

Supplementary Information

Towards a probabilistic understanding about the
context-dependency of species interactions

Chuliang Song¹, Sarah Von Ahn², Rudolf P. Rohr³, Serguei Saavedra¹

¹Department of Civil and Environmental Engineering, MIT,
77 Massachusetts Av., 02139 Cambridge, MA, USA

²Department of Mathematics, MIT,
77 Massachusetts Av., 02139 Cambridge, MA, USA

³Department of Biology - Ecology and Evolution, University of Fribourg
Chemin du Musée 10, CH-1700 Fribourg, Switzerland.

The probability of persistence

Following previous work on structural stability in ecological research [1–3], it is possible to calculate the probability of persistence $\Omega(\mathbf{A})$ of a given community structure \mathbf{A} [3]. Persistence is guaranteed by the existence of positive (feasible) and stable equilibrium abundances of the system as a function of model parameters [4]. Note that feasibility is the necessary condition for persistence, while feasibility and stability are the necessary and sufficient conditions [4]. Assuming that ecological dynamics can be described by any model topologically equivalent to the Lotka-Volterra population dynamics model [5], it has been proved that the domain of feasibility $D_F(\mathbf{A})$ is described by a convex cone with the edges defined by the columns of the interaction matrix \mathbf{A} [6] (see Fig. S1). This cone is made of vectors, whose elements are phenomenological intrinsic growth rate values leading to feasible solutions. Then, to obtain persistence, one has to restrict the domain of feasibility to the stable and feasible abundances. That is, one has to determine the domain of stability $D_S(\mathbf{A})$. Note that $D_S(\mathbf{A})$ is necessarily contained inside $D_F(\mathbf{A})$ as stability is defined only for feasible equilibria. Therefore, the intersection of the domains of feasibility and stability can be called the domain of persistence $D_P(\mathbf{A}) = D_F(\mathbf{A}) \cap D_S(\mathbf{A})$ (see Fig. S1). The larger $D_P(\mathbf{A})$, the larger the structural stability of persistence of a community with community structure \mathbf{A} . Consequently, following a classical probabilistic approach, the probability of persistence $\Omega(\mathbf{A})$ is given by the proportion of $D_P(\mathbf{A})$ within the parameter space of phenomenological intrinsic growth rates [2, 3]:

$$\Omega(\mathbf{A}) = \text{proportion of } D_P(\mathbf{A}) \text{ in the parameter space.}$$

Formally speaking, $\Omega(\mathbf{A})$ is the normalized solid angle of the convex cone of persistence $D_P(\mathbf{A})$ [2, 3]. Finally, one can constrain the parameter space of phenomenological intrinsic growth rates to a domain \mathcal{C} (e.g., considering only positive or negative intrinsic growth rates) and define the conditional probability of persistence $\Omega(\mathbf{A}|\mathcal{C})$:

$$\Omega(\mathbf{A}|\mathcal{C}) = \text{proportion of } D_P(\mathbf{A}) \text{ inside } \mathcal{C},$$

which is computed as the fraction (conditional probability)

$$\Omega(\mathbf{A}|\mathcal{C}) = \frac{\Omega(\mathbf{A} \cap \mathcal{C})}{\Omega(\mathcal{C})}.$$

Finally, the probability of persistence of a randomly chosen species within the community structure \mathbf{A} (assuming a Binomial process) is given by

$$\omega(\mathbf{A}) = \Omega(\mathbf{A})^{1/n},$$

where n is the number of species in the community.

