Appendix

A guideline to study the feasibility domain of multi-trophic and changing ecological communities

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A Definition of feasibility domain

Here, we briefly present the formal definitions associated with the feasibility domain.

Definition 1 (Feasibility Domain)**.** *The feasibility domain for a non-singular interaction matrix* $\mathbf{A}$ *is defined as the parameter space of intrinsic growth rates that leads to a feasible (positive) equilibrium, i.e., the set of* $\mathbf{r}$ *such that* $-\mathbf{A}^{-1}\mathbf{r} > 0$.

Definition 2 (Cone)**.** *A cone in* $\mathbb{R}^S$ *is defined as a space spanned by positive linear combinations of* S *linearly independent vectors.*

Remark 1. *This is also referred as a simplicial cone (Ribando, 2006). For simplicity, we will call it cone. However, it is important to note that this is not the common definition of cone (James, 1992).*

Definition 3 (Spanning Vector)**.** *The vector* $\mathbf{v}_i$ *is defined as the* i^{th} *spanning vector of the feasibility domain if* $\mathbf{v}_i$ *is the negation of the* i^{th} *column of* $\mathbf{A}$.

Remark 2. *A spanning vector is sometimes referred to as an extreme ray in convex geometry (Bertsimas & Tsitsiklis, 1997).*

With the above definitions, the feasibility domain of $\mathbf{A}$ is proved to be (Svirezhev & Logofet, 1983)

$$D_F(\boldsymbol{A}) = \{\boldsymbol{r} = N_1^* \boldsymbol{v}_1 + \cdots + N_S^* \boldsymbol{v}_S, \text{ with } N_1^* > 0, \ldots, N_n^* > 0\}, \tag{A1}$$

where $\mathbf{v}_i$ is the negation of the i^{th} column of $\mathbf{A}$.

Remark 3. *This definition is the reason why we restrict the parameters, in the definition of cone, to be strictly greater than* 0*, instead of the standard definition where the boundary is also included.*

Remark 4. *The non-singularity condition* $\mathsf{det}(\mathbf{A}) \neq 0$ *is equivalent to the situations where* $(\mathbf{v}_1, ..., \mathbf{v}_S)$ *are linearly independent. The non-singular interaction matrix* $\mathbf{A}$ *gives a one-to-one linear mapping from the feasibility domain to the space of positive equilibrium of species abundances. Mathematically, these two spaces are equivalent. However, the geometric representation and the clear link to the interaction matrix makes this transformation useful for feasibility analysis (Saavedra et al., 2017b).*

B Least upper bound of the relative volume

Here, we prove a basic property of the normalized solid angle $\Omega(\mathbf{A})$ (defined in eqn. 5).

Theorem 1. *Least upper bound of* $\Omega(\mathbf{A})$ *is* $\frac{1}{2}$.

Proof. First we prove that $\frac{1}{2}$ is an upper bound for $\Omega(\mathbf{A})$, then we prove that this upper bound is a limit point.

The relative volume is generated by the positive linear combinations of S linearly independent vectors $\mathbf{v}_1, ..., \mathbf{v}_S$. The end-points of those vectors form a hyperplane that does not pass through the origin because of the assumption of linear independence. Let us consider the hyperplane that passes through the origin and is parallel to the hyperplane formed by the end-points of our S vectors. By construction, all the end-points are on the same side of the hyperplane. Because the normalized solid angle of the whole side of a hyperplane is $\frac{1}{2}$, it is proved that $\frac{1}{2}$ is an upper bound of $\Omega(\mathbf{A})$.

Then we prove that $\frac{1}{2}$ is a limit point. Let us construct the following set of S vectors:

$$\mathbf{v}_1 = \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, \mathbf{v}_2 = \begin{pmatrix} 0 \\ 1 \\ \vdots \\ 0 \end{pmatrix}, \cdots, \text{ and } \mathbf{v}_S = \begin{pmatrix} -1 \\ -1 \\ \vdots \\ \delta \end{pmatrix}.$$

For $\delta > 0$, those S vectors are linearly independent and generate a cone of a normalized solid angle $\Omega(\mathbf{A}) < \frac{1}{2}$. By taking the limit$\delta \to 0^+$, the normalized solid angle $\Omega(\mathbf{A}) \to \frac{1}{2}$. This proves that $\frac{1}{2}$ is a least upper bound of $\Omega(\mathbf{A})$.

