

As stated in the introduction, our ultimate goal is to study equilibria points of the set of coupled differential equations (??). In particular we want to know how *stable* a given equilibrium is. However there is no consensual definition of stability: what does it mean exactly that a system is stable under a given perturbation? How is a perturbation even defined? Throughout this thesis different notions of stability will be tackled: the first is *dynamical stability*. The main idea behind dynamical stability is simple. We want to answer the following question:

Given an equilibrium point $\{R_\mu^, S_i^*\}$, does the system go back to a positive-valued equilibrium when the consumers and resources abundances are changed? If yes, how much can they be changed before the system evolves in such a way that it does not reach a positive-valued equilibrium?*

0.0.1 Definitions

Local dynamical stability

We first introduce *local dynamical stability*. A system is said to be *locally dynamically stable* if it goes back to *its initial equilibrium point* $\{R_\mu^*, S_i^*\}$ after R_μ^* and S_i^* have been perturbed by an infinitesimal amount $\{\Delta R_\mu(t_0), \Delta S_i(t_0)\}$ at time t_0 .

More precisely, consider a system which is at equilibrium at time before $t = t_0$. Right after $t = t_0$, we perturb the equilibria abundances $\{R_\mu^*, S_i^*\}$ by an infinitesimal amount $\{\Delta R_\mu(t_0), \Delta S_i(t_0)\}$. We want to know how the perturbations away from equilibrium, written $\{\Delta R_\mu(t), \Delta S_i(t)\}$, and defined as

$$\Delta R_\mu(t) \equiv R_\mu(t) - R_\mu^* \text{ and } \Delta S_i(t) = S_i(t) - S_i^*. \quad (1)$$

will evolve qualitatively. Namely, will they go to zero or increase indefinitely as t increases? Perturbation analysis tells us **insert ref** that the quantity which drives the evolution of $\{\Delta R_\mu(t), \Delta S_i(t)\}$ is the *jacobian matrix of the system at equilibrium* J^* , given by :

$$J^* \equiv J(t_0), \quad (2)$$

where $J(t)$ is the *jacobian* of the system *i.e.* the jacobian matrix of its temporal evolution (??) evaluated at time t . $J(t)$ has a block matrix structure which is given by:

$$J(t) \equiv \begin{pmatrix} \frac{\partial \dot{R}_\mu}{\partial R_\nu} & \frac{\partial \dot{R}_\mu}{\partial S_j} \\ \frac{\partial \dot{S}_i}{\partial R_\nu} & \frac{\partial \dot{S}_i}{\partial S_j} \end{pmatrix} = \begin{pmatrix} \left(-m_\mu - \sum_j \gamma_{j\mu} S_j(t) \right) \delta_{\mu\nu} & -\gamma_{j\mu} R_\mu(t) + \alpha_{\mu j} \\ \sigma_{i\nu} \gamma_{i\nu} S_i(t) & (\sum_\nu \sigma_{i\nu} \gamma_{i\nu} R_\nu(t) - d_i - \sum_\nu \alpha_{\nu i}) \delta_{ij} \end{pmatrix}, \quad (3)$$

where δ is the ubiquitously occurring Kronecker delta symbol defined as:

$$\delta_{ij} = \begin{cases} 1 & \text{if } i = j, \\ 0 & \text{else.} \end{cases} \quad (4)$$

J^* is then precisely J with $\{R_\mu, S_i\}$ taken at the considered equilibrium point $\{R_\mu^*, S_i^*\}$, which simplifies its structure. Indeed, since we are interested only in positive valued equilibria (*i.e.* $S_i^* > 0 \forall i$), then Eq.(??) is equivalent to:

$$\sum_{\nu} \sigma_{i\nu} \gamma_{i\nu} R_\nu^* - d_i - \sum_{\nu} \alpha_{\nu i} = 0, \quad (5)$$

which means that the lower right block of the jacobian in Eq.(3) will be zero. Hence at equilibrium the jacobian J^* will have the following block form:

$$J^* = \begin{pmatrix} -\Delta & \Gamma \\ B & 0 \end{pmatrix}, \quad (6)$$

where

- $\Delta_{\mu\nu} = \text{diag}(m_\mu + \sum_j \gamma_{j\mu} S_j^*) = \text{diag}\left(\frac{l_\mu + \sum_j \alpha_{\mu j} S_j^*}{R_\mu^*}\right)$ 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.

For reasons explained later in the manuscript, we say that a given equilibrium is *locally dynamically stable* if the largest real part of the eigenvalues of J^* is negative.

The locally dynamically stable volume $\mathcal{D}_{L,x}^{G,A}$

Similarly to what was conducted in Methods ??, one can define the *parameters set local dynamical stability function* $\mathfrak{D}_L : \mathcal{P} \rightarrow \{0, 1\}$, which tells you whether a given set of parameters $p \in \mathcal{P}$ is locally dynamically stable or not:

$$\mathfrak{D}_L(p) \equiv \begin{cases} 1 & \text{if } p \text{ is locally dynamically stable} \\ 0 & \text{else.} \end{cases} \quad (7)$$

Of course, p has to be feasible in order to be locally dynamically stable:

$$\mathfrak{D}_L(p) = 1 \implies \mathfrak{F}(p) = 1. \quad (8)$$

We also define the *metaparameters set local dynamical stability function* $\mathcal{D}_L : \mathcal{M} \times \mathcal{B}_{N_S \times N_R} \times \mathcal{B}_{N_R \times N_S} \rightarrow [0, 1]$ which tells you, given a set of metaparameters $m \in \mathcal{M}$ and a consumption-syntrophy network $B = (G, A)$ the chance that the procedure $\mathcal{A}(m, B)$ gives a locally dynamically stable set of parameters:

$$\mathcal{D}_L(m, B) \equiv \text{Probability} \{ \mathfrak{D}_L(\mathcal{A}(m, B)) = 1 \}. \quad (9)$$

We also define the x locally dynamically stable (lds) region $\mathcal{D}_{L,x}^{G,A}$ by the region of the metaparameters space that gives rise to a percentage of at least x dynamically stable systems:

$$\mathcal{D}_{L,x}^{G,A} \equiv \{m \in \mathcal{M} : \mathcal{D}_L(m, (G, A)) \geq x\} \quad (10)$$