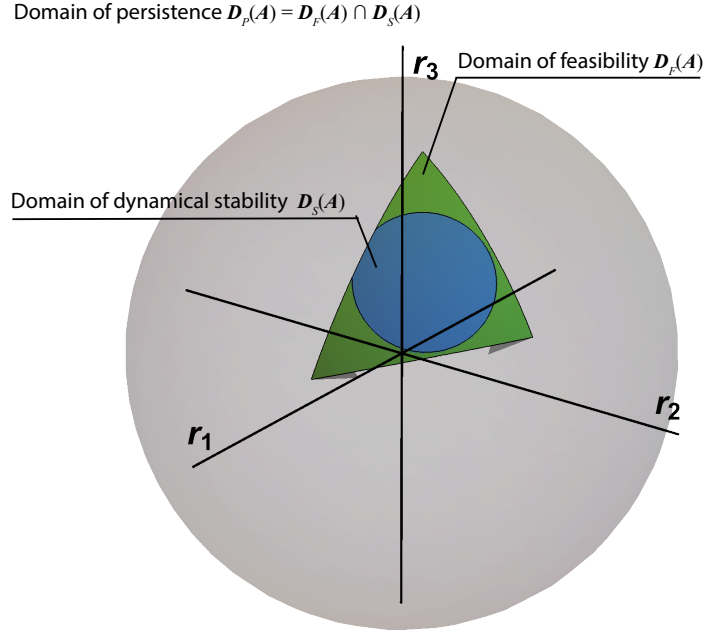


Figure S1: **Graphical example of the domain of persistence for a 3-species community.** For a hypothetical interaction matrix (community structure) \mathbf{A} with 3 species, following LV dynamics, the figure shows the 3-dimensional parameter space of phenomenological intrinsic growth rates (r_1 , r_2 , and r_3). It is proved that the effective parameter space is equivalent to the unit sphere \mathbb{S}^2 (gray region). The green region corresponds to the feasibility domain $D_F(\mathbf{A})$, while the blue region corresponds to the dynamical stability domain $D_S(\mathbf{A})$. The size and shape of these domains are modulated by the interaction matrix \mathbf{A} . We define the domain of persistence $D_P(\mathbf{A}) = D_{F \cap S}(\mathbf{A})$ as the region compatible with feasible and locally stable systems.

Proof of invariant theorem

Here we prove that the shape of the feasible domain uniquely determines the domain of dynamical stability. That is, once the shape of the feasibility domain is known, whether a growth rate would give rise to feasibility and/or dynamical stability is also determined.

Lemma 1. *Suppose there are two interaction matrices A and B , which only differ in the columns by multiplication of some positive constants. Then, for the same intrinsic growth rates, the two generalized Lotka-Volterra systems have the same feasibility and stability properties. Furthermore, all eigenvalues of their Jacobians are the same.*

Proof. Denote the fixed intrinsic growth rates \mathbf{r} as

$$\mathbf{r} = \begin{bmatrix} r_1 & r_2 & \dots & r_n \end{bmatrix}^\top$$

and denote the interaction matrix \mathbf{A} to be

$$\mathbf{A} = \begin{bmatrix} \mathbf{L}_1 & \mathbf{L}_2 & \dots & \mathbf{L}_n \end{bmatrix}$$

and the interaction matrix \mathbf{B}

$$\mathbf{B} = \begin{bmatrix} m_1 \mathbf{L}_1 & m_2 \mathbf{L}_2 & \dots & m_n \mathbf{L}_n \end{bmatrix}$$

where all $m_k > 0$.

The interior equilibrium of the system with interaction matrix \mathbf{A} is defined by

$$\frac{d\mathbf{N}}{dt} = 0 = \mathbf{A}\mathbf{N}^* + \mathbf{r}$$

or equivalently

$$\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{r}$$

The Jacobian matrix corresponding to this equilibrium point is

$$\mathbf{J} = \text{diag}(\mathbf{N}^*) \cdot \mathbf{A} = \text{diag}(-\mathbf{A}^{-1}\mathbf{r}) \cdot \mathbf{A}$$

Thus, we only need to show that the the eigenvalues of $\text{diag}(\mathbf{A}^{-1}\mathbf{r}) \cdot \mathbf{A}$ and $\text{diag}(\mathbf{B}^{-1}\mathbf{r}) \cdot \mathbf{B}$ are the same up to the ordering of eigenvalues.

Given that the determinant of a matrix is defined by

$$\det(\mathbf{A}) = s_p \prod_{k=1}^n a_{k,p(k)},$$

where $s_p = 1$ if p is even, $s_p = -1$ if p is odd, and p is a permutation of $1, 2, \dots, n$. Because each product contains exactly one element from each column of the matrix, the product of all m can be factored out, resulting in

$$\det(\mathbf{B}) = \prod_{k=1}^n m_k \cdot \det(\mathbf{A}).$$

In the process of taking the inverse of matrix \mathbf{B} , while making the matrix of minors, each element is defined by the elements of every other row and column. This makes each element a product of the constants m of every other column except the one element that it belongs to. Also during this process, the elements are transposed. This means that the constant that was

found in the n^{th} column is now found in the n^{th} row. Because of this

$$\mathbf{B}_{ij}^{-1} = \frac{\det(\mathbf{A}) \prod m_k}{\det(\mathbf{B}) m_i} \cdot \alpha_{ij} = \frac{1}{m_i} \cdot \alpha_{ij}$$

Multiplying by the same r and taking the diagonal are the same processes for \mathbf{A} and \mathbf{B} so

$$(\text{diag}(\mathbf{B}^{-1}\mathbf{r}))_{ij} = \frac{1}{m_i} \cdot \alpha_{ij} \tag{S1}$$

