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Solvable model of a complex ecosystem with randomly interacting species†

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Abstract. A stochastic model for a dynamical system containing a great number of randomly interacting species is introduced. In the limit of infinitely many interacting species this model becomes exactly solvable and shows a stability–instability transition driven by the typical interaction strength and the noise parameter. The dynamical behaviour of the system in the stability region of the phase diagram is investigated and compared with numerical simulations. The implications of the results on natural ecosystems are discussed.

1. Introduction

The population dynamics of complex ecosystems is conveniently described by generalised Lotka–Volterra equations [1]. Recent work using such a description has concentrated on modelling the idiotopic network of the immune system [2]. The nonlinearity of these equations complicates their analytical investigation, especially in the case of a great number of interacting species. Nevertheless the linear stability analysis [3], the investigation of Lyapunov functions [4], graph-theoretical methods [5] as well as numerical simulations [6] gave some insight into the behaviour of complex ecosystems. In general, persistency and stability is predicted if certain requirements concerning the self-regulation and/or the interaction strength are fulfilled. If, for example, in completely connected networks the interaction strength exceeds some value of the order $O(N^{-1/2})$, where N is a big number of interacting species, an explosive increase of population occurs. This is due to so-called ‘ghost species’ with negative equilibrium populations [7].

The aim of the present work is to introduce a model of a complex ecosystem that becomes exactly solvable in the limit $N \rightarrow \infty$ and to look for its stability–instability transition. The paper is organised as follows. In § 2 the model is presented and the stability of its steady state is analysed. The solution of the model is performed in § 3 and is compared with computer simulations of systems with a large but finite number of interacting species. In § 4 the results are summarised and their implications for the real world are discussed. Some calculations are delegated to appendices 1–3.

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2. The model

I investigate the stochastic dynamics of a system of randomly interacting species. Consider the generalised Lotka–Volterra equation

$$\frac{d}{dt} n_i(t) = n_i(t) \left(f_i(n_i(t)) + \sum_{j(\neq i)} J_{ij} n_j(t) + \xi_i(t) \right) \quad (1)$$

where $n_i(t)$ ($i = 1, \dots, N$) is the population density of the i th species at time t (clearly $n_i(t) \geq 0$). The function $f_i(x)$ describes the development of the i th species without interacting with other species. The case $f_i(x) = -b_i < 0$ means exponential decrease of the population density of species i (i.e. species i is a ‘consumer’), and $f_i(x) = b_i > 0$ means exponential increase (i.e. species i is a ‘producer’). In both cases there is no self-regulation of the i th population, which has a destabilising effect on the whole system. Typical mechanisms for self-regulation in natural ecosystems are, for example, a territorial breeding requirement or the crowding effect caused by competition for a resource [3]. Therefore it is convenient to consider

$$f_i(x) = \frac{1}{\alpha} \left[1 - \left(\frac{x}{\theta_i} \right)^\alpha \right] \quad (2)$$

with $\alpha \geq 0$. θ_i is the saturation population density of the i th species. The case $\alpha = 1$ is the Verhulst model for self-regulation [8] and the case $\alpha = 0$, i.e. $f_i(x) = -\log(x/\theta_i)$, is the Gompertz model for self-regulation [9].

$\xi_i(t)$ is a stochastic noise that takes into account the influence of the environment, e.g. climate, disease, etc. This multiplicative noise is defined as the Stratonovich type. (J_{ij}) , $i, j = 1, \dots, N$, is the so-called interaction matrix or coupling matrix. If $J_{ij} < 0$, then $J_{ij} n_i n_j$ represents the loss rate of species i due to collision with species j , if $J_{ij} > 0$ that term represents the growth rate. If $J_{ij} < 0$ and $J_{ji} > 0$ the i th species is in prey–predator relationship with species j . The case $J_{ij} < 0$ and $J_{ji} < 0$ means that species i and j interact competitively and the case $J_{ij} > 0$ and $J_{ji} > 0$ means positive symbiosis between species i and j .

I consider (J_{ij}) , $i, j = 1, \dots, N$, as a random matrix whose elements are independently distributed according to a probability distribution $P(J_{ij})$ which is symmetric relative to zero. This means that the present ecosystem contains 50% prey–predator relationships, 25% competitive interactions and 25% positive symbiotic interactions. Because I am interested in the case of infinitely many interacting species, only the first two cumulants of the distribution $P(J_{ij})$ are important provided the higher cumulants are of lower order than $O(1/N)$. The distribution

$$P(J_{ij}) = \frac{1}{2} \delta(J_{ij} - J/N^{1/2}) + \frac{1}{2} \delta(J_{ij} + J/N^{1/2}) \quad (3)$$

and the distribution

$$P(J_{ij}) = \frac{1}{\sqrt{2\pi} J^2 N^{-1/2}} \exp\left(-\frac{(J_{ij})^2}{2J^2 N^{-1/2}}\right) \quad (4)$$

lead to the same results for $N \rightarrow \infty$. I define J to be the ‘typical interaction strength’, although the interaction strengths are proportional to J/\sqrt{N} .

For analytical reasons I have chosen the Gompertz model and for simplicity set the saturation population densities θ_i equal to 1. The effect of randomly distributed

θ_i will be considered later. The stochastic noise $\xi(t)$ is a stationary Gaussian process with the cumulants

$$\langle \xi_i(t) \rangle = 0 \quad \langle \xi_i(t) \xi_j(t') \rangle = 2\sigma \delta_{ij} \delta(t - t'). \quad (5)$$

The parameter σ is a measure for the strength of the noise, also called the noise intensity.