Clearly, $\mathcal{D}_{L,0}^{G,A} = \mathcal{M}$, $\text{Vol}(\mathcal{D}_{L,x}^{G,A}) \leq \text{Vol}(\mathcal{D}_{L,y}^{G,A}) \forall x \geq y$, and more importantly, Eq.(8) is equivalent to $\mathcal{D}_{L,x}^{G,A} \subset \mathcal{V}_x^{G,A}$. We can also define for a set of N couples of matrices $S = \{(G_1, A_1) \dots, (G_N, A_N)\}$ their common x lds-region $\mathcal{D}_{L,x}^S$:

$$\mathcal{D}_{L,x}^S \equiv \bigcap_{(G,A) \in S} \mathcal{D}_{L,x}^{G,A}. \quad (11)$$

For such a set S we define also its critical local dynamical stability $d_L^*(S)$ which is the largest local dynamical stability we can achieve while still having a non-zero common volume:

$$d_L^*(S) = \max_{x \in [0,1]} \{x : \text{Vol}(\mathcal{D}_{L,x}^S) > 0\}. \quad (12)$$

Finally the critical common local dynamical stability volume \mathcal{D}_L^S is the common lds-region at the critical local dynamical stability:

$$\mathcal{D}_L^* \equiv \mathcal{D}_{L,d_L^*(S)}^S. \quad (13)$$

The hope is that we can work most of the time with systems that have $d_L^*(S) = 1$.

Global dynamical stability

If we establish that a system is locally dynamically stable, we know that it will come back to the same equilibrium after an infinitesimal perturbation of the resources and consumers abundances. The next natural question is:

How much can these equilibria points be perturbed before the system goes to a point where either at least a species has gone extinct or reaches another positive valued equilibrium $\{\tilde{R}_\mu^, \tilde{S}_i^*\}$ or simply does not reach a new dynamical equilibrium?*

One way of studying this [1] is to simply take an equilibrium point $\{R_\mu^*, S_i^*\}$ and perturb the abundance of the species and resources at that point by a fixed number $\Delta_D \in [0, 1]$ which allows us to quantify the perturbation:

$$\begin{cases} R_\mu^* \rightarrow R_\mu(t_0) \equiv R_\mu^* (1 + \Delta_D \nu_\mu), \\ S_i^* \rightarrow S_i(t_0) \equiv S_i^* (1 + \Delta_D \nu_i), \end{cases} \quad (14)$$

$$\quad (15)$$

where the $\nu_{\mu,i}$ are random numbers drawn from a uniform distribution between -1 and +1 and t_0 is the time where the previously at equilibrium system is perturbed. The system with the initial values $\{R(t_0), S(t_0)\}$ can then be time evolved from $t = t_0$ until it reaches an equilibrium $\{\tilde{R}^*, \tilde{S}^*\}$ which may be different from the equilibrium $\{R^*, S^*\}$ initially considered. This procedure is essentially a generalized version of local dynamical stability, since we allow the perturbation Δ_D to be non-infinitesimal. The question we will ask is precisely how big Δ_D can get.

A certain number of quantities, that all depend on the perturbation Δ_D , can then be measured to quantify the dynamical stability of the system:

- The resilience t_R : the time scale over which the system reaches its new equilibrium.

- The number of extinctions E : the number of species or resources which died during the time it took the system to reach its new equilibrium.
- The angle α between two equilibria: this quantifies how close the old and new equilibria are. α is defined through its standard scalar product formula:

$$\cos(\alpha) \equiv \frac{\sum_{\mu} R_{\mu}^* \tilde{R}_{\mu}^* + \sum_j S_j^* \tilde{S}_j^*}{\sqrt{\sum_{\mu} (R_{\mu}^*)^2 + \sum_i (S_i^*)^2} \sqrt{\sum_{\mu} (\tilde{R}_{\mu}^*)^2 + \sum_i (\tilde{S}_i^*)^2}}. \quad (16)$$

These quantities have either been already introduced in previous papers or are natural extensions of standard quantities [1, 2]. They allow us to quantify the robustness of a given equilibrium.

0.0.2 The quest for a full solution

The question of global dynamical stability is mathematically tedious, so we focus on local dynamical stability. We aim to find the spectrum of the jacobian at equilibrium, which will tell us whether the system is locally dynamically stable or not.

How to determine local dynamical stability

We stated above that the sign of the largest real part of all the eigenvalues of J^* determines the local dynamical stability. More precisely, we are interested in the real part of λ_1 , which is defined by the following property:

$$\boxed{\forall \lambda \in \sigma(J^*), \operatorname{Re}(\lambda) \leq \operatorname{Re}(\lambda_1)}, \quad (17)$$

where $\sigma(J^*)$ is the set of eigenvalues of J^* , called the *spectrum* of J^* . Perturbation analysis tells us that the sign of the real part of λ_1 governs the local stability of the system at equilibrium **add source**. There are three cases:

- $\operatorname{Re}(\lambda_1) < 0$: any perturbation on the abundances is exponentially suppressed. The system is stable.
- $\operatorname{Re}(\lambda_1) > 0$: any perturbation on the abundances is exponentially amplified. The system is unstable.
- $\operatorname{Re}(\lambda_1) = 0$: a second order perturbation analysis is required to assess the system's local dynamical stability. We call such systems *marginally stable* [3].

The master equation for local dynamical stability

In order to get $\operatorname{Re}(\lambda_1)$, we have to get the full spectrum of J^* , as a straight forward application of easier standard techniques like the Perron-Frobenius theorem [4] does not work. The eigenvalues of J^* are obtained through the eigenvalue problem:

$$\det(J^* - \lambda) = 0. \quad (18)$$

More explicitly, using Eq.(6), we state the *master equation for local dynamical stability*:

$$\boxed{\det \begin{pmatrix} -\Delta - \lambda & \Gamma \\ B & 0 - \lambda \end{pmatrix} = 0} \quad (19)$$

That equation is not trivially solved. We then seek regimes where it could be made simpler.

