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Complex systems in Ecology:
a guided tour with large
Lotka-Volterra models and
random matrices
[supplementary material]

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1. May's model

(a) The mathematics behind May's result

Inspired by Gardner and Ashby's numerical results [1], Robert May proposed a first mathematical model [2] to link the stability of an ecosystem with its complexity. In this model, the ecosystem is represented by a vector of N functions $\mathbf{n} : t \mapsto (n_i(t))_{i \in [N]}$, the quantity $n_i(t)$ corresponding to the abundance of species number i at time t .

The vector of the abundances \mathbf{n} satisfies a system of first order nonlinear differential equations of the form:

$$\frac{dn_i}{dt} = F_i(\mathbf{n}). \quad (1.1)$$

(May did not particularly consider the form of the differential equation given by Eq.(1.1) in [3]). The main interest of May lies in the study of stability of equilibria of such systems. We assume the existence of an equilibrium $\mathbf{n}^* = (n_i^*)_{i \in [N]}$ and write the abundance of species number i as $n_i(t) = n_i^* + \varepsilon_i(t)$. Near the equilibrium, the stability of the nonlinear system (1.1) boils down to the stability of the linear system

$$\frac{d\varepsilon}{dt} = J(\mathbf{n}^*)\varepsilon, \quad (1.2)$$

where $J := J(\mathbf{n}^*)$ is the $N \times N$ Jacobian matrix

$$J_{ij} := \frac{\partial F_i}{\partial n_j}(\mathbf{n}^*). \quad (1.3)$$

In particular, the equilibrium is Lyapunov-stable if and only if all the eigenvalues of J have negative real parts.

The main contribution of May was to model the Jacobian as a random matrix in order to use mathematical results from RMT. More precisely, May chose to replace the self-interaction coefficients by -1 and all the other coefficients by independent centered random variables so that:

$$J = -I + M, \quad (1.4)$$

where $M_{ii} = 0$ and for $i \neq j$, M_{ij} are i.i.d centered random variables with variance $V := \text{Var}(M_{ij})$, and with a distribution independent from N .

May addressed the problem of determining what are the conditions on N and V to ensure that all the eigenvalues have negative real part. He relied on the result by Ginibre [4] who proved that asymptotically in N , the eigenvalues of matrix J are contained in a disk centered at $(-1, 0)$ with radius \sqrt{NV} . This lead May to state the following phase transition :

Proposition 1.1. (May [2], 1972) *If the matrix J is given by (1.4), the equilibrium is stable with high probability if*

$$V < \frac{1}{N} \quad (1.5)$$

and unstable with high probability if

$$V > \frac{1}{N}. \quad (1.6)$$

In fact, Ginibre's result is not enough to justify this phase transition but we need to understand the spectral radius of the matrix J . The first results on the spectral radius were obtained by Füredi and Komlós [5] in the Hermitian case and by Bai and Yin [6], Geman [7] and Geman and Hwang [8] in the general case. Recently, Bordenave et al. [9] show its convergence in probability under optimal moment assumption.

As the condition to get stability involves the number N of species, what we need to deduce May's result rigorously is a concentration inequality for the spectral radius. Such an inequality has been established in [10].

Theorem 1.1. *Let $X_N = (X_{ij})$ denote the random $N \times N$ matrix, where X_{ij} are independent copies of a given symmetric complex random variable, with $\mathbb{E}[|X_{11}|^2] \leq 1$. If there exists $\epsilon > 0$ and $B > 0$ such that $\mathbb{E}[|X_{11}|^{2+\epsilon}] \leq B$, then, for any $\delta > 0$, there exists a constant $K := K(\epsilon, \delta, B) > 0$, such that for any $N \in \mathbb{N}$, we have*

$$\mathbb{P} \left[\rho(X_N) \geq (1 + \delta)\sqrt{N} \right] \leq \frac{K}{(\log N)^2}. \quad (1.7)$$

It means that, in this first model¹, for N large enough, with high probability, there is no eigenvalue of J outside the disk centered at -1 and of radius \sqrt{NV} .

The spectrum of the Jacobian matrix is illustrated in Figure 1.

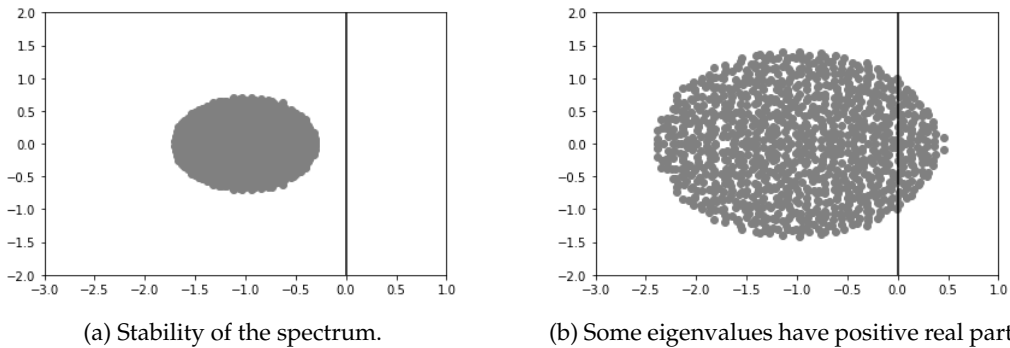


Figure 1: Spectrum of the Jacobian matrix $J = -I + M$, for $N = 1000$ species with $C = 1$, the entries M_{ij} , for $i \neq j$ are independent normal centered variables with variance V , with $V = \frac{1}{2N} < \frac{1}{N}$ in (A) and $V = \frac{2}{N} > \frac{1}{N}$ in (B).

May already considered a sparse version of his initial model in [2], where each possible interaction takes place with probability C (connectance), independently of all the other interactions, see Section 4(a) in [3] for an introduction to sparsity. It means that in average, each species effectively interacts with a proportion C of all the other species. The phase transition can be now stated as :

Proposition 1.2. (May [2], 1972) *If C is the connectance of the model, the equilibrium is stable with high probability if*

$$CV < \frac{1}{N} \quad (1.8)$$

and unstable with high probability if

$$CV > \frac{1}{N}. \quad (1.9)$$

Mathematically speaking, it is convenient to use the following formalism. Denote by Δ_{ER} the adjacency matrix of the Erdős-Rényi graph (see Section 4(b) in [3] for details) meaning that each entry of Δ_{ER} has probability C to be equal to 1 and is 0 otherwise. In other words, each species has

¹There are slight differences between the model in [10] and the model (1.4) : in [10], the symmetry of the law of the entries is required and all the entries of the matrix, including the diagonal entries, are i.i.d copies of the same variable while in (1.4), the diagonal entries are put to zero.

an effect on another species with probability C . Then, the matrix M introduced in (1.4) is replaced by \widetilde{M} equal to :

$$\widetilde{M} := \Delta_{\text{ER}} \circ M = ([\Delta_{\text{ER}}]_{ij} M_{ij}) . \quad (1.10)$$

The parameter C can therefore be interpreted as the average number of neighbours of a given vertex of the graph.

In this new model, the matrix \widetilde{M} has the same distribution as M except that $\text{Var}(\widetilde{M}_{ij}) = CV$, for $i \neq j$, leading to Proposition 1.2.