First of all I consider the steady-state solution of (1) for vanishing noise ($\sigma = 0$). A steady state $\mathbf{n}^0 = (n_1^0, \dots, n_N^0)$ of (1) is defined to be a solution of the fixed-point equation

$$n_i^0 \left(-\log(n_i^0) + \sum_{j(\neq i)} J_{ij} n_j^0 \right) = 0. \quad (6)$$

When none of the n_i^0 vanish and a steady state does exist, they must satisfy

$$n_i^0 = \exp \left(\sum_{j(\neq i)} J_{ij} n_j^0 \right). \quad (7)$$

In the case of a pure prey-predator system (i.e. (J_{ij}) is any antisymmetric matrix) one can easily show [1] that the function $G(t) = \sum_i n_i^0 [\exp(y_i(t)) - y_i(t)]$ with $y_i(t) = \log(n_i(t)/n_i^0)$ is a Lyapunov function (i.e. $d/dt G(t) < 0$) for the dynamics described by (1) and hence the system develops in time towards the steady state $n_i(t) = n_i^0$ for $t \rightarrow \infty$. In what follows I give some arguments for the contention that this steady state is also reached for $t \rightarrow \infty$ in the model described above, where the matrix (J_{ij}) is not antisymmetric.

Firstly, all finite systems simulated on a computer reach, after a short time ($t \approx 10$), the steady-state solution n_i^0 —if this solution of (7) does exist—no matter which initial state was chosen. If no solution of (7) exists—this happens for a typical interaction strength J greater than $J_c \approx 0.18$ —every initial state leads the divergence of some population densities and indicates the instability of the system. Thus one can assume that this scenario is not much different in a system with a much greater number of species than that, which can be simulated on a computer. Secondly, it is possible to prove analytically the stability of the steady-state solution for a low enough interaction strength J (see appendix 1). Finally in the next section it is shown that at the critical interaction strength, where the transition from stability to instability takes place, the steady-state solution is the only solution of (1) for $N \rightarrow \infty$ if the initial time is shifted to $-\infty$.

From the last two remarks one concludes that the dynamical behaviour of the system (1) is described by a relaxation to the steady-state solution for low interaction strengths and for the highest possible one. Bearing in mind the results of the computer simulations mentioned above, one can assume the same behaviour for intermediate values of the interaction strength and thus preclude any oscillatory behaviour of the dynamics after an infinitely long time has passed since starting from any initial state. In the case of non-vanishing noise $\sigma \neq 0$ the population densities fluctuate around their mean values, which for low enough σ are not very different from the steady state solution of equation (7). If the system is in equilibrium, the time-dependent correlation functions are expected to decrease monotonically with time. These considerations are important for the selection of the right solution of the saddle point equations that are derived in the next section.

3. The solution

Defining

$$y_i(t) = \log n_i(t) \quad (8)$$

equation (1) can be written as

$$\dot{y}_i(t) = -y_i(t) + b_i(t) + \sum_{j(\neq i)} J_{ij} \exp(y_j(t)) + \xi_i(t). \quad (9)$$

The dot refers to derivative with respect to time. The 'external fields' $b_i(t)$ represent time-dependent saturation population densities $b_i(t) = \log[\theta_i(t)]$. I have set $\theta_i(t) = 1$, consequently $b_i(t) = 0$. Equation (9) connects $y(t)$ with the stochastic process $\xi(t)$ and has to be used to calculate the generating functional for all correlation and response functions of the process $y(t)$. The quenched disorder in the system caused by the random interaction matrix forces one to average this generating functional over the distribution (3) or (4). Thus one is led to proceed in the same way as was done earlier [10] in the dynamical mean-field theory of spin glasses. Averaging out the quenched disorder leads to a complete decoupling of the time development of the different species and yields in the limit $N \rightarrow \infty$ a self-consistent one-species dynamics

$$\dot{y}_i(t) = -y_i(t) + \varphi_i(t) \quad (10)$$

where $\varphi_i(t)$ is a stationary Gaussian process with cumulants

$$\begin{aligned} \langle \varphi_i(t) \rangle_{\{\varphi_i\}} &= 0 \\ \langle \varphi_i(t) \varphi_i(t') \rangle_{\{\varphi_i\}} &= 2\sigma\delta(t-t') + J^2 C(t-t'). \end{aligned} \quad (11)$$

The averaged autocorrelation function $C(t-t')$ has to be determined self-consistently via

$$C(t-t') = \langle \exp[y_i(t) + y_i(t')] \rangle_{\{\varphi_i\}}. \quad (12)$$

Remembering (8), the physical meaning of $C(t-t')$ becomes clear:

$$C(t-t') = \frac{1}{N} \sum_i \langle n_i(t) n_i(t') \rangle \quad (13)$$

where the brackets $\langle \dots \rangle$ refer to average with respect to the probability distribution of the stochastic process $\xi(t)$ and to average over the distribution (3) or (4) of the random interactions J_{ij} . In writing $C(t-t')$ instead of $C(t, t')$, I have assumed that the initial time has gone to $-\infty$ and that the system has reached equilibrium. Once the correlation function $C(t)$ is known all other averaged autocorrelation functions can be calculated via

$$\langle n(t_1) \dots n(t_k) \rangle = \frac{1}{N} \sum_i \langle n_i(t_1) \dots n_i(t_k) \rangle = \langle \exp[y(t_1) + \dots + y(t_k)] \rangle_{\{\varphi_i\}}. \quad (14)$$

