

Supplementary Material

Title needed

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1 Supplementary Methods

1.1 Parameterization of the model

We parameterized the model considering that each parameter X is modelled following a uniform distribution $\text{Unif}(X_0 - \delta, X_0 + \delta)$ with $\delta = 0.05X_0$. Hereafter and in Main Text, we call the parameters X_0 and δ metaparameters. For the matrices, $\gamma_{i\mu} = g_{i\mu} \odot G_{i\mu}$ and $\alpha_{\mu i} = a_{i\mu} \odot A_{i\mu}$, where $g_{i\mu} = \text{Unif}(\gamma_0 - \delta, \gamma_0 + \delta)$, $a_{i\mu} = \text{Unif}(\alpha_0 - \delta, \alpha_0 + \delta)$ and $G_{i\mu}(A_{i\mu})$ is a binary matrix describing the consumption (secretion) of resource μ by species i . The specific metaparameter values are summarized in Table [Ref].

In our analysis, we vary three metaparameters controlling the consumption rate (γ_0), secretion rate (α_0) and abundances at equilibrium (S_0). The remaining parameters are fixed as follows. The external input of resources $l_0 = 1$ and equilibrium abundances of resources $R_0 = 1$ set the units of time and biomass, respectively. To choose the efficiency of transformation of nutrients into cell biomass, σ_0 , we noted (see Eq. 4 below) that the feasibility of the system depends on $\min(\sigma_0, 1 - \sigma_0)$, suggesting the existence of two regimes $\sigma_0 < 0.5$ and $\sigma_0 > 0.5$. Estimating the efficiency is difficult since it depends on the context in which is measured such as the presence of nutrients. Current data suggests that it is small and independent of body size [DeLong], so we fix it to a constant value $\sigma_0 = 0.25$. The remaining parameters, m_μ and d_i are fixed choosing a value of the variable metaparameters γ_0 , α_0 and S_0 and solving the system of equations at steady state.

	Metaparameter
S_i^*	$S_0 \in (0, 1]$
$\gamma_{i\mu}$	$\gamma_0 \in (0, 1]$
$\alpha_{i\mu}$	$\alpha_0 \in [0, 1]$
l_μ	$l_0 = 1$
R_μ^*	$R_0 = 1$
σ_i	$\sigma_0 = 0.25$
m_μ	Solved at fixed point
d_i	Solved at fixed point

Table 1: **Metaparameters** considered in the model.

1.2 Set of matrices

Léo please explain the new Monte Carlo algorithm here.

2 Supplementary Notes

2.1 Determination of the feasibility volume

To determine the feasibility conditions we start considering the dynamical equations at a fixed point given by positive equilibrium abundances S^* , R^* :

$$\begin{aligned} 0 &= l_\mu - \sum_j \gamma_{j\mu} S_j^* R_\mu^* + \sum_j \alpha_{\mu j} S_j^* - m_\mu R_\mu^* \\ 0 &= \sum_\nu \sigma_\nu \gamma_{i\nu} R_\nu^* S_i^* - \sum_\nu \alpha_{\nu i} S_i^* - d_i S_i^*, \end{aligned} \quad (1)$$

and we impose two conditions. Firstly, conservation of biomass

$$\sum_\nu (1 - \sigma_{i\nu}) \gamma_{i\nu} R_\nu^* \geq \sum_\nu \alpha_{\nu i} \quad \forall i = 1, \dots, N_S \quad (2)$$

and, secondly, positivity of all metaparameters

$$\begin{aligned} d_i &= \sum_\nu (\sigma_{i\nu} \gamma_{i\nu} R_\nu^* - \alpha_{\nu i}) > 0 \quad \forall i = 1, \dots, N_S \\ m_\mu &= \frac{l_\mu - \sum_j (\gamma_{j\mu} R_\mu^* - \alpha_{\mu j}) S_j^*}{R_\mu^*} > 0 \quad \forall \mu = 1, \dots, N_R. \end{aligned} \quad (3)$$

In the following derivation, we considered the mean values of variables at steady state and parameters, represented by their respective metaparameters (see Table 1). By doing so, the most restrictive conditions imposed by Eqs. 2 and 3, will be given by the species (resources) with the most extreme matrix degrees.

