

As explained in Methods ??, before addressing the question of the stability of a system, be it dynamical or structural, it is important to study whether that system is *feasible*. In short we must answer the question: “does it make sense to talk about this system? Does it even exist?”.

We will say that it makes sense to talk about a system if it is *feasible* (see Methods ??). In order to be feasible, a system should respect two conditions: it must conserve biomass and its parameters must have a direct biological interpretation.

0.0.1 The feasibility volume $\mathcal{V}_x^{G,A}$

Formally we can define $\forall x \in [0, 1]$ the x -feasibility volume $\mathcal{V}_x^{G,A} \subset \mathcal{M}$ of the consumption network coupled with the syntrophy network $(G, A) \in \mathcal{B}_{N_S \times N_R} \times \mathcal{B}_{N_R \times N_S}$ (see Methods ??). Every metaparameter set $m \in \mathcal{M}$ contained in the x -feasibility volume $\mathcal{V}_x^{G,A}$ will give rise to a percentage x of feasible systems. A first order approximation of the fully feasible volume $\mathcal{V}_1^{G,A}$ is given by Eq.(??). In the absence of syntrophy $\alpha_0 = 0$, it becomes:

$$\gamma_0 R_0 \lesssim \frac{l_0}{\max_{\nu} \{\deg(G, \nu)\} S_0}. \quad (1)$$

This relation is interesting in many ways. First of all it tells us that at fixed consumption rate γ_0 and resource equilibrium abundance R_0 , feasibility increases when:

- the external resource input rate increases. This result was somewhat expected: if you give more food to a goldfish you expect it to thrive more.
- the consumer equilibrium abundance S_0 increases. What this means is that if you want to maintain the same consumption interaction but get a higher abundance of resources at equilibrium, you must at the same time decrease the consumers equilibrium abundance.
- the largest column-degree of the consumption matrix decreases. The degree of a given column ν of the consumption matrix tells you how many species eat from resource ν . This encourages communities of specialists, where each consumer eats from its own and no other resource.

Overall we see that feasibility increases when the *consumption flow* $\simeq \gamma_0 S_0 \deg(G, \nu)$ is low $\forall \nu$. Eq.(??) can be confronted to simulations. First of all note that for all the matrices in the set we chose, there existed a fully feasible zone. Fortunately, there was an overlap between all of these, such that the critical feasibility $f^*(S) = 1$ and the critical volume is the fully feasible volume which we denote \mathcal{V}^1 .

Figure ?? shows the proportion of feasible systems without syntrophy $\mathcal{F}(\gamma_0, S_0, \alpha_0 = 0, G)$ and $R_0 = l_0 = 1$, $\sigma_0 = 0.25$ (see Methods ??), for two matrices G_1 and G_2 of our set. G_1 has connectance $\kappa_1 = 0.17$ and nestedness $\eta_1 = 0.2$, G_2 is more connected and more nested: $\kappa_2 = 0.37$ and $\eta_2 = 0.4$.

We observe a very sharp transition from a fully feasible to a fully unfeasible regime. Theoretically, this sharp transition happens when both sides of the inequality (??) are equal,

i.e. at $\gamma_0 R_0 = l_0 / \max_{\nu} \{\deg(G, \nu)\} S_0$. Numerically we fit the points which are at “the boundary” of the common feasible volume, *i.e.* points where $0.4 \leq \mathcal{F}(\gamma_0, S_0, G) \leq 0.6$.

For G_1 , the theoretical expectation is $S_0 = 0.125/\gamma_0$ and a fit on the numerical results gives $S_0 = (0.124 \pm 7 \times 10^{-8})/\gamma_0 - (6.8 \times 10^{-4} \pm 3 \times 10^{-7})$ so the theoretical relation is already very good. For G_2 , we expect $S_0 = 0.077/\gamma_0$. A fit gives $S_0 = (0.075 \pm 2 \times 10^{-8})/\gamma_0 + (3.6 \times 10^{-4} \pm 1 \times 10^{-7})$. Again, the theoretical value is very close to the measured value.