Simplifying the master equation

Equation (19) may be simplified if

$$\lambda \neq 0. \quad (20)$$

Indeed¹, a non-zero λ implies

$$\det(\lambda \mathbb{1}_{N_S}) \neq 0, \quad (21)$$

where $\mathbb{1}_{N_S}$ stands for the $N_S \times N_S$ identity matrix. One can use this condition to simplify Eq.(19) using the properties of block matrices [5]:

$$\det \begin{pmatrix} -\Delta - \lambda \mathbb{1}_{N_R} & \Gamma \\ B & 0 - \lambda \mathbb{1}_{N_S} \end{pmatrix} = \det(-\lambda \mathbb{1}_{N_S}) \det \left(-\Delta - \lambda \mathbb{1}_{N_R} + \frac{1}{\lambda} \Gamma B \right). \quad (22)$$

Hence Eq.(19) becomes:

$$\boxed{\det(\lambda^2 \mathbb{1}_{N_R} + \Delta \lambda - \Gamma B) = 0.} \quad (23)$$

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. We see from the previous expression that the dynamics is essentially dictated by the ΓB N_R -dimensional square matrix, which is given by:

$$(\Gamma B)_{\mu\nu} = \sum_i \Gamma_{\mu i} B_{i\nu} = \sum_i (\alpha_{\mu i} - \gamma_{i\mu} R_{\mu}^*) \sigma_{i\nu} \gamma_{i\nu} S_i^*. \quad (24)$$

There are many strategies here to find regimes of stability. One is the so-called “Reductio ad absurdum”, which is explored later in Methods 0.0.4.

0.0.3 Bounds on the eigenvalues

Before studying Equation (23), we would like to know more about the spectrum of J^* . The most critical question is knowing *where* we expect the eigenvalues of J^* to lie on the complex plane.

Gerschgorin circle theorem

Gerschgorin circle theorem [6] states that every eigenvalue of a $N \times N$ square matrix A is located in one of the N discs D_i defined by:

$$D_i \equiv \left\{ z \in \mathbb{C} : |z - A_{ii}| \leq \sum_{j \neq i} |A_{ij}| \right\}. \quad (25)$$

¹Appendix ?? elaborates on when that condition is fulfilled.

In a more mathematical language:

$$\sigma(A) \subset \bigcup_{i=1}^N D_i. \quad (26)$$

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. It is then easy to see that if all the discs 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 corresponds to the following lemma:

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

$$\operatorname{Re}(A_{ii}) + \sum_{j \neq i} |A_{ij}| < 0, \forall i = 1, \dots, N, \quad (27)$$

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

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

$$|\lambda - A_{kk}| \leq \sum_{j \neq k} |A_{kj}|. \quad (28)$$

We now use the complex identity:

$$|\lambda - A_{kk}| \geq \operatorname{Re}(\lambda - A_{kk}) = \operatorname{Re}(\lambda) - \operatorname{Re}(A_{kk}). \quad (29)$$

Equation (27) implies:

$$\sum_{j \neq k} |A_{kj}| < -\operatorname{Re}(A_{kk}). \quad (30)$$

Combining the two previous inequalities yields:

$$\operatorname{Re}(\lambda) - \operatorname{Re}(A_{kk}) \leq |\lambda - A_{kk}| \leq \sum_{j \neq k} |A_{kj}| < -\operatorname{Re}(A_{kk}). \quad (31)$$

Comparing the RHS and LHS of this inequality yields:

$$\operatorname{Re}(\lambda) < 0. \quad (32)$$

□

The Gerschgorin circle theorem allows us to get a precious bound on the modulus of each eigenvalue and hence on the one that decides the dynamics of the system λ_1 . Indeed we know that all eigenvalues of J^* will be located in one of the $N_R + N_S$ discs of J^* . These are the “resources” discs:

$$D_\mu^R \equiv \left\{ z \in \mathbb{C} : |z + \Delta_\mu| \leq \sum_j |\Gamma_{\mu j}| \right\} \quad \forall \mu = 1, \dots, N_R, \quad (33)$$

and the “consumers” discs:

$$D_i^C \equiv \left\{ z \in \mathbb{C} : |z| \leq \sum_{\nu} |B_{i\nu}| \right\} \quad \forall i = 1, \dots, N_S. \quad (34)$$

According to the circle theorem Eq.(26), 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:

$$|\lambda| \leq \sum_{\nu} |B_{i^*\nu}| \quad (35)$$

or

$$|\lambda + \Delta_{\mu^*}| \leq \sum_j |\Gamma_{\mu^*j}| \quad (36)$$

The triangle inequality implies:

$$|\lambda| \leq |\lambda + \Delta_{\mu^*}| + |-\Delta_{\mu^*}| \leq \sum_j |\Gamma_{\mu^*j}| + |-\Delta_{\mu^*}| = \sum_j |\Gamma_{\mu^*j}| + \Delta_{\mu^*}. \quad (37)$$

The only way both Eq.(35) and (37) 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. More precisely:

$$\boxed{|\lambda| \leq R_C \quad \forall \lambda \in \sigma(J^*),} \quad (38)$$

where we defined the critical radius R_C as:

$$R_C \equiv \max \left\{ \max_i \left\{ \sum_{\nu} |B_{i\nu}| \right\}, \max_{\mu} \left\{ \sum_j |\Gamma_{\mu j}| + \Delta_{\mu} \right\} \right\}. \quad (39)$$

This gives us an estimation of how big the eigenvalues can get: we know that all the eigenvalues *have* an absolute value smaller than or equal to the critical radius R_C . The next step is to estimate R_C in terms of metaparameters, so that we can get a qualitative insight on how the eigenvalues change when the metaparameters are changed.

Using techniques very similar to previous computations, we estimate:

$$\sum_j |\Gamma_{\mu j}| + \Delta_{\mu} = \sum_j |\alpha_{\mu j} - \gamma_{j\mu} R_{\mu}^*| + \frac{l_{\mu} + \sum_j \alpha_{\mu j} S_j^*}{R_{\mu}^*} \approx \deg(\Gamma, \mu) |\alpha_0 - \gamma_0 R_0| + \frac{l_0 + \deg(A, \mu) \alpha_0 S_0}{R_0}. \quad (40)$$

It is difficult to simplify $\deg(\Gamma, \mu) \approx \deg(A - G^T, \mu)$. If we assume that A and G have a low connectance then $\deg(A, \mu), \deg(G^T, \mu) \ll N_S$ and we may use the very loose approximation

$$\deg(A - G^T, \mu) \approx \deg(A, \mu) + \deg(G, \mu). \quad (41)$$

In that regime we then have:

$$\max_{\mu} \left\{ \sum_j |\Gamma_{\mu j}| + \Delta_{\mu} \right\} \approx \max_{\mu} \left\{ (\deg(A, \mu) + \deg(G, \mu)) |\alpha_0 - \gamma_0 R_0| + \frac{l_0 + \deg(A, \mu) \alpha_0 S_0}{R_0} \right\}. \quad (42)$$

Similarly we find

$$\sum_{\nu} |B_{i\nu}| \approx \deg(G, i) \sigma_0 \gamma_0 S_0, \quad (43)$$

such that R_C can be estimated roughly as:

$$R_C \approx \max \left\{ \max_i (\deg(G, i)) \sigma_0 \gamma_0 S_0, \max_{\mu} \left\{ (\deg(A, \mu) + \deg(G, \mu)) |\alpha_0 - \gamma_0 R_0| + \frac{l_0 + \deg(A, \mu) \alpha_0 S_0}{R_0} \right\} \right\} \quad (44)$$

0.0.4 Low intra resources interaction (LRI) regime

Now that we have a bound on how big the eigenvalues can be, we need strategies to find regimes where we *know* $\text{Re}(\lambda_1) < 0$, *i.e.* local dynamical stability is guaranteed. We inspire ourselves from the general idea of the mathematical proofs of [7].