Multiplying the matrix by \mathbf{B} , it multiplies every element in the j^{th} column by m_j :

$$(\text{diag}(\mathbf{B}^{-1}\mathbf{r}) \cdot \mathbf{B})_{ij} = J_{\mathbf{B}_{ij}} = \frac{m_j}{m_i} \cdot J_{\mathbf{A}_{ij}}$$

Thus, we can find the eigenvalues of J_B using the characteristic equation

$$\det(J_B - \lambda I) = s_p \prod_{k=1}^n \frac{m_j}{m_i} \cdot \alpha_{k,p(k)}.$$

Every product includes exactly one element from each row i and each column j , so we can factor out the constants

$$\det(J_B - \lambda I) = \frac{\prod m}{\prod m} \cdot s_p \prod_{k=1}^n \alpha_{k,p(k)} = s_p \prod_{k=1}^n \alpha_{k,p(k)} = \det(J_A - \lambda I)$$

□

Lemma 2. *Norm of growth rate does not affect the stability nor feasibility*

Proof. Let a system with growth rate r have the solution N^* , the Jacobian J and eigenvalues λ . If instead we apply the growth rate cr to that system for some constant $c > 0$, the new solution is $N_c^* = cN^*$ and the new Jacobian is $J_c = cJ$. To find the eigenvalues of J_c we write

$$J_c v = (cJ)v = c(Jv) = c\lambda v,$$

so $c\lambda$ is an eigenvalue of J_c . Since $c > 0$ all of the eigenvalues of J_c are the same sign as the eigenvalues of the original Jacobian. Because of this, both systems have the same stability properties. □

Lemma 3 (Characterization of the shape of the feasibility domain). *The feasibility domain is a simplicity cone generated as negative linear combination of the column space.*

Proof. See [7]. □

With Lemma 1-3, we have

Theorem 1. *The shape of the feasibility domain uniquely determines the dynamical stability and feasibility for any growth rate.*

Note that the shapes of the feasible cones of \mathbf{A} and \mathbf{B} are exactly the same by lemma 3, but the same growth rate corresponds to different feasible abundances.

Instead of column changes, which preserve the shape of the feasible cone, row changes might change the feasible cone. By the invariant theorem, this would affect stability. Ecological interpretation of row changes in Jacobian is taking the role of species abundance distribution into stability analysis of LV system [8–10].

This has pointed out the asymmetry of a_{ij} and a_{ji} , which carries a different ecological meaning but has received less attention.

Grid-approximation algorithm to sample the domain of persistence

To find the domain of persistence in the numerical example of Box 3, we used a grid-approximation algorithm. We used this algorithm to sample the domain of local asymptotic stability inside the feasibility domain $D_S(\mathbf{A})$, which allowed us to compute the domain of persistence $D_P(\mathbf{A}) = D_{F \cap S}(\mathbf{A})$ compatible with feasible and locally stable states. The algorithm evenly samples (given a step size) normalized points (i.e., the sum of species abundances equals to 1) in the feasibility domain. Each point is a set of elements $a_1 - a_n$ and all elements are strictly positive. The algorithm works as follows:

Step 1: We set the first $n - 2$ coordinates to be “fixed” at the given step size. The second to last coordinate starts at the given step size and steps up incrementally while the last coordinate steps down incrementally as $1 - \sum_{k=1}^{n-1} a_k$ (so the coordinates always sum to one). At each increment, the unique point is saved in a list.

Step 2: All “fixed” coordinates increment one step size up and Step 1 is repeated for all increments.

Step 3: The original list made in Steps 1 and 2 is copied and more points are created out of all of the permutations of the order of coordinates. (For example: all of the points in the first list but in the order a_2, a_4, a_1, a_3 are added.)

Step 4: All non-unique points are eliminated.

Numerical example of the domain of persistence

In Box 3, we used the volume $\omega(\mathbf{A})$ of the domain of persistence $D_P(\mathbf{A})$ as the probability of persistence. This is an adequate approximation under the assumption that the environmental conditions (parameter values) is uniformly random. Of course, as the environment becomes directional, it is important to understand the specific shape of $D_P(\mathbf{A})$. Although the systematic examination of this shape is beyond the scope of this work, here we give one concrete example to show that the shape is not a trivial problem.

