Supplementary Information of ”Artificial selection of communities drives the emergence of structured interactions”

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Contents

1 Phase diagram 2
2 First order perturbation theory of Lotka-Volterra equations 2
3 Maximum over Gaussian samples 3
4 Mutation-Selection Process for any $\gamma$ 4
5 Correlation of the eigenvector with the abundances at equilibrium 5
6 Limit of small $\sigma$ and large $S$ 5
7 Community changes in the absence of selection 7
8 Evolution of species diversity 8
9 Comparison with synthetic interaction matrix 9
10 Generalisations 9
11 Numerical integration method 9
1 Phase diagram

The phase diagram of the random Lotka-Volterra model (equation (12) of the main text) in the space of the parameters $\mu$ and $\sigma$, for the case $\gamma = 0$, was derived in [Bunin, 2017] and is reproduced in Figure 1. In the unbounded growth phase, some population sizes diverge in finite time: this is a pathological feature of the Lotka-Volterra equations, that can only be corrected by modifying the equations [Sidhom and Galla, 2020]. The chaotic phase is characterised by a chaotic dynamics with multiple unstable equilibria. In the unique-equilibrium phase, the community converges, independently of the initial conditions, toward a unique ecological equilibrium where numerous species coexist. In light of this result, we decided to draw our initial interaction matrix in the unique-equilibrium phase as the ecological equilibrium is well defined. In the last two phases, a long-term value of the mean abundance can be computed, depending only on $\mu$, $\sigma$ and $\gamma$: the contour plot of the log of this mean value is represented in Figure 1. Since the total abundance is proportional to the mean abundance, this surface is used in Figure 4 of the main text for the comparison between a purely random and the evolved interaction matrix.

2 First order perturbation theory of Lotka-Volterra equations

The equilibrium condition for the Lotka-Volterra equations is:

$$0 = N_i \left[ K_i - N_i - \sum_j \alpha_{ij} N_j \right] = N_i \left[ K_i - \left( I + \alpha \right) N \right]$$  \hspace{1cm} (1)

We define $\chi_{ij} = \frac{\partial N_j}{\partial K_i}$ the perturbation matrix that measure the effect of a perturbation of the carrying capacities on the equilibrium abundances. We will denote with a $^*$ the vectors or matrices reduced to the set of extant species $\{i = 1, \ldots, S \mid N_i > 0\}$.

The solution of equation (1) is:

$$(I^* + \alpha^*)N^* = K^*$$

$$N^* = (I^* + \alpha^*)^{-1}K^*$$  \hspace{1cm} (2)

We now differentiate equation (1) with respect to $K_j$:

$$0 = \chi_{ij} \left[ K_i - N_i - \sum_k \alpha_{ik} N_k \right] + N_i \left[ \delta_{ij} - \chi_{ij} - \sum_k \alpha_{ik} \chi_{kj} \right]$$  \hspace{1cm} (3)

For the set of extant species the first term is equal to zero and $N_i \neq 0$ so we must have:

$$\chi_{ij} + \sum_k \alpha_{ik} \chi_{kj} = \delta_{ij}$$  \hspace{1cm} (4)

That is to say, in matrix notation:

$$\chi^* + \alpha^* \chi^* = I^*$$  \hspace{1cm} (5)
This gives us an expression for \( \chi^* \):
\[
\chi^* = (I^* + \alpha^*)^{-1}
\]
and from equations (2) and (6) we get that at equilibrium:
\[
N^* = \chi^* K^*
\]

3 Maximum over Gaussian samples

Let \( x_1, \ldots, x_n \) be independent Gaussian random vectors of dimension \( d \) and of law \( \mathcal{N}(0, I_d) \). For \( u \in \mathbb{R}^d \), we define \( f_i = x_i \cdot u \). We want to find the distribution of \( f_* = \max(f_i) \) and of the associated \( x_* \).