□

C Computation of the relative volume

Here, we discuss the computation of the normalized solid angle $\Omega(\mathbf{A})$. In the main text (Eqn. (6)), we have presented an analytic formula. In fact, Ribando (2006) proved a closed form to compute the normalized solid angle $\Omega(A)$ (Theorem 2.2. in (Ribando, 2006)). However, this formula is computationally expensive in high dimension, and an exact solution is not actually needed. Thus, we use a quasi-Monte Carlo method to efficiently compute the relative volume following Genz & Bretz (2002); Saavedra et al. (2016b). One important computational consideration is the numerical error of $(\mathbf{A}^T\mathbf{A})^{-1}$, which is a quantity required for the computation of the normalized solid angle. For instance, the tolerance level of the function *solve* in R is too low for high dimensions. In order to correct for these numerical errors, we encourage to use the function *chol2inv* in R, or any other function incorporating the QR decomposition to compute the inverse of the matrix (Trefethen & Bau III, 1997).

D Intersection of feasibility cones

Here, we turn our attention to the overlap (intersection) of two (or more) feasibility cones corresponding to two (or more) interaction matrices of the same dimension. Without loss of generality, we will focus on two cones. To calculate this overlap, one can think about the problem of computing the probability of the intersection of two events U_1 and U_2, namely $\Omega(U_1 \cap U_2)$. This intersection is needed to calculate the combined $\Omega(\mathbf{A} \cup \mathbf{B})$ and shared $\Omega(\mathbf{A} \cap \mathbf{B})$ normalized solid angles between two (or more) feasibility cones $D_F(\mathbf{A})$ and $D_F(\mathbf{B})$ (see main text): $\Omega(\mathbf{A} \cup \mathbf{B}) = \Omega(\mathbf{A}) + \Omega(\mathbf{B}) - \Omega(\mathbf{A} \cap \mathbf{B})$.

The overlap of two feasibility cones is not a trivial problem in computation. However, using convex geometry, we can translate the overlap problem into an *affine space* of the cones problem (Leichtweiß, 1999). That is, we can take the advantage of the fundamental fact that any spanning vector starting from the origin is uniquely determined by any point on it except for its initial point. Importantly, this guarantees that any feasibility cone can be compressed without loss of information into its intersection with a hyperplane (polyhedron), which can be chosen arbitrarily as long as the intersection is not empty.

Therefore, we can study the geometric properties corresponding to the overlap between two S-dimensional cones simply by choosing a hyperplane that intersects both feasibility cones when the overlap is nonempty, and then investigate the overlap of two polyhedrons on the $(S-1)$-dimensional hyperplane. Because the intersection of two polyhedrons can be triangulated (Hatcher, 2002), all we have to do (if the overlap is a non-empty set) is to locate the extreme points that generated the intersection. This is the key observation that simplifies the computation of the overlap between two feasibility cones. That is, the intersection is generated by two types of points: one type belongs to the original extreme points of each polyhedron, and the other type belongs to the intersection of the edges of two polyhedrons. Note that the affine transformation only preserves the relative position rather than the relative volume of a geometric object (Kostrikin, 1982), the volume of intersection cannot be simply calculated as the absolute volume of the intersection over the volume of the two polyhedrons on the hyperplane. Below, we provide the full derivation.

The overlap is mathematically defined as Eqn. (8) in the main text. It may not be a cone, and the following theorem describes its shape.

Theorem 2. *The overlap of two feasibility cones is a union of cone(s), or an empty set.*

Proof. An empty overlap is obviously possible. We discuss the case when the overlap is not empty. Let us denote two feasibility cones as $D_F(\boldsymbol{A})$ and $D_F(\boldsymbol{B})$, respectively.