The numerical estimate does not always match that well the theoretical value. Fig.?? shows the relative error $\Delta_G = 1 - (\text{theoretical value})/(\text{numerical estimate})$. We see that in general the theoretical expectation tends to overestimate the fully feasible region. This is probably due to the noise (*i.e.* the deviations away from the metaparameters) in the actual systems and the structure of the G matrix. Indeed Fig.?? shows that the lower the nestedness and connectance of G , the worse the theoretical estimate. In the future a better approximation can surely be found taking into account the variance of the metaparameters and the nestedness of G .

We can similarly measure the common fully feasible volume \mathcal{V}^* , which according to Eq.(??) is inversely proportional to the largest maximal row degree of the matrix set. For the set we considered, this yields in theory: $S_0 = 0.053\gamma_0$. A fit on the points at the edge yields the critical boundary $S_0 = (0.043 \pm 10^{-8})/\gamma_0 - (4.6 \times 10^{-3} \pm 3 \times 10^{-8})$. The theoretical prediction is not as good as before with an error of $\sim 20\%$. The discrepancy is probably due to the fact that numerically we determine the common feasibility volume by counting the points for which $\mathcal{F}(\gamma_0, S_0, G) = 1 \forall G \in S_G$, while the theoretical value matches better a fit of the points $0.4 \leq \mathcal{F} \leq 0.6$ **make this more understandable**.

0.0.2 Evolution of the feasible volume with syntrophy

Above we computed feasible volumes when there is no syntrophy *i.e.* $\mathcal{V}_1^G(\alpha_0 = 0)$. Since $\alpha_0 = 0$, we did not need to specify what the structure of A was. The next naturally arising question is then: what happens to the feasible volume of a given matrix G when we add a syntrophic interaction? More precisely, how does \mathcal{V}_1^G 's shape change?

The problem gets a bit more complex here. When we computed $\mathcal{V}_1^G(\alpha_0 = 0)$, we only had to take into account the structure of G , since there was no syntrophy. Now, we have an additional complexity because we have to think about the structure of the syntrophy network A as well. The choice of A , which is at the core of the problem, is far from trivial. We investigated three different cases:

- “fully connected”: A is filled with ones only, $A_{\mu i} = 1$. This corresponds to a so-called “mean-field” approximation. Every consumer releases every resource at (up to some noise) the same intensity.
- “no intraspecific syntrophy”: the structure of A is such that consumers are not allowed to release what they consume, *i.e.* there is no coprophagy.
- “optimal LRI”: A is the outcome of the Monte Carlo algorithm ¹ described in Meth-

¹Note that we took a constant value α_0 (given in Methods ??) and $\gamma_0 = 0.2$. A more thorough analysis should build the optimal LRI matrix *corresponding to each* (γ_0, α_0) . That would take too much time which is why we decided to keep γ_0 and α_0 constant.

ods ??, whose purpose is to make systems “more dynamically stable” and hence more feasible.

The maximal common feasible syntrophy can be estimated with the help of Eq.(??):

$$\alpha_0 \lesssim \frac{\min(1 - \sigma_0, \sigma_0)\gamma_0 R_0}{\max_{(G,A) \in S} \left\{ \max_i \left\{ \frac{\deg(A,i)}{\deg(G,i)} \right\} \right\}} \approx 0.01\gamma_0 \leq 0.01. \quad (2)$$

So we will look at ten different α_0 values from 0 to 0.015. We first consider the effect of syntrophy on each consumption network G then on the common fully feasible volume.

The influence of matrix structure

Because Eq.(?) depends on the structure of G and of A , we expect $\mathcal{F}_1^{G,A}$ to depend heavily on the topology of both consumption and syntrophy matrices. Figure ?? shows that indeed \mathcal{F}_1^G not only changes with syntrophy but also with the network structure of the consumption matrix.

First of all, we observe a general trend among all matrices, the fully feasible region moves horizontally to the right towards a higher γ_0 . This can be explained with Eq.(?): when $\alpha_0 > 0$, it provides a lower bound to γ_0 . Note that S_0 remains unbounded, so at a fixed γ_0 , every S_0 from 0 to the upper boundary critical curve $\sim \gamma_0^{-1}$ discussed before will be a fully feasible point. So in general, as syntrophy increases, systems with a high consumption rate and a low consumers abundance at equilibrium will remain feasible.