(b) Relation between May's model and Lotka-Volterra framework

Consider Eq. (2.1) in [3] (Lotka-Volterra model) and assume that there exists an equilibrium \mathbf{x}^* . If $\mathbf{x}^* > 0$ then one can easily compute the Jacobian at equilibrium. We provide hereafter a quick computation. Write $x_i(t) = x_i^* + \varepsilon_i(t)$ and notice that at equilibrium, since $x_i^* > 0$, one has

$$r_i = x_i^* - (\Gamma \mathbf{x}^*)_i .$$

Now

$$\begin{aligned} \frac{dx_i}{dt} &= x_i(r_i - x_i + (\Gamma \mathbf{x})_i) , \\ &= (x_i^* + \varepsilon_i)(r_i - (x_i^* + \varepsilon_i) + (\Gamma(\mathbf{x} + \boldsymbol{\varepsilon}))_i) , \\ &= (x_i^* + \varepsilon_i)(x_i^* - (\Gamma \mathbf{x}^*)_i - (x_i^* + \varepsilon_i) + (\Gamma(\mathbf{x} + \boldsymbol{\varepsilon}))_i) , \\ &= (x_i^* + \varepsilon_i)(-\varepsilon_i + (\Gamma \boldsymbol{\varepsilon})_i) , \\ &= [\text{diag}(\mathbf{x}^*)(-I + \Gamma)\boldsymbol{\varepsilon}]_i + o(\boldsymbol{\varepsilon}) . \end{aligned}$$

Hence the Jacobian

$$J(\mathbf{x}^*) = \text{diag}(\mathbf{x}^*)(-I + \Gamma) . \quad (1.11)$$

Formally, this Jacobian resembles May's Jacobian, with important differences:

- the underlying equilibrium \mathbf{x}^* must be feasible (i.e. $\mathbf{x}^* > 0$). If Γ is random, then conditions for feasibility are provided in Section 3(d) in [3]. Under these conditions, stability is granted (see for instance [11, Corollary 1.4]).
- in the Jacobian formula $\text{diag}(\mathbf{x}^*)(-I + \Gamma)$, there is the product of an extra matrix, namely $\text{diag}(\mathbf{x}^*)$, with matrix $-I + \Gamma$ that appears. Notice that if Γ is random, then $\text{diag}(\mathbf{x}^*)$ and Γ are dependent since $\mathbf{x}^* = \mathbf{r} + \Gamma \mathbf{x}^*$ for a feasible equilibrium.

Stone [12] considered a Jacobian matrix of this form, but with the simplifying assumption that the entries of $\text{diag}(\mathbf{x}^*)$ are independent from Γ . Then J is unstable only if Γ is unstable, and thus May's criterion would still hold.

This independence assumption between D and Γ is strong as the subset of surviving species and their abundances are function of the interaction matrix Γ , hence not independent.

Notice that Stone [12] does not consider the normalization under which the equilibrium \mathbf{x}^* is feasible. It is thus not clear that the considered formula for the Jacobian is associated to a LV system.

(c) Other models

Some authors have used more involved models for the Jacobian matrix, such as the elliptic model (see Eq. (2.6) in [3] and [13]) and derived from there similar criteria for stability expressed in terms of the parameters of the model.

We also mention other possible random models, such as studied in Ben Arous et al. [14,15]:

$$\frac{dx_i}{dt} = -x_i(t) + f_i(\mathbf{x}), \quad (1.12)$$

where $f_i(\mathbf{x})$ is a smooth random vector field which models the complexity and nonlinearity of interactions. It is assumed that for all $i \in [N]$,

$$f_i(\mathbf{x}) = -\frac{\partial V}{\partial x_i}(\mathbf{x}) + \frac{1}{\sqrt{N}} \sum_{j=1}^N \frac{\partial A_{ij}}{\partial x_j}(\mathbf{x}), \quad (1.13)$$

where the matrix A is a random antisymmetric matrix independent of the random scalar potential V .

2. Lotka-Volterra system in two dimensions

The question of long-time behavior of Lotka-Volterra system is a very delicate one that has motivated an already large literature. Let us first discuss briefly the results for a deterministic matrix Γ with N small. The $N=2$ setting provides some basic heuristics for understanding when the dynamics admits a single equilibrium with or without species going extinct, multiple equilibria, or oscillatory behaviors (e.g. Section 2, and also [16,17]).

Recall the Lotka-Volterra system (2.1) in [3] for $N=2$ species and with a deterministic matrix Γ (e.g. [16,17]). This system generally admits four equilibria:

$$(0, 0), \quad \left(0, \frac{r_2}{1 - \Gamma_{22}}\right), \quad \left(\frac{r_1}{1 - \Gamma_{11}}, 0\right), \quad \text{or} \\ \left(\frac{(1 - \Gamma_{22})r_1 + \Gamma_{12}r_2}{(1 - \Gamma_{11})(1 - \Gamma_{22}) - \Gamma_{12}\Gamma_{21}}, \frac{\Gamma_{21}r_1 + (1 - \Gamma_{11})r_2}{(1 - \Gamma_{11})(1 - \Gamma_{22}) - \Gamma_{12}\Gamma_{21}}\right). \quad (2.1)$$

The stability of these equilibria can be discussed from the computation of the Jacobian matrix at these critical points.

If either $x_1 < 0$ or $x_2 < 0$ at the equilibrium (2.1), that particular equilibrium is unfeasible and does not correspond to an admissible solution. We generally find that in these cases one species goes asymptotically to extinction, and is said to be excluded by the other species (e.g. competitive exclusion). The fact that only one species survives is a classic setting of adaptive dynamics, see Metz et al. [18] and Champagnat [19]: this corresponds to the rule that *invasion implies fixation*, meaning that the weakest species is lost when a favourable mutant arises. Provided new mutant species arrive sufficiently slowly into the system, the evolution of the population can be described by the sequence of successive dominating species or *trait substitution sequence*.

If both $x_1 > 0$ and $x_2 > 0$ at the equilibrium (2.1): the fixed point (x_1, x_2) is feasible. Linear stability analysis reveals that the feasible equilibrium is stable if $\Gamma_{12}\Gamma_{21} < (1 - \Gamma_{11})(1 - \Gamma_{22})$, unstable otherwise (see e.g. chapter 6 in [20]).

When the equilibrium (2.1) is unstable, the dynamics admits two stable fixed points, with either species 1 or species 2 extinct (both equilibria are uninvadable, insofar as the extinct species, if introduced with small abundance, will decay exponentially). This phenomenon, known as mutual exclusion, provides a basic template for the existence of multiple stable states in Lotka-Volterra dynamics.

The case $\Gamma_{12}\Gamma_{21} = (1 - \Gamma_{11})(1 - \Gamma_{22})$ is singular and corresponds to a situation where one species always goes extinct [21].

Let us now discuss the possible existence of cycles. The original predator-prey model of Lotka and Volterra had antisymmetric interactions $\Gamma_{12} = -\Gamma_{21}$, and $\Gamma_{11} - 1 = \Gamma_{22} - 1 = 0$ and r 's of

opposite signs, so that the dynamics reduces to

$$\frac{dx_1}{dt} = x_1(r_1 + \Gamma_{12}x_2), \quad \frac{dx_2}{dt} = x_2(r_2 - \Gamma_{12}x_1) \quad (2.2)$$

In that case, the dynamics admits neutral cycles around the marginally stable fixed point $(r_2/\Gamma_{12}, -r_1/\Gamma_{12})$. Indeed, it can be checked that the function $F(t) = \Gamma_{12}(x_1(t) + x_2(t)) + r_1 \log x_2(t) - r_2 \log x_1(t)$, called a first integral of Eq. (2.1) in [3], remains constant over time.