We denote \( \hat{u} = \frac{u}{\|u\|} \). Let \( P_u \) and \( P_{u^\bot} \) be the projection matrices on \( \hat{u} \) and on its orthogonal space \( \hat{u}^\bot \) such that we have \( f_i = \|u\| P_u x_i \). By Cochran theorem \( P_u x_i \) and \( P_{u^\bot} x_i \) are independent Gaussian variables of law \( \mathcal{N}(0, P_u) \) and \( \mathcal{N}(0, P_{u^\bot}) \).

As \( P_u x_i \) is aligned with \( \hat{u} \) and because \( \hat{u} \) is normalized, we have \( P_u x_i = y_i \hat{u} \) with \( y_i \sim \mathcal{N}(0, 1) \). We thus have \( f_i > f_j \Leftrightarrow y_i > y_j \). We define \( M_n = \max(y_1, \ldots, y_n) \) such that \( y_* = y_\star \) if \( \forall i \neq \star, y_i < y_* \). By Bayes formula, \( M_n \) has the probability density :
\[
p(M_n = y) = p(y_* = y) \frac{1}{Z} \prod_{i \neq \star} \mathbb{P}(y_i < y) p(y_* = y) = \frac{1}{Z} \Phi(y)^{n-1} \phi(y)
\]
with \( \Phi \) and \( \phi \) the CDF and PDF of Gaussian law and \( Z \) a normalisation constant :
\[
Z = \int_{-\infty}^{+\infty} \Phi(y)^{n-1} \phi(y) \, dy = \frac{1}{n}[\Phi(y)^n]_{-\infty}^{+\infty} = \frac{1}{n}
\]
Finally, \( p(M_n = y) = n\Phi(y)^{n-1} \phi(y) \). This distribution is represented in Figure 2. It is asymptotic to a shifted Gumbel distribution [Gumbel, 2004].

We now use the decomposition \( x_* = P_u x_* + P_{u^\bot} x_* = M_n \hat{u} + P_{u^\bot} x_* \). We thus have :
\[
x_* = M_n \hat{u} + b \quad \text{with} \quad b \sim \mathcal{N}(0, P_{u^\bot})
\]
or, in another notation :
\[
x_* = M_n \hat{u} + P_{u^\bot} z = (M_n - z \cdot \hat{u}) \hat{u} + z \quad \text{with} \quad z \sim \mathcal{N}(0, I_d)
\]
4 Mutation-Selection Process for any $\gamma$

Let $N$ be the equilibrium for the community described by the Lotka-Volterra equations. Each species’ abundance obeys the equation:

$$0 = N_i \left[ K_i - N_i - \sum_j \alpha_{ij} N_j \right].$$  \hfill (12)

After a mutational step, the interaction matrix becomes, at first order in $\varepsilon$:

$$\hat{\alpha}_{ij} = \alpha_{ij} + \varepsilon \sigma \sqrt{S} \eta_{ij}$$  \hfill (13)

with $\eta$ a Gaussian matrix of expected value zero, variance 1 and symmetric correlation $\gamma$.

Let $\hat{N}$ be the equilibrium abundances associated to the interaction matrix $\hat{\alpha}$. To first order in $\varepsilon$, the equation for $\hat{N}$ is:

$$0 = \hat{N}_i \left[ K_i - \hat{N}_i - \sum_j \alpha_{ij} \hat{N}_j - \varepsilon \sigma \sqrt{S} \sum_j \eta_{ij} N_j \right].$$  \hfill (14)

The variable $\hat{N}$ is the solution of equation (12), where we added a perturbation field $\delta K = -\varepsilon \sigma \sqrt{S} \eta N$ of order $\varepsilon$. Defining $\chi_{ij} = \frac{\partial N_i}{\partial K_j}$ as in section 2, for small $\varepsilon$ we can compute the resulting change in abundances $\delta N$ as:

$$\delta N = \chi \delta K = -\varepsilon \sigma \sqrt{S} \chi \eta N$$  \hfill (15)