Now one is left with the problem of determining $C(t)$ by equations (10-12). Introducing $Z(t) = \log C(t)$, it can be shown (see appendix 3) that for all times $Z(t) \geq 0$ (i.e. $C(t) \geq 1$) and that $Z(t)$ must obey the Newtonian equation of motion

$$\ddot{Z}(t) = -\frac{\partial}{\partial Z} V(Z) \quad (15)$$

with the 'potential'

$$V(Z) = -\frac{1}{2}Z^2 + J^2 e^Z + \frac{1}{2}Z_0 Z. \tag{16}$$

$Z_0 = Z(0)$ is for $J^2 \neq 0$ a free parameter which has to be determined with the help of the considerations made in the last section. For $J^2 = 0$ it is $Z_0 = 2\sigma$. The 'initial velocity' is given by $\dot{Z}(0) = -\sigma$.

Firstly I consider the deterministic case $\sigma = 0$, i.e. $\dot{Z}(0) = 0$. Because the initial time has gone to $-\infty$, the system is in the steady state, i.e. $\mathbf{n}(t) = \mathbf{n}^0$. Therefore the correlation function $C(t)$ is time independent and equal to $\exp(Z_0)$. For $J^2 < 1/2e$ the potential $V(Z)$ possesses two extrema if Z_0 is low enough and no extremum if Z_0 exceeds a critical value depending on J^2 . The former case is depicted in figure 1. Depending on Z_0 , the position of the maximum Z_{\max} is to the left or to the right of Z_0 . The requirement for constant $C(t)$ implies $Z_0 = Z_{\max}$, where $V'(Z_{\max}) = 0$ and $V''(Z_{\max}) < 0$. The prime means differentiation with respect to Z . This leads to a transcendental equation for Z_0 :

$$Z_0 = 2J^2 e^{Z_0}. \tag{17}$$

From the two solutions of (17) which exists as long as $J^2 < 1/2e$, the lower one has to be chosen. The bigger one would also fulfil the requirement of constant $C(t)$. But choosing that solution would imply a discontinuity in the dependence of $\langle n^2 \rangle$ on the interaction strength at $J^2 = 0$, in contradiction with a result of appendix 2.

Figure 2 shows the mean square population density $C_0 = \langle n^2 \rangle = \exp(Z_0)$ computed by equation (17) in comparison with numerical results for systems with $N = 100, 200$ and 400 . With the help of the mean-field equations (10)-(12) one can easily calculate the generating function $g(k) = \langle \exp(iky) \rangle$ from which it follows that the population density n of a species is a random variable that obeys the distribution

$$P(n) = \frac{1}{\sqrt{\pi \log(C_0)}} \frac{1}{n} \exp\left(-\frac{(\log n)^2}{\log(C_0)}\right) \quad n \geq 0. \tag{18}$$

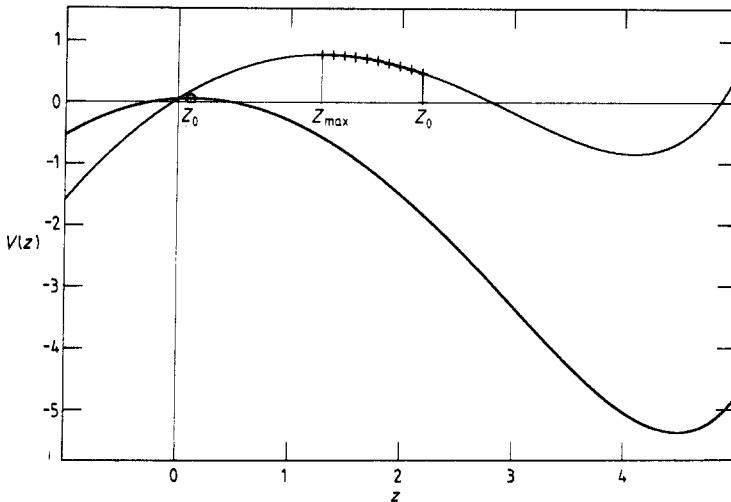


Figure 1. The potential $V(Z)$ given by (16) for two different values of Z_0 and $J^2 = 0.05$. For the lower curve Z_0 is the solution of (17), i.e. Z_0 merges with Z_{\max} . This is indicated by the small circle and corresponds to the solution of (15) and (16) for $\sigma = 0$. Z_0 of the upper curve is determined by (22) and (23) with $\sigma = 0.8$. The marked section between the two vertical lines indicates the path of a particle in the potential $V(Z)$ with just enough kinetic energy to reach the local maximum (see text).