For more general matrices Γ , the Bendixson-Dulac theorem gives a sufficient condition to show that there is no cycle ([16]. We also refer to [22], who proved that attractors of competitive or cooperative N -species systems could only be manifold of $N - 1$ or fewer dimensions). The Bendixson-Dulac theorem in the case of the 2d-Lotka-Volterra equation is as follows:

Proposition 2.1. *If there exists a function $\varphi(x_1, x_2)$ such that*

$$\frac{\partial}{\partial x_1} \left(\varphi(x_1, x_2) (r_1 x_1 + (\Gamma_{11} - 1)x_1^2 + \Gamma_{12}x_1 x_2) \right) + \frac{\partial}{\partial x_2} \left(\varphi(x_1, x_2) (r_2 x_2 + \Gamma_{21}x_1 x_2 + (\Gamma_{22} - 1)x_2^2) \right) \quad (2.3)$$

has a constant sign in the positive quarter plane, then there is no cycle solution of the Lotka-Volterra system (2.1) in [3].

Let us discuss further the case where $\Gamma_{11} - 1 = \Gamma_{22} - 1 = 0$, but now with symmetric interactions, $\Gamma_{12} = \Gamma_{21}$, which may arise for some competitive or mutualistic interactions.

If $r_1, r_2 > 0$ and $\Gamma_{12} > 0$ (mutualistic interactions), we can choose $\varphi(x_1, x_2) = 1$ and (2.3) becomes $r_1 + r_2 + \Gamma_{12}(x_1 + x_2)$, which is positive on positive quarter plane, so the dynamics do not exhibit cycling.

If $r_1, r_2 > 0$ and $\Gamma_{12} < 0$ (competition), there is a saddle point at $(-r_1/\Gamma_{12}, -r_2/\Gamma_{12})$ and $(0, 0)$ is repulsive, so there is also no possible cycle.

As a general heuristic, antisymmetric interactions (as in the original prey-predator model (2.2)) favor cycling around fixed points, whereas symmetric interactions favor taking a shortest path toward fixed points.

Let us now consider the general case with an arbitrary matrix Γ . Choosing $\varphi(x_1, x_2) = 1/(x_1 x_2)$ for example, we obtain that (2.3) is equal to

$$\frac{(\Gamma_{11} - 1)x_1 + (\Gamma_{22} - 1)x_2}{x_1 x_2}$$

so there is no cycle if $\Gamma_{11} > 1$ and $\Gamma_{22} > 1$ or if $\Gamma_{11} < 1$ and $\Gamma_{22} < 1$.

In all generality, the Bendixson-Dulac theorem proves that the two-species Lotka-Volterra system admits no *isolated* periodic orbit, whatever the values of the Γ_{ij} and r_i [16, p.33] (the cycles exhibited above being non isolated).

Let us briefly say that in higher dimensions, the complexity increases exponentially. For three competing species, Zeeman [23] described the compact limit sets of these systems, which are either fixed points or periodic orbits (conforming to the general result of [22]), and found 33 different equivalence classes. For the general case of N competitive species, Zeeman and Zeeman [24] have studied the carrying simplex that attracts all non-zero orbits and carries the asymptotic dynamics.

3. From individual-based models to Lotka-Volterra system

As explained in the main text, the Lotka-Volterra multidimensional ordinary differential equation (2.1) or its stochastic analogue (5.12) in [3] can both be obtained as the large population limit of a stochastic individual based *birth-death model with interactions*, see, e.g., [25–28].

The goal of the present appendix will be to derive Eq. (2.1) from individual-based models, the other variants will be presented in Section 4. In both Sections 3 and 4, our exposition will be mainly inspired by [26].

(a) One species as a birth and death process

Our starting point will be to describe the birth and death model for a single species. This is done by means of a homogeneous Markov jump process $(Y(t))_{t \geq 0}$ with values in \mathbb{N} . The transition probabilities of Y , defined by $P_{nm}(h) = \mathbb{P}(Y(t+h) = m \mid Y(t) = n)$ for $h \geq 0$ and $n, m \in \mathbb{N}$ are such that:

$$\begin{aligned} P_{n,n+1}(h) &= b_n h + o(h), & \text{for } n > 0, \\ P_{n,n-1}(h) &= d_n h + o(h), & \text{for } n > 0, \\ P_{n,m}(h) &= o(h), & \text{for } |n - m| > 1, \end{aligned} \quad (3.1)$$

where $(b_n)_{n \in \mathbb{N}}$ and $(d_n)_{n \in \mathbb{N}}$ are two sequences of real non-negative numbers. For example, if individuals are exchangeable with individual birth rate b and death rate d , then, $b_n = b \times n$ and $d_n = d \times n$, so that b_n and d_n are respectively the birth and death rates when the population is of size n . We refer to [26] for more details.

We note for further use that such processes can be advantageously described by stochastic differential equations involving random Poisson point measures [25,29]. Denoting as $\mathbf{N}(ds, du)$ the random Poisson measure on $\mathbb{R}_+ \times \mathbb{R}_+$ with the intensity measure the product of the Lebesgue measures $ds \otimes du$, a birth and death process with respective birth and death rate sequences (b_n) and (d_n) can be written as

$$Y(t) = Y(0) + \int_0^t \int_{\mathbb{R}_+} \left(\mathbf{1}_{u \leq b_{Y(s^-)}} - \mathbf{1}_{b_{Y(s^-)} \leq u \leq b_{Y(s^-)} + d_{Y(s^-)}} \right) \mathbf{N}(ds, du). \quad (3.2)$$

Such stochastic differential equations correspond to the individual-based simulation algorithms often used by biologists (see, e.g., Gillespie [30]). In these equations, the Poisson point measure models the possible births or deaths and the indicators correspond to an acceptance-rejection algorithm which ensures that the events occur with the correct time-dependent and random rate $b_{Y(s^-)}$ or $d_{Y(s^-)}$.

Using Poisson stochastic calculus, and introducing the compensated Poisson measure $\widetilde{\mathbf{N}}(ds, du) = \mathbf{N}(ds, du) - ds \otimes du$, we have:

$$Y(t) = Y(0) + \int_0^t (b_{Y(s)} - d_{Y(s)}) ds + M(t), \quad (3.3)$$

where:

$$M(t) := \int_0^t \int_{\mathbb{R}_+} \left(\mathbf{1}_{u \leq b_{Y(s^-)}} - \mathbf{1}_{b_{Y(s^-)} \leq u \leq b_{Y(s^-)} + d_{Y(s^-)}} \right) \widetilde{\mathbf{N}}(ds, du)$$

is a centered martingale with variance $\mathbb{E}(\int_0^t (b_{Y(s)} + d_{Y(s)}) ds)$. It is possible to rewrite (3.3) in differential form as:

$$dY(t) = (b_{Y(t)} - d_{Y(t)}) dt + dM(t). \quad (3.4)$$

(b) Asymptotics for one species

We now assume that the population size is large and introduce a parameter $K > 0$, which is seen as a scaling parameter for the initial population size (*carrying capacity*). More precisely, we now

denote our process as $Y^K(t)$ and the rescaled version

$$X^K(t) := \frac{Y^K(t)}{K}.$$

We assume that

$$X^K(0) = \frac{Y^K(0)}{K} \xrightarrow{K \rightarrow \infty} x_0 \quad \text{in probability,}$$

where $x_0 > 0$ is some deterministic or random positive real number. We also assume that the birth and death rates depend on the scaling parameter K , and denote them as b_n^K and d_n^K respectively. Our purpose is to study the dynamics of $X^K(t)$ in the asymptotic regime $K \rightarrow \infty$, given different types of dependencies of the birth and death rates on K . Note that since the jumps of $X^K(t)$ are of amplitude $1/K$, the limiting process can take any value in \mathbb{R}_+ .