This change in abundance $\delta N$ will result in a change in the community function $f(N)$ that we can characterise:

$$\delta f = \nabla f(N) \cdot \delta N$$
$$= -\varepsilon \frac{\sigma}{\sqrt{S}} \nabla f(N) \chi \eta N$$
$$= -\varepsilon \frac{\sigma}{\sqrt{S}} ([\chi \nabla f(N)] \otimes N) : \eta$$
$$= -\varepsilon \frac{\sigma}{\sqrt{S}} [v \otimes N] : \eta$$  \hfill (16)

with $v = \chi \nabla f(N)$, $\otimes$ the tensor product ($(u \otimes v)_{ij} = u_i v_j$) and $: \eta$ the tensor contraction ($A : B = \sum_{ij} A_{ij} B_{ij}$). Because in the case $\gamma \neq 0$, the $\eta_{ij}$ are not all independent, we can’t directly apply the results of section 3. For this reason, we use the decomposition of $\eta$ (see SI of [Barbier et al., 2018]):

$$\eta = x + \kappa x^\top \frac{1}{\sqrt{1 + \kappa^2}}$$  \hfill (17)

with $\kappa = \frac{1 - \sqrt{1 - \gamma^2}}{\gamma}$ and $x$ a Gaussian matrix of mean 0, variance 1 with no correlations between $x_{ij}$ and $x_{ji}$ for $i \neq j$.

Using $A : x^\top = A^\top : x$, we have

$$\delta f = -\varepsilon \frac{\sigma}{\sqrt{S} \sqrt{1 + \kappa^2}} [v \otimes N + \kappa N \otimes v] : x$$  \hfill (18)

We now denote $u = -\varepsilon \frac{\sigma}{\sqrt{S} \sqrt{1 + \kappa^2}} [v \otimes N + \kappa N \otimes v]$ so that $\delta f = u : x$ as in section 3, but this time $x$ and $u$ are matrices instead of vectors and the scalar product is replaced by a tensor contraction. However, by packing the two indices $ij$ of $x_{ij}$ and $u_{ij}$ into a general index $\alpha$ we can interpret the exact same form as the scalar product of two large vectors of dimension $d = S^2$. In this way, the tensor contraction reduces to a simple scalar product so that we can directly apply the results of section 3.

Among $n$ different realisations of the random matrix $x$ (and thus of $\eta$), the one that will give rise to the highest score can be written:

$$x_* = M_n \frac{u}{\| u \|} = -\frac{M_n}{N} [v \otimes N + \kappa N \otimes v] + B$$  \hfill (19)
and is associated with a change in score:

$$\delta f_* = u : x_* = \frac{\varepsilon \sigma N}{\sqrt{S \sqrt{1 + \kappa^2}}} M_n$$  \tag{20}$$

with $N = \|v \otimes N + \kappa N \otimes v\|$, $M_n$ the random variable defined in section 3 and $B$ a Gaussian matrix "orthogonal to the selected direction" ($u : B = 0$). This equation reduces to equation (9) of the main text when $\gamma = 0$.

Putting the expression of $x_*$ in the formula for $\eta$ and using $\frac{2\varepsilon}{1+\kappa^2} = \gamma$ we get an expression for the selected $\eta_*:

$$\eta_* = -\frac{M_n}{N \sqrt{1 + \kappa^2}} \left[ (1 + \kappa^2) v \otimes N + 2\kappa N \otimes v \right] + \tilde{B}$$  \tag{21}$$

with $\tilde{B} = \frac{B + sB^T}{\sqrt{1 + \kappa^2}}$ being a Gaussian matrix of mean 0 and variance 1 with symmetric correlation $\gamma$ (it is the same construction as equation (17)).

