We discovered in the previous section that we expect microbial communities where a large syntrophic interaction is observed to have a large consumption rate γ_0 and a small abundance of consumers at equilibrium S_0. It is time to work with feasible systems and investigate their dynamics. We now spend our energy on studying the local dynamical stability of feasible microbial communities. In short, we want to know what happens to them when their populations (of both resources and microbes) at equilibrium are perturbed. The question of the stability of ecosystems has always been and still remains of prime importance for ecologists and constitutes a whole scientific field. Many results have been derived, for linear systems [**may_will_1972**], Lotka-Volterra systems [**bunin_ecological_2017**, **takeuchi_global_1996**] or MacArthur's consumer

0.0.1 LRI regime – Outcome of the MCMC algorithm

Methods **??** explains how we designed an algorithm whose goal is to find, for a given consumption matrix G, the syntrophy matrix A that should bring us closer to the satisfaction of Eq.(**??**), which we know is a dynamically stable regime. The shape of the A-matrix that is the outcome of the algorithm minimizes the energy $E(G, A)$ (Eq.**??**). Namely, A should have the following properties:

- The sum of the diagonal elements of AG is minimized. Because $(AG)_{\mu\mu} = \sum_{i=1}^{N_S} A_{\mu i} G_{i\mu}$ corresponds to the number of species that both consume and release resource μ, we expect the algorithm to yield A-matrices that minimize intraspecific syntrophy.

- The sum of the off-diagonal elements of $\left| \alpha_0 AG - \gamma_0 R_0 G^T G \right|$ is minimized. This means that outside the diagonal, we should have $\frac{\alpha_0}{\gamma_0 R_0} AG \approx G^T G$. A direct ecological interpretation is harder to draw. For a couple of different resources (μ, ν), $(AG)_{\mu\nu} = \sum_{i=1}^{N_S} A_{\mu i} G_{i\nu}$ is the number of species that at the same time consume resource ν and release resource μ and $(G^T G)_{\mu\nu} = \sum_{i=1}^{N_S} G_{i\mu} G_{i\nu}$ is the number of consumers that eat both ν and μ. **TO DO: add something here, transition is a bit rough**

So intuitively the LRI MCMC algorithm should give us a syntrophy matrix that both limits intraspecific syntrophy and such that for every couple of different resources (μ, ν), the number of consumers that eat both μ and ν is proportional to the number of consumers that eat μ and release ν. The proportionality constant, which is the same for all (μ, ν) is equal to the ratio of the syntrophy and consumption interactions. Since the connectance and the dimensions of A are fixed, the number of links of A is already decided and the algorithm simply determines how to optimally distribute them. Figure **??** shows that typically the algorithm will put links in a cell (μ, i) if (i, μ) is zero, meaning that not only intraspecific syntrophy tries to be avoided but also species that consume a lot of resources will tend to release few of them and vice-versa.

Figure **??** shows that indeed we obtain for a given G matrix a syntrophy matrix A such that the two requirements above are best satisfied. Note that the algorithm works better for matrices with a low connectance. **TO DO: explain why** It is worth noticing that this procedure produces highly nested syntrophy matrices (Fig.**??**) where only a few species produce most of the syntrophic flow. The obtained matrices have an even larger nestedness

if we increase the number of resources. **TO DO : check if can speak of syntrophic overlap for nestedness of syntrophy matrix**

0.0.2 Typical dynamical stability

We observed in Results **??** that, for all $(G, A) \in S_{25}$, at fixed α_0 the metaparameters feasibility function $\mathcal{F}(m, G, A)$ has a typically sharp transition from fully feasible ($\mathcal{F} = 1$) to fully unfeasible ($\mathcal{F} = 0$) regimes in the (γ_0, S_0) plane. Figure **??** shows that a similar although more complicated behaviour is observed in the case of the dynamical stability function $\mathcal{D}_L((\gamma_0, S_0, \alpha_0), G, A)$. On one hand, the (γ_0, S_0) plane is split in two distinct zones, which are also separated by a very narrow boundary. The first zone is characterised by complete dynamical instability, *i.e.* $\mathcal{D}_L = 0$. On the other hand, the second zone is not described by full dynamical stability, but rather *almost* full dynamical stability: $\mathcal{D}_L$ is very close to but not always exactly equal to 1. The consequence is that the fully dynamically stable region $\mathcal{D}_{L,1}^{G,A}$ will be very patchy (see below for a longer discussion on this).

That patchiness could come from purely numerical effects: $\mathcal{D}_L$ is estimated by generating N_{sys} parameters sets and counting the proportion that is dynamically stable, which inevitably leads to an uncertainty on $\mathcal{D}_L$ that could explain the patchiness. Or it could come from a genuine complicated topology of $\mathcal{D}_{L,1}^{G,A}$. In a future project, increasing N_{sys} would allow to reduce the relative uncertainty on $\mathcal{D}_L$ and truly discover the origin of this interesting phenomenon.