First, we prove that the overlap is a polyhedron with only extreme rays. Suppose $\sum_{i=1}^{S} a_i \mathbf{v}_i$ is inside the overlap, then for any positive $\lambda > 0$, $\lambda \sum_{i=1}^{S} a_i \mathbf{v}_i$ is inside the overlap, too. Also, the overlap of two cones is still a polyhedron. Thus, by the resolution theorem (Bertsimas & Tsitsiklis, 1997), there exist extreme rays $\mathbf{v}_1, .., \mathbf{v}_N$ such that the overlap is equivalent to

$$\{\sum_{i=1}^{N} \lambda_i \mathbf{v}_i | \lambda_1, ..., \lambda_N > 0\}. \tag{D1}$$

Second, we prove that $N = S$ if the borders of the two cones do not intersect. From the view of the parameter space, $D_F(\boldsymbol{A})$ separates the Euclidean space into three disjoint sets: $\mathscr{C}_1 = \{\lambda|\lambda_i < 0, \exists i\}$ (outside the cone), $\mathscr{C}_2 = \{\lambda|\lambda_i = 0, \exists i\}$ (the borders of the cone), $\mathscr{C}_3 = \{\lambda|\lambda_i > 0, \forall i\}$ (inside the cone). If the feasibility cone $D_F(\boldsymbol{B})$ intersects with both $\mathscr{C}_1$ and $\mathscr{C}_3$ of $D_F(\boldsymbol{A})$, then by continuity, $D_F(\boldsymbol{B})$ also intersects with $\mathscr{C}_2$ of $D_F(\boldsymbol{A})$. Since the overlap is assumed to be non-empty, $D_F(\boldsymbol{B})$ must be contained in either $\mathscr{C}_1$ or $\mathscr{C}_3$ of $D_F(\boldsymbol{A})$. In both cases, $N = S$.

Finally, we prove that $N \geq S$ if the borders of the two simplexes intersect. If $N < S$, then the overlap is null (Stein & Shakarchi, 2009). Since the borders intersect, the border of a cone is not in the cone. Then by the assumption of non-emptiness, there must exist one point x_0 inside the overlap. Because this point is in the interior of $D_F(\boldsymbol{A})$, there exists a $\epsilon_A > 0$ such that the neighborhood $\{x \mid |x - x_0| < \epsilon_A\}$ of x_0 is inside $D_F(\boldsymbol{A})$. Similarly, there exists an $\epsilon_B > 0$ such that the neighborhood $\{x \mid |x - x_0| < \epsilon_B\}$ of x_0 is inside $D_F(\boldsymbol{B})$. Thus, the neighborhood $\{x \mid |x - x_0| < min\{\epsilon_A, \epsilon_B\}\}$ of x_0 is in the overlap whose measure is nonzero, which leads to a contradiction. Thus, $N \geq S$ if the overlap is not empty. The set of N vectors can be $\cup U_i$, where the cardinality of each U_i is S, and any element in U_i is not in the interior of the polyhedron spanned by $U_j, \forall j \neq i$. This can easily be proved by mathematical induction. □

The problem left now is to compute the extreme rays. We reformulate it by transforming it into an equivalent problem.

Definition 4 (Characteristic Simplex of a Cone)**.** *A characteristic simplex of a cone is defined as the interior of the convex set whose extreme points are located on the spanning vectors. See Fig. D1 for an illustration.*

Corollary 1. *The characteristic simplex of a feasibility cone is an $(S-1)$-dimensional simplex.*

Proof. Let us denote the intersection points as $v_i,\ i = 1, ..., S$. Then, the simplex is equivalent to

$$\{\mathbf{r} = \sum_{i=1}^{S} \lambda_i \mathbf{v}_i \in \mathrm{R}^n | \exists \lambda_1, .., \lambda_S > 0, \sum_{i=1}^{S} \lambda_i = 1\}. \tag{D2}$$

Since we only consider non-degenerate cases, $\mathbf{v}_i$ are linearly independent. Thus, it satisfies the standard definition of a simplex. □

Remark 5. *The border is included in the standard definition of a simplex, while the definition of a characteristic simplex excludes the border.*