The first model for b_n^K and d_n^K will be the so-called *logistic model*. Given three parameters $b, d, c > 0$, this model reads

$$b_n^K = b n \quad \text{and} \quad d_n^K = d n + \frac{c}{K} n^2. \quad (3.5)$$

According to this model, there is no interaction between the individuals that constitute the species regarding the births, since b_n^K grows linearly with the population size. This is not the case of the deaths, since d_n^K has a quadratic component accounting for a *competition* among the individuals within the species to access the limited amount of resources.

From the equations (3.1), we easily see that

$$\mathbb{E} \left(Y^K(t+h) - Y^K(t) \mid Y^K(t) = n \right) = \sum_m (m-n) P_{n,m}(h) = (b_n^K - d_n^K)h + o(h),$$

$$\text{Var} \left(Y^K(t+h) - Y^K(t) \mid Y^K(t) = n \right) = (b_n^K + d_n^K)h + o(h).$$

On the other hand, the birth and death rates for the logistic model satisfy: for all $x \geq 0$,

$$\lim_{K \rightarrow \infty} \frac{b_{[Kx]}^K - d_{[Kx]}^K}{K} = \lim_{K \rightarrow \infty} (b-d) \frac{[Kx]}{K} - c \frac{[Kx]^2}{K^2} = rx - cx^2$$

$$\lim_{K \rightarrow \infty} \frac{b_{[Kx]}^K + d_{[Kx]}^K}{K^2} = \lim_{K \rightarrow \infty} (b+d) \frac{[Kx]}{K^2} + c \frac{[Kx]^2}{K^3} = 0,$$

where $r = b - d$. We therefore get from the previous equations that

$$\begin{aligned} \frac{\mathbb{E}[X^K(t+h) - X^K(t) \mid X^K(t)]}{h} &\simeq \frac{b_{Y^K(t)}^K - d_{Y^K(t)}^K}{K} \simeq rX^K(t) - cX^K(t)^2, \\ \frac{\text{Var}[X^K(t+h) - X^K(t) \mid X^K(t)]}{h} &\simeq \frac{b_{Y^K(t)}^K + d_{Y^K(t)}^K}{K^2} \simeq 0 \end{aligned}$$

for large K . This argument shows that the variance of the increments of $X^K(\cdot)$ decreases faster than h , thus, heuristically, the stochasticity of this process disappears for large K . Assuming that x_0 is deterministic and using the expression of the conditional mean above, we thus infer that $X^K(\cdot)$ converges in probability, and uniformly on every time interval $[0, T]$, to a deterministic process $x(\cdot)$ defined as the unique solution of the ODE

$$\dot{x}(t) = rx(t) - cx(t)^2, \quad x(0) = x_0. \quad (3.6)$$

Formally, this means

$$\forall \varepsilon > 0, \quad \mathbb{P} \left\{ \sup_{t \leq T} |X^K(t) - x(t)| > \varepsilon \right\} \xrightarrow{K \rightarrow \infty} 0.$$

Observe that $r = b - d$ can be seen as the population “natural increase rate” in the limit of the small population size. When $r > 0$, which is usually the case, the competition for the available resources regulates the population.

Obviously, the ODE (3.6) is the particular case of Eq. (2.1) in [3] obtained for $N = 1$.

The argument for showing the convergence towards the solution of (3.6) can be made rigorous by establishing a compactness result over the laws of the trajectories $X^K(\cdot)$ in the space $D([0, 1], \mathbb{R}_+)$ of the so-called càdlàg processes before identifying the equation satisfied by the limiting values $x(\cdot)$. The convergence finally results from the uniqueness of the limiting value. A complete proof can be found in [25].

(c) Asymptotics for N species with interactions

We now address the case of N species with interactions. Our (vector) process \mathbf{Y}^K is now valued in \mathbb{N}^N and writes $\mathbf{Y}^K(t) = (Y_i^K(t))$ where $Y_i^K(t)$ is the population size of the species i at time t . Let $\mathbf{b}^K = (b_i^K)$ and $\mathbf{d}^K = (d_i^K)$ be two $N \times 1$ vectors with positive elements, and let $\Gamma^K = (\Gamma_{ij}^K)$ be a $N \times N$ matrix.

According to the model with interactions, the individuals in the species i reproduce with an individual rate proportional to b_i^K , die with the individual natural death rate proportional to d_i^K , and can interact with other individuals, say of the species j , with a rate proportional to $\Gamma_{ij}^K - \mathbf{1}_{i=j}$ resulting in an extra birth or death term. The indicator $\mathbf{1}_{i=j}$ corresponds to the logistic competition term inside each species, as in Section 3(b). The matrix Γ^K of the interactions may be deterministic or random. When it is random, all the computations that are presented below are made conditionally to Γ^K . As previously, it is possible to write a stochastic differential equation involving a random Poisson point measure which generalizes (3.2).

Denote as \mathbf{e}_i the i^{th} canonical vector of \mathbb{R}^N and consider a population represented by vector $\mathbf{k} = (k_i) \in \mathbb{N}^N$. We can now express the transition probabilities:

$$\mathbb{P}\left(\mathbf{Y}^K(t+h) = \mathbf{k} + \mathbf{e}_i \mid \mathbf{Y}^K(t) = \mathbf{k}\right) = \underbrace{\left(b_i^K k_i + \sum_{j: \Gamma_{ij}^K > 0} \Gamma_{ij}^K k_i k_j\right)}_{\text{birth rate for species } i} h + o(h). \quad (3.7)$$

$$\mathbb{P}\left(\mathbf{Y}^K(t+h) = \mathbf{k} - \mathbf{e}_i \mid \mathbf{Y}^K(t) = \mathbf{k}\right) = \underbrace{\left(d_i^K k_i + k_i^2 + \sum_{j: \Gamma_{ij}^K < 0} |\Gamma_{ij}^K| k_i k_j\right)}_{\text{death rate for species } i} h + o(h). \quad (3.8)$$

Now if $\boldsymbol{\ell} = (\ell_i) \in \mathbb{N}^N$ represents another population distribution with

$$\|\boldsymbol{\ell} - \mathbf{k}\|_1 = \sum_i |\ell_i - k_i| > 1,$$

then:

$$\mathbb{P}\left(\mathbf{Y}^K(t+h) = \boldsymbol{\ell} \mid \mathbf{Y}^K(t) = \mathbf{k}\right) = o(h). \quad (3.9)$$

Note that there is here a slight abuse of notations in (3.7) and (3.8), where b_i^K (resp. d_i^K) denotes to the individual birth (resp. death) rate of species i , whereas in (3.5), b_n^K (resp. d_n^K) denotes the birth (resp. death) rate of a single species with population size n . In the sequel, we will use index $i \in [N]$ for numbering the species and index $n \in \mathbb{N}$ for the size of a population.