Combining both conditions we find, after some algebra, that feasibility is determined by the inequalities

$$\max_i \left\{ \frac{\deg(A, i)}{\deg(G, i)} \right\} \alpha_0 \lesssim \min(1 - \sigma_0, \sigma_0) \gamma_0 R_0 \lesssim \min(1 - \sigma_0, \sigma_0) \min_\nu \left\{ \frac{l_0}{\deg(G, \nu) S_0} + \frac{\deg(A, \nu)}{\deg(G, \nu)} \alpha_0 \right\}, \quad (4)$$

where $\deg(X, i)$ ($\deg(X, \nu)$) indicates the degree of matrix X for species i (resource ν) and whose limiting cases determine the more strict conditions. [APG: We could consider adding the derivation as an Appendix]

In the absence of syntrophy, the second inequality in Eq. 4 becomes

$$\gamma_0 \lesssim \frac{l_0}{\max_\nu \{\deg(G, \nu)\} R_0 S_0}, \quad (5)$$

indicating that the upper bound of the consumption strength is relaxed if the external rate of supplied resources increases (higher l_0), while it becomes more strict for larger steady state abundances (R_0 , S_0) or if species consume more resources (in particular the one consumed the most, i.e. $\max_\nu \{\deg(G, \nu)\}$).

Figure [Ref] shows the proportion of feasible systems for 200 realizations of the parameters, for two consumption matrices G_1 and G_2 . We observe a sharp transition between a region in which all realizations are feasible and another region in which all are unfeasible, with a thin transition region in which feasibility depends on the specific realization. The boundary between both regions can be determined by imposing the equality in Eq. 5, which yields $\gamma_0 = K S_0^{-1}$ with $K = l_0 / \max_{\nu} \{\deg(G, \nu)\} R_0$. Considering the metaparameters in the examples, we obtain $S_0 = 0.125 \gamma_0^{-1}$ for G_1 and $S_0 = 0.077 \gamma_0^{-1}$ for G_2 , showing good agreement with a fit to the empirical values ($S_0 = (0.124 \pm 3 \times 10^{-8}) \gamma_0^{-1}$ for G_1 and $S_0 = (0.076 \pm 7 \times 10^{-9}) \gamma_0^{-1}$ for G_2).

In Main Text, we showed that the feasibility volume shrinks when the syntrophy strength α_0 increases. This is explained by the first inequality of Eq. 4, which shows that γ_0 is lower bounded by

$$\gamma_0 \gtrsim \frac{\max_i \left\{ \frac{\deg(A, i)}{\deg(G, i)} \right\}}{\min(1 - \sigma_0, \sigma_0) R_0} \alpha_0.$$

As we showed when there is no syntrophy, also the abundance of consumers S_0 is upper bounded when there is syntrophy. Following the second inequality of Eq. 4 we find

$$\gamma_0 \lesssim \frac{1}{R_0} \min_{\nu} \left\{ \frac{l_0}{\deg(G, \nu) S_0} + \frac{\deg(A, \nu)}{\deg(G, \nu)} \alpha_0 \right\},$$

which, if the resource more consumed is also the one less secreted (which would be expected e.g. if there is no intraspecific syntrophy) the analytical expression found for the case with no syntrophy could be recovered.