The resulting selected interaction matrix can be written:

$$\hat{\alpha}_* = \alpha - \frac{\varepsilon \sigma}{\sqrt{S}} \left( \frac{M_n \sqrt{1 + \kappa^2}}{N} [v \otimes N + \gamma N \otimes v] - \tilde{B} \right)$$  \tag{22}$$

In the case $\gamma = 0$, we obtain equation (12) of the main text.

5 Correlation of the eigenvector with the abundances at equilibrium

Fig. 3 shows that at a late generation ($\tau = 2000$), the vector of abundances at equilibrium is strongly correlated with the eigenvector associated to the left-most isolated eigenvalue of $\alpha$ and to the vector $v = \delta N_T = \delta K$. Theses correlations explain the structure of $\alpha$: Fig. 4 shows that the species that are the most abundant are also the most mutualist.

![Figure 3: Coefficients of $N_*, v_*$ (as defined in the main text) and of the left eigenvector $q_*$ associated to the isolated eigenvalue of $\alpha$ at generation $\tau = 2000$ reduced to extant species, all normalised, with indices sorted by decreasing carrying capacity. It is evident that $N_*, v_*$ and $q_*$ are strongly correlated. Their dependence on $K$ is weaker, but still sufficient for the structure to emerge in Fig. 5 of the main text.](image)

This correlation is caused by two effects that feed back onto one another. First, species with mutualistic interactions are more likely to be abundant than those with competitive interactions. Secondly, as shown in Eq. 7 (Main text), the most abundant species will see their interactions evolve faster toward mutualism.

6 Limit of small $\sigma$ and large $S$

For simplicity, we consider here that all the carrying capacities are equal (we set $K_i = 1$, without loss of generality). When $S \gg 1$, $\sigma(\tau)$ is almost constant, and we assume here that it is initially small.
Figure 4: Coefficients of the interaction matrix $\alpha$ at generations 1 (left) and 2000 (right) with rows and columns sorted by decreasing equilibrium abundances at $\tau = 2000$ for the same simulation as described in Materials and Methods. Only the species that have positive abundance at generation 2000 are shown.

For small $\sigma$, the interaction matrix $\alpha(\tau)$ can be characterised only by its mean value:

$$\alpha_{ij}(\tau) = \frac{\mu(\tau)}{S} + \mathcal{O}(\sigma)$$  \hspace{1cm} (23)

that we write in matrix notation:

$$\alpha(\tau) = \frac{\mu(\tau)}{S} \mathbf{1}\mathbf{1}^\top + \mathcal{O}(\sigma)$$  \hspace{1cm} (24)

Then, following eq (6), the perturbation matrix can be expressed as:

$$\chi(\tau) = (\mathbb{I} + \alpha(\tau))^{-1}$$

$$= \left( \mathbb{I} + \frac{\mu(\tau)}{S} \mathbf{1}\mathbf{1}^\top + \mathcal{O}(\sigma) \right)^{-1}$$

$$= \mathbb{I} - \frac{\mu(\tau)}{1 + \mu(\tau)} \mathbf{1}\mathbf{1}^\top + \mathcal{O}(\sigma)$$  \hspace{1cm} (25)

using Sherman–Morrison formula. With this, we can compute the abundances at equilibrium:

$$\mathbf{N}(\tau) = \chi(\tau)\mathbf{1}$$

$$= \frac{1}{1 + \mu(\tau)} \mathbf{1} + \mathcal{O}(\sigma)$$  \hspace{1cm} (26)

The total abundance along the evolutionary trajectory depends, as well as the interaction matrix, only on the mean interaction strength:

$$\frac{N_T(\tau)}{S} = \langle N_i(\tau) \rangle = \frac{1}{1 + \mu(\tau)} + \mathcal{O}(\sigma).$$  \hspace{1cm} (27)

In the same fashion, we get that:

$$\mathbf{v}(\tau) = \frac{1}{1 + \mu(\tau)} \mathbf{1} + \mathcal{O}(\sigma)$$  \hspace{1cm} (28)