Definition 5 (Associated Polyhedron)**.** *The associated polyhedron of a feasibility cone is defined as the polyhedron whose extreme points are the origin point and the spanning vectors (taken as points). The associated face of the polyhedron corresponds to the face spanned by the spanning vectors of the original cone.*

Theorem 3. *The spanning vectors of the intersection of two feasibility cones are extreme points of the overlap of the corresponding characteristic simplexes.*

Proof. Let us denote the two feasibility cones as $D_F(\boldsymbol{A})$ and $D_F(\boldsymbol{B})$, and the interaction matrices as $\boldsymbol{A}, \boldsymbol{B}$. Also, denote the intersection with the associated face of $\boldsymbol{A}$ as F_A, and with $\boldsymbol{B}$ as F_B.

The overlap of $D_F(\boldsymbol{A})$ and $D_F(\boldsymbol{B})$ can be written as

$$\{\mathbf{r}|A^{-1}\mathbf{r}, B^{-1}\mathbf{r} \in (\mathbb{R}_{-})^S\}. \tag{D3}$$

The overlap of F_A and F_B can be written as

$$\{\mathbf{r}|A^{-1}\mathbf{r}, B^{-1}\mathbf{r} \in (-1,0)^S\}. \tag{D4}$$

where $(-1,0)^S$ is the Cartesian product.
The intersection of the overlap and the associated face of any cone is equivalent to the overlap. By uniqueness of extreme points and extreme rays in convex geometry, the proof is complete. □

Remark 6. *By convex geometry, the overlap of F_A and F_B can be uniquely determined by its extreme points, and the overlap of $D_F(\boldsymbol{A})$ and $D_F(\boldsymbol{B})$ can be uniquely determined by its extreme rays (spanning vectors). Thus, this theorem proves the equivalence of these two definitions via construction.*

The vertexes of the simplex and the intersection points of simplexes are candidates as extreme points of the overlap.

Theorem 4. *The extreme points of the overlap of characteristic simplexes are the extreme points of the joint of the set of all vertexes of one simplex in another simplex's closure. This closure has the set of the intersection points of the edges of one simplex with borders of another simplex.*

Proof. We consider the closure of the overlap. This is only for mathematical simplicity due to the fact that an extreme point is equivalent to a basic feasible solution under this setup (Bertsimas & Tsitsiklis, 1997). All vertexes of the simplexes are basic solutions, thus, it is an extreme point if and only if it is feasible.

All extreme points must be in the intersection of the borders of the simplexes. Let us consider a face which has a subset that is in the border of the overlap. We show that any extreme point x_0 of the overlap that is in this face must be on some edge of another simplex. Otherwise, x_0 must be in the interior of some face F_2 of another simplex. Thus, F_A transverse F_B is restricted to the overlap part of F_1 and F_2 (Guillemin & Pollack, 2010), which in turn gives that x_0 is not in the border of the overlap part. See Fig. D2 for a visualization of this geometric idea. □

In general, to enumerate all vertexes of a polyhedron is difficult (Khachiyan et al., 2008). No algorithm in polynomial time has been found for solving the general case (Murty, 2009). For a particular case, the total number of vertexes might be exponential by the constraints. Due to the geometric essence of the problem, the maximum number of extreme points grows only squarely with the dimension.

Definition 6 (Notations)**.** *For a set of vectors $\mathbf{v}_1, ..., \mathbf{v}_N$, expression $(\mathbf{v}_1, .., \bar{\mathbf{v}}_i, ..., \mathbf{v}_N)$ denotes the space spanned by all vectors but $\mathbf{v}_i$. For a set $\mathscr{A}$, $\bar{\mathscr{A}}$ denotes the closure of $\mathscr{A}$, and $\mathscr{A}^o$ denotes the interior of $\mathscr{A}$.*

Theorem 5. *The maximum number of the spanning vectors of the intersection of two feasibility cones is $S(S-1)$.*