Not only does $\mathcal{F}_1^{G,A}$ change its location, it also shrinks in size: as syntrophy is increased, the set of possible consumption rate and average consumers abundance is more restricted. Figure ?? shows that $\text{Vol}(\mathcal{F}_1^G(\alpha_0))$ decays exponentially as α_0 increases. We can define the *feasibility decay rate* by performing a fit in order to find the constants $c_1, c_2, d_F \in \mathbb{R}^+$ that satisfy best:

$$\text{Vol}(\mathcal{F}_1^{G,A}(\alpha_0)) \approx c_1 \exp(-d_F x) - c_2. \quad (3)$$

The value of $d_F(G, A)$ tells us how fast the feasible volume shrinks for a given consumption-syntrophy couple (G, A) . In that sense $d_F(G, A)$ provides a measure of how good a consumption-syntrophy network (G, A) can sustain an increase in syntrophy². If d_F is low then the system can bear an increase of syntrophy and stay feasible. If d_F is high, the system will quickly not be feasible at all anymore.

Figure ?? shows how d_F changes for different matrices and different structures of the syntrophy matrix. A few comments can be made. First of all it seems like the structure of A does not provide any real difference, except for G with $\eta_G = 0.15$ and $\kappa_G = 0.18$. For that specific matrix, the optimal LRI structure for A reduced by a factor of three the decay rate, compared to the fully connected case. That result is only true for this specific matrix and does not hold for the others, where $d_F(G, A)$ seems to almost not depend on A . Furthermore

²One could also desire to define a *critical feasible syntrophy* as the smallest syntrophy that gives a zero fully feasible volume. This would be a very interesting quantity to study and could be easily found as the root of the RHS of Eq.(?). We tried doing this, because the errors on d_F and on the two other fitting coefficients are already quite large (see the caption of Fig. ??), the errors on the critical feasible syntrophy we obtained were way too large, making our results essentially meaningless.

a very strong trend can be observed, for all matrices and all structures of A : for a given connectance, d_F is increased if the ecological overlap is increased and for a given ecological overlap d_F decreases if the connectance is increased. This means clearly that systems where there is a small ecological overlap but a lot of links in the food consumption network will be favoured. Microbial communities where consumers eat from a lot of different resources (*i.e.* each their own) can sustain a larger syntrophic interaction than others.

Common fully feasible volume

After studying the structure of each matrix individually, we can focus on the common fully feasible volume $\mathcal{F}_1^{S_M}$. Figure ?? show the evolution of the common feasible volume as syntrophy increases. Once again, the structure of the syntrophy matrix does not seem to play a significant role in the shape of $\mathcal{F}_1^{S_M}$. Note that at $\alpha_0 = 9.1 \times 10^{-3}$, $\text{Vol}(\mathcal{F}_1^{S_M}) = 0$ but at $\alpha_0 = 7.8 \times 10^{-3}$ the common feasible region was still non-zero. So the *critical common feasibility* α_0^F , defined as the smallest syntrophy which gives rise to a zero fully feasible volume respects $7.8 \times 10^{-3} < \alpha_0^F \leq 9.1 \times 10^{-3}$. It was estimated above that $\alpha_0^F \approx 0.01$, which is the right order of magnitude.

Figure ?? shows that unsurprisingly $\text{Vol}(\mathcal{F}_1^{S_M}(\alpha_0))$ also decays exponentially with a rate $d_F(S_M) = 480 \pm 50$ per unit of syntrophy which is a bit larger than the largest $d_F(G, A)$ observed in Fig.?. Without any surprise as well we observe the same shift of $\mathcal{F}_1^{S_M}$ towards points with a high γ_0 and consequently a small S_0 **Add interpretation on this?**

The influence of the matrix dimensions

For now we only focused on systems with the same number of consumers and resources: $N_R = N_S = 25$. But such a system lies at what has been called in the literature as May's stability bound [biroli_marginally_2018], which is precisely defined as an ecological community where the number of resources is equal to the number of species. According to the competitive exclusion principle³, an ecological system which has as many resources as consumers is the border case where coexistence, *i.e.* feasibility of our system, starts to exist, so in a way the study conducted before can be seen as a borderline case and it can be very fruitful to investigate the behaviour of systems where the number of resources has been increased to $N_R = 50$.