The Lotka-Volterra equation (2.1) in [3] can be obtained along the same principle as for the single species case, when the number of species N is fixed and their initial sizes are large. Consider again that the scaling parameter $K > 0$ goes to infinity and assume that each $Y_i(0)$ is of order K . As before, we consider

$$\mathbf{X}^K(t) := \frac{\mathbf{Y}^K(t)}{K}.$$

Assume that $\mathbf{X}^K(0)$ converges in probability to a deterministic vector $\mathbf{x}^0 \in (0, \infty)^N$. The competition coefficient is rescaled as $\Gamma_{ij}^K = \Gamma_{ij}/K$, while the individual birth and death rates $b_i^K = b_i$ and $d_i^K = d_i$ are kept fixed. This model can be seen as a multiple species generalization of the logistic model introduced by Equation (3.5).

Write $\Gamma = (\Gamma_{ij})$, define the vector $\mathbf{r} = (b_1 - d_1, \dots, b_N - d_N)$ and recall the Hadamard product notation \circ which also applies to two vectors $\mathbf{u} = (u_i)$ and $\mathbf{v} = (v_i)$ and yields $\mathbf{u} \circ \mathbf{v} = (u_i v_i)$. Mimicking the conditional expectation and conditional variance derivations that follow Equation (3.5), one can compute that

$$\begin{aligned} \frac{\mathbb{E}\left(\mathbf{X}^K(t+h) - \mathbf{X}^K(t) \mid \mathbf{X}^K(t)\right)}{h} &\simeq \mathbf{X}^K(t) \circ \left(\mathbf{r} - \mathbf{X}^K(t) + \Gamma \mathbf{X}^K(t)\right), \\ \frac{\text{Cov}\left(\mathbf{X}^K(t+h) - \mathbf{X}^K(t) \mid \mathbf{X}^K(t)\right)}{h} &\simeq 0, \end{aligned}$$

for large K . With these heuristical derivations, we infer that the sequence of processes (\mathbf{X}^K) converges in probability to the deterministic process \mathbf{x} defined as the solution of the multivariate ODE

$$\frac{d\mathbf{x}}{dt}(t) = \mathbf{x}(t) \circ (\mathbf{r} - \mathbf{x}(t) + \Gamma \mathbf{x}(t)), \quad \mathbf{x}(0) = \mathbf{x}^0.$$

which writes componentwise

$$\frac{dx_i}{dt}(t) = x_i(t) (r_i - x_i(t) + (\Gamma \mathbf{x}(t))_i), \quad x_i(0) = x_i^0.$$

This is exactly Eq. (2.1) in [3].

4. From individual-based models to community models with noise

The present appendix is devoted to the derivation of various models arising in Section 5 in [3] from individual birth-and-death processes.

(a) From the stochastic individual-based process to the Feller diffusions

We go back to the individual model defined in Section 3(b) but we now consider a different popular model for the birth and death rates. Given an additional parameter $\sigma > 0$, we replace the rates given by (3.5) with

$$b_n^K = bn + \sigma nK \quad \text{and} \quad d_n^K = dn + \frac{c}{K} n^2 + \sigma nK. \quad (4.1)$$

According to this model, the *individual* birth and death rates scale with K , the order of the population size. This can be realistic when one deals with very small individuals such as unicellular organisms, which have small life expectancy [31].

Doing the same computation as above, we see that the conditional mean is unchanged :

$$\frac{\mathbb{E}[X^K(t+h) - X^K(t) \mid X^K(t)]}{h} \simeq \left(rX^K(t) - cX^K(t)^2\right),$$

while this time, the conditional variance becomes

$$\frac{\text{Var}[X^K(t+h) - X^K(t) \mid X^K(t)]}{h} \simeq 2\sigma X^K(t).$$

This computation shows that, here, the stochasticity does not disappear as $K \rightarrow \infty$. More precisely (see e.g. [25]), $(X^K(t))_{t \geq 0}$ converges to the solution of the so-called Feller stochastic differential equation

$$dX(t) = (rX(t) - cX(t)^2)dt + \sqrt{2\sigma X(t)}dB(t), \quad X(0) = x_0, \quad (4.2)$$

where again $r = b - d$ and B is a standard Brownian Motion. Note that this equation coincides with the Feller equation (5.11) in [3] for $N = 1$.

The multivariate analogue of the Feller equation (4.2), $N \geq 1$, can be obtained in a similar manner. Let $\sigma > 0$ be fixed. Getting back to Equations (3.7)-(3.9), let us replace the natural birth and death rates $b_i k_i$ and $d_i k_i$ in the definition of the transition probabilities with $b_i k_i + \sigma k_i K$ and $d_i k_i + \sigma k_i K$ respectively. As before, $\Gamma_{ij}^K = \Gamma_{ij}/K$. This operation is similar to the change from (3.5) to (4.1) above. In this situation, the limit in distribution of the sequence of processes $(X^K(t))_{t \geq 0}$ is given as follows :

$$dX(t) = X(t) \circ (r - X(t) + \Gamma X(t)) dt + \sqrt{2\sigma X(t)} \circ dB(t),$$

where $B(t)$ is a N -dimensional standard Brownian Motion, which is (5.11) in [3] in the case when $\sigma_i = \sigma$ is the same for each species $i \in [N]$.

(b) Mean-Field approaches

In [32], the limit when the number of species N grows to infinity is considered, starting from the SDE (5.12) in [3] that we recall here:

$$dX(t) = X(t) \circ (\mathbf{1}_N - X(t) + \Gamma X(t)) dt + \lambda \mathbf{1}_N dt + f(X(t)) \circ dB(t),$$

and that is considered on a finite time window $[0, T]$, for a given $T > 0$. More precisely, we consider the limit of

$$\widehat{Q}_N(dx) := \frac{1}{N} \sum_{i=1}^N \delta_{X_i}(dx), \quad (4.3)$$

which is an empirical measure on $\mathcal{C}([0, T], \mathbb{R}_+)$.

The limit Q depends on the choice of a model for Γ . When the correlation $\xi = 0$ (see Eq. (2.7) in [3], Γ is then a non-centered Ginibre matrix), this limit Q solves the equation

$$Q = \mathbb{E}\pi(G^Q), \quad (4.4)$$

where, for a probability measure ν on $\mathcal{C}^+([0, T])$, G^ν is an independent Gaussian process supported by $[0, T]$ and whose law is defined by

$$\mathbb{E}(G_t^\nu) = \int z(t)\nu(dz), \quad \text{Cov}(G_t^\nu, G_s^\nu) = \int z(t)z(s)\nu(dz),$$

and where, for a deterministic function $h(\cdot) \in L^2([0, T])$, $\pi(h)$ is the probability distribution on $\mathcal{C}([0, T], \mathbb{R}_+)$ of the diffusion process

$$dX(t) = X(t) (1 - X(t) + h(t)) dt + \lambda dt + f(X(t))dB(t),$$

where $B(t)$ is a one-dimensional Brownian Motion.

As mentioned in the main text, the mathematical justification for this limit uses an approach of Ben Arous and Guionnet: in [33] and in the subsequent contributions, this convergence is established for related models by means of the large deviations theory, characterizing Q as the unique minimum of an adequate rate function. This work remains to be done in the context of the SDE (5.12) in [3].

Then, a known result, due to Sznitmann [34] asserts that if the components of X are exchangeable, the convergence of \widehat{Q}_N to Q is equivalent to the propagation of chaos: given an arbitrary integer $k > 0$ and a fixed arbitrary set of integers $\{i_1, \dots, i_k\}$, the vector $(X_{i_1}, \dots, X_{i_k})$ converges in distribution to a vector with probability distribution $Q^{\otimes k}$ as $N \rightarrow \infty$.