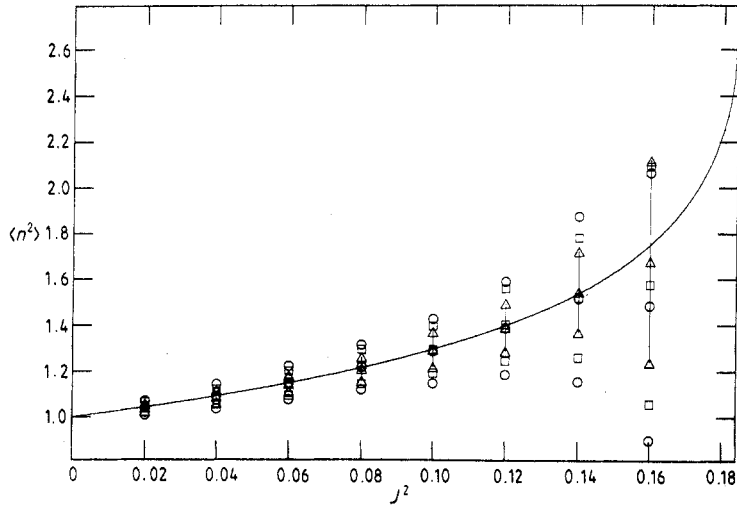


Figure 2. The dependence of the mean square population density $C(0) = \langle n^2 \rangle$ on the typical interaction strength J^2 for simulated systems with $N = 100$ (open circles), $N = 200$ (open squares) and $N = 400$ (open triangles) species ($\sigma = 0$). There are 500 systems in each ensemble for a certain value of J^2 . The points near the full curve are those for $\langle n^2 \rangle$, where the overbar refers to the ensemble average. The upper and lower points are those for $\langle n^2 \rangle \pm (\langle n^2 \rangle^2 - \langle n^2 \rangle)^{1/2}$. The upper and lower points for $N = 400$ are connected by a vertical straight line to indicate error bars. The full curve is the analytical result calculated with the help of equation (17).

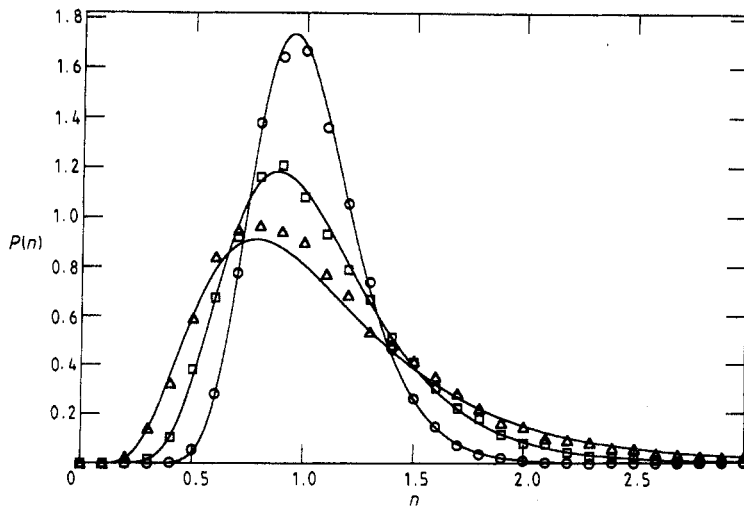


Figure 3. The probability distribution (18) of the population densities for three different values of the typical interaction strength in comparison with the histograms arising from numerical simulations of 500 systems with $N = 100$ species: $J^2 = 0.05$ (open circles), $J^2 = 0.10$ (open squares) and $J^2 = 0.15$ (open triangles) ($\sigma = 0$).

The moments of this distribution are given by

$$\langle n^k \rangle = \langle n^2 \rangle^{k/2}. \tag{19}$$

It should be remarked that these formulae are valid also for the case of non-vanishing noise $\sigma \neq 0$, which is treated below. The central quantity for all static distributions is the mean square population density. Figure 3 shows histograms for the population densities arising from computer simulations for systems with $N = 100$ species and different values of the typical interaction strength J^2 .

Until now I have assumed $J^2 < J_c^2 = 1/2e \approx 0.184$. If $J^2 > J_c^2$, the potential $V(Z)$ has no extremum, regardless of the value of Z_0 , and no non-negative solution of (15) exists. In that case the system is unstable; the population density of at least one species diverges. This transition has the following form in systems with a finite number of species that can be simulated on the computer. Even for $J^2 < J_c^2$ some systems which belong to an ensemble of systems with given J^2 are unstable, just as for $J^2 > J_c^2$ some systems of the ensemble are still stable. The former occur more often for $J^2 \nearrow J_c^2$ and the latter become more rare for increasing J^2 . As one would expect, this transition region localised around J_c^2 shrinks more and more for an increasing number N of species. From figure 2 one can see that the fluctuations of the mean square population densities around its mean value for the whole ensemble decrease for increasing N . For $J^2 > 0.16$ more than a quarter of all systems of a given ensemble are unstable and the fluctuations grow rapidly. Therefore I have not inserted any data for that region. Nevertheless one can conclude that for $N \rightarrow \infty$ the analytical curve will be reproduced.

Now I come to the case $\sigma \neq 0$. In recent investigations [1, 11] the influence of all other species on a certain species in a complex ecosystem was substituted by a Langevin force, which means no distinction was made between the stochastic noise caused by the environment and by the other species. This corresponds to the case $J^2 = 0$ and $\sigma \neq 0$. The potential (16) is then a parabola which is opened in the negative direction. It has zeros at 0 and $Z_0 = 2\sigma$ and a maximum at $Z_0/2 = \sigma$. The ‘total energy’

$$E = V(Z_0) + \frac{1}{2}\dot{Z}(0)^2 \tag{20}$$

is conserved, so that the motion starts at Z_0 in the direction of decreasing Z and approaches, but never reaches Z_{\max} within finite times. Hence one gets

$$C(t) = \exp[\sigma \cdot (1 + e^{-|t|})]. \tag{21}$$

This picture does not change qualitatively if one smoothly switches on the interaction strength. This is indicated in figure 1. Now one has to determine Z_0 in such a way that the initial kinetic energy $\sigma^2/2$ just suffices to reach the local maximum at Z_{\max} (otherwise $Z(t)$ would oscillate or become negative). That means

$$J^2 \exp(Z_0) + \frac{1}{2}\sigma^2 = \frac{1}{2}Z_{\max}^2 + J^2 \exp(Z_{\max}) + \frac{1}{2}Z_0 Z_{\max}. \tag{22}$$