Figure ?? is the $N_R = 50$ equivalent to Figure ?. We may observe that increasing N_R has a non-trivial effect, which will be different for each consumption-syntrophy network. For instance, for G with $\eta_G = 0.6$ and $\kappa_G = 0.32$, adding more resources increases the maximal syntrophy bearable by the system (Fig.?). On the contrary, for G with $\eta_G = 0.15$ and $\kappa_G = 0.12$, it decreases it from 1.4×10^{-2} to 7.8×10^{-3} .

A global trend can however be discovered by looking at the common feasibility region (Fig.?). We see that, compared with the $N_R = 25$ case (Fig.?), an overall lesser syntrophy can be achieved. Finally Figure ?? shows that indeed it is really hard to predict the effect that

³The heavily debated and often misunderstood [hardin_competitive_1960] *competitive exclusion principle*, also known as Gause's principle, states that "Complete competitors cannot coexist" [hardin_competitive_1960], or more generally that "the number of consumer species in steady coexistence cannot exceed that of resources" [wang_overcome_2019].

increasing the number of resources will have on a specific consumption-syntrophy network. Indeed d_F , which we use to measure how big of a syntrophy a consumption-syntrophy network (G, A) can bear, does not have a clear pattern, at least not under the matrix metrics we chose to measure. It is a sign that this question needs a further and deeper investigation.

Figure 1: Plot of the feasibility region. The color curve indicates the feasibility function $\mathcal{F}(\gamma_0, S_0, \alpha_0 = 0, G)$ for G_1 (left) and G_2 (right). We observe a steep descent which marks a very clear transition from a totally feasible regime to a totally unfeasible regime, which allows us to precisely get the boundary of \mathcal{V}_1^G . The dashed lines indicate the theoretical predictions, which for both G_1 and G_2 are accurate to the order of 0.1%.

Figure 2: Relative error in the determination of the boundary of $\mathcal{V}_1^{G,0}$ (a) varying connectance at fixed nestedness and (b) varying nestedness at fixed connectance. The theoretical prediction tends to overestimate the measured value. The larger the nestedness and connectance, the better the estimate.

Figure 3: Plot of the common feasibility region. The blue area indicates the common feasibility volume, computed numerically, while the dashed line shows the analytical prediction. Although the match is not as good as before, the relative error is only of the order of 20%. The red part is the area where not all matrices are fully feasible. From now on, it will not be considered anymore.

feasibility_region_wt_wc_NR25_NS25_Nest0.6_Conn0.3168.pdf

(a)