Reductio ad absurdum

Using standard properties of determinants, we rewrite Eq.(23) as²:

$$\det(-\Delta^{-1}) \det(-\Delta^{-1} \lambda^2 - \lambda + \Delta^{-1} \Gamma B) = 0 \iff \boxed{\det(S(\lambda) - \lambda) = 0} \quad (45)$$

with

$$\boxed{S(\lambda) = \Delta^{-1} \Gamma B - \Delta^{-1} \lambda^2}, \quad (46)$$

or, component-wise:

$$S_{\mu\nu} = \frac{1}{\Delta_{\mu}} \left[\left(\sum_i \Gamma_{\mu i} B_{i\nu} \right) - \lambda^2 \delta_{\mu\nu} \right] \quad (47)$$

The strategy is to assume we are in an unstable regime, *i.e.* there exists at least one $\lambda \in \sigma(J^*)$ with $\text{Re}(\lambda) \geq 0$ that satisfies Eq.(23) and such that $\text{Re}(\lambda) > 0$. By Eq.(45), 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 stable³.

Hence, the general idea is to find regimes where we know that the spectrum of S , written as $\sigma(S)$, will be entirely negative for a positive λ . Thanks to the help of the two following theorems, we found such a regime, called *low intra-resource interaction* or LRI.

Strong LRI regime

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*

$$(\Gamma B)_{\mu\mu} < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| - R_C^2 \quad \forall \mu, \quad (48)$$

are verified, then p is dynamically stable.

²We can do this because since $m_{\mu} > 0$, we know Δ will always be invertible.

³Indeed, Eq.(23) assumes already that either $\text{Re}(\lambda_1) > 0$ or $\text{Re}(\lambda_1) < 0$.

Proof. We assume

$$(\Gamma B)_{\mu\mu} < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| - R_C^2 \quad \forall \mu. \quad (49)$$

This implies:

$$(\Gamma B)_{\mu\mu} + R_C^2 < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu. \quad (50)$$

Using Eq.(38) and $\text{Im}(\lambda)^2 \leq |\lambda|^2$, we get:

$$(\Gamma B)_{\mu\mu} + \text{Im}(\lambda)^2 < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu. \quad (51)$$

It is not difficult to prove that for any complex number:

$$\text{Im}(c)^2 \geq -\text{Re}(c^2) \quad \forall c \in \mathbb{C}. \quad (52)$$

Using this result and dividing Eq.(51) by⁴ Δ_μ , we get:

$$\frac{1}{\Delta_\mu} \left[\left(\sum_i \Gamma_{\mu i} B_{i\mu} \right) - \text{Re}(\lambda^2) \right] < - \sum_{\nu \neq \mu} \left| \frac{\sum_i \Gamma_{\mu i} B_{i\nu}}{\Delta_\mu} \right| \quad \forall \mu. \quad (53)$$

Looking at Eq.(47), we see that Eq.(53) is equivalent to:

$$\text{Re}(S_{\mu\mu}) + \sum_{\nu \neq \mu} |S_{\mu\nu}| < 0 \quad \forall \mu. \quad (54)$$

Lemma 1 implies that all the eigenvalues of $S(\lambda)$ have a negative real part. As explained before that means that if $\text{Re}(\lambda_1) \geq 0$ in Eq.(46) (unstable or marginally stable regime), then $\text{Re}(\lambda_1) < 0$, which leads to a contradiction. This then implies that the equilibrium is dynamically stable. \square

Theorem 1 is a strong statement but it asks a lot 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. That is why we do not expect to find many parameters sets which would be in such a regime. We need to find another more relaxed regime in which more parameters sets could be.

Weak LRI regime

Another version of Theorem 1 can be stated. Its proof is in Appendix ???. Its assumptions are less restrictive, but that comes with a price : its statement is weaker.

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*

$$(\Gamma B)_{\mu\mu} < - \sum_{\nu \neq \mu} |(\Gamma B)_{\mu\nu}| \quad \forall \mu, \quad (55)$$

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

⁴That step is valid because $\Delta_\mu > 0, \forall \mu$.

Intuitive interpretation of the LRI regimes

Feasibility of the LRI regimes

So we found that if a system has parameters that respect Eq.(48) then it is dynamically stable. A naturally arising question is then to ask in what measure this is compatible with the feasibility equations Eqs.(??) and (??). The path is simple : we need to find a metaparameters approximation of the resource interaction matrix $(\Gamma B)_{\mu\nu}$, which will allow us to give a “metaparameters-version” of Eq.(48) and compare it with the metaparameters feasibility equation (??).

Using the metaparameters approximations Eqs.(??), Eq.(24) can be simplified as:

$$(\Gamma B)_{\mu\nu} \approx \sigma_0 \gamma_0 S_0 \left(\alpha_0 \sum_i A_{\mu i} G_{i\nu} - \gamma_0 R_0 \sum_i G_{i\mu} G_{i\nu} \right) \equiv \sigma_0 \gamma_0 S_0 (\alpha_0 O_{\mu\nu} - \gamma_0 R_0 C_{\mu\nu}) \quad (56)$$

where we defined the *syntrophy overlap matrix* $O_{\mu\nu}$ and the *consumption overlap matrix* $C_{\mu\nu}$ as:

$$O_{\mu\nu} \equiv (AG)_{\mu\nu} \text{ and } C_{\mu\nu} \equiv (G^T G)_{\mu\nu}. \quad (57)$$

The clash syntrophy versus consumption between these two binary matrices essentially builds the dynamics of our model and an intuitive understanding of them can be very helpful.