2.2 Sufficient conditions for dynamical stability

The characteristic equation

To study the dynamical stability of the system we start computing its Jacobian matrix:

$$J = \begin{pmatrix} \left(-m_{\mu} - \sum_j \gamma_{j\mu} S_j \right) \delta_{\mu\nu} & -\gamma_{j\mu} R_{\mu} + \alpha_{\mu j} \\ \sigma_{i\nu} \gamma_{i\nu} S_i & (\sum_{\nu} \sigma_{i\nu} \gamma_{i\nu} R_{\nu} - d_i - \sum_{\nu} \alpha_{\nu i}) \delta_{ij} \end{pmatrix}, \quad (6)$$

where δ is the Kronecker delta. Since we are interested in the stability of the system at an equilibrium point $\{R_{\mu}^*, S_i^*\}$, from Eq. 1 we can see that

$$\sum_{\nu} \sigma_{i\nu} \gamma_{i\nu} R_{\nu}^* - d_i - \sum_{\nu} \alpha_{\nu i} = 0. \quad (7)$$

Hence, at equilibrium the Jacobian J^* will have the following block form:

$$J^* = \begin{pmatrix} -D & \Gamma \\ B & 0 \end{pmatrix}, \quad (8)$$

where

- $D_{\mu\nu} = \text{diag}(m_{\mu} + \sum_j \gamma_{j\mu} S_j^*) = \text{diag}\left(\frac{l_{\mu} + \sum_j \alpha_{\mu j} S_j^*}{R_{\mu}^*}\right)$ is a positive $N_R \times N_R$ diagonal matrix,
- $\Gamma_{\mu j} = -\gamma_{j\mu} R_{\mu}^* + \alpha_{\mu j}$ is a $N_R \times N_S$ matrix which does not have entries with a definite sign.
- $B_{i\nu} = \sigma_{i\nu} \gamma_{i\nu} S_i^*$ is a $N_S \times N_R$ matrix with positive entries.

The stability of the system is analysed studying the eigenvalue problem determined by the characteristic equation

$$\det(J^* - \lambda) = 0 \quad (9)$$

or, more explicitly,

$$\det \begin{pmatrix} -D - \lambda & \Gamma \\ B & -\lambda \end{pmatrix} = 0. \quad (10)$$

If $\lambda \neq 0$, we can simplify this equation using the properties of block matrices [Ref Powell 2011]:

$$\det \begin{pmatrix} -D - \lambda 1_{N_R} & \Gamma \\ B & 0 - \lambda 1_{N_S} \end{pmatrix} = \det(-\lambda 1_{N_S}) \det \left(-D - \lambda 1_{N_R} + \frac{1}{\lambda} \Gamma B \right). \quad (11)$$

Hence, Eq. (10) becomes:

$$\det(\lambda^2 1_{N_R} + D\lambda - \Gamma B) = 0. \quad (12)$$

The complexity here is already reduced because we go from the determinant of a $N_R + N_S$ square matrix to a N_R square matrix. Using standard properties of determinants, we can rewrite Eq. (12) as¹:

$$\det(-D) \det(-D^{-1}\lambda^2 - \lambda + D^{-1}\Gamma B) = 0 \iff \det(S(\lambda) - \lambda) = 0 \quad (13)$$

with

$$S(\lambda) = D^{-1}\Gamma B - D^{-1}\lambda^2, \quad (14)$$

or, component-wise,

$$S_{\mu\nu} = \frac{1}{D_\mu} \left[\left(\sum_i \Gamma_{\mu i} B_{i\nu} \right) - \lambda^2 \delta_{\mu\nu} \right], \quad (15)$$

where the ΓB N_R -dimensional square matrix is given by:

$$(\Gamma B)_{\mu\nu} = \sum_i \Gamma_{\mu i} B_{i\nu} = \sum_i (\alpha_{\mu i} - \gamma_{i\mu} R_\mu^*) \sigma_{i\nu} \gamma_{i\nu} S_i^*. \quad (16)$$

The strategy we use to solve Eq. (13) is inspired by the one followed in Ref. [butler_stability_2018]. We assume the system is in an unstable regime, *i.e.* there exists at least one $\lambda \in \sigma(J^*)$ with $\text{Re}(\lambda) \geq 0$ that satisfies Eq. (12) and such that $\text{Re}(\lambda) > 0$. By Eq. (13), λ is also an eigenvalue of $S(\lambda)$. If we find conditions under which the real part of the spectrum of $S(\lambda)$ is entirely negative, we will know that $\text{Re}(\lambda) \leq 0$. As this is a contradiction to the hypothesis that the regime is unstable, we must conclude that the regime is stable². Hence, the general idea is to find regimes where we know that the spectrum of S will be entirely negative for a positive λ .