Note that for exchangeable initial conditions and Γ drawn from an elliptic model, the exchangeability of the components of X in $\mathcal{C}([0, T], \mathbb{R}_+)$ holds. Beyond the elliptical model, one can imagine more sophisticated exchangeable models, such as a model with randomized trophic levels or a randomized space.

The last step is to rigorously study the mean-field equation (4.4) satisfied by the law Q . In the context of the elliptical model, the mean-field equation was studied in [32], where, among other conclusions, the stationary and chaotic phases of [35] were recovered.

(c) Lotka-Volterra in models of adaptive dynamics

A last class of Lotka-Volterra equations with noise can be obtained in the context of Adaptive Dynamics [18,28,36–38]. Start from the individual-based model with N species of large size, so that the Proposition (5.1) in [3] applies and $X_i^K(t) \approx Kx_i(t)$, and assume that the solution of Eq. (5.6) in [3] converges to a stable equilibrium \mathbf{x}^* . Now, add mutations: upon birth, say with probability μ_i^K , the new offspring may be a mutant who can found a new species. If the rates of appearance of mutants are sufficiently small (mutations are rare), *i.e.*

$$e^{-CK} \ll \mu_K \ll \frac{C}{K \log K}, \quad (4.5)$$

(see [19,28]) the time-scales of ecology (*i.e.* births and deaths) and of mutations can be separated. Then, the dynamics can be separated into three phases.

Before going into their precise description, one can mention that adaptive dynamics can be seen as an example of what is called *invasion analysis* in ecology. Other examples have been analyzed through statistical physics tools such as the cavity method (see e.g. Arnoldi et al. [39] for more details) and understanding them fully remains an interesting future task (see Section 6 in [3]).

First phase: invasion probability of the mutant population. Assume that the resident species $i \in [N]$ have abundancies close to the equilibrium state \mathbf{x}^* when the mutant appears. The mutant descendance constitutes the $N + 1$ th specie, let us denote its birth rate by b_{N+1} , its natural death rate by d_{N+1} and by $\Gamma_{j,N+1}$ and $\Gamma_{N+1,j}$ its interaction coefficient with the specie $j \in [N]$. The intraspecific competition rate is assumed to be -1 , as for the other species. Let us also denote by $r_{N+1} = b_{N+1} - d_{N+1}$ the natural growth rate. As long as the new mutant population remains negligible, say with a size smaller than $[K\varepsilon]$ with some small $\varepsilon > 0$, its dynamics is very close to a linear birth and death process whose parameters are functions of \mathbf{x}^* while the other species are unaffected by the new population. More precisely, the rates of this birth and death process are:

$$b_{N+1}, \quad \text{and} \quad d_{N+1} + \sum_{j=1}^N \Gamma_{N+1,j} x_j^*.$$

Note that the non-linearities have disappeared as the state has been frozen to $(x^*, 0)$. For such a birth and death process, the probability of invasion or extinction depends on their fitness

$$\phi_{N+1}(\mathbf{x}^*) = (r_{N+1} - \mathbf{x}^* + \Gamma \mathbf{x}^*) = r_{N+1} - \sum_{j=1}^N \Gamma_{N+1,j} x_j^*.$$

computed in Section 3(a). The probability that the tree associated with the above birth death process is infinite, is

$$p_{N+1}(\mathbf{x}^*) = \frac{[\phi_{N+1}(\mathbf{x}^*)]_+}{b_{N+1}}, \quad (4.6)$$

where $[\cdot]_+$ denotes the positive part. It is also, for the original process, the probability that the mutant population stemming from a single founder reaches size $[K\varepsilon]$ without becoming extinct, and hence it is also called the *invasion probability*. With probability $1 - p_{N+1}(\mathbf{x}^*)$, the descendance of the mutant individual gets extinct before reaching the macroscopic size $[K\varepsilon]$. Notice that $p_{N+1}(\mathbf{x}^*)$ belongs by definition to $[0, 1]$. When the fitness $\phi_{N+1}(\mathbf{x}^*)$ is negative, the new population has no chance of invading the equilibrium \mathbf{x}^* .

By coupling the original individual-based process with linear birth and death processes, it is

possible to show that the time taken by the mutant population to reach the size $\lfloor K\varepsilon \rfloor$ is roughly the same as the time taken by the birth-death process to increase from 0 to $\lfloor K\varepsilon \rfloor$, which is of order

$$T_1^K \propto \log \frac{K}{\phi_{N+1}(\mathbf{x}^*)}.$$

Second phase: approximation by an ODE system. Once the mutant population has reached a size $\lfloor K\varepsilon \rfloor$, following the same path as in Section 3(c), the evolution of the $N + 1$ populations can be approximated by a system of ordinary equations as Eq. (1.1) in [3] but in \mathbb{R}_+^{N+1} and started from the initial condition $(\mathbf{x}^*, \varepsilon)$. Assume that the solutions converge to an equilibrium $\tilde{\mathbf{x}}^*$, some components of which might be zero. This indicates that the appearance of the mutant population can result in wiping out some other species.

The duration of the second phase, *i.e.* the time taken by the random individual-based process to enter a neighborhood of $\tilde{\mathbf{x}}^*$, is of order 1: it is the time predicted by the deterministic dynamical system.

Third phase: extinction of the species corresponding to the zeros of $\tilde{\mathbf{x}}^*$. Once the stochastic individual-based process has entered a neighborhood of $\tilde{\mathbf{x}}^*$, say of width $\varepsilon > 0$, we can show using the theory of large deviations that it stays there during an exponentially long time of order e^{CK} with $C > 0$ (see [19]). The species of sizes less than $\lfloor K\varepsilon \rfloor$ correspond to species $i \in [N]$ can be coupled with subcritical birth-death processes such that $\phi_i(\tilde{\mathbf{x}}^*) \leq 0$. These processes have birth and death rates:

$$b_i, \quad \text{and} \quad \tilde{d}_i = d_i + \sum_{j=1}^{N+1} \Gamma_{i,j} \tilde{x}_j^*.$$

They get almost surely extinct, and the expected time to extinction is

$$\mathbb{E}_{\lfloor \varepsilon K \rfloor} [T_i] = \frac{1}{b_i} \sum_{\ell \geq 1} \left(\frac{b_i}{\tilde{d}_i} \right)^\ell \sum_{k=1}^{\lfloor \varepsilon K \rfloor - 1} \frac{1}{k + \ell} \quad (4.7)$$

(see [26, Section 5.5.3, p.190]).

In Metz et al. [18] and Champagnat [19], the case where a system of $N = 2$ species always ends with the disappearance of one of the species is considered: this corresponds to the rule that *invasion implies fixation*, meaning that the weakest species is lost when a favourable mutant arises. Provided new mutant species arrive sufficiently slowly into the system, the evolution of the population can be described by the sequence of successive dominating species or *trait substitution sequence*. Later, Champagnat and Méléard [36] generalized this construction to the case where species can coexist and construct the *polymorphic evolution sequence* that alternates phases where the dynamics is described by the Lotka-Volterra system (2.1) in [3] and phases of invasion of new arriving species. Lepers et al. [40] built on such construction to provide new models of population genetics, for populations with demographies and competition. In particular, the consideration of a neutral marker (see also [38]) allows to describe the evolution of the genetic diversity in a Lotka-Volterra system between each occurrence of (rare) mutations and to show that the demographic variance of the marker in the species $i \in [N]$ is

$$\frac{2b_i}{x_i^*},$$

which also allows to recover a definition of the effective population size:

$$Ne_i := x_i^*. \quad (4.8)$$

Notice that the population effective size, which partially governs the evolution of the diversity at the neutral marker, depends on the birth and death rates in the specie i , but also on the ones of all the species interacting with specie i (which is hidden in our notation). In particular, it means that

the variance in the neutral diversity within the specie i depends on the competitive interactions of the latter with all the other strains.