The syntrophy overlap matrix $O_{\mu\nu}$ is defined as:

$$O_{\mu\nu} \equiv \sum_k A_{\mu k} G_{k\nu}. \quad (58)$$

Although A and G are binary, O does not have to and usually will not be. A given consumer k contributes to $O_{\mu\nu}$ if and only if both $A_{\mu k}$ and $G_{k\nu}$ are non zero, that is if consumer k releases resource μ and consumes resource ν . Hence $O_{\mu\nu}$ essentially tells how many species effectively “link” resource μ to resource ν through the indirect interaction of the species consumption.

Similarly, the consumption overlap matrix is defined as:

$$C_{\mu\nu} = \sum_k G_{k\mu} G_{k\nu}. \quad (59)$$

Like O , C usually is not binary. The intuition behind $C_{\mu\nu}$ is straight forward: it counts how many species eat both resource μ and ν .

We then find a lowerbound for the RHS of Eq.(48):

$$- \sum_{\nu \neq \mu} |\Gamma B|_{\mu\nu} \geq - \sum_{\nu \neq \mu} \max_{\nu \neq \mu} |\Gamma B|_{\mu\nu} \geq - \deg(\mu, O - C) \max_{\nu \neq \mu} |\Gamma B|_{\mu\nu}. \quad (60)$$

Combining this with the approximation of ΓB above we get an approximative LRI regime condition on the metaparameters:

$$\boxed{\alpha_0 O_{\mu\mu} - \gamma_0 R_0 C_{\mu\mu} \lesssim - \deg(\mu, O - C) \max_{\nu \neq \mu} |\alpha_0 O_{\mu\nu} - \gamma_0 R_0 C_{\mu\nu}| - \frac{R_C^2}{\sigma_0 \gamma_0 S_0} \quad \forall \mu.} \quad (61)$$

Since R_C gets smaller as the largest degree of G decreases (see Eq.44) we only expect systems with a low connectance food consumption adjacency matrix to be able to achieve an LRI state.

This allows to give a necessary condition on the magnitude of α_0 . Indeed, since the RHS of the previous equation is negative, we need:

$$\alpha_0 O_{\mu\mu} - \gamma_0 R_0 C_{\mu\mu} < 0 \quad \forall \mu \implies \alpha_0 \max_{\mu} \left\{ \frac{O_{\mu\mu}}{C_{\mu\mu}} \right\} < \gamma_0 R_0. \quad (62)$$

It is clear that systems with the maximal ratio of $O_{\mu\mu}$ and $C_{\mu\mu}$ is small will be more easily into a LRI regime. The most favoured systems will be those where $S_{\mu\mu} = 0 \quad \forall \mu$, *i.e.* systems where no species consumes what it itself produces. In that way we may say that coprophagy tends to destabilize microbial communities. Combining Eq.(??) and (62) gives us a necessary condition on α_0 for feasible systems (need more details?):

$$\alpha_0 \left[\max_{\mu} \{O_{\mu\mu}\} - \min_{\mu} \left\{ \frac{k_{\mu}^{\alpha}}{k_{\mu}^{\gamma}} \right\} \right] \leq \frac{l_0}{\min_{\mu} (k_{\mu}^{\gamma}) S_0}. \quad (63)$$

Although that equation gives us a necessary condition, it is not sufficient. Eq.(61), on the other hand, is and provides an intuitive way of finding a syntrophy adjacency matrix $A_{\mu i}$ that would put a system with a given consumption adjacency $G_{\mu i}$ in an LRI regime. Section ?? explains in details how this can be achieved numerically.

Monte Carlo algorithm for the optimal syntrophy matrix

We want to find a general algorithm which, for a given food consumption adjacency matrix G gives back an optimal syntrophy adjacency matrix A . Strategically, we would like an A such that Eq.(61) is as close to being satisfied as possible. If it were satisfied, it would put the system in an LRI regime, which we have proven is dynamically stable.

One way of trying to satisfy Eq.(61) is to increase the magnitude of its LHS and minimize the magnitude of the RHS. The LHS is minimized if $(AG)_{\mu\mu}$ is set to its lowest possible value for every μ , that is zero. On the other hand, the RHS is minimized if $\alpha_0 (AG)_{\mu\nu} \approx \gamma_0 R_0 (G^T G)_{\mu\nu} \quad \forall \nu \neq \mu$.

Intuitively, we then search for systems where AG is zero on the diagonal, *i.e.* where no coprophagy is observed, and $AG \approx \frac{\gamma_0 R_0}{\alpha_0} G^T G$ outside the diagonal. It can be formalized by writing a proper Metropolis-Hastings Markov Chain Monte Carlo (MCMC) method. We designed the following algorithmic procedure to build a syntrophy adjacency matrix A :

1. Create a random A . Its connectance is chosen as the one of the consumption matrix G .
2. Do the following for a given number of steps:
 - Choose a random row or, every other iteration, a column.
 - In that row/column, try to swap a zero and a one while preserving the “releasers”: if a species releases some resource, it has to keep releasing something (the resource

can change though). The “releasees” are preserved as well: if a resource is being released by some species, it has to keep being released (but it does not have to be by the same species). **why do we impose those conditions?**

- The swap is accepted, *i.e.* A is modified, if the energy difference ΔE is negative or if a random number drawn uniformly between zero and one is smaller than $e^{-\Delta E/T}$ where T is the current temperature. More on ΔE and T below.