Proof. We first prove that any edge of $D_F(\boldsymbol{A})$ will not intersect with more than interiors of two faces of $D_F(\boldsymbol{C})$. Suppose that an edge has passed three faces of $D_F(\boldsymbol{B})$. Without loss of generality, let us suppose the middle one is on the face spanned by $(\bar{\mathbf{v}}_1, .., \mathbf{v}_{S-1}, \mathbf{v}_S)$, and the other two are on the face spanned by $(\mathbf{v}_1, .., \mathbf{v}_{S-1}, \bar{\mathbf{v}}_S)$ and $(\mathbf{v}_1, .., \bar{\mathbf{v}}_{S-1}, v_S)$, respectively. Then, there exists $k_1, k_2 > 0$, such that

$$k_1\lambda_1 + k_2\lambda_2 = 0, \tag{D5}$$

where λ_1, λ_2 are the positive coefficients of $\mathbf{v}_1$ in the two border points. This is in fact not possible.

Thus, there are no more than $S-1$ extreme points on each face. In total, there can be no more than $2S(S-1)$ on all faces of two simplexes. If an extreme point is on the interior of some face, then it is counted at least twice; if an extreme point is on the interior of some edge, then it is counted at least $S-1$ times; if an extreme point is on some vertex, then it is counted at least S times. Thus, there can be no more than $S(S-1)$ different extreme points.

The positioning of the simplexes that gives the highest number of extreme points can be constructed: for each face of $D_F(\boldsymbol{A})$, there are $S-1$ vertexes of $D_F(\boldsymbol{B})$ on the side of the face where the vertex of $D_F(\boldsymbol{A})$ that does not belong to this face, and only one vertex of $D_F(\boldsymbol{B})$ on the other side. In this case, the number of extreme points is $(S-1)S$. Thus, the upper bound is tight. $\square$

By theorem 2, 3, and 5, the non-empty overlap of the original feasibility cones has at most $S(S-1)$ spanning vectors and at least S spanning vectors. Now the problem is reduced to separate the overlap of cones into several disjoint cones.

Definition 7 (Border set)**.** *A subset of spanning vectors with S elements is defined as a border set if all spanning vectors that are not in this subset are on one side of the space spanned by this subset.*

Theorem 6. *Let us suppose a set of N vectors where any S elements are linearly independent. The problem is to partition this set into $\cup U_i$, where by cardinality of each U_i is S, and any element in U_i is not in the interior of the polyhedron spanned by $U_j, \forall j \neq i$. Each U_i is defined as a partitioning set. The computational complexity of this problem is in polynomial time.*

Proof. The simplexes referred following are characteristic simplexes. This approach is justified by theorem 3.

We first prove that the total number of these partitioning sets is $N-S+1$. This is because each of the two cones whose corresponding characteristic simplexes share a face have S_1 spanning vectors in common. Note that two different characteristic simplexes cannot share two faces. This is because two faces involve all the spanning vectors, which uniquely determine a partitioning set. The characteristic simplex of any cone must share at least one face with another simplex. Note that the points in one border set must be on the same face of some simplex. See Fig. D3 for a visualization of this geometric idea. $\square$

Following Ribando (2006) and Theorem 6, the problem of computing analytically the overlap is solved.

Remark 7. *Our results show that the overlap of two arbitrary cones can be analytically computed as there is a closed form (Ribando, 2006). Note that our results do not contradict the classical result: that computing the precise volume of the polyhedron in high dimension is an #P-complete problem (Khachiyan, 1989; Dyer & Frieze, 1988).*

Clearly, the methodology above can be applied to the intersection of multiple feasibility cones. All the code in R will be archived on Github.