0.0.3 Fully dynamically stable region

The same way we studied the fully feasible volume $\mathcal{F}_1^{G,A}(\alpha_0)$, we investigate now the behaviour of its special subset, the locally fully dynamically stable region $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$, which is defined[1] as

$$\mathcal{D}_{L,1}^{G,A}(\alpha_0) \equiv \left\{ (\gamma_0, S_0) : (\gamma_0, S_0, \alpha_0) \in \mathcal{D}_{L,1}^{G,A} \right\}. \tag{1}$$

Intuitively, $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$ corresponds to the set of all (γ_0, S_0) such that $\mathcal{A}((\gamma_0, S_0, \alpha_0), G, A)$ is a feasible, locally dynamically stable parameters set with probability 1. Since we require $\mathcal{A}((\gamma_0, S_0, \alpha_0), G, A)$ to be feasible, it is clear that $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$ is indeed a subset of $\mathcal{F}_1^{G,A}(\alpha_0)$.

As explained above, $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$ is geometrically more complex than $\mathcal{F}_1^{G,A}(\alpha_0)$ (Figure **??**) because of the *almost* fully dynamically stable points[2] . It may sometimes have holes, even without syntrophy, and sometimes not, even for matrices that are topologically very close. Compare for instance Fig.**??** with Fig.**??**, these two networks have the same ecological overlap, but even though their connectance is very similar, their fully locally dynamically stable regions have a very different shape: one of them can sustain only a tiny bit of syntrophy before becoming dynamically unstable (Fig.**??**) while the second can endure basically any

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[1]A formal definition of the fully dynamically stable region $\mathcal{D}_{L,1}^{G,A}$ is provided in Methods **??**.

[2]One may argue then that we should also consider the almost fully dynamically stable points in the analysis. That position is intellectually appealing but would require to either work in a completely different framework or choose a "stability threshold" which separates almost fully feasible points from the others. The arbitrariness of said threshold (should we take into account points above $\mathcal{D}_L = 0.99$? Or above $\mathcal{D}_L = 0.98$? What about 0.995?) would make such a point of view hard to hold.

feasible syntrophic interaction (Fig.**??**). A general trend is hence harder to find but it seems that points with a larger γ_0 are in general more dynamically stable (more on this below).

We required that a system had to be feasible in order to be dynamically stable, which is the mathematical equivalent of $\mathcal{D}_{L,1}^{G,A}(\alpha_0) \subset \mathcal{F}_1^{G,A}(\alpha_0)$, *i.e.* local dynamical stability implies feasibility. We may also ask the reverse question, does feasibility imply local dynamical stability? The answer to this is, again, unsurpisingly, "it depends on the matrix", as shows Figure **??**. For instance, for G with $\kappa_G = 0.13$ and $\eta_G = 0.1$, we have $\text{Vol}\left(\mathcal{D}_{L,1}^{G,A}(\alpha_0)\right) < \text{Vol}\left(\mathcal{F}_{L,1}^{G,A}(\alpha_0)\right) \forall \alpha_0$, which means that for this consumption matrix feasibility does not imply stability. The fully connected case gives a larger dynamically stable volume than the regime without intraspecific syntrophy which is itself better than the LRI regime. This hints that the LRI regime, despite what it was designed for, apparently does not give better results than other structures of A. On the contrary, for G with $\kappa_G = 0.32$ and $\eta_G = 0.6$, both volumes are equal at every syntrophy that is feasible, for the three structures of A considered, which shows that for this specific matrix, feasibility implies local dynamical stability.

A good way to measure how systems react to syntrophy is to compute the *critical locally dynamically stable syntrophy* $\alpha_0^D(G, A)$ (see Methods **??**). An easy way this can be done is by getting some points of the volume of $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$ curve and finding its intercept to zero. Figure **??** shows the typical shrinkage of the fully locally dynamically stable volume.

To find $\alpha_0^D(G, A)$ for each G, we fit with a linear function the last four points of the curve corresponding to Fig.**??** and find its intercept to zero $\alpha_0^D(G, A)$. Figure **??** shows a very interesting and clear behaviour[3]: for a given connectance of the consumption matrix, systems that can sustain the largest syntrophy have a small ecological overlap. And for a given ecological overlap, systems with a larger connectance will stay stable longer under the action of syntrophy. In the end, optimal systems have a small ecological overlap and a large connectance: many resources are eaten by the consumers, but they do not share them.

Finally, one can take a look at the *common fully locally dynamically stable region*, which is the intersection of the $\mathcal{D}_{L,1}^{G,A}(\alpha_0) \forall (G, A) \in S_M$ (Figure **??**). Because of the fractured and heterogenous nature of each $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$, we observe a very fractured and small common fully locally dynamically stable region, which is the same for all structures of A considered. It has a non-zero volume for $\alpha_0 = 0$, but for the next point investigated $\alpha_0 = 1.3 \times 10^{-3}$, no point is fully locally dynamically stable for every matrix considered, which means that the critical common syntrophy is smaller than this.

0.0.4 Largest eigenvalue of the jacobian

Equation (**??**) from Methods **??** gives a relationship that the metaparameters should approximately follow in order to give rise to locally dynamically stable systems. Although strictly speaking it is only valid for the case where both G and A are fully connected, we expect it to work as well when G and A are *not too far away* from the fully connected case. It tells us that in order to get more local dynamically stable systems you should:

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[3]Those results have to be taken with a grain of salt because we did not check whether $\alpha_0^D(G, A)$ was feasible, *i.e.* the actual critical locally dynamically stable syntrophy is the minimum between the value measured in Fig.**??** and the largest feasible α_0 for that couple (G, A).

