distribution of r_i is symmetric around zero, $p_i = 1/2$ independently of the distribution of $a_{ii} < 0$. Thus, $P(n|n) = 1/2^n$ for any particular system. This result is consistent with our numerical analysis as $P(4|4) = 0.063$ (see Figure 4 (b)).

In [4] the same situation is studied with the strong assumption that the real matrix A is negative definite, i.e. all the eigenvalues of $A + A^T$ are negative. Under this hypothesis, Lotka-Volterra model has a single global-

ally stable equilibrium. This requisite implies that the parameters are such that $K < |d_i|$ is always satisfied, since it ensures stability. One can meet this condition by choosing a sufficiently negative d_i. In [4] it is shown that the number of coexisting species follows the binomial distribution with probability $1/2$, and neither the network structure nor the exact shapes of the distributions (for example its σ value) have any effect. Hence,

$$P(k|n) = \binom{n}{k} \frac{1}{2^n}. \tag{8}$$

If $k = n$, we recover the same result of the particular case computed above.

This beautiful simple result is admissible provided that A is strongly stable (i.e. A is negative definite). This assumption is not always true in real ecosystems. As we can see in Figure 4 (b), when σ is such that $K(\sigma) \gtrsim |d_i|$ the coexistence deviates from its binomial behavior and stability begins to fall down. The way in which the system loses its stability is similar to the behavior described in the previous section. Stability first drops in the feasible solutions, then in three coexisting solutions, etc. Figure 5 shows a histogram where this aspect is shown clearly. For $\sigma = 0$, we are in strongly stable conditions and the distribution fits a binomial as we expected. For $\sigma = 1.5$, we are not under the conditions mentioned above and we observe a drop in stability of 19%, 37% and 47% with respect to the binomal with $k = 2, 3, 4$, respectively.
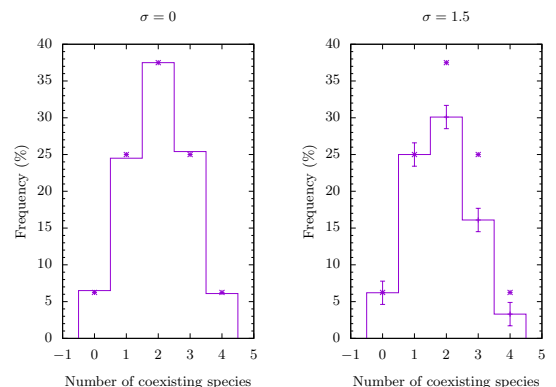

FIG. 5: Frequency histogram of stable solutions with k persistent species for $\sigma = 0$ and $\sigma = 1.5$. Points superimposed on histogram represent the binomial distribution with parameters $n = 4$ and $p = 1/2$, $B(4, 1/2)$.

V. MODELING THE MOVEMENT OF WILD ANIMALS

In the previous section we have sampled the parameters randomly following a Normal distribution. Nevertheless, real ecosystems are influenced by their composition, by the way these species move, by the number of individuals in each population, etc. Our goal here is to build the interaction matrix from a very simple lattice model that represents animal movement in 2D and to study its stability and coexistence.

We consider the simplest case in which all species move isotropically following a random walk. This movement is diffusive as far as it satisfies $\langle (\vec{r} - \vec{r}_0)^2 \rangle = 2d'Dt$, where t is the time elapsed since the individual begins to move from $\vec{r}_0$, d' is the dimensionality and D is the diffusion coefficient. The absolute values of the a_{ij} are directly related to the number of encounters with near neighbors of different species. Both the sign of the interaction and the initial distribution of individuals in the motion lattice are uniformly sampled. Furthermore, we consider the intrinsic parameters invariant with movement. Intra-specific interactions are fixed, and growth (death) rates are randomly distributed. To avoid finite size effects, periodic boundary conditions have been imposed.

We have performed the same coexistence analysis as in section IV for different times, t. For small t, individuals only explore their closest environment in such a way that they have not had time to interact at all or their interaction is very weak. In this case, the distribution of a_{ij} peaks at zero (small σ and K). As t increases, the greater the space explored by the individuals and the greater the interactions become. Now the distribution does not have a peak at zero but it is still symmetric (moderate σ and K). For large t, all individuals have interacted with nearly equal intensity, although favoring or disfavoring their existence. Finally, the distribution contains two symmetric peaks (large σ and K).

After generating 1000 interaction matrices with different random seeds, we expect the number of coexisting species follows a binomial distribution. However, as t increases, $K(\sigma)$ gets closer to the fixed $|a_{ii}| = d$ value and the strong stability constraint relaxes. What we can see in Figure 6 is that the stability of this "real" ecosystem falls in the same way that we have seen when the parameters are sampled at random.

VI. CONCLUSIONS

Implementing and analysing Lotka and Volterra equations we have first seen how is the coexistance of two particular populations. Coexistence or extinction between prey and predator is only given by the ratio between growth and death rates (r_x/r_y) as well as the ratio between the effect that preys exerts on the predators and onto itself (a_{xx}/a_{yx}). In addition, when inter-specific in-

teractions are randomly sampled, we have verified May's criterion seeing that stability is strongly linked to complexity (K) and intra-specific interactions (d_i). Introducing r_i and a_{ii} sampled at random but keeping $d_i \sim -1$, we have not observed appreciable changes in the total stability of the system. However, the number of species that coexist changes radically and follows the binomial distribution with probability $1/2$ in strongly stable conditions. This result is only due to the r_i sampling and network structure has no influence on it. In all cases, the stability is first lost for n coexisting species, then for $n - 1$, etc. Finally, we have verified that the results obtained with random interaction matrices are applicable to diffusive species in a heterogeneous ecosystem.
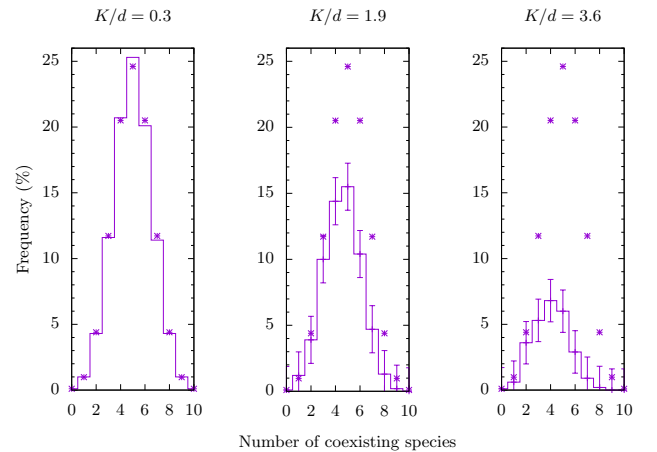

FIG. 6: Frequency histogram of stable solutions with k persistent species for different K/d values as a function of time. Points superimposed on histogram represent the binomial distribution with parameters $n = 10$ and $p = 1/2$, $B(10, 1/2)$.

Our results show that large ecosystems can stably coexist when we start from a much larger species pool and let the dynamics evolve. We conclude that stability and coexistence can be studied separately since they depend on the independent parameters d_i and r_i, respectively.

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