Derived conditions from Gerschgorin circle theorem

The Gerschgorin circle theorem *gerschgorin_u ber_1931 states that every eigenvalue of a $N \times N$ square matrix A is located in one of the N discs \tilde{D}_i defined by:*

$$\tilde{D}_i \equiv \left\{ z \in \mathbb{C} : |z - A_{ii}| \leq \sum_{j \neq i} |A_{ij}| \right\}. \quad (17)$$

¹We can do this because since $m_\mu > 0$, we know D will always be invertible.

²Indeed, Eq.(12) assumes already that either $\text{Re}(\lambda_1) > 0$ or $\text{Re}(\lambda_1) < 0$.

Intuitively, the circle theorem tells us that the eigenvalues of a matrix deviate from the diagonal elements by a value bounded by the sum of the off-diagonal elements. We note that, if all the discs \tilde{D}_i are located to the left of the imaginary axis (*i.e.* the discs contain only numbers with a negative real part), then the eigenvalues of A are all negative. This theorem allow us to consider two results in our problem. Firstly, it provides the following bound for the eigenvalues

$$|\lambda| \leq R_c \quad \forall \lambda \in \sigma(J^*), \quad (18)$$

where R_C is the *critical radius* and $\sigma(J^*)$ stands for the spectrum of the Jacobian at equilibrium. To estimate R_C we note that all eigenvalues of J^* will be located in one of the $N_R + N_S$ discs of J^* , among the N_R “resources discs”:

$$\tilde{D}_\mu^R \equiv \left\{ z \in \mathbb{C} : |z + D_\mu| \leq \sum_j |\Gamma_{\mu j}| \right\} \quad \forall \mu = 1, \dots, N_R, \quad (19)$$

and the “consumers discs”:

$$\tilde{D}_i^C \equiv \left\{ z \in \mathbb{C} : |z| \leq \sum_\nu |B_{i\nu}| \right\} \quad \forall i = 1, \dots, N_S. \quad (20)$$

According to the circle theorem Eq.(??), all eigenvalues will be in the union of these circles, *i.e.* there exists $\forall \lambda \in \sigma(J^*)$ at least one μ^* or one i^* such that:

$$|\lambda| \leq \sum_\nu |B_{i^*\nu}| \quad (21)$$

or

$$|\lambda + D_{\mu^*}| \leq \sum_j |\Gamma_{\mu^* j}|. \quad (22)$$

The triangle inequality implies:

$$|\lambda| \leq |\lambda + D_{\mu^*}| + |-D_{\mu^*}| \leq \sum_j |\Gamma_{\mu^* j}| + |-D_{\mu^*}| = \sum_j |\Gamma_{\mu^* j}| + D_{\mu^*}. \quad (23)$$

The only way both Eq.(21) and (23) are satisfied for all eigenvalues, and especially the one with the highest real part λ_1 is if they are bound by the maximum of both RHS of these equations, which allow us to determine R_c as:

$$R_c \equiv \max \left\{ \max_i \left\{ \sum_\nu |B_{i\nu}| \right\}, \max_\mu \left\{ \sum_j |\Gamma_{\mu j}| + D_\mu \right\} \right\}. \quad (24)$$

The second result derived from the theorem is the following Lemma, which puts an upper bound on the real part of the spectrum³ of any square matrix.