- decrease N_S, l_0 **WEIRD RESULT: would expect that increasing l0 would make systems more dynamically stable (observed in simulations I think)** or α_0,

- if $\alpha_0 - \gamma_0 R_0 < 0$, increase N_R, σ_0 and γ_0,

- be careful in how you handle S_0: increasing S_0 reduces the l_0^2/S_0 term but increases the $N_S^2\alpha_0^2 S_0$ term. It is very easy to show (Appendix **??**) that if $S_0 > l_0/(N_S\alpha_0)$ it should be decreased, and otherwise it should be increased until it reaches $l_0/(N_S\alpha_0)$.

Combining these with the feasibility conditions Eq.(**??**) we expect that – for all other metaparameters fixed – systems get more and more locally dynamically stable as γ_0 is increased and S_0 is the largest possible. In short, points at the upper border of $\mathcal{D}_{L,1}^{G,A}$ should have a lower and lower $\mathrm{Re}\,(\lambda_1)$ as γ_0 increases. Figure **??** shows that indeed this trend is followed. This tells us that if we keep the consumption flux $N_S\gamma_0 S_0$ constant, increasing γ_0 (and hence decreasing S_0) will give rise to more stable systems. Notice that contrarily to the prediction made above, increasing α_0 does not decrease stability but increases the maximal $|\mathrm{Re}\,(\lambda_1)|$ observed as shows Fig.**??**. This is coupled with the shrinkage of the fully locally dynamically stable volume seen on Fig.**??**. This means that overall increasing syntrophy makes the system *more stable* but at *fewer points*. This hints that systems in a high syntrophic regime, where consumers produce a lot of resources, should be very fine-tuned and occur for very specific consumption strength and average abundance of consumers.

0.0.5 The influence of the matrix dimension

As said above, because of Eq.(**??**), we expect stability to increase when the number of resources is increased for a fixed number of consumers. The following subsection shows what happens when the number of resources is doubled $N_R = 25 \rightarrow N_R = 50$ and every other metaparameter, as well as the number of consumers, keeps the same value as before.

Figure **??** shows that the effect of adding resources can be quite dramatic on the stability of the system. For that specific matrix for instance, adding resources allowed for a way larger $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$ at each α_0. It even allows full dynamical stability in the feasibility region for larger syntrophic interactions than before. Even though more syntrophy can be sustained, it seems that the volume of $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$ is smaller at $N_R = 50$ than at $N_R = 25$ (compare for instance Fig.**??** with Fig.**??**). This is compensated by the fact that way larger eigenvalues are observed at $N_R = 50$: although there are (a bit) fewer equilibrium points, these are more stable (compare Fig.**??** and Fig.**??**). This is a trend that we believe holds for all the matrices considered but a more thorough investigation should be conducted before claiming those results to be absolutely true.

Since matrices are individually more locally dynamically stable, the *common locally dynamically stable* region is larger with $N_R = 50$ resources than with $N_R = 25$. The difference between Figure **??** and Figure **??** is very striking: when the number of resources is increased not only is $\mathcal{D}_{L,1}^{S_M}(\alpha_0)$ larger, it also can overall bear a larger syntrophy. Remember that for $N_R = 25$, the critical common syntrophy was between 0 and 1.3×10^{-3}, and for $N_R = 50$, it is way larger, between 3.9×10^{-3} and 5.2×10^{-3}. **Is there anything more to add? I have some plots but I am not sure if they are the most relevant**

Figure 1: *Typical shape of the consumption G_i and syntrophy A_i matrices. The white cells symbolize a zero matrix element and the black cells, a one. A_i here is the outcome of the LRI MC algorithm described in Methods* **??**. *The first row has a consumption matrix with $\eta_1 = 0.6$ and $\kappa_1 = 0.32$, the LRI MC solver gives rise to a syntrophy matrix with same connectance and ecological overlap ≈ 0.85. The second row has G_2 with $\eta_2 = 0.1$ and $\kappa_2 = 0.13$ and the corresponding syntrophy matrix A_2 has ecological overlap ~ 0.42. We observe that under this optimisation, species that consume few resources end up releasing many and the other way around.*