feasibility_region_wt_wc_NR25_NS25_Nest0.35_Conn0.2208.pdf

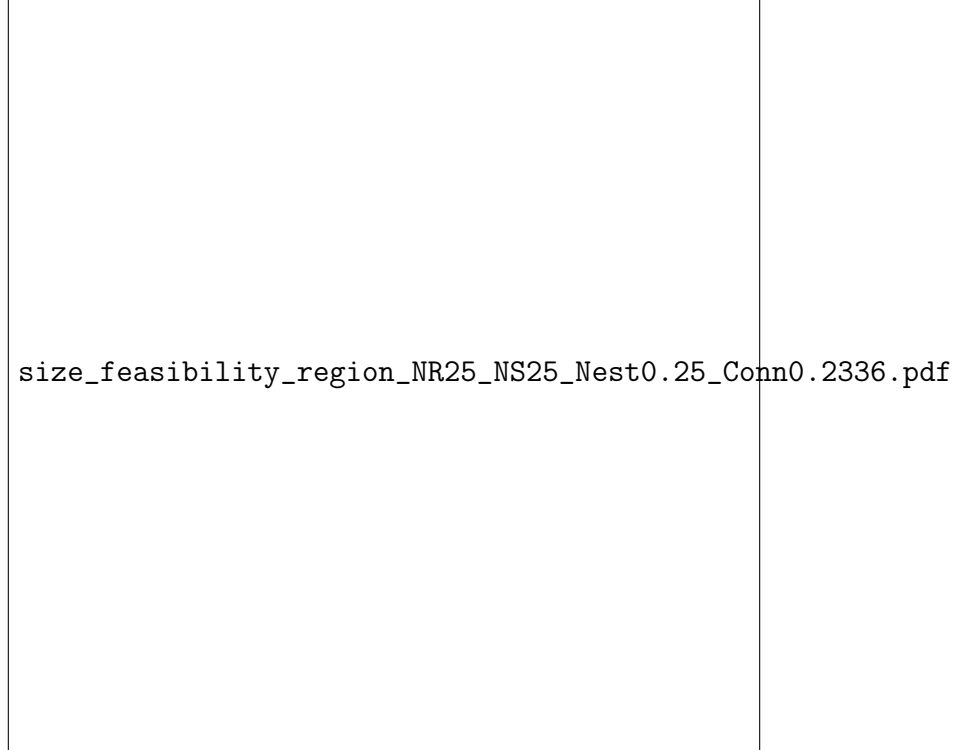


Figure 5: Decay of the volume of the fully feasible region $\mathcal{F}_1^G(\alpha_0)$ for a matrix consumption G with ecological overlap $\eta_G = 0.25$ and connectance $\kappa_G = 0.23$ on a logarithmic scale. The solid lines represent the exponential fit explained in the main text. The three different colors represent the three different structures considered for the syntrophy matrix. The decay of $\text{Vol}(\mathcal{F}_1^G)$ seems well approximated by an exponential decay and the structure of the A -matrix seems to not play a large role in that prospect.

(a)

feasibility_NR25_NS25_feasibility_decay_rate_fixed
feasibility_NR25_NS25_feasibility_decay_rate_fixed

(b)

feasibility_NR25_NS25_feasibility_decay_rate_fixed
feasibility_NR25_NS25_feasibility_decay_rate_fixed

(c)

feasibility_NR25_NS25_feasibility_decay_rate_fixed
feasibility_NR25_NS25_feasibility_decay_rate_fixed

(d)

feasibility_NR25_NS25_feasibility_decay_rate_fixed
feasibility_NR25_NS25_feasibility_decay_rate_fixed

(e)

feasibility_NR25_NS25_feasibility_decay_rate_fixed
feasibility_NR25_NS25_feasibility_decay_rate_fixed

(f)

feasibility_NR25_NS25_feasibility_decay_rate_fixed
feasibility_NR25_NS25_feasibility_decay_rate_fixed

(b)

(c)

Figure 7: Surface plot of the fully feasible volume $\mathcal{V}^1(\alpha_0)$. The color bar on the side indicates the value of α_0 to which the surface corresponds. The white part of the plot corresponds to points that *never* are fully feasible. Note that even though it is not very clear on the figure $\mathcal{V}^1(\alpha_0^+) \subset \mathcal{V}^1(\alpha_0^-) \forall \alpha_0^+ > \alpha_0^-$, *i.e.* the common fully feasible region of higher syntrophy is included in the one of lower syntrophy. The different subplots correspond to different structures for the syntrophy matrix: (a) A is fully connected, (b) A has a structure such that intraspecific syntrophy is restricted and (c) A is obtained through the LRI MC algorithm described in Methods ??.

Figure 8: Volume of the common feasibility region $\mathcal{V}^1(\alpha_0)$ as a function of syntrophic interaction strength α_0 . The curves indicate the different structures used for the syntrophy network A .

feasibility_region_wt_NR50_NS25_Nest0.6_Conn0.3344.pdf

(a)

feasibility_region_wt_NR50_NS25_Nest0.35_Conn0.2296.pdf

(b)

(c)

Figure 10: Common feasibility region $\mathcal{F}_1^{SM}(\alpha_0)$ for $N_R = 50$ and $N_S = 25$, to compare with ???. We considered different structures of the syntrophy matrix: (a) fully connected, (b) intraspecific syntrophy restricted and (c) LRI matrix. As the number of resources increases, the feasibility volume for a given α_0 decreases.

(a)

decay_rate_25_vs_50_nestedness_random_structure.pdf

(b)

decay_rate_25_vs_50_connectance_random_structure.pdf

(c)

decay_rate_25_vs_50_nestedness_no_release_when_empty.pdf

(d)

decay_rate_25_vs_50_connectance_no_release_when_empty.pdf

(e)

decay_rate_25_vs_50_nestedness_optimal_matrix.pdf

(f)

decay_rate_25_vs_50_connectance_optimal_matrix.pdf