3. Return A .

A couple comments on this algorithm can be made:

- The algorithm preserves the connectance of A but not its nestedness. The question of what value to choose is open, but we choose $\kappa(A) = \kappa(G)$ as a first approach, *i.e.* syntrophy and consumption networks have the same connectance.
- The temperature T changes dynamically during the simulation. It is obtained in a way close to the spirit of simulated annealing techniques [8]: the temperature T is multiplied by a factor $\lambda = 0.99$ at a fixed frequency (for instance every 1000 steps). We add the requirement that if new moves are rejected during too many consecutive steps, we multiply the temperature by $1/\lambda$.
- The energy difference ΔE between the new proposed A' and the old A is computed by assigning an energy E to both A' and A and subtracting them:

$$\Delta E \equiv E(A', G) - E(A, G). \quad (64)$$

The choice of the energy function E is crucial. In essence, this MCMC algorithm will find the specific A which minimizes $E(A)$. Since we want to work with systems in the LRI regime, we use the simplest and most natural function that is compatible with the intuitively expected characteristics of A explained above (*i.e.* AG is zero on the diagonal and equal to $\frac{\gamma_0 R_0}{\alpha_0} G^T G$ outside of it):

$$E(A, G) \equiv \sum_{\mu} \left(|\alpha_0 (AG)_{\mu\mu}| + \sum_{\nu \neq \mu} |(\alpha_0 AG - \gamma_0 R_0 G^T G)_{\mu\nu}| \right). \quad (65)$$

The energy function and hence the optimal syntrophy adjacency matrix A depend on the ratio $\frac{\alpha_0}{\gamma_0 R_0}$. This prompts then the question of which α_0 can be deemed sensible. As a first step, we will take the value of Eq.(??): $\alpha_0 = \min(1 - \sigma_0, \sigma_0) \gamma_0 R_0 N_R$. This means that the outcome of the algorithm is an optimized A **for the largest feasible syntrophy**. Since the expression we have for the largest feasible syntrophy is independent of the G matrix, this choice of α_0 provides us a sensible way of comparing different consumption networks.

0.0.5 Flux analysis - a way to get a sense of scales

A natural scale free order parameter that at first sight controls the behaviour of the system is the ratio of the syntrophy and consumption fluxes.

The rate of consumption (or *consumption flux*) of species i is given by $\sum_{\nu} \sigma_{i\nu} \gamma_{i\nu} R_{\nu} S_i$. Hence the total consumption flux C_{tot} is given by:

$$C_{\text{tot}} = \sum_{i,\nu} \sigma_{i\nu} \gamma_{i\nu} R_{\nu} S_i. \quad (66)$$

We can similarly define the total syntrophy flux of the system S_{tot} :

$$S_{\text{tot}} = \sum_{i,\nu} \alpha_{\nu i} S_i. \quad (67)$$

A natural order parameter O is then

$$O \equiv \frac{S_{\text{tot}}}{C_{\text{tot}}} = \frac{\sum_{i,\nu} \alpha_{\nu i} S_i}{\sum_{i,\nu} \sigma_{i\nu} \gamma_{i\nu} R_{\nu} S_i} \approx \frac{N_S N_R \alpha_0 S_0}{\sigma_0 R_0 S_0 N_S N_R \gamma_0} = \frac{\alpha_0}{\sigma_0 R_0 \gamma_0}. \quad (68)$$

0.0.6 Application: fully connected consumption and syntrophy networks

As an application, we consider the very special case of the fully connected consumption and syntrophy networks. In this “mean-field” theory, every consumer consumes from and releases each resource, *i.e.*

$$G_{i\mu} = A_{\mu i} = 1 \quad \forall \mu = 1, \dots, N_R \quad \forall i = 1, \dots, N_S. \quad (69)$$

Our goal is to find the spectrum of systems with such matrices as their consumption and syntrophy networks. We follow the path explained by Barbier and Arnoldi in [9] and perform a *standard deviation expansion*. They showed that the variance of the interaction matrix drives the strength of the interactions in their model [9], so it is worth a try to follow their path.

Standard deviation expansion The idea behind the standard deviation expansion (abbreviated SDE) is the following. Let $q_{i\mu}$ be an arbitrary matrix of size $N_S \times N_R$. Then the nice trick done in [9] is to write the elements of the q matrix in terms of new variables $\tilde{q}_{i\mu}$:

$$q_{i\mu} = \langle q \rangle + \sigma_q \tilde{q}_{i\mu}. \quad (70)$$

In that expression, $\langle q \rangle$ is the average of q , element-wise

$$\langle q \rangle \equiv \frac{\sum_{\mu,i} q_{i\mu}}{N_S N_R}, \quad (71)$$

and σ_q is the standard deviation of q , again element-wise:

$$\sigma_q \equiv \sqrt{\langle q^2 \rangle - \langle q \rangle^2} \quad \text{with} \quad \langle q^2 \rangle \equiv \frac{\sum_{\mu,i} q_{i\mu}^2}{N_S N_R}. \quad (72)$$

The main advantage of this procedure is that we get a clear idea about the scales involved. A matrix element $q_{i\mu}$ is roughly the mean $\langle q \rangle$ plus a deviation σ_q multiplied by a factor of magnitude *sim* 1. Indeed the $\tilde{q}_{i\mu}$ are not large since they follow the two equalities [9]:

$$\langle \tilde{q} \rangle = 0 \quad \text{and} \quad \langle \tilde{q}^2 \rangle = 1. \quad (73)$$

We apply this framework to our problem by noticing that if the $q_{i\mu}$ are all random samples coming from the same distribution law $\mathbf{\Omega}$, we can write the following approximation in the case $N_R, N_S \gg 1$:

$$\langle q \rangle \approx \langle \mathbf{\Omega} \rangle \equiv q_0. \quad (74)$$

We can then rewrite the free parameters of our model⁵:

$$\left\{ \begin{array}{l} l_\nu \approx l_0 + \sigma_l \tilde{l}_\nu \end{array} \right. \quad (75a)$$

$$R_\nu^* \approx R_0 + \sigma_R \tilde{r}_\nu \quad (75b)$$

$$S_i^* \approx S_0 + \sigma_S \tilde{s}_i \quad (75c)$$

$$\gamma_{i\nu} \approx \gamma_0 + \sigma_\gamma \tilde{g}_{i\nu} \quad (75d)$$

$$\alpha_{\nu i} \approx \alpha_0 + \sigma_\alpha \tilde{a}_{\nu i} \quad (75e)$$

$$\sigma_{i\nu} \approx \sigma_0 + \sigma_\sigma \tilde{\sigma}_{i\nu} \quad (75f)$$

The general idea is then to assume that the standard deviations are small and proceed to a first order Taylor expansion.