Figure 2: *Plotting of AG and $G^T G - \alpha_0/(\gamma_0 R_0)AG$. The A and G matrices of the first and second rows correspond to the respective A and G of Figure* **??**. *As expected, we obtain an A such that intraspecific coprophagy is limited (the diagonal of AG is roughly zero) and, outside the diagonal, $G^T G - \alpha_0/(\gamma_0 R_0)AG \approx 0$. Both relations are better satisfied for consumption (and hence syntrophy) matrices with a low connectance.*
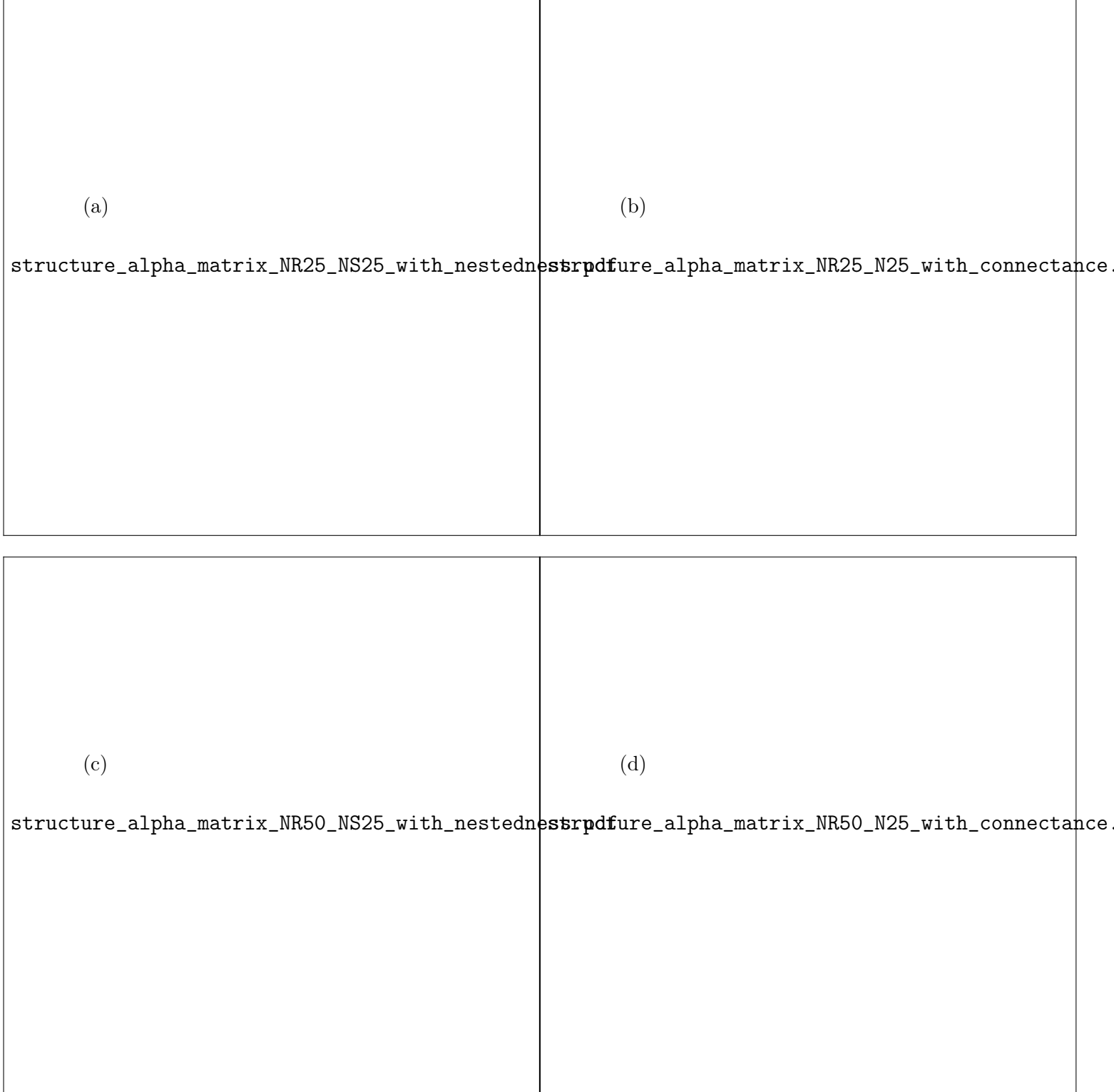
Figure 3: *Properties of the syntrophy matrix against the consumption matrix. (a)-(c) Ecological overlap of A as a function of the ecological overlap of G for $N_S = 25$ and $N_R = 25$ (a) or $N_R = 50$ (c). (b)-(d) Ecological overlap of A as a function of the connectance of G for $N_S = 25$ and $N_R = 25$ (b) or $N_R = 50$ (d). The nestedness of the "intraspecific syntrophy restricted" is also plotted as a matter of comparison. As η_G or κ_G increase, the two results will without surprise give matrices with similar properties.* **Explain this?**

probability_dynamical_stability_NR25_NS25_Nest0.5_Conn0.416_low_colorbar.pdf

(a)

local_dynamical_stability_wt_wc_region_NR25_NS25_Nest0.35_Conn0.2208.pdf

(a)