The condition $V'(Z_{\max}) = 0$ yields

$$Z_0 = 2Z_{\max} - 2J^2 \exp(Z_{\max}). \tag{23}$$

Inserting the latter equation into the former, one gets a transcendental equation for Z_{\max} , which can be solved as long as J^2 remains below a critical value $J_c^2(\sigma)$. Within the picture of the motion in the potential (16) this means that too large an initial kinetic energy drives a particle behind the well at Z_{\max} and then into the region $Z(t) < 0$, which is forbidden. Hence one obtains a phase diagram shown in figure 4 separating the region of stable systems from that of unstable ones.

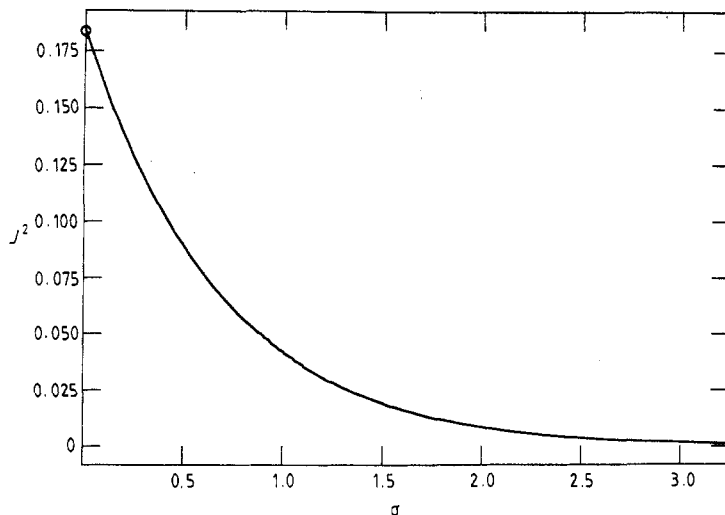


Figure 4. The critical line $J_c^2(\sigma)$. The stability-instability transition takes place when crossing this line from below. Critical slowing down occurs if the point indicated by the circle is approached.

The asymptotic behaviour of $Z(t)$ for $t \rightarrow \infty$ is dictated by the curvature of $V(Z)$ at the local maximum Z_{\max} . It is $Z(t) - Z_{\max} \propto \exp(-t/\tau)$ with

$$\tau^{-1} = \sqrt{-V''(Z_{\max})} = \sqrt{1 - J^2 \exp(Z_{\max})}. \quad (24)$$

For given $J^2 \neq 0$ the relaxation time τ increases monotonically with decreasing σ . If σ is fixed, τ grows with J^2 . Critical slowing down, i.e. $\tau \rightarrow \infty$, occurs only for $\sigma \rightarrow 0$ and $J^2 \rightarrow J_c^2(0) = 1/2e$ simultaneously. This can be easily seen from the fact that only in this case do the two extrema of the potential merge into a critical point with $V''(Z_{\max}) = 0$.

The system is, of course, non-ergodic; the correlations do not decay completely. We have e.g. $\lim_{t \rightarrow \infty} \langle n(t)n(0) \rangle > \langle n \rangle^2$ because $\lim_{t \rightarrow \infty} C(t) = \exp(Z_{\max})$ and $\langle n \rangle^2 = \exp(Z_{\max}/2)$. The distribution of the population densities obey again (20) and (21). In figure 5 I have depicted the mean square population density as a function of the noise parameter for different values of the interaction strength.

Concluding, I insert some remarks about the response function which is defined as follows:

$$G_{ij}(t, t') = \left. \frac{\delta}{\delta b_j(t')} \right|_{b=0} \langle n_i(t) \rangle. \quad (25)$$

This describes the linear response of the population density of species i at time t caused by a small change at time t' in the saturation population density θ_j of the j th species. The averaged local response function

$$G(t-t') = \frac{1}{N} \sum_i G_{ii}(t-t') \quad (26)$$

has the same form for all values of J^2 and σ given by

$$G(t) = \exp(e^{-t}) \quad \text{for } t > 0. \quad (27)$$

This is due to the lack of correlations between the interaction strengths J_{ij} and J_{ji} . In pure prey-predator systems, where $J_{ij} = -J_{ji}$, an oscillatory time dependency of $G(t)$ is expected, as will be discussed below.