5. Mathematical aspects of structured models

(a) Deterministic networks

We gather hereafter mathematical results related to sparse networks when the adjacency matrix Δ of the network is deterministic.

In this paragraph, we propose the following model, where a single quantity $d := d_N$ accounts for the sparsity of the network. This parameter d may depend on the number of species N or be finite.

Consider a d -regular oriented graph with N vertices, each vertex having d neighbours. Matrix Δ had d non-null entries per row and per column and $L := d \times N$ non-null entries overall.

One can now write the interaction matrix Γ as

$$\Gamma = \frac{\Delta \circ A}{\sqrt{d}},$$

where $A = (A_{ij})$ has i.i.d. centered entries. A first question concerns the feasibility of the equilibrium of Lotka-Volterra system stemming from such interaction matrix. In other words, the crux of the issue is the componentwise positivity of the $N \times 1$ vector $\mathbf{x}_N = (x_i)_{1 \leq i \leq N}$, solution of the linear system

$$\mathbf{x}_N = \mathbf{1}_N + \frac{\Gamma}{\alpha_N} \mathbf{x}_N, \quad (5.1)$$

where $\mathbf{1}_N$ is the $N \times 1$ vector of ones.

Notice that since the matrix is sparse the natural normalization is \sqrt{d} instead of \sqrt{N} [41].

The first set involves *block interaction matrix*. Let $N = d \times m$. Denote by \mathcal{S}_m the group of permutations of $[m] = \{1, \dots, m\}$ into itself, by $P_\sigma = (\delta_{i, \sigma(i)})_{i \in [m]}$ the permutation matrix associated to $\sigma \in \mathcal{S}_m$ with δ_{ik} the Kronecker delta function and by $J_d = \mathbf{1}_d \mathbf{1}_d^T$ the $d \times d$ matrix of ones. We shall focus hereafter on $N \times N$ *block-permutation* adjacency matrices Δ_N , of the form

$$\Delta_N = P_\sigma \otimes J_d = \left(\delta_{i, \sigma(i)} J_d \right)_{i \in [m]}, \quad (5.2)$$

where $N = d \times m$ and \otimes designates the Kronecker product.

Such matrix Δ_N gathers species by blocks. Species of block i affect species of block $\sigma(i)$ and are affected by species of block $\sigma^{-1}(i)$.

Let's provide an example to illustrate this. Let $m = 4$ and $\sigma \in \mathcal{S}_4$ defined by :

$$\sigma = \begin{pmatrix} 1 & 2 & 3 & 4 \\ 2 & 4 & 3 & 1 \end{pmatrix}.$$

Matrices P_σ , Δ_N and $\Delta_N \circ A$ are respectively given by :

$$P_\sigma = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 \end{pmatrix}, \quad \Delta = \begin{pmatrix} 0 & J_d & 0 & 0 \\ 0 & 0 & 0 & J_d \\ 0 & 0 & J_d & 0 \\ J_d & 0 & 0 & 0 \end{pmatrix}, \quad \Delta \circ A = \begin{pmatrix} 0 & A^{(1)} & 0 & 0 \\ 0 & 0 & 0 & A^{(2)} \\ 0 & 0 & A^{(3)} & 0 \\ A^{(4)} & 0 & 0 & 0 \end{pmatrix},$$

where $A^{(i)}$, $i = 1, \dots, 4$, is a $d \times d$ random matrix.

In particular, one may assume that, for each i , $A^{(i)}$ has i.i.d. $\mathcal{N}(0, 1)$ entries. With a condition on d depending on N , the same phase transition phenomenon as in the i.i.d. model 3.4 in [3] occurs, even if the normalisation parameter of the interaction matrix Γ passes from \sqrt{N} to \sqrt{d} .

Theorem 5.1. Let $d \geq \log(N)$, $\alpha_N \xrightarrow{N \rightarrow \infty} \infty$ and denote by $\alpha_N^* = \sqrt{2 \log N}$. Let $\mathbf{x}_N = (x_k)_{k \in [N]}$ be the solution of (5.1) with Δ_N given by (5.2) and A_N a random matrix with i.i.d $\mathcal{N}(0, 1)$ entries, then

(i) If $\exists \varepsilon > 0$ such that eventually $\alpha_N \leq (1 - \varepsilon)\alpha_N^*$ then

$$\mathbb{P} \left\{ \min_{k \in [n]} x_k > 0 \right\} \xrightarrow{N \rightarrow \infty} 0.$$

(ii) If $\exists \varepsilon > 0$ such that eventually $\alpha_N \geq (1 + \varepsilon)\alpha_N^*$ then

$$\mathbb{P} \left\{ \min_{k \in [N]} x_k > 0 \right\} \xrightarrow{N \rightarrow \infty} 1.$$

Furthermore, under the assumptions of the second point of theorem 5.1, feasibility and global stability occur simultaneously.

Theorem 5.2. Let $d \geq \log(N)$, $\alpha_N \xrightarrow{N \rightarrow \infty} \infty$ and denote by $\alpha_N^* = \sqrt{2 \log N}$. Let $\mathbf{x}_N = (x_k)_{k \in [N]}$ be the solution of (5.1) with Δ_N given by (5.2) and A_N a random matrix with i.i.d $\mathcal{N}(0, 1)$ entries.

Then, the probability that \mathbf{x}_N is a nonnegative and globally stable equilibrium converges to 1.

Moreover, if $\exists \varepsilon > 0$ such that eventually $\alpha_N \geq (1 + \varepsilon)\alpha_N^*$, then the probability that globally stable equilibrium \mathbf{x}_N is feasible converges to 1.

One can remark that under the first assumptions of theorem 5.2, the equilibrium of the Lotka-Volterra equation is globally stable even if its feasibility is not guaranteed. In other words, some species can get abundances set to zero.

With less structure, one can get an interest in d -regular graphs without this block structure. Henceforth, two different approaches are possible.

The first one is to select a d -regular graph which can have or not have a particular chosen structure and then study the feasibility and the stability of the equilibrium.

The second one consists in choosing a random d -regular graph. A random d -regular graph is a graph randomly selected from $\mathcal{G}_{N,d}$, where $\mathcal{G}_{N,d}$ is the probability space of all d -regular graphs on N vertices. In particular, if the distribution on $\mathcal{G}_{N,d}$ is the discrete uniform distribution, then all the graphs have the same probability to be taken.

Furthermore, the order of magnitude of d is an important factor in the mathematics study of the feasibility and stability issues, notably if d is larger or smaller than $\log(N)$.

(b) Kernel matrices

The goal of this section is to gather some known results in the mathematical literature on kernel matrices. As announced in Section 4 in [3], the take-home message will be that in many situations, the limiting spectrum of a kernel matrix will be a simple deformation (in fact a linear transformation) of the Marcenko-Pastur distribution.