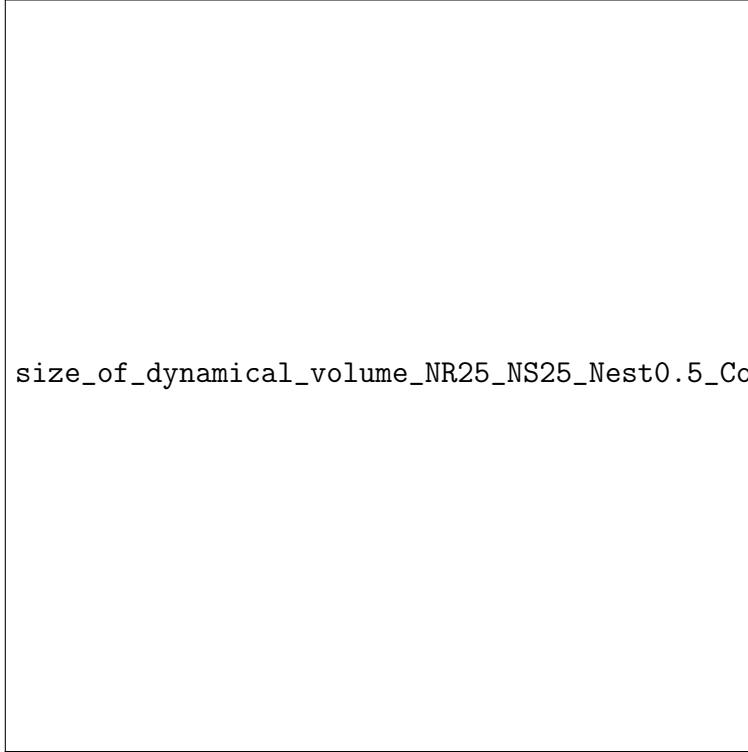feasibility_vs_lds_NR25_NS25_Nest0.1_Conn0.1296.pdf

(a)

Figure 7: Evolution of the volume of $\mathcal{D}_{L,1}^{G,A}(\alpha_0)$ with α_0 for a consumption matrix G with $\eta_G = 0.5$ and $\kappa_G = 0.42$. The size of the fully locally dynamically feasible region shrinks as syntrophy increases. A linear fit is performed on the last four points to determine $\alpha_0^D(G, A)$ (see Fig.??), the point where this curves reaches zero.

(a)

largest_eigenvalue_NR25_NS25_critical_alpha0_fixed...largest_eigenvalue_NR25_NS25_critical_pdf_alpha0_fixe

(b)

(c)

largest_eigenvalue_NR25_NS25_critical_alpha0_fixed...largest_eigenvalue_NR25_NS25_critical_pdf_alpha0_fixe

(d)

(e)

largest_eigenvalue_NR25_NS25_critical_alpha0_fixed...largest_eigenvalue_NR25_NS25_critical_pdf_alpha0_fixe

(f)

11

(a)
common_local_dynamical_stability_volume_NR25_NS25_varying_syntrophy_random_structure.p...

(b)
common_local_dynamical_stability_volume_NR25_NS25...

(c)
common_local_dynamical_stability_volume_NR25_NS25_varying_syntrophy_opti...
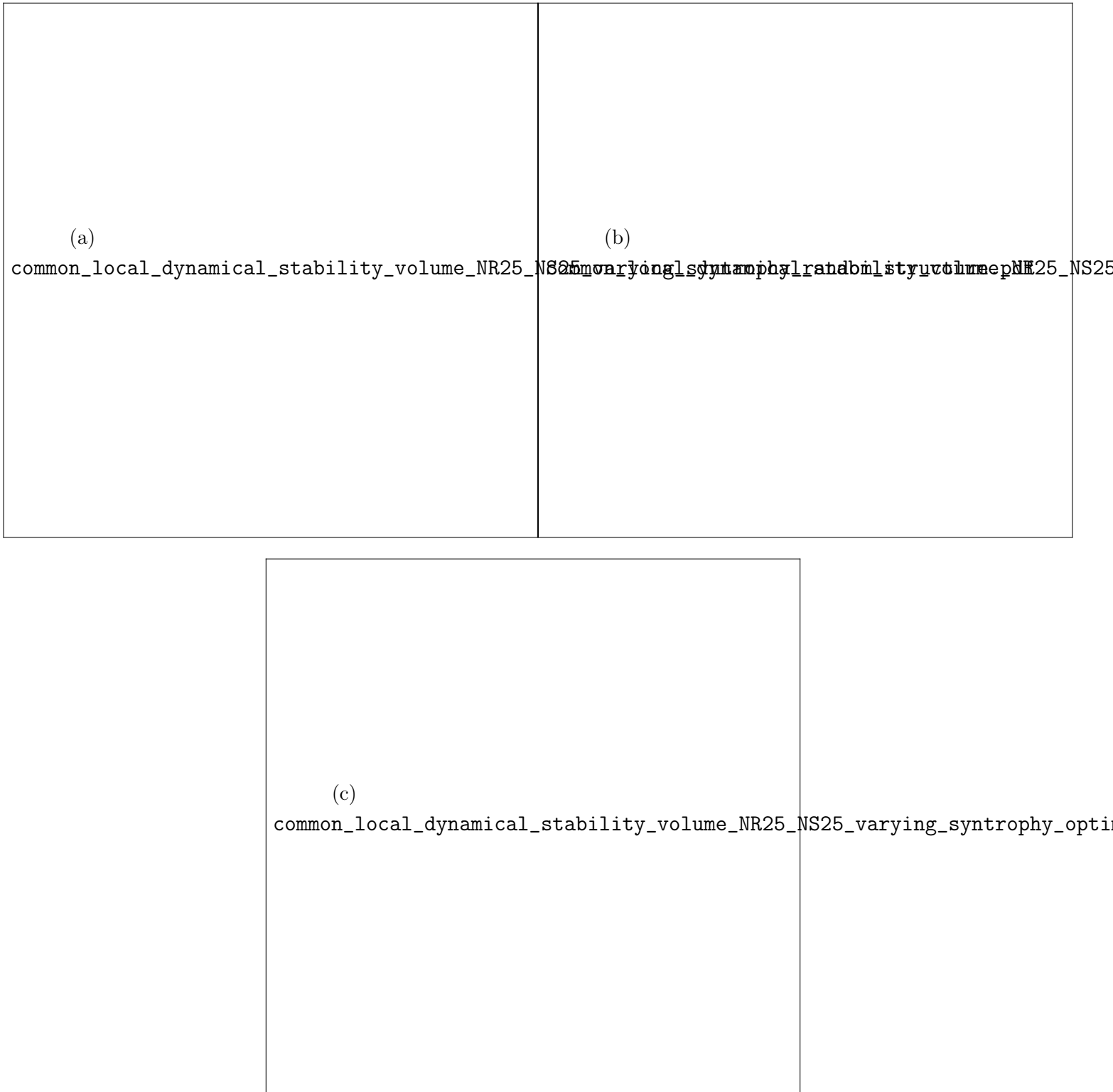
Figure 9: Common full local dynamical stability volume for different A structures: (a) fully connected, (b) no intraspecific syntrophy and (c) LRI algorithm. The points coloured in dark red give rise to locally dynamically stable systems with probability 1 for all the matrices considered. Very few spots verify this property when there is no syntrophic interaction, and no point gives rise to a fully dynamically stable system for $\alpha_0 = 1.3 \times 10^{-3}$. This is independent of the structure of A that we chose. The white points never give rise to fully dynamically stable systems.