Lemma 1. *If a N -dimensional square matrix A verifies the equations:*

$$\text{Re}(A_{ii}) + \sum_{j \neq i} |A_{ij}| < 0, \quad \forall i = 1, \dots, N, \quad (25)$$

then $\text{Re}(\lambda) < 0 \quad \forall \lambda \in \sigma(A)$.

Proof. Let $\lambda \in \sigma(A)$. By the circle theorem, there exists $k \in \{1, \dots, N\}$ such that :

$$|\lambda - A_{kk}| \leq \sum_{j \neq k} |A_{kj}|. \quad (26)$$

³We denote the spectrum of a matrix M with the symbol $\sigma(M)$.

We now use the complex identity:

$$|\lambda - A_{kk}| \geq \operatorname{Re}(\lambda - A_{kk}) = \operatorname{Re}(\lambda) - \operatorname{Re}(A_{kk}). \quad (27)$$

Equation (25) implies:

$$\sum_{j \neq k} |A_{kj}| < -\operatorname{Re}(A_{kk}). \quad (28)$$

Combining the two previous inequalities yields:

$$\operatorname{Re}(\lambda) - \operatorname{Re}(A_{kk}) \leq |\lambda - A_{kk}| \leq \sum_{j \neq k} |A_{kj}| < -\operatorname{Re}(A_{kk}). \quad (29)$$

Comparing the RHS and LHS of this inequality yields:

$$\operatorname{Re}(\lambda) < 0. \quad (30)$$

□

Sufficient condition for dynamical stability (strong)

Theorem 1. *Let p be a parameter set with a Jacobian at equilibrium J^* . If 0 is not an eigenvalue of J^* and the equations*

$$(\Gamma B)_{\mu\mu} < -\sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| - R_c^2 \quad \forall \mu, \quad (31)$$

are verified, then p is dynamically stable.

Proof. We assume

$$(\Gamma B)_{\mu\mu} < -\sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| - R_c^2 \quad \forall \mu. \quad (32)$$

This implies:

$$(\Gamma B)_{\mu\mu} + R_c^2 < -\sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu. \quad (33)$$

If the previous inequality is verified, since $\operatorname{Re}(\lambda)^2 \leq |\lambda|^2 < R_c^2$, the following one is also trivially verified,

$$(\Gamma B)_{\mu\mu} - \operatorname{Re}(\lambda)^2 < -\sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu. \quad (34)$$

Using this result and dividing Eq.(34) by D_μ ($D_\mu > 0, \forall \mu$), we get:

$$\frac{1}{D_\mu} \left[\left(\sum_i \Gamma_{\mu i} B_{i\mu} \right) - \operatorname{Re}(\lambda^2) \right] < -\sum_{\nu \neq \mu} \left| \frac{\sum_i \Gamma_{\mu i} B_{i\nu}}{D_\mu} \right| \quad \forall \mu. \quad (35)$$

Looking at Eq.(15), we see that Eq.(35) is equivalent to:

$$\operatorname{Re}(S_{\mu\mu}) + \sum_{\nu \neq \mu} |S_{\mu\nu}| < 0 \quad \forall \mu. \quad (36)$$

Lemma 1 implies that all the eigenvalues of $S(\lambda)$ have a negative real part. Using the “Reductio ad absurdum” reasoning from Section ??, that means that if $\operatorname{Re}(\lambda) \geq 0$ in Eq. (14) (unstable or marginally stable regime), then $\operatorname{Re}(\lambda) < 0$ in Eq. (35), which leads to a contradiction. This then implies that the equilibrium is dynamically stable. □

Note that Theorem 1 is a sufficient condition, and there may be dynamically stable systems that do not fulfill it. It demands strong constraints on the parameters set, namely ΓB must have diagonal elements that are “very negative”, which imposes severe conditions especially on the α and γ matrices.

