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Feasibility conditions of ecological models: Unfolding links between model parameters

Mohammad AlAdwani, Serguei Saavedra *

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

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ABSTRACT

Over more than 100 years, ecological research has been striving to derive internal and external conditions compatible with the coexistence of a given group of interacting species. To address this challenge, numerous studies have focused on developing ecological models and deriving the necessary conditions for species coexistence under equilibrium dynamics, namely feasibility. However, due to mathematical limitations, it has been impossible to derive analytic expressions for equilibria locations if the isocline equations have five or more roots, which can be easily reached even in 2-species models. Here, we propose a general formalism to obtain the set of analytical conditions of feasibility for any polynomial population dynamics model of any dimension without the need to solve for the equilibrium locations. We illustrate the application of our methodology by showing how it is possible to derive mathematical relationships between model parameters in modified Lotka–Volterra models with functional responses and higher-order interactions (model systems with at least five equilibrium points)—a task that is impossible to do with simulations. This work unlocks the opportunity to increase our understanding of how parameters and their interconnections affect our conclusions of species coexistence as a function of model choice.

1. Introduction

Over more than 100 years, ecological research has been striving to derive the biotic and abiotic conditions compatible with the co-existence of a given group of interacting species (also known as an ecological system or community) (Tansley, 1920; Lotka, 1920; Volterra, 1926; Gause, 1932; Case, 2000). These conditions can provide the keys to understand the mechanisms responsible for the maintenance of biodiversity and the tolerance of ecological systems to external perturbations (Levins, 1968; Sugihara, 1994; Loreau and De Mazancourt, 2013; Kerr et al., 2002). Because of the complexity of this question, many efforts have been centered on developing phenomenological and mechanistic models to represent the dynamics of ecological systems and predict their behavior (MacArthur, 1970; Turchin, 2003; Svirezhev and Logofet, 1983; Vandermeer and Goldberg, 2013). However, even if we had knowledge about the exact equations governing the dynamics of interacting species, extracting and solving the set of conditions compatible with the coexistence of such species would remain a big mathematical challenge (Grilli et al., 2017; AlAdwani and Saavedra, 2020; Song et al., 2019). Indeed, most of the analytical work looking at these coexistence conditions has focused on relatively simple 2-species systems or strictly particular cases of higher-dimensional systems (Cox et al., 2010; Strogatz, 2015; Ong and Vandermeer, 2015; Barabás et al., 2018; Fort, 2018; Yacine and Loeuille, 2022; Novoa-Muñoz et al., 2021). In fact, even at the 2-species level, currently there is no general methodology that can provide us with a full analytical understanding about coexistence conditions for any arbitrary model (AlAdwani and Saavedra, 2020). Therefore, the majority of work has relied on numerical simulations (Valdovinos, 2019; Letten and Stouffer, 2019; Aliyu and Mohd, 2022), which provide a partial view of the dynamics conditioned by the choice of model and parameter values (AlAdwani and Saavedra, 2019).

Recent work has started to address the challenge above by focusing on the necessary conditions for species coexistence under equilibrium dynamics: feasibility (Hofbauer and Sigmund, 1998; Song et al., 2018). Mathematically, the feasibility of a generic n-species dynamical system $dN_i/dt = N_i f_i(\mathbf{N})/q_i(\mathbf{N})$, where the f's and q's are multivariate polynomials in species abundances $\mathbf{N} = (N_1, N_2, \ldots, N_n)^T$, corresponds to the existence of at least one equilibrium point (i.e., $dN_i/dt = 0\ \forall i$) whose components are all real and positive (i.e., $\mathbf{N}^* = (N_1^*, N_2^*, \ldots, N_n^*)^T > \mathbf{0}$). Feasibility conditions are typically represented by inequalities as a function of model parameters (Vandermeer, 1975; Barabás et al., 2018). Traditionally, feasibility conditions have been attained by finding the isocline equations $f_i(\mathbf{N}^*) = 0\ \forall i$ and then solving for $\mathbf{N}^*$ before

* Corresponding author.
E-mail address: sersaa@mit.edu (S. Saavedra).