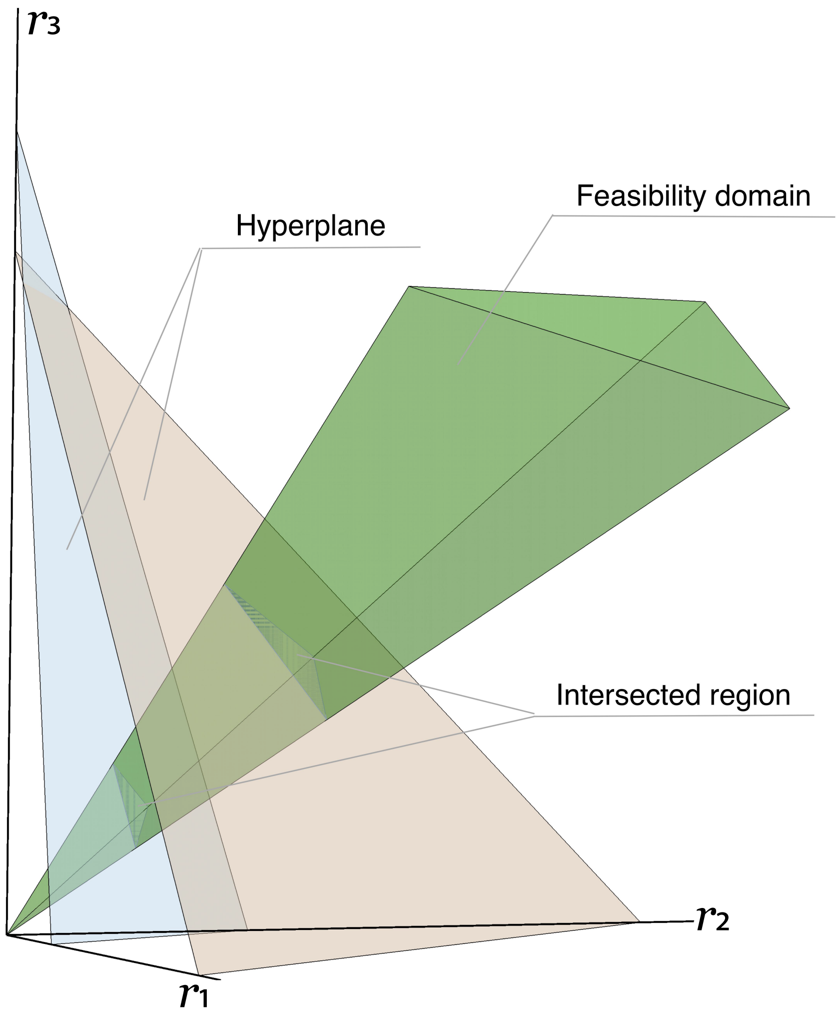

Figure D1: **Characteristic Cones**. The nonempty intersections of the feasibility cone with any hyperplane are equivalent up to affine transformation.