Sufficient condition for dynamical stability (weak)

Another Theorem can be stated with less restrictive assumptions which, however, leads to a less general condition.

Theorem 2. *Let p be a parameter set with a Jacobian at equilibrium J^* . If 0 is not an eigenvalue of J^* and the equations*

$$(\Gamma B)_{\mu\mu} < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu, \quad (37)$$

are verified, then the real eigenvalues of J^ are negative.*

Proof. We assume

$$(\Gamma B)_{\mu\mu} < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu. \quad (38)$$

Let $\lambda \in \mathbb{R}$, then the following will also trivially hold:

$$(\Gamma B)_{\mu\mu} - \lambda^2 < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu. \quad (39)$$

Dividing Eq.(39) by D_μ , we get:

$$\frac{1}{D_\mu} \left[\left(\sum_i \Gamma_{\mu i} B_{i\mu} \right) - \lambda^2 \right] < - \sum_{\nu \neq \mu} \left| \frac{\sum_i \Gamma_{\mu i} B_{i\nu}}{D_\mu} \right| \quad \forall \mu. \quad (40)$$

Looking at Eq.(15), we see that this is equivalent to:

$$S_{\mu\mu} + \sum_{\nu \neq \mu} |S_{\mu\nu}| < 0 \quad \forall \mu. \quad (41)$$

Using Lemma 1, we know that all the real eigenvalues of $S(\lambda)$ will have a negative real part. We can conclude with the statement of the theorem. \square

The condition is less general because it only applies for real eigenvalues of J^* , hence excluding complex eigenvalues.

Objective function derivation

The two theorems derived suggest that dynamical stability would more likely be fulfilled if the matrix ΓB is diagonally dominant, i.e. if the condition in Eq. (38) is fulfilled. Therefore, we propose an objective function whose minimization allow us to search for topologies more likely leading to dynamically stable systems

$$E = \sum_{\mu} \left((\Gamma B)_{\mu\mu} + \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \right)$$

which we can make more explicit in terms of the metaparameters and binary matrices, to get the expression presented in Main Text:

$$E(A, G) = \sum_{\mu} (\alpha_0 A G - \gamma_0 R_0 G^T G)_{\mu\mu} + \sum_{\mu \neq \nu} |(\alpha_0 A G - \gamma_0 R_0 G^T G)_{\mu\nu}|.$$

2.3 The effective competition framework

Derivation of the effective competition parameter

Next, we show that, at steady state, the stability of the whole system can be approximated by an effective system whose dynamical stability is fulfilled if the effective competition matrix defined below is positive definite. Assuming that the dynamics of resources achieves steady-state faster than the dynamics of species, i.e.

$$\frac{dR_\mu}{dt} \approx 0, \forall \mu, \quad (42)$$

and using Eq. (1), we get an explicit value for the resources at equilibrium:

$$R_\mu \approx \frac{l_\mu + \sum_j \alpha_{\mu j} S_j}{m_\mu + \sum_k \gamma_{k\mu} S_k}. \quad (43)$$

This expression can be substituted in the ODEs (Eq. [Eq] in Main Text) to get an effective system which describes the dynamics of the N_S consumers near the equilibrium:

$$\frac{dS_i}{dt} = \left(\sum_\nu \left(\frac{\sigma_{i\nu} \gamma_{i\nu} l_\nu}{m_\nu + \sum_k \gamma_{k\nu} S_k} - \alpha_{\nu i} \right) - d_i + \sum_{\nu j} \frac{\sigma_{i\nu} \gamma_{i\nu} \alpha_{\nu j}}{m_\nu + \sum_k \gamma_{k\nu} S_k} S_j \right) S_i. \quad (44)$$