Equation (22) for $\gamma = 0$ or equation (6) of the main text then gives the recursive equation for $\mu(\tau)$:

$$\mu(\tau + 1) = \mu(\tau) - \sqrt{1 + \gamma} \varepsilon \frac{M_n \sigma}{\sqrt{S}}$$  \hspace{1cm} (29)

that has for solution:

$$\mu(\tau) = \mu(0) - \tau \varepsilon \frac{\sigma}{\sqrt{S}} \frac{M_n}{\sqrt{1 + \gamma}}$$  \hspace{1cm} (30)

Fig. 5 shows that equations (27) and (30) match the numerical simulations remarkably well in the case of an initial $\sigma = 0.1$ and $S = 100$. 
7 Community changes in the absence of selection

We now look at the evolutionary dynamics of the interaction matrix in the neutral regime, when any community leaves an offspring with equal probability. In this subsection only, we denote for simplicity \( d = S(S - 1) \) the number of interaction terms and every sum \( \sum \) are index on \( i \neq j \). The notations \( b_{ij} \) is not the same as before.

The process is the following:

- We have \( a_{ij}^{(t)} = m_t + \text{std}_t b_{ij}^{(t)} \) with \( m_t = \frac{1}{d} \sum a_{ij}^{(t)} \) the empirical mean and \( \text{std}_t = \sqrt{\frac{1}{d} \sum (a_{ij}^{(t)} - m_t)^2} \) the empirical standard deviation.

- We then define \( a_{ij}^{(t+1)} = m_t + \text{std}_t b_{ij}^{(t+1)} \) with \( b_{ij}^{(t+1)} = \frac{a_{ij}^{(t)} + \varepsilon \eta_{ij}^{(t+1)}}{\sqrt{1 + \varepsilon^2}} \).

- We repeat the operation.

Note that by definition, \( a_{ij} \) have the following properties: \( \sum a_{ij}^{(t)} = 0 \) and \( \frac{1}{d} \sum (a_{ij}^{(t)})^2 = 1 \).

We now wish to get an expression of \( \mu_{t+1} \) as a function of \( \mu_t \) and \( \eta \). We start with the empirical mean:

\[
m_{t+1} = \frac{1}{d} \sum a_{ij}^{(t+1)} = m_t + \frac{\text{std}_t}{d} \sum b_{ij}^{(t+1)} = m_t + \frac{\text{std}_t \varepsilon}{\sqrt{1 + \varepsilon^2}} \frac{1}{d} \sum \eta_{ij}^{(t+1)}
\]

Using the Central Limit Theorem and writing with \( \mu, S \) and \( \sigma \) we get:

\[
\mu_{t+1} \sim \mathcal{N}(\mu_t, \sigma_t \frac{\varepsilon}{\sqrt{S(1 + \varepsilon^2)}})
\]

To have a similar expression for \( \sigma \) the computation is a bit longer. We start with the empirical variance:

\[
\text{Var}_{t+1} = \frac{1}{d} \sum (a_{ij}^{(t+1)} - m_{t+1})^2 = \frac{1}{d} \sum (m_t - m_{t+1} + \text{std}_t b_{ij}^{(t+1)})^2
\]

\[
= \frac{\text{Var}_t}{d} \sum \left( \frac{a_{ij}^{(t)} + \varepsilon \eta_{ij}^{(t+1)}}{\sqrt{1 + \varepsilon^2}} - \frac{\text{std}_t \varepsilon}{\sqrt{1 + \varepsilon^2}} \frac{1}{d} \sum \eta_{k,l}^{(t+1)} \right)
\]