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finding the conditions that satisfy $\mathbf{N}^* > \mathbf{0}$ (Strogatz, 2015; Case, 2000; Vandermeer and Goldberg, 2013).

For example, let us focus on the linear Lotka–Volterra (LV) model of the form $dN_i/dt = N_i(r_i + \sum_{j=1}^{n} a_{ij}N_j)$, where a's and r's represent the interaction coefficients and the intrinsic growth rates, respectively. In the linear LV model, the isocline equations (for any dimension) can be written as $\mathbf{r} + \mathbf{A}\mathbf{N}^* = \mathbf{0}$, whose unique root is given by $\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{r}$. Therefore, feasibility conditions in this case are simply given by the inequality $-\mathbf{A}^{-1}\mathbf{r} > \mathbf{0}$. However, adding nonlinear functional responses or higher-order terms can increase exponentially the number of roots of the system (AlAdwani and Saavedra, 2019). Importantly, it can be shown from elimination theory (via Grobner basis) and Abel's impossibility theorem that it is impossible to solve analytically for $\mathbf{N}^*$ when the number of roots of the system is five or more (Abel, 1824, 1826; Adams et al., 1994). Similarly, using numerical approaches, it has been demonstrated that the probability of feasibility (the probability of finding at least one equilibrium point whose components are all positive by randomly choosing parameter values) is an increasing function of the model's complexity (i.e., number of complex roots of the isocline equations with generic coefficients) regardless of the invoked mechanism, whether they are ecologically motivated or have no meaning whatsoever (AlAdwani and Saavedra, 2020). This implies that traditional approaches can be unsuitable for finding the necessary conditions for coexistence in generic systems.

Here, we propose a general formalism to obtain for any polynomial population dynamics model and any dimension the set of necessary conditions leading to species coexistence without the need to solve for the equilibrium locations. We show how to reduce these conditions into a small set of expressions. We illustrate this methodology with an example of a univariate system. Additionally, we show how to identify the feasibility conditions that are compatible with a given range of parameter values. That is, we show how to find analytic relationships between model parameters while maintaining feasibility. We illustrate this methodology with examples of multispecies systems using modified LV models with functional responses and higher-order interactions, where isocline analysis cannot be performed. Finally, we discuss advantages and limitations of our formalism, and future avenues of research derived from our study.

2. Obtaining feasibility conditions

Our methodology can be applied to any dynamical system of the form:

$$\frac{dN_1}{dt} = \frac{N_1 f_1(N_1,\dots,N_n)}{q_1(N_1,\dots,N_n)} \\ \vdots \\ \frac{dN_n}{dt} = \frac{N_n f_n(N_1,\dots,N_n)}{q_n(N_1,\dots,N_n)}, \quad (1)$$

where the f's and q's are multivariate polynomials in species abundances. Let $\boldsymbol{\Psi}$ be the vector of model parameters that include, for example, species growth rates and species interaction coefficients. Feasibility conditions become consequently conditions on model parameters $\boldsymbol{\Psi}$ that guarantee at least one feasible equilibrium point in the system (Svirezhev and Logofet, 1983; AlAdwani and Saavedra, 2020). That is, we require that the number of roots of the system defined by polynomial equations $f_i(N_1,\dots,N_n) = 0$ for $i = 1,\dots,n$ whose components are all real and positive is at least one. To find such feasibility conditions, we develop a 3-step methodology: (1) Find symmetric sums of the roots of the polynomial. (2) Assemble a function that counts the number of feasible roots. (3) Use the function of the number of feasible roots to deduce feasibility conditions, reduce them and eliminate redundant conditions. Below, we give details of these three steps. We also provide MATLAB code for its implementation.