largest_eigenvalue_wt_NR25_NS25_Nest0.1_Conn0.1296_alpha0=0.0.pdf

(a)

largest_eigenvalue_wt_NR25_NS25_Nest0.1_Conn0.1296_alpha0=0.0039.pdf
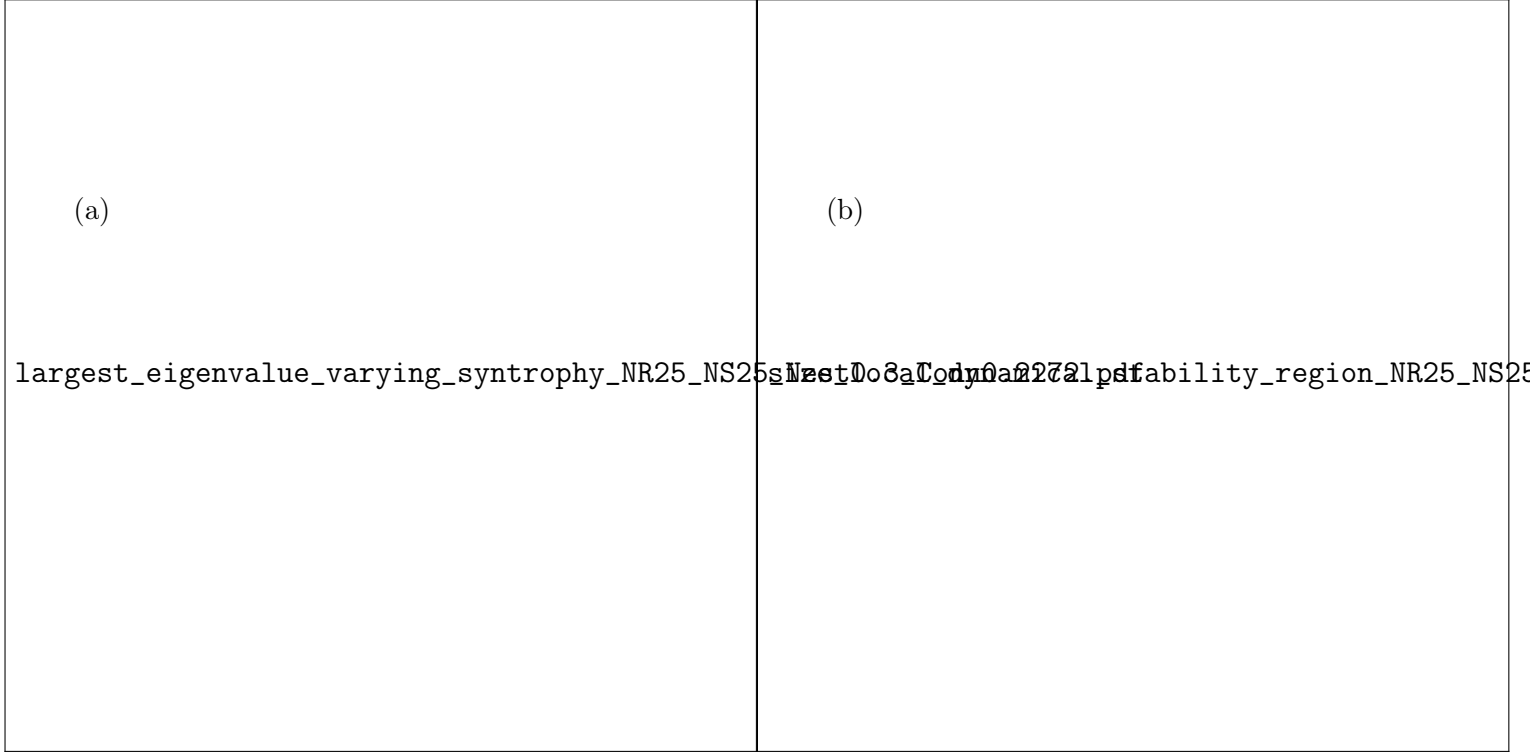
(b)