We denote \( \langle \eta \rangle = \frac{1}{d} \sum_{k \neq l} \eta_{k,l}^{(t+1)} \) the empirical mean of \( \eta \) so that:

\[
\text{Var}_{t+1} = \frac{\text{Var}_t}{(1 + \varepsilon^2)d} \sum (a_{ij}^{(t)} + \varepsilon (\eta_{ij} - \langle \eta \rangle)) = \frac{\text{Var}_t}{(1 + \varepsilon^2)d} \left[ \sum (a_{ij}^{(t)})^2 + \varepsilon \sum (\eta_{ij} - \langle \eta \rangle)^2 + 2\varepsilon \sum a_{ij}^{(t)} (\eta_{ij} - \langle \eta \rangle) \right]
\]
We now use the fact that $\sum a_{ij}^{(t)} = 0$ and $\frac{1}{d} \sum (a_{ij}^{(t)})^2 = 1$. Furthermore, as $\eta$ is a Gaussian random variable, $\sum (\eta_{ij} - \langle \eta \rangle)^2 \sim \chi^2_{d-1}$ (chi-square distribution).

As $a_{ij}$ and $\eta_{ij}$ are uncorrelated we have by the Central Limit Theorem:

$$\frac{1}{d} \sum a_{ij} \eta_{ij} \sim \mathcal{N}(0, \frac{1}{\sqrt{d}}) \quad (33)$$

We then use the asymptotic expression: $\chi^2_{d-1} \rightarrow d - 1 + \sqrt{2(d-1)} \mathcal{N}(0,1)$ so that in the large $S$ (and thus $d$) limit:

$$\text{Var}_{t+1} = \frac{\text{Var}_{t}}{(1 + \varepsilon)^2} \left[ 1 + \varepsilon^2 + \varepsilon^2 \sqrt{\frac{2}{d}} \mathcal{N}(0,1) + \frac{2\varepsilon}{\sqrt{d}} \mathcal{N}(0,1) \right]$$

But as $\varepsilon \ll 1$ we can neglect the first normal distribution:

$$\text{Var}_{t+1} = \text{Var}_{t} \left( 1 + \frac{2\varepsilon}{1 + \varepsilon^2} \sqrt{\frac{2}{d}} \mathcal{N}(0,1) \right)$$

Using the Taylor expansion of the square root we get the expression for $\sigma$:

$$\sigma_{t+1} \sim \mathcal{N}(\sigma_t, \sigma_t \frac{\varepsilon}{S(1 + \varepsilon^2)}) \quad (35)$$

We thus observe that this process is a isotropic random walk in the space $(\mu, \sigma)$ and that the variation in $\sigma$ are small compared to the one in $\mu$: it scales like $\frac{1}{S}$ for $\sigma$ and $\frac{1}{\sqrt{S}}$ for $\mu$. Thus, for large $S$, $\sigma$ evolves with a longer time-scale than $\mu$ and so can be approximated as constant. These results are consistent with the numerical observation in Figure 6.

Figure 6: Evolution of the empirical $\mu$ (top-left), $\sigma$ (top-right) and mean population $\langle N \rangle$ (bottom-right) in absence of selection, with the parameters $S = 100$, $\varepsilon = 0.1$, $\tau_{\text{max}} = 100$, $n = 50$ and $\gamma = 0$. For the panels in the top and in the bottom-right, the red lines are the mean of the quantity of interest and the blue area is bounded by the maximum and minimum values. The green line in the bottom-right panel represent the predicted value from the cavity method. The panel in the bottom-left is the evolution of the communities in the $(\mu, \sigma)$ space.

8 Evolution of species diversity

Fig. 7 represents the evolution of the diversity (or species richness) $\phi = \frac{S^*}{S}$ along the same evolutionary trajectory as the figures of the main text. This shows that diversity decreases along the evolutionary trajectory but the number of extant species does not collapse, and the community maintains a substantial amount of diversity.
Figure 7: Changes of species richness along an evolutionary trajectory. Selection for increased total abundance leads to a decrease in the species richness. The parameters of the simulation are described in the Methods section.