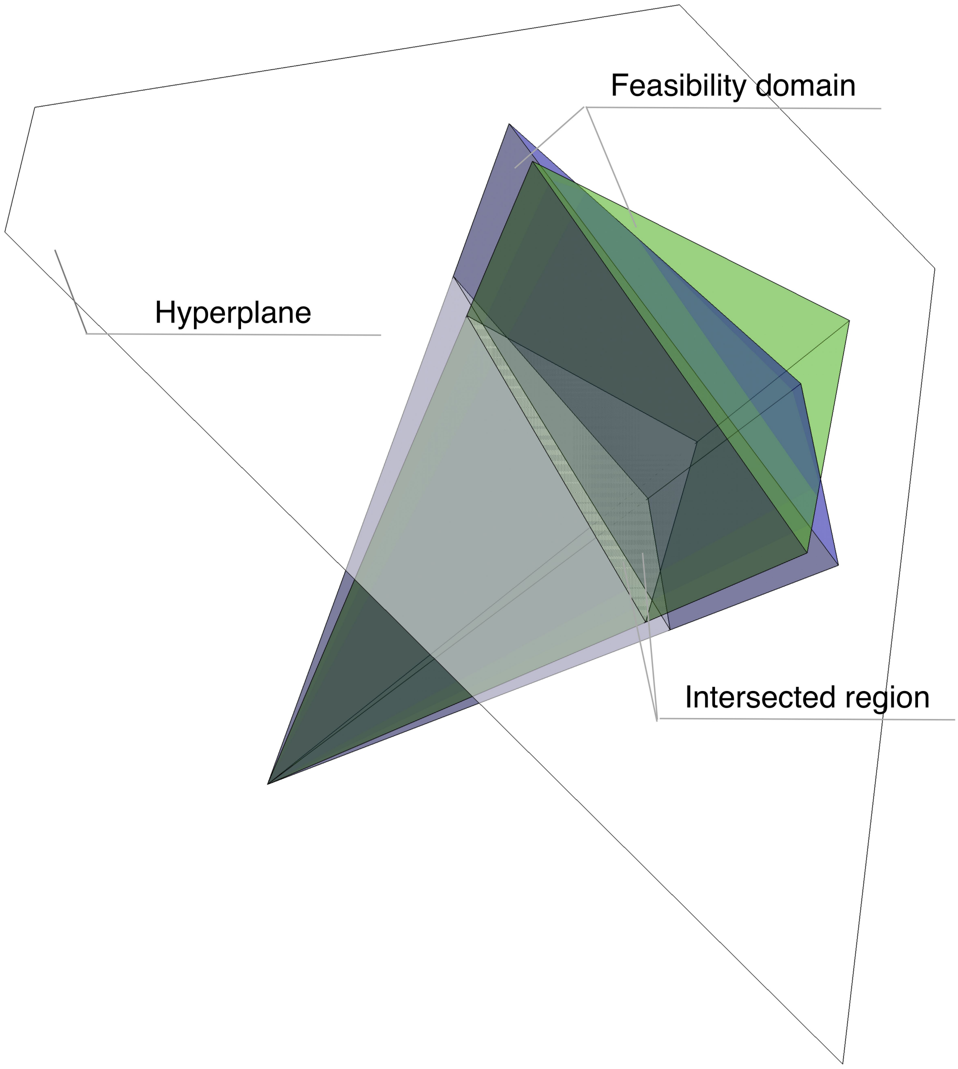

Figure D2: **Intersection of Cones**. This transforms the original problem into an equivalent question, the extreme points of the intersection of two $S-1$ closed simplex.

a **b**

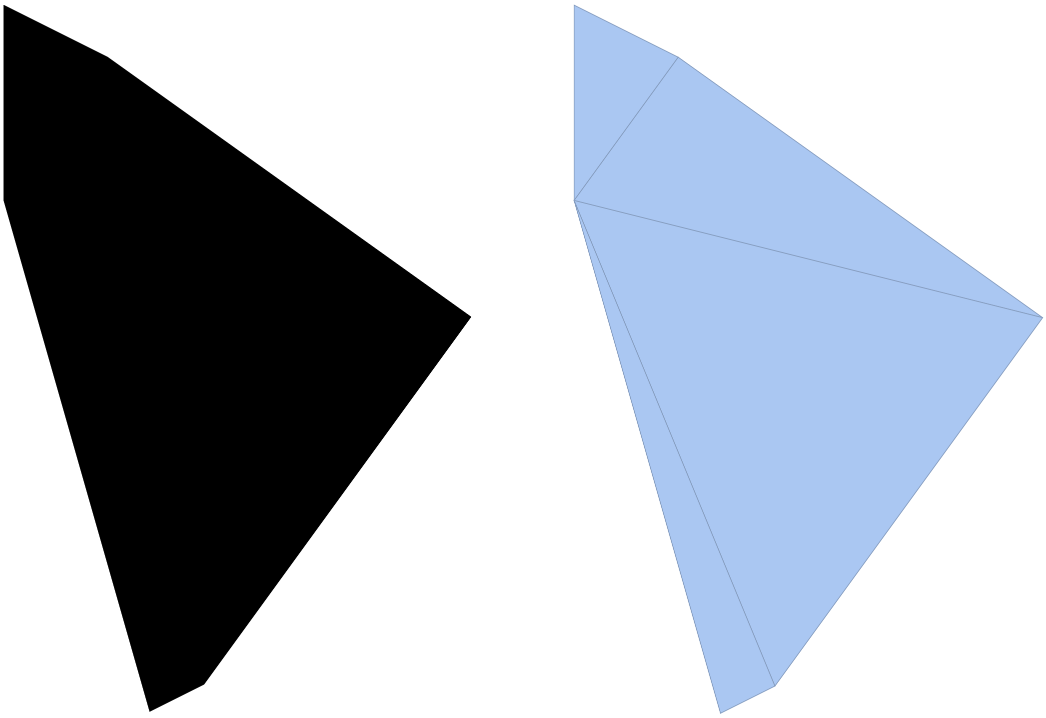

Figure D3: **Triangulating the plane**. Panel (a) shows the shape of the intersection; note that the volume of this region has no direct relationship with the volume of the original overlap. Panel (b) shows the triangulation of the intersection simplex.