Finally, I consider the effect of randomly distributed saturation population densities θ_i , which was set to 1 until now. The probability distribution of the population densities suggests the following distribution for the θ_i , which must be positive:

$$P(\theta_i) = \frac{1}{\sqrt{2\pi\beta^2}} \frac{1}{\theta_i} \exp\left(-\frac{(\log \theta_i / \theta_0)^2}{2\beta^2}\right) \quad \theta_i \geq 0. \tag{28}$$

$P(\theta)$ has a maximum at $\theta_{\max} = \theta_0 \exp(-\beta^2)$ which becomes more and more sharp for $\beta \rightarrow 0$. The distribution of θ_i is constructed in such a way that the external fields $b_i = \log \theta_i$ in equation (9) obey a Gaussian distribution with mean $b_0 = \log \theta_0$ and variance β^2 . Now one has to average the generating functional for all correlation and response functions of the process $y(t)$ also over this additional disorder and gets a self-consistent one-species dynamics in the same way as mentioned above. One ends again at (15) and (16) with a modified potential

$$V(Z) = -\frac{1}{2}Z^2 + J^2 e^Z + \frac{1}{2}(Z_0 + \gamma)Z \tag{29}$$

with $\gamma = 2b_0 + \beta^2/2$. For vanishing noise parameter, $\sigma = 0$, the new critical interaction strength is

$$J_c^2 = \frac{1}{2} \exp[-(1 + \gamma)]. \tag{30}$$

If $\theta_0 < 1$, i.e. $b_0 < 0$, the interval in which J^2 can vary without destabilising the system becomes greater than for $\theta_0 = 1$ and this interval shrinks for $\theta_0 > 1$. A finite variance β^2 diminishes J_c^2 . These effects are qualitatively the same for $\sigma \neq 0$.

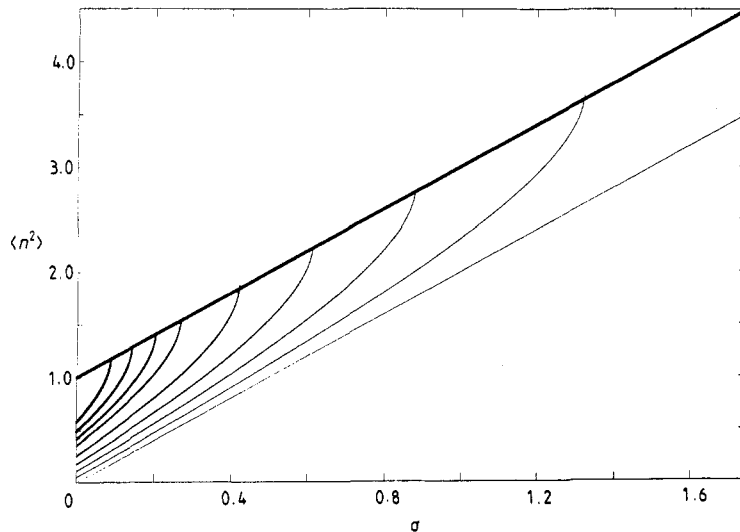


Figure 5. The dependence of the mean square population density $\langle n^2 \rangle$ on the noise parameter σ calculated with the help of equations (22) and (23) for different values of the typical interaction strength. The lower straight line is $\langle n^2 \rangle$ for $J^2 = 0$, the upper straight line indicates the upper bound of $\langle n^2 \rangle$. From right to left (with increasing thickness) the curves are drawn for $J^2 = 0.025$, $J^2 = 0.05$, $J^2 = 0.075$, $J^2 = 0.10$, $J^2 = 0.125$, $J^2 = 0.1375$, $J^2 = 0.15$ and $J^2 = 0.1625$.

4. Discussion

The proof and localisation of the transition from stability to instability in complex ecosystem described by (1) is the essential result of the above investigation. This transition takes place when the typical interaction strength, the noise (i.e. the influence of the environment) and the saturation population densities exceed a certain critical value. This transition is accompanied by a critical slowing down of the dynamics only in an exceptional case mentioned above. Remembering the fact that the interaction strengths were scaled with a factor $1/\sqrt{N}$ the following conclusion is obvious.

In stable ecosystems with many species the typical interaction strength should be lower than in systems with a smaller number of species. This is a feature of many ecosystems, as was already noted earlier. 'From empirical evidence it seems that species that interact feebly with others do so with a great number of other species. Conversely, species with strong interactions are often part of a system with a small number of species' [12].

I have demonstrated these features for a system that gives no priority to a prey-predator relationship between two species. Because natural ecosystems also exhibit symbiotic and competitive interactions, a restriction to prey-predator systems seems not to be desirable. Nevertheless, the investigation of systems containing a large number of prey-predator relationships is interesting, the more so since computer simulations show a greater stability for these systems. This indicates that in natural ecosystems the prey-predator relationship dominates the type of interaction.

Of special relevance for a model of the immune system is the requirement for a symmetric coupling matrix (J_{ij}) [13]. This is due to the functional equivalence of paratope and epitope of the antigens. Both cases mentioned here can be treated if one allows correlations between the distributions of J_{ij} and J_{ji} . That means, instead of dealing with independently distributed interaction strengths, one has to consider now a bivariate distribution for the pairs (J_{ij}, J_{ji}) with $N\langle J_{ij}J_{ji} \rangle = \lambda J^2$, where the correlation parameter λ varies between -1 and 1 . The case $\lambda = -1$ is a pure prey-predator model, $\lambda = 1$ implies a symmetric coupling matrix which is relevant for the immune system, and $\lambda = 0$ was treated above. Work investigating the model described in § 2 for all values of λ is in progress.