9 Comparison with synthetic interaction matrix

Following [Barbier et al., 2021], we can compute the inferred interaction matrix $\beta$ that gives rise to the observed equilibrium abundances and has a given mean interaction $\bar{\beta}$. Neglecting the correlations between different matrix elements (which are sub-leading in the large $S$ limit), such matrix is of the form:

$$\beta_{ij}^* = \bar{\beta} + \frac{(K_i - N_i - \bar{\beta})N_j}{\sum_k N_k^2} + \sigma B_{ij}$$  \hspace{1cm} (36)

with $B$ a Gaussian matrix of mean 0 and variance 1. Fig. 8 shows the eigenvalue distribution of such matrix, compared to the one obtained from the evolutionary process. The agreement is remarkable.

10 Generalisations

We checked that the features presented in the main text hold for a broad range of parameters in the numerical simulations, in particular for most initial values of $(\mu, \sigma)$ as long as we are in the unique equilibrium phase (see section 1), for any values of $m$ and $n$ (when selecting $m$ communities out of $n$) as long as $n > 1$ and $m < n$ (theses two extreme cases lead to no selection) and for any value of $\gamma$ with the exception of $\gamma = -1$, as expected from the equations discussed in the main text. The addition of a small immigration term to the ecological dynamics, moreover, doesn’t qualitatively alter the results.

We considered different selection functions, such as $f = \sum w_i N_i$ with all weights $w_i$ being positives. Similar results keep holding. This can be understood by interpreting the selection process as a modification of selection for the total abundance, obtained by rescaling species abundances as $w_i N_i$, so that species $i$ has carrying capacities $w_i K_i$ and an interaction matrix $\alpha_{ij} w_i / w_j$. The same computations explained in the main text and in Section 4 then allow us to obtain the exact same recursive equations for $f$ and $\alpha$ but with $v = \delta f / \delta K$ and $v^*(\tau) = (\mathbb{I}^* + \alpha^*(\tau)^T)^{-1} w^*$.

11 Numerical integration method

We here present an integration method for the Lotka-Volterra equations:

$$\frac{dN_i}{dt} = r_i N_i \left( K_i - N_i - \sum_{j \neq i} \alpha_{ij} N_j \right),$$  \hspace{1cm} (37)

with $K_i$ the carrying capacities, $r_i$ the growth rates (all equals to one in the paper) and $\alpha$ the interaction matrix.

In contrast to the Euler method where one assumes that the derivative is constant during a short interval of time $dt$, potentially leading to negative populations for strong derivatives, we assume that only the abundances of the other species $(N_j(t))_{j \neq i}$ are constant. During this time interval $[t, t + dt]$, the equations are reduced to uncoupled logistic equations of effective carrying capacities $\tilde{K}_i = K_i - \sum_{j \neq i} \alpha_{ij} N_j(t)$ and effective growth
Figure 8: Evolved and synthetic matrix have similar structure of eigenstates. Comparison between the eigenvalues of the evolved interaction matrix $\alpha^*$ (blue) and of the maximum entropy matrix $\beta^*$ (green) at generation $\tau = 1500$ (Top) and the coefficient of the eigenvector of the minimal eigenvalue (middle). Evolution of the minimum eigenvalue of both matrices for every generations (Bottom).
rates $\tilde{r}_i(t) = r_i \tilde{K}_i(t)/K_i$. These logistic equations can be analytically solved in the interval $[t, t+dt]$, giving the recursive formula:

$$N_i(t+dt) = \frac{N_i(t)\tilde{K}_i(t)}{N_i(t) + (\tilde{K}_i(t) - N_i(t)) \exp \left( -\tilde{r}_i(t) dt \right)}$$

(38)

with

$$\begin{cases}
\tilde{K}_i(t) = K_i - \sum_{j \neq i} \alpha_{ij} N_j(t) \\
\tilde{r}_i(t) = r_i \frac{\tilde{K}_i(t)}{K_i}
\end{cases}$$

(39)

We then have a logistic-by-part curve that avoids abundances to become negative. We can show by Taylor expansion that we get back the Euler method at first order in $dt$.

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