(a)

(b)

largest_eigenvalue_varying_syntrophy_NR25_NS25sNeet0o3aCodyaa272lpsfability_region_NR25_NS25_N

Figure 11: For a consumption matrix G with $\eta_G = 0.3$ and $\kappa_G = 0.23$. (a) Evolution of the maximal $|\langle Re(\lambda_1) \rangle|$ observed in the $(\gamma_0, S_0) \in [0,1]^2$ region. The maximal eigenvalue increases in magnitude, making the system more dynamically stable, as syntrophy increases. That trend is true for all matrices we considered. (b) Volume of $\mathcal{D}_{L,1}^G(\alpha_0)$. As syntrophy increases, fewer and fewer points become fully dynamically stable. For both figures, the different lines show the different stand for the different structure of the syntrophy matrix that we considered.

local_dynamical_stability_region_NR25_NS25_Nest0.45_Conn0.3168.pdf
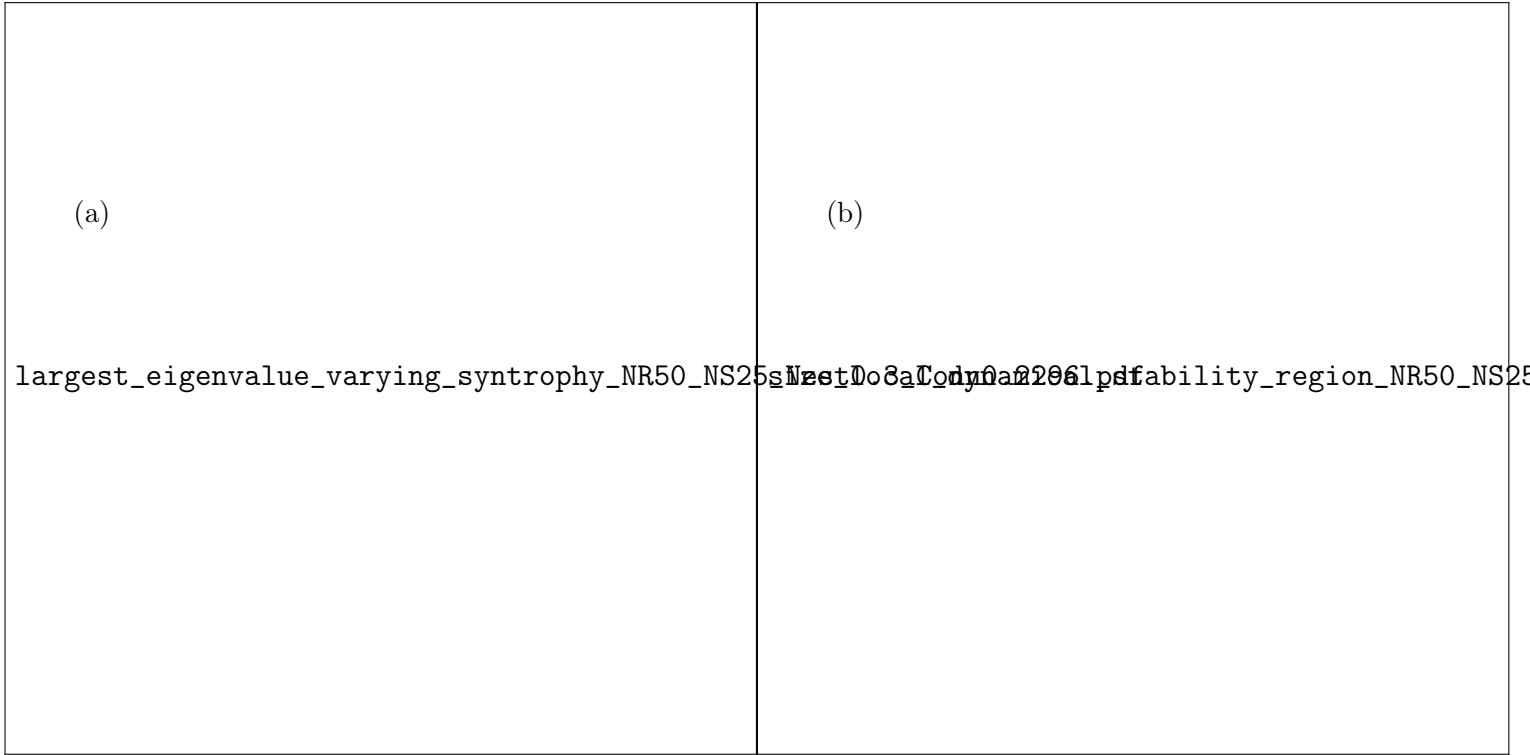
(a)