Rewriting the jacobian at equilibrium The different blocks of the jacobian at equilibrium (??) can be written with the new variables :

$$\left\{ \begin{array}{l} \frac{l_\mu + \sum_j \alpha_{\mu j} S_j^*}{R_\mu^*} = \frac{l_0 + N_S \alpha_0 S_0 + \sigma_l \tilde{l}_\mu + \sigma_\alpha S_0 \sum_j \tilde{a}_{\mu j} + \sigma_\alpha \sigma_S \sum_j \tilde{a}_{\mu j} \tilde{s}_j}{R_0 + \sigma_R \tilde{r}_\mu} \end{array} \right. \quad (76)$$

$$\left\{ \begin{array}{l} -\gamma_{j\mu} R_\mu^* + \alpha_{\mu j} = -\gamma_0 R_0 + \alpha_0 + \sigma_\gamma R_0 \tilde{g}_{j\mu} + \sigma_R \gamma_0 \tilde{r}_\mu + \sigma_\alpha \tilde{a}_{\mu j} + \sigma_\gamma \sigma_R \tilde{g}_{j\mu} \tilde{r}_\mu \end{array} \right. \quad (77)$$

$$\left\{ \begin{array}{l} \sigma_{i\nu} \gamma_{i\nu} S_i^* = \sigma_0 \gamma_0 S_0 + \sigma_\sigma \gamma_0 S_0 \tilde{\sigma}_{i\nu} + \sigma_\gamma \sigma_0 S_0 \tilde{g}_{i\nu} + \sigma_S \sigma_0 \gamma_0 \tilde{s}_i + \sigma_\sigma \sigma_\gamma S_0 \tilde{\sigma}_{i\nu} \tilde{g}_{i\nu} \\ + \sigma_\sigma \sigma_S \gamma_0 \tilde{\sigma}_{i\nu} \tilde{s}_i + \sigma_\gamma \sigma_S \sigma_0 \tilde{g}_{i\nu} \tilde{s}_i + \sigma_\sigma \sigma_\gamma \sigma_S \tilde{\sigma}_{i\nu} \tilde{g}_{i\nu} \tilde{s}_i \end{array} \right. \quad (78)$$

It's easier to work with relative standard deviations, *i.e.* we rewrite for all parameters :

$$\sigma_P \equiv \epsilon_P \langle P \rangle, \quad \forall P \in \{l_\nu, R_\nu^*, S_i^*, \gamma_{i\nu}, \alpha_{\nu i}, \sigma_{i\nu}\}. \quad (79)$$

The previous relations then become :

$$\left\{ \begin{array}{l} \frac{l_\mu + \sum_j \alpha_{\mu j} S_j^*}{R_\mu^*} = \frac{l_0 (1 + \epsilon_l \tilde{l}_\mu) + \alpha_0 S_0 (N_S + \epsilon_\alpha \sum_j \tilde{a}_{\mu j} + \epsilon_\alpha \epsilon_S \sum_j \tilde{a}_{\mu j} \tilde{s}_j)}{R_0 (1 + \epsilon_R \tilde{r}_\mu)} \end{array} \right. \quad (80)$$

$$\left\{ \begin{array}{l} -\gamma_{j\mu} R_\mu^* + \alpha_{\mu j} = -\gamma_0 R_0 (1 + \epsilon_\gamma \tilde{g}_{j\mu} + \epsilon_R \tilde{r}_\mu + \epsilon_\gamma \epsilon_R \tilde{g}_{j\mu} \tilde{r}_\mu) + \alpha_0 (1 + \epsilon_\alpha \tilde{a}_{\mu j}) \end{array} \right. \quad (81)$$

$$\left\{ \begin{array}{l} \sigma_{i\nu} \gamma_{i\nu} S_i^* = \sigma_0 \gamma_0 S_0 (1 + \epsilon_\sigma \tilde{\sigma}_{i\nu} + \epsilon_\gamma \tilde{g}_{i\nu} + \epsilon_S \tilde{s}_i + \epsilon_\sigma \epsilon_\gamma \tilde{\sigma}_{i\nu} \tilde{g}_{i\nu} + \epsilon_\sigma \epsilon_S \tilde{\sigma}_{i\nu} \tilde{s}_i \\ + \epsilon_\gamma \epsilon_S \tilde{g}_{i\nu} \tilde{s}_i + \epsilon_\sigma \epsilon_\gamma \epsilon_S \tilde{\sigma}_{i\nu} \tilde{g}_{i\nu} \tilde{s}_i) \end{array} \right. \quad (82)$$

⁵This works with γ and α because G and A have a trivial topology. Otherwise we would have to take it into account and the computations would not be as easy.

Standard deviation expansion at first order

We can then assume the relative standard deviations are small :

$$\epsilon_P \ll 1, \quad \forall P \in \{l_\nu, R_\nu^*, S_i^*, \gamma_{i\nu}, \alpha_{\nu i}, \sigma_{i\nu}\}. \quad (83)$$

The previous equations can be rewritten as :

$$\left\{ \begin{array}{l} \frac{l_\mu + \sum_j \alpha_{\mu j} S_j^*}{R_\mu^*} = \frac{l_0 + N_S \alpha_0 S_0}{R_0} - \epsilon_R \frac{l_0 + N_S \alpha_0 S_0}{R_0} \tilde{r}_\mu + \epsilon_l \frac{l_0}{R_0} \tilde{l}_\mu + \epsilon_\alpha \frac{\alpha_0 S_0}{R_0} \sum_j \tilde{\alpha}_{\mu j} \end{array} \right. \quad (84)$$

$$\left\{ \begin{array}{l} -\gamma_{j\mu} R_\mu^* + \alpha_{\mu j} = -\gamma_0 R_0 + \alpha_0 - \epsilon_\gamma \gamma_0 R_0 \tilde{\gamma}_{j\mu} - \epsilon_R \gamma_0 R_0 \tilde{r}_\mu + \epsilon_\alpha \alpha_0 \tilde{\alpha}_{\mu j} \end{array} \right. \quad (85)$$

$$\sigma_{i\nu} \gamma_{i\nu} S_i^* = \sigma_0 \gamma_0 S_0 (1 + \epsilon_\sigma \tilde{\sigma}_{i\nu} + \epsilon_\gamma \tilde{\gamma}_{i\nu} + \epsilon_S \tilde{s}_i) \quad (86)$$

where we neglect all terms of order $\mathcal{O}(\epsilon^2)$. We now assume furthermore that the relative standard deviations of every parameter in the model more or less have the same value which again is assumed small, *i.e.* we set :

$$\epsilon_P \approx \epsilon \ll 1, \quad \forall P \in \{l_\nu, R_\nu^*, S_i^*, \gamma_{i\nu}, \alpha_{\nu i}, \sigma_{i\nu}\}. \quad (87)$$