This can be rewritten in a more compact way:

$$\frac{dS_i}{dt} = q_i(S) S_i + \sum_j M_{ij}(S) S_i S_j \quad (45)$$

with

$$q_i(S) = \sum_\nu \frac{\sigma_{i\nu} \gamma_{i\nu} l_\nu}{m_\nu + \sum_k \gamma_{k\nu} S_k} - \left(d_i + \sum_\nu \alpha_{\nu i} \right) \quad (46)$$

interpreted as the effective biomass productivity of the species, whose positive increase is reduced by competition for resources with other species ($\sum_\nu \sum_k \gamma_{k\nu} S_k$), and

$$M_{ij}(S) = \sum_\nu \frac{\sigma_{i\nu} \gamma_{i\nu} \alpha_{\nu j}}{m_\nu + \sum_k \gamma_{k\nu} S_k} \quad (47)$$

representing the mutualistic benefit that species i exerts on species j by means of cross-feeding interactions, again reduced by the competition for resources. The fact that both cross-feeding and competitive interactions appear in these objects hinders their interpretation. In addition, we aim for a direct connection between the stability of the effective system and the full system. To achieve this goal and to gather a more direct interpretation, we shall look for a purely competitive Lotka-Volterra expression of the form

$$\frac{dS_i}{dt} = \left(p_i - \sum_j C_{ij} S_j + \text{higher order interactions} \dots \right) S_i, \quad (48)$$

in which p_i is again interpreted as the effective productivity of the species and C_{ij} as an effective competition matrix, effectively incorporating both competitive and syntrophic interactions. Performing a Taylor expansion of the term in 46 and ??

$$\frac{1}{m_\nu + \sum_k \gamma_{k\nu} S_k} \approx \frac{1}{m_\nu + \gamma_{k\nu} S_k^*} \left[\left(1 + \sum_k \frac{\gamma_{k\nu} S_k^*}{m_\nu + \sum_l \gamma_{l\nu} S_l^*} \right) - \sum_j \frac{\gamma_{j\nu}}{m_\nu + \sum_l \gamma_{l\nu} S_l^*} S_j \right], \quad (49)$$

we may connect with the definition of the Jacobian at equilibrium of the full system by noting that:

$$m_\nu + \sum_k \gamma_{k\nu} S_k^* = \frac{l_\nu + \sum_k \alpha_{\nu k} S_k^*}{R_\nu^*} = D_\nu \quad (50)$$

with D_ν being a strictly positive quantity. Substituting in Eq. 49 yields:

$$\approx \frac{1}{m_\nu + \sum_k \gamma_{k\nu} S_k^*} \quad (51)$$

$$\approx \frac{1}{D_\nu} \left[\left(1 + \sum_j \frac{\gamma_{j\nu} S_j^*}{D_\nu} \right) - \sum_j \frac{\gamma_{j\nu}}{D_\nu} S_j \right] = \left(\frac{1}{D_\nu} + \sum_j \frac{\gamma_{j\nu} S_j^*}{D_\nu^2} \right) - \sum_j \frac{\gamma_{j\nu}}{D_\nu^2} S_j, \quad (52)$$

which allows us to write Eq. (??) as:

$$\frac{dS_i}{dt} = \left[p_i - \sum_{\nu j} \frac{\sigma_{i\nu} \gamma_{i\nu}}{D_\nu^2} \left(\gamma_{j\nu} l_\nu - \alpha_{\nu j} \left(D_\nu + \sum_k \gamma_{k\nu} S_k^* \right) \right) S_j + \dots \right] S_i \quad (53)$$

We obtain the following expression for the effective competition matrix:

$$C_{ij} = \sum_\nu \frac{\sigma_{i\nu} \gamma_{i\nu}}{D_\nu^2} \left(\gamma_{j\nu} l_\nu - \alpha_{\nu j} \left(D_\nu + \sum_k \gamma_{k\nu} S_k^* \right) \right). \quad (54)$$