(a)

(b)

largest_eigenvalue_varying_syntrophy_NR50_NS25_NnestDo3aColman206lpdf size_dynamical_stability_region_NR50_NS25_N

Figure 13: To be compared with Fig.??. The consumption matrix G considered here has $\eta_G = 0.3$ and $\kappa_G = 0.23$. (a) Maximal average $|Re\,(\lambda_1)|$ observed in the unit square. (b) Percentage of the unit square occupied by the fully dynamically stable region of G as a function of syntrophy. The matrix considered has almost equal properties to the one in Fig.??, with the only difference that $N_R = 50$ here. Even though the size of $\mathcal{D}_{L,1}^{G,A}$ is smaller, the eigenvalues are larger in magnitude.

(a)
common_local_dynamical_stability_volume_NR50_NS25_varying_syntrophy_random_structure_NR50_NS25

(b)
common_local_dynamical_stability_volume_NR50_NS25

(c)
common_local_dynamical_stability_volume_NR50_NS25_varying_syntrophy_opti
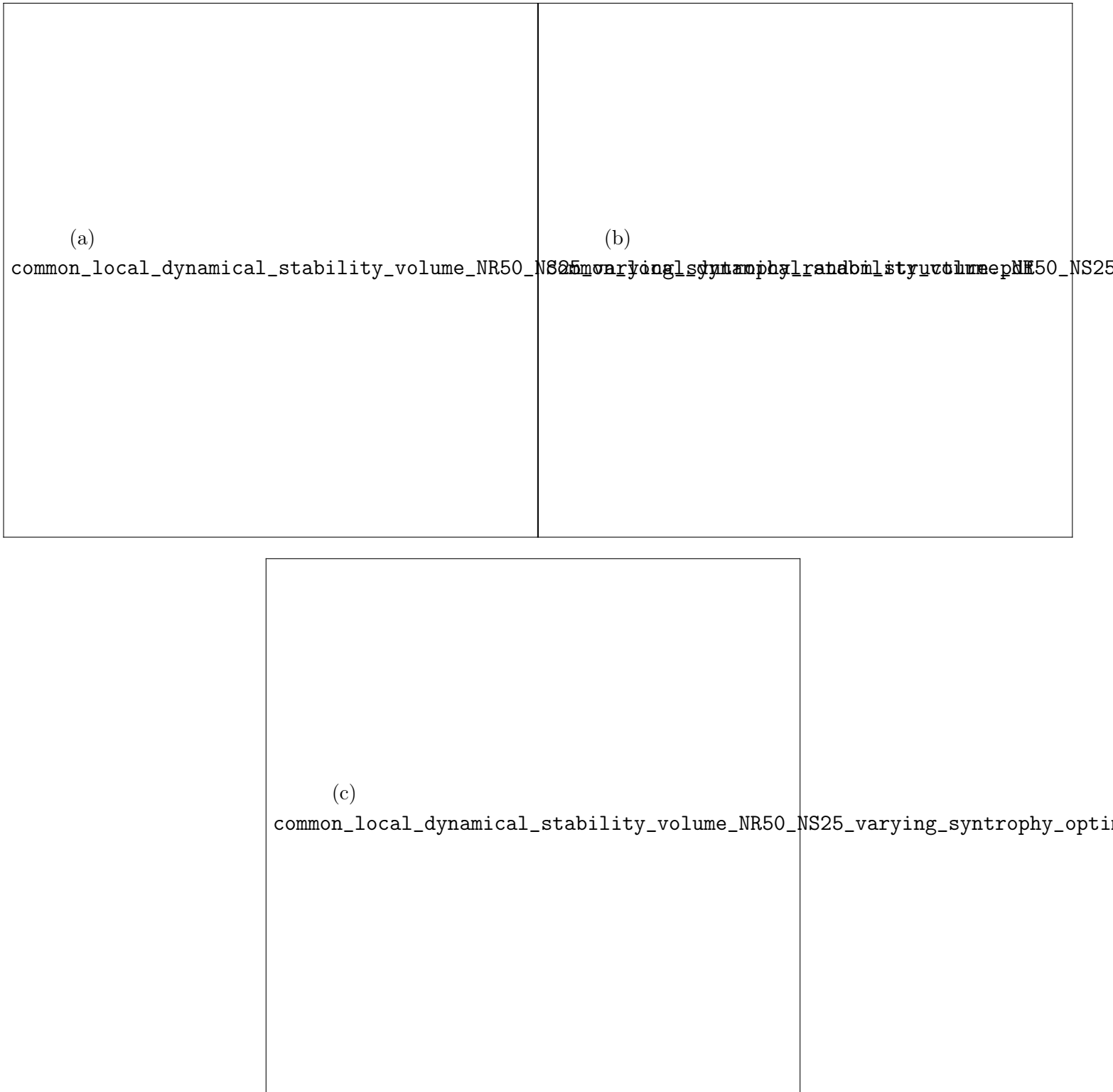
Figure 14: Common fully dynamically stable volume. It is larger with a larger number of resources -> even though individually it is not always better, it is better for the worse matrices (since the common volume can handle more syntrophy)