This allows us to rewrite the jacobian at equilibrium as :

$$J^* = J_0 + \epsilon \tilde{J}, \quad (88)$$

with

$$J_0 = \begin{pmatrix} -\Delta_0 & \Gamma_0 \\ B_0 & 0 \end{pmatrix} \quad (89)$$

where

$$(\Delta_0)_{\mu\nu} \equiv \Delta_0 \delta_{\mu\nu} = \frac{l_0 + N_S \alpha_0 S_0}{R_0} \delta_{\mu\nu} \quad (90)$$

$$(\Gamma_0)_{\mu i} \equiv \Gamma_0 = -\gamma_0 R_0 + \alpha_0 \quad (91)$$

$$(B_0)_{i\nu} \equiv B_0 = \sigma_0 \gamma_0 S_0 \quad (92)$$

and

$$\tilde{J} = \begin{pmatrix} \tilde{\Delta} & \tilde{\Gamma} \\ \tilde{B} & 0 \end{pmatrix} \quad (93)$$

with

$$\tilde{\Delta}_{\mu\nu} \equiv \left(-\Delta_0 \tilde{r}_\mu + \frac{l_0}{R_0} \tilde{l}_\mu + \frac{\alpha_0 S_0}{R_0} \sum_j \tilde{\alpha}_{\mu j} \right) \delta_{\mu\nu} \quad (94)$$

$$\tilde{\Gamma}_{\mu i} \equiv \alpha_0 \tilde{\alpha}_{\mu i} - \gamma_0 R_0 (\tilde{\gamma}_{i\mu} + \tilde{r}_\mu) \quad (95)$$

$$\tilde{B}_{i\mu} \equiv B_0 (\tilde{\sigma}_{i\mu} + \tilde{\gamma}_{i\mu} + \tilde{s}_i) \quad (96)$$

Using Jacobi's formula [10], the equation $\det(J^* - \lambda) = 0$ can be rewritten as :

$$\boxed{\det(J_0 - \lambda + \epsilon J^*) = \det(J_0 - \lambda) + \epsilon \operatorname{Tr} \left(\operatorname{adj}(J_0 - \lambda) \tilde{J} \right) = 0.} \quad (97)$$

where $\operatorname{adj}(\dots)$ is the adjugate operator (*i.e.* which yields the transpose of the cofactor matrix). This equation is a complicated polynomial of degree $N_R + N_S$. As of now it does not seem to have an easily computable solution for $\epsilon > 0$. An explicit solution can however be computed when $\epsilon = 0$.

Zero variance case When $\epsilon = 0$, Eq.(97) becomes:

$$\det(J_0 - \lambda) = \det \begin{pmatrix} -\Delta_0 - \lambda & \Gamma_0 \\ B_0 & -\lambda \end{pmatrix} = 0 \quad (98)$$

If we assume that $\lambda \neq 0$, using a reasoning similar to Section ?? we can write the previous equation as:

$$\det(\lambda^2 + \Delta_0\lambda - \Gamma_0 B_0) = 0 \quad (99)$$

Component-wise, we have :

$$(\lambda^2 + \Delta_0\lambda - \Gamma_0 B_0)_{\mu\nu} = (\lambda^2 + \Delta_0\lambda) \delta_{\mu\nu} - \Gamma_0 B_0. \quad (100)$$

Using Eq.(??), the non-zero solutions of Eq.(99) are immediately found:

$$(\lambda + \Delta_0)^{N_R-1} (\lambda^2 + \Delta_0\lambda - N_R \Gamma_0 B_0) = 0. \quad (101)$$

That equation gives us $N_R - 1 + 2 = N_R + 1$ non-zero eigenvalues, which means that there are $N_S - 1$ zero eigenvalues. The two eigenvalues different from $-\Delta_0$ or 0 are the roots of the second degree polynomial:

$$\lambda^2 + \Delta_0\lambda - N_R \Gamma_0 B_0 = 0. \quad (102)$$

In the end, the spectrum is given by:

- if $\Gamma_0 < -\frac{\Delta_0^2}{4N_R B_0}$:

$$\sigma(J_0) = \left\{ 0, \dots, 0, -\Delta_0, \dots, -\Delta_0, -\frac{\Delta_0}{2} \left(1 \pm i \sqrt{-\left(1 + \frac{4N_R \Gamma_0 B_0}{\Delta_0^2} \right)} \right) \right\} \quad (103)$$

- if $\Gamma_0 = -\frac{\Delta_0^2}{4N_R B_0}$:

$$\sigma(J_0) = \left\{ 0, \dots, 0, -\Delta_0, \dots, -\Delta_0, -\frac{\Delta_0}{2}, -\frac{\Delta_0}{2} \right\} \quad (104)$$

- if $\Gamma_0 > -\frac{\Delta_0^2}{4N_R B_0}$:

$$\sigma(J_0) = \left\{ 0, \dots, 0, -\Delta_0, \dots, -\Delta_0, -\frac{\Delta_0}{2} \left(1 \pm \sqrt{1 + \frac{4N_R \Gamma_0 B_0}{\Delta_0^2}} \right) \right\} \quad (105)$$

It then becomes clear that the system is dynamically unstable if and only if $\frac{4N_R \Gamma_0 B_0}{\Delta_0^2} > 0$. Because $N_R, B_0 > 0$, we get the condition:

The non-variance system is dynamically unstable $\iff \Gamma_0 > 0$.

(106)

If $\Gamma_0 \leq 0$, the fully connected system will be marginally stable. Note that the RHS of the feasibility condition Eq.(??) is equivalent in the fully connected case to :

$$\alpha_0 \lesssim \min(1 - \sigma_0, \sigma_0) \gamma_0 R_0 \iff \Gamma_0 \lesssim [\min(1 - \sigma_0, \sigma_0) - 1] \gamma_0 R_0 < 0, \quad (107)$$

so we expect the fully connected case to be feasible and the non-zero eigenvalues to be negative. We see that the non-zero part of the spectrum is essentially given by Δ_0 . However the sign of the parameter $4N_R\Gamma_0 B_0 + \Delta_0^2$ plays an essential role in the stability. Looking at its sign allows us to find possibly more locally dynamically stable zones of the metaparameters space \mathcal{M} . Indeed we expect to find more stable systems if

$$4N_R\Gamma_0 B_0 + \Delta_0^2 \ll 0 \iff 4N_R\sigma_0\gamma_0(\alpha_0 - \gamma_0 R_0) + \frac{l_0^2}{S_0} + 2N_S\alpha_0 l_0 + N_S^2\alpha_0^2 S_0 \ll 0. \quad (108)$$