The interaction matrix is

$$\begin{bmatrix} -1.00000 & 13.15238 & 20.74604 \\ 16.53817 & -1.00000 & -12.75578 \\ -19.29366 & 22.41098 & -1.00000 \end{bmatrix}$$

And the corresponding shape of the domain of persistence is

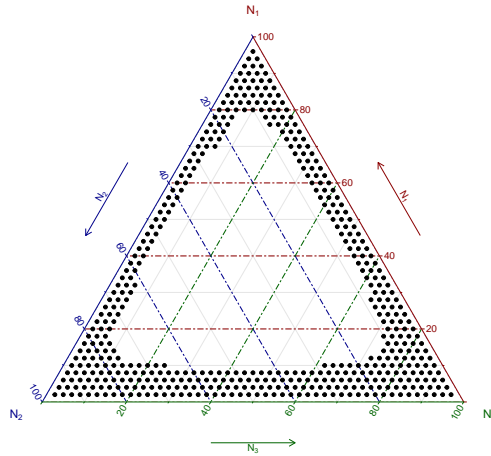


Figure S2: The triangle is a transformed feasibility domain $D_F(\mathbf{A})$. The black dots represent the domain of persistence $D_P(\mathbf{A})$.

Permanence as the criterion for persistence

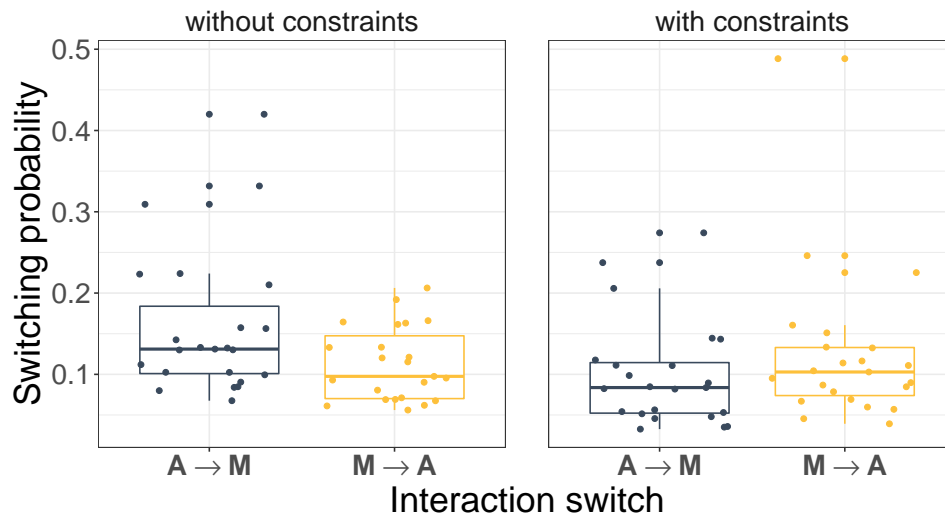


Figure S3: This figure is the same as Figure IIIC-D except that persistence is now defined as permanence. That is, (i) the 3-species community has to be feasible, (ii) the determinant of the 3-dimensional matrix has to be positive, and (iii) the determinants of the three 2-dimensional sub-matrices have to be positive—this is only valid for 3-species communities [4]. Note that permanence include cyclic populations (as the condition for dynamical stability is not required). The qualitative results remain the same as Figure IIIC-D.

References

- [1] Rohr, R.P. *et al.* (2014) On the structural stability of mutualistic systems. *Science* 345, 1253497
- [2] Saavedra, S. *et al.* (2017) A structural approach for understanding multispecies coexistence. *Ecol. Monogr.* 87, 470–486
- [3] Song, C. *et al.* (2018) A guideline to study the feasibility domain of multi-trophic and changing ecological communities. *J. Theor. Biol.* 450, 30–36
- [4] Hofbauer, J. and Sigmund, K. (1998) *Evolutionary games and population dynamics*. Cambridge University Press
- [5] Case, T.J. (2000) *An Illustrated Guide to Theoretical Ecology*. Oxford Univ. Press, Oxford
- [6] Cenci, S. and Saavedra, S. (2018) Structural stability of nonlinear population dynamics. *Phys. Rev. E* 97, 012401
- [7] Logofet, D.O. (1993) Matrices and graphs. *Stability Problems in Mathematical Ecology*, CRC, Boca Ratón, FL
- [8] Song, C. and Saavedra, S. (2018) Will a small randomly-assembled community be feasible and stable? *Ecology* 99, 743–751
- [9] Gibbs, T. *et al.* (2018) Effect of population abundances on the stability of large random ecosystems. *Phys. Rev. E* 98, 022410
- [10] Stone, L. (2018) The feasibility and stability of large complex biological networks: a random matrix approach. *Sci. Rep.* 8, 8246