The expression shows that syntrophy reduces the competition for resources between species. Indeed, if there is no syntrophy all the elements of the effective competition matrix are positive, and we expect that most of them are for stable systems when there is syntrophy. If most elements are positive and assuming that the matrix is irreducible, i.e. the complete space is the only spaces that is invariant under the action of C , the Perron-Frobenius theorem [Ref] states that each matrix C has a dominant eigenvalue λ_1 of order N_S associated with left and right eigenvectors u^1 and v^1 whose elements are all positive. The dominant eigenvalue λ_1 is the weighted mean of the competition values $\lambda_1 = \sum C_{ij} u_i^1 u_j^1 = \sum C_{ij} v_i^1 v_j^1$ which, following previous work [Refs], allow us define the effective competition parameter ρ_{eff} as the ratio of the interspecific to intraspecific competition:

$$\rho_{\text{eff}} = \frac{1}{N_S - 1} \left(\frac{\lambda_1(C)}{\sum_i C_{ii}/N_S} - 1 \right). \quad (55)$$

This parameter is sensitive to both the parameterization and the topology of the system, which allowed us to explore the effect that variations in the effective competition have on other properties such as the feasibility volume.

Positivity of the effective competition is a necessary condition to fulfill the dynamical stability theorems

Considering a more stringent feasibility condition (Eq. 3) in which $m_\nu \gg \sum_k \gamma_{k\nu} S_k^*$ allow us to assume

$$D_\nu + \sum_k \gamma_{k\nu} S_k^* \approx D_\nu. \quad (56)$$

Such a condition can be set if e.g. the input of resources, l_ν , are large —which is a parameter that can be controlled in an experimental setup. With that approximation, Eq.(54) becomes:

$$C_{ij} \approx \sum_\nu \frac{\sigma_{i\nu} \gamma_{i\nu}}{D_\nu} \left(\gamma_{j\nu} \frac{l_\nu}{D_\nu} - \alpha_{\nu j} \right) \quad (57)$$

Since we are assuming that l_ν is large, we can also approximate

$$D_\nu = \frac{l_\nu + \sum_k \alpha_{\nu k} S_k^*}{R_\nu^*} \approx \frac{l_\nu}{R_\nu^*}, \quad (58)$$

and, hence

$$\frac{l_\nu}{D_\nu} \approx R_\nu^*. \quad (59)$$

Inserting these approximations in Eq.(57) yields

$$C_{ij} \approx \sum \frac{\sigma_{i\nu} \gamma_{i\nu} S_i^* R_\nu^*}{S_i^* l_\nu} (\gamma_{j\nu} R_\nu^* - \alpha_{\nu j}), \quad (60)$$

which can be expressed in terms of the B and Γ matrices:

$$C_{ij} \approx - \left(\sum_\nu \frac{R_\nu^*}{S_i^* l_\nu} \right) (B\Gamma)_{ij}. \quad (61)$$

We will finally show the connection between the stability of the effective system and the whole system.

Theorem 3. *If all eigenvalues of $(\Gamma B)_{\mu\nu}$ are non-zero, a necessary condition to fulfill the theorems 1 and 2 is that the effective competition matrix is positive definite.*

Proof. We start considering the following Lemma demonstrated in Ref. [Johnson].

Lemma 2. *Let C and D be $m \times m$ and $n \times n$ complex matrices, respectively, with $m \leq n$. Then C may be written AB while a necessary condition for D to be BA is that the Jordan structure associated with nonzero eigenvalues is identical in C and D .*

Therefore, if $(\Gamma B)_{\mu\nu}$ has nonzero eigenvalues, which is necessary for the system to be stable, all eigenvalues of $(B\Gamma)_{ij}$ are identical to those of $(\Gamma B)_{\mu\nu}$. Since all eigenvalues of $(\Gamma B)_{\mu\nu}$ must have negative real parts for theorems to hold, and all the eigenvalues of $(B\Gamma)_{ij}$ have negative real parts if and only if the effective competition matrix is positive definite, we conclude that positivity of the effective competition matrix is necessary for the theorems to hold.

□