E Constraints on intrinsic growth rates

In the majority of feasibility studies, it is assumed that there are no constraints acting on energy flows across trophic levels, i.e., the intrinsic growth rates of different species are independent and can have any possible value. We focus on linear constraints to provide a starting point for addressing this problem, where an analytic description of constraints can be incorporated.

There are two types of linear constraints: linear inequalities and linear equalities. Although they are equivalent by introducing auxiliary variables in the sense of mathematics (Bertsimas & Tsitsiklis, 1997), they have different meanings in ecology. First we focus on linear inequalities. The general form of constraints (lower and upper bounds) on one species i is:

$$L_i \leq r_i \leq U_i. \tag{E1}$$

The most simple example is that the sign of intrinsic growth rates can be fixed (Logofet, 1993); for instance, a given predator and prey may have negative and positive intrinsic growth rates, respectively. Biologically speaking, a finite L_i and U_i exist for any $i \in \{1, ..., S\}$. Thus, we always have the following constraints on equilibrium abundances:

$$L_i \leq \sum_{l=1}^{S} \mathbf{v}_i^l \lambda_l \leq U_i \quad , \quad i = 1, .., S; \tag{E2}$$

$$\lambda_i > 0 \quad , \quad i = 1, ..., S, \tag{E3}$$

where $\mathbf{v}_i^l$ stands for the i-th component of the spanning vector corresponding to species l.

Note that these constraints are in essence different from the overlap of feasibility cones. The feasibility cone is shrinked to a bounded polytope. There is no restraint on its shape (Ball, 1997) except that it is a convex subset of the original feasibility cone. In particular, this cone might be an empty set, which is also another indication of why the structure of intrinsic growth rates is so important. Besides the inequality constraints on one species, it is also common to see equality constraints on the relationship of several species, as metabolic rates may also be similar among species.

With regard to linear equalities, we check the most simple case first. Suppose two species i, j have exactly the same growth rates. This constraint can be written explicitly as

$$\sum_{l=1}^{S} \lambda_l \mathbf{v}_i^l = \sum_{l=1}^{S} \lambda_l \mathbf{v}_j^l. \tag{E4}$$

By denoting $\delta v = (v_i^1 - v_j^1, ..., v_i^S - v_j^S)$ and $\lambda = (\lambda_1, ..., \lambda_S)$, this constraint can be equivalently written as

$$\delta v \cdot \lambda = 0. \tag{E5}$$

Although this constraint seems to be local, it turns out that it introduces a global relationship among abundances of all species. A direct consequence of the constraint (E5) is that the dimension of the sampling space is reduced by 1.

All the reasoning above can be easily generalized to different types of constraints. Consider a constraint $\sum_{k \in T} a_k r_k = 0$ where $a_k \neq 0$ and T is a subset of $\{1, ..., S\}$ whose cardinality is strictly greater than 1. It would generically pose one linear constraint on λ, which is the cardinality of T. Note that there are only S components of λ, thus generically there cannot be more than S constraints. This is a very important distinction from inequalities.

The computation of a general polyhedra (constraints) in high dimension can be done through a Markov chain Monte Carlo method (Dyer et al., 1991; Jerrum & Sinclair, 1996). It is important to note that the it is time-consuming in high dimension. In the main text, we have focused on the relative volume of the feasible region as it has a natural probabilistic interpretation. However, in many cases, the interests might be on the optimization of some functions of species abundances (Goh, 2012). Because most of convex nonlinear constraints can be efficiently computed (Boyd & Vandenberghe, 2004), this kind of problem can be solved via setting the species growth rates as undetermined parameters. Of course, the optimization of any linear function whose variables are species abundances can be easily computed (Bertsimas & Tsitsiklis, 1997). All the code in R will be archived on Github.