In this context it is worth noting that a generalised Gompertz model

$$\frac{d}{dt}n_i(t) = n_i(t) \left[\log\left(\frac{n_i(t)}{\theta_i}\right) + \sum_{j(\neq i)} J_{ij} \log[n_j(t)] + \xi_i(t) \right] \quad (31)$$

which was proposed firstly for two-species systems [14] to explain some experimental invalidation of the principle of competitive exclusion [15], can easily be solved in the limit $N \rightarrow \infty$ for all values of the correlation parameter λ . This is due to the linearity of that model, which becomes evident if we again introduce $y_i(t) = \log n_i(t)$. But the transition from stability to instability at the critical interaction strength (independent of the noise parameter σ)

$$J_c^2 = \frac{1}{(1+\lambda)^2} \quad (32)$$

can immediately be seen by analysing the stability of the fixed point $\mathbf{y} = \mathbf{0}$. The complete solution of the dynamical problem shows at this line a divergence of the mean square population density. The tendency to greater stability for decreasing λ following from

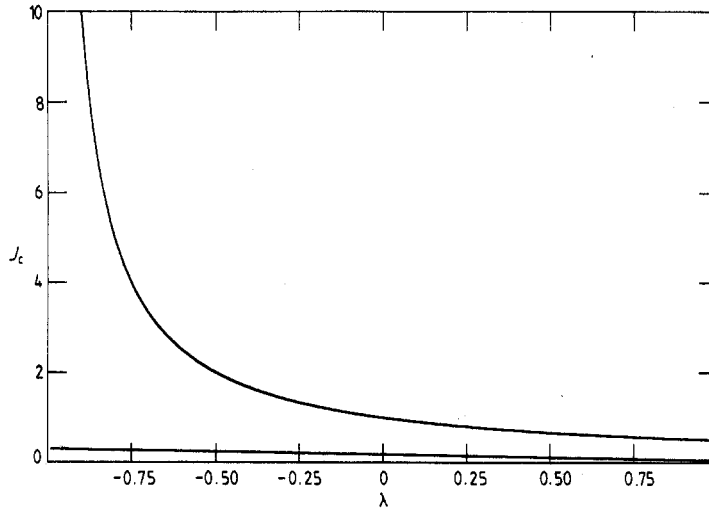


Figure 6. The dependence of the critical interaction strength J_c on the correlation parameter λ for the generalised Gompertz model (31). The case $\lambda = -1$, where $J_c = \infty$, corresponds to a pure prey-predator system. The lower curve is the critical line $J_c(\lambda, \sigma = 0)$ for the generalised Lotka-Volterra model (1) extrapolated from computer simulations for different values of λ .

equation (32) is, as already mentioned, also a feature of Lotka-Volterra models (see figure 6) just as is the case for oscillations of the response function (26), which for the generalised Gompertz model (31) is

$$G(t) = e^{-t} \frac{\mathcal{J}'_0(2t\sqrt{\lambda J^2})}{t\sqrt{\lambda J^2}} \langle n \rangle \quad t \geq 0. \tag{33}$$

\mathcal{J}'_0 is the derivative of the zeroth modified Bessel function, and $\langle n \rangle$ is the mean population density.

Finally I want to remark that all systems considered in this paper have an unique determined steady state that does not depend on the initial conditions. This is not the case in competition communities in which all interaction strengths are negative [16]. The dynamics of such systems, the number and size of their basins of attractions, are a field of further investigation.

Appendix 1

Defining the deviation of the population densities from their steady-state values as $\delta n_i(t) = n_i(t) - n_i^0$, equation (1) can be written as

$$\frac{d}{dt} \delta n_i = (\delta n_i + n_i^0) \left[-\log \left(1 + \frac{\delta n_i}{n_i^0} \right) + \sum_{j(\neq i)} J_{ij} \delta n_j \right]. \tag{A1.1}$$

Retaining only linear terms in δn_i one sees that the eigenvalues of the matrix

$$A_{ij} = -\delta_{ij} + n_i^0 J_{ij} \tag{A1.2}$$

decide the stability of the equilibrium. The matrix (J_{ij}) is random matrix whose elements obey the distribution (3) or (4). The eigenvalues of such a matrix are, for $N \rightarrow \infty$, uniformly distributed in a circle of radius J in the complex plane [17] (the probability of finding a finite number of eigenvalues outside this circle is supposed to vanish in

the limit $N \rightarrow \infty$ in analogy to the case of a random matrix J_{ij} belonging to the Gaussian orthogonal ensemble). Hence the eigenvalue of the matrix (A_{ij}) that has the greatest real part is lower than $-1 + J \max_{i=1, \dots, N} \{n_i^0\}$. In appendix 2 it is shown that for J low enough the steady state population densities are of order one with probability one. Therefore one can choose J low enough (independent of N) so that all eigenvalues of (A_{ij}) have a negative real part. From this follows the stability of the steady state \mathbf{n}^0 for low enough interaction strength J .