The kernel matrices we will consider are of the following form : let Y be a random vector in \mathbb{R}^p such that $\mathbb{E}(Y) = 0$ and $\mathbb{E}(\|Y\|^2) = 1$. Let X_1, \dots, X_N be i.i.d. copies of Y . Let $g : \mathbb{R}^p \times \mathbb{R}^p \rightarrow \mathbb{R}$ be a symmetric matrix, denoted as the kernel, and $f : \mathbb{R} \rightarrow \mathbb{R}$ a function called the envelope. Typical examples will be $g(x, y) = x^T y$, or $\|x - y\|^2$ and $f(x) = \exp(ex)$ or $(1 + x)^a$ etc.

We will consider the (symmetric) kernel matrix $A = (A_{ij})_{1 \leq i, j \leq N}$ where,

$$A_{ij} := f(g(X_i, X_j)), \quad (5.3)$$

and will be interested in the asymptotics of the empirical spectral measure $\hat{\mu}_N := \frac{1}{N} \sum_{i=1}^N \delta_{\lambda_i(A)}$ in the regime when p and N grows at the same rate that is $\frac{p}{N} \rightarrow \tau \in (0, \infty)$. In random matrix theory, this is called the global regime.

The first interesting and well studied case is the so-called Wishart case, when $g(x, y) = x^T y$ and $f(x) = x$. The matrix A is now just the empirical covariance matrix of the vectors X_1, \dots, X_N .

If the entries of Y are i.i.d., then it is well known (see [42]) that $\hat{\mu}_N$ converges almost surely to the Marcenko-Pastur distribution with parameter τ :

$$d\mu_{MP,\tau}(x) := \left(1 - \frac{1}{\tau}\right) \mathbf{1}_{\tau > 1} \delta_0 + \frac{1}{2\pi x \tau} \sqrt{(b-x)(x-a)} \mathbf{1}_{[a,b]} dx, \quad (5.4)$$

where $a, b := (1 \pm \sqrt{\tau})^2$. In this model, X_i represents the p features of the species i and A_{ij} is a way to measure the similarity of species i and j . Note that these convergence hold for more general random vectors Y , not necessarily with i.i.d. entries, for example when Y is uniformly distributed on the unit sphere in \mathbb{R}^p .

We will now study the case of a regular (differentiable) envelope f that does not depend on the dimension p of the features. There are several papers studying this problem, in particular [43–46]. We present now a general result, found in [43], which can be seen as a transference principle.

Theorem 5.3. *Let $a := \mathbb{E}(g(X_i, X_j))$ for $i \neq j$ and $b := \mathbb{E}(g(X_i, X_i))$. Assume that $\text{Var } g(X_i, X_j) = O(1/p)$ and*

$$\forall \delta > 0, \mathbb{P} \left(\max_{i \neq j} |g(X_i, X_j) - \mathbb{E}(g(X_i, X_j))| > \delta \right) = o(1).$$

Assume that f is differentiable at a and continuous at b . Then, if we denote by G the matrix with entries

$$G_{ij} := \begin{cases} g(X_i, X_j), & \text{if } i \neq j, \\ 0, & \text{otherwise,} \end{cases}$$

and A is defined in (5.3), then A has the same limiting spectral distribution as the matrix

$$B := (af'(a) - f(a) + f(b))\mathbb{I}_N + f'(a)G.$$

In particular, when Y has i.i.d. entries or is uniform on the sphere and $g(x, y) = x^T y$, then the asymptotic spectral distribution of A is a linear transformation of $\mu_{MP,\tau}$.

Let us now give a few ideas of the proof. The main idea is to perform a Taylor expansion of the function f around a (or b) and to use the concentration hypotheses we have made on the quantities $g(X_i, X_j)$ to justify that the two matrices have indeed the same global asymptotic regime.

More precisely, let us define the matrix

$$C := (f(a) - af'(a))\mathbb{J}_N + (af'(a) - f(a) + f(b))\mathbb{I}_N + f'(a)G,$$

with \mathbb{I}_N the identity matrix and \mathbb{J}_N the $N \times N$ matrix whose entries are all one's.

Let us remark that with this description, one can also identify that possible outliers, arising from the rank one deformation $(f(a) - af'(a))\mathbb{J}_N$. We know that they can be of crucial importance for stability.

For $z \in \mathbb{C} \setminus \mathbb{R}$, let $m_A(z) := \int \frac{1}{z-x} d\mu_N(x)$ the trace of the resolvent of the matrix A (also called the Stieltjes transform μ_N) and $m_C(z)$ the trace of the resolvent of the matrix C . To show that the two sequences of matrices have the same limiting spectral measure, it is enough to prove (see [43] for the details) that $m_A(z) - m_C(z)$ converges to zero for all z such that $\Im z > 0$. By Cauchy-Schwarz inequality and then using that $\Im z > 0$, there exists a constant C_z (depending only on z) such that

$$\begin{aligned} |m_A(z) - m_C(z)|^2 &\leq \frac{1}{N} \sum_{i=1}^N \left| \frac{1}{z - \lambda_i(A)} - \frac{1}{z - \lambda_i(C)} \right|^2 \\ &\leq C_z \frac{1}{N} \sum_{i=1}^N |\lambda_i(A) - \lambda_i(C)|^2. \end{aligned}$$

Now, by Hoffman-Wielandt inequality (see e.g. [47]), we have that

$$|m_A(z) - m_C(z)|^2 \leq C_z \frac{1}{N} \sum_{i,j} |A_{ij} - C_{ij}|^2.$$

We now go to the comparison of A and C entrywise. For $i \neq j$, using the regularity of f at point $a = \mathbb{E}(f(g(X_i, X_j)))$, we have

$$\begin{aligned} A_{ij} &= f(g(X_i, X_j)) = f(a) + f'(a)(g(X_i, X_j) - a) + o(g(X_i, X_j) - a) \\ &= C_{ij} + o(g(X_i, X_j) - a), \end{aligned}$$

and the rest is controlled using the concentration hypothesis on $g(X_i, X_j)$ (see [43, lemma 1] for more details), whereas

$$A_{ii} = f(b) + o(f(g(X_i, X_j)) - b) = C_{ii} + o(f(g(X_i, X_j)) - b).$$

To end this review of the mathematical literature on kernel matrices, we want to mention two interesting results. The first one can be stated in the same framework (5.3) as above. In [44], the authors show that, considering an envelope f depending on the dimension p of the features, it is possible to construct an example such that the unenveloped model converges to the Marcenko-Pastur law but the enveloped model converges to a limiting measure which is not a simple linear transformation of the Marcenko-Pastur distribution. In [48], with motivations from neural networks, the authors considered a somehow different kernel matrix. Their starting point is two matrices X of size $N_0 \times M$ and W of size $N_0 \times N_1$ with i.i.d. entries with distribution ν_1 and ν_2 respectively, having both a second moment. The matrix W can be interpreted as a matrix of weights and X a matrix of features. They form a new $N_1 \times m$ matrix R with entries

$$R_{ij} := f\left(\frac{WX}{\sqrt{n_0}}\right)$$

and finally consider the empirical covariance matrix associated to R given as the $N_1 \times N_1$ matrix

$$M := \frac{1}{m} RR^*.$$

In both examples, the limiting measures are described through a functional equation satisfied by their respective Stieltjes transform.

It is not clear to us whether these mathematical results can be helpful for the study of ecological systems.

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