Appendix 2

Consider a certain realisation of the random matrix (B_{ij}) with $\langle B_{ij} \rangle = 0$, $N \langle B_{ij}^2 \rangle = 1$ and all other cumulants vanishing. Define the matrix $(J_{ij})(\varepsilon) = \varepsilon (A_{ij})$ and the function $F: [0, \infty)^N \times [0, \infty) \rightarrow \mathbb{R}^N$ by

$$F_i(\mathbf{n}, \varepsilon) = n_i \left(-\log(n_i) + \sum_{j(\neq i)} J_{ij}(\varepsilon) n_j \right). \tag{A2.1}$$

The stable solution of the equation $F(\mathbf{n}, \varepsilon) = \mathbf{0}$ is denoted by $\mathbf{n}^0(\varepsilon)$. It is $n_i^0(0) = 1$ for $i = 1, \dots, N$. The function F is continuously differentiable in $(\mathbf{n}^0, 0)$ and

$$\left. \frac{\partial F_i}{\partial n_j} \right|_{(\mathbf{n}^0, 0)} = -\delta_{ij}. \tag{A2.2}$$

i.e. the Jacobi matrix of F is non-singular in $(\mathbf{n}^0, 0)$. From the theorem regarding implicitly defined functions follows the existence of a $\delta > 0$ and a differentiable function $\mathbf{n}^0: (-\delta, +\delta) \rightarrow [0, \infty)^N$ with $\mathbf{n}^0(0) = (1, \dots, 1)$ and $F(\mathbf{n}^0(\varepsilon), \varepsilon) = \mathbf{0}$ for $\varepsilon \in (-\delta, +\delta)$. For low enough ε all $n_i^0(\varepsilon)$ are positive and not much different from one. Furthermore we have

$$\left. \frac{\partial n_i^0}{\partial \varepsilon} \right|_{\varepsilon=0} = \sum_{j(\neq i)} A_{ij} \tag{A2.3}$$

which is a random variable with mean zero and variance one. Therefore all moments

$$\langle n^k \rangle(\varepsilon) = \frac{1}{N} \sum_{i=1}^N [n_i^0(\varepsilon)]^k \tag{A2.4}$$

are continuous in $\varepsilon = 0$. Until now only a certain realisation of the random matrix was considered and their elements were multiplied by ε . Because of the property of self-averaging with respect to the interaction strengths, it follows that in large systems, $N \gg 1$, the above conclusions hold for any realisation of the matrix (J_{ij}) and low enough typical interaction strength J .

Appendix 3.

From equation (10) one concludes that the process $y_i(t)$ is given by

$$y_i(t) = \int_{-\infty}^t d\tau e^{\tau-t} \varphi_i(\tau). \tag{A3.1}$$

The lower bound of the integral is identical with the initial time which was shifted to $-\infty$. The equation (A3.1) describes a linear transformation from the process $\varphi_i(t)$ to the process $y_i(t)$. Therefore $y_i(t)$ is also a stationary Gaussian process, all of whose cumulants vanish except the second. Now, using the identity

$$\langle e^A \rangle = \exp\left(\sum_{m=1}^{\infty} \frac{1}{m!} \langle\langle A^m \rangle\rangle\right) \quad (\text{A3.2})$$

where $\langle\langle A^m \rangle\rangle$ means the m th cumulant, equation (12) can be written as

$$C(t) = \exp\left(\frac{1}{2}\langle\langle [y(t) + y(0)]^2 \rangle\rangle\right). \quad (\text{A3.3})$$

Inserting (A3.1), this yields

$$C(t) = \exp\left(\int_{-\infty}^t d\tau \int_{-\infty}^0 d\tau' e^{\tau-t} e^{\tau'} \langle\langle \varphi(\tau)\varphi(\tau') \rangle\rangle + \int_{-\infty}^0 d\tau \int_{-\infty}^0 d\tau' e^{\tau} e^{\tau'} \langle\langle \varphi(\tau)\varphi(\tau') \rangle\rangle\right) \quad (\text{A3.4})$$

where I have used the stationarity of the process $\varphi(t)$ (i.e. $\langle\langle \varphi(\tau)\varphi(\tau') \rangle\rangle = \langle\langle \varphi(\tau-t)\varphi(\tau'-t) \rangle\rangle$). Remembering equation (11), one gets

$$C(t) = \exp\left(\sigma(1 + e^{-|t|}) + \int_{-\infty}^t d\tau \int_{-\infty}^0 d\tau' e^{\tau-t} e^{\tau'} J^2 C(\tau - \tau') + \int_{-\infty}^0 d\tau \int_{-\infty}^0 d\tau' e^{\tau} e^{\tau'} J^2 C(\tau - \tau')\right). \quad (\text{A3.5})$$

Introducing the variable $Z(t) = \log C(t)$ yields an integral equation for $Z(t)$:

$$Z(t) = \frac{1}{2}Z(0)(1 + e^{-|t|}) + \int_0^t d\tau \int_{-\infty}^0 d\tau' e^{\tau-t} e^{\tau'} J^2 \exp(Z(\tau - \tau')) \quad (\text{A3.6})$$

with

$$Z(0) = 2\sigma + 2 \int_{-\infty}^0 d\tau \int_{-\infty}^0 d\tau' e^{\tau} e^{\tau'} J^2 \exp(Z(\tau - \tau')). \quad (\text{A3.7})$$

After differentiating (A3.6) twice with respect to time ($t > 0$) one gets

$$\ddot{Z}(t) = Z(t) - J^2 \exp(Z(t)) - \frac{1}{2}Z(0) \quad (\text{A3.8})$$

which is identical with equations (15) and (16). Solving equation (A3.8) with respect to $J^2 e^Z$ and inserting the result into (A3.7), one gets

$$\dot{Z}(0) = -\sigma. \quad (\text{A3.9})$$

Furthermore, it can be seen from equations (A3.6) and (A3.7) that $Z(t) > 0$ for all times t . (Except for $J^2 = 0$ and $\sigma = 0$, in which case $Z(t) = 0$, i.e. all population densities are one. This follows trivially from the steady-state solution of $\dot{n}_i(t) = -n_i(t) \log n_i(t)$.)

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