2.1. Finding symmetric sums of the roots

The first step involves in finding the symmetric sums of the roots that are needed to build the analytic formula of the number of feasible roots. Such sums can be obtained via different methodologies (Serret, 1849; Macaulay, 1902; Pedersen, 1991). One approach is outlined below:

1. Fix i, assume that variable N_i is constant, and find the total degree of each polynomial equation $f_j(N_1,\dots,N_n) = 0$ for $j = 1,\dots,n$. The total degree of f_j is the maximum sum of the variables' exponents in each term of f_j while treating N_i as constant. Denote the total degree of polynomial f_j by $d_{i,j}$ for $j = 1,\dots,n$. Next, homogenize each term in each of the f's with an artificial variable W so that the total degree of each term in f_j is $d_{i,j}$. Denote to the homogenized equation by $F_{N_i,j}$. For example, if $f_2(N_1,N_2,N_3) = 1+N_1^3+N_1N_2N_3$ and N_1 is assumed to be constant, then $d_{1,2} = 2$ and the homogenized equation is $F_{N_1,2} = W^2 + N_1^3W^2 + N_1N_2N_3$.
2. Let $L_i = 1 + \sum_{j=1}^{n}(d_{i,j} - 1)$ and form the set H_i as a union of n monomial sets, where $H_i = (W^{d_{i,1}} \cdot H_{i,1}^{L_i-d_{i,1}}) \cup (\cup_{1\le j\le i-1} N_j^{d_{i,j+1}} \cdot H_{i,j+1}^{L_i-d_{i,j+1}}) \cup (\cup_{i+1\le j\le n} N_j^{d_{i,j}} \cdot H_{i,j}^{L_i-d_{i,j}})$. Define the outer-term of $H_{i,k}^{L_i-d_{i,k}}$ to be the one that is dotted or multiplied by it. For example $W^{d_{i,1}}$ is the outer-term of $H_{i,1}^{L_i-d_{i,1}}$. Here, $H_{i,k}^{L_i-d_{i,k}}$ is the set of all monomials in $W, N_1,\dots,N_n$ not including N_i that are of total degree $L_i - d_{i,k}$ and does not contain the outer-terms of any of $H_{i,1}^{L_i-d_{i,1}},\dots,H_{i,k-1}^{L_i-d_{i,k-1}}$. For example, if $d_{2,1} = 2, d_{2,2} = 2$ and $d_{2,3} = 1$, then using variables W, N_1, N_3 where N_2 is constant, we have $L_2 = 3$ and $H_2 = W^2 \cdot \{W, N_1, N_3\} \cup N_1^2 \cdot \{W, N_1, N_3\} \cup N_3 \cdot \{N_3^2, WN_1, WN_1, N_1N_3\}$. Note that the second curly bracket does not contain W^2 (i.e., outer term of the first curly bracket) and the third curly bracket does not contain W^2 nor N_1^2 (i.e., the outer-terms of the first and second curly brackets).
3. Form the set $H_{i,\text{row}} = \cup_{1\le j\le n} f_j \cdot H_{i,j}^{L_i-d_{i,j}}$ evaluated at $W = 1$. Note that $H_{i,\text{row}}$ is simply H_i with outer-term of every $H_{i,j}^{L_i-d_{i,j}}$ being replaced by f_j. Next, form the monomial set $H_{i,\text{col}}$ which is simply H_i evaluated at $W = 1$. After that, form the Macaulay matrix M_{N_i}, which is a square matrix whose size is $\binom{n-1+L_i}{n-1}$ and whose (i,j) entry is the coefficient of $H_{i,\text{col}}(j)$ in the expression of $H_{i,\text{row}}(i)$ assuming that N_i is a constant. Then, find the resultant $\text{Res}_{N_1,\dots,N_{i-1},N_{i+1},\dots,N_n}(f_1,\dots,f_n)$ which equals to the determinant of M_{N_i}. This resultant is a univariate polynomial in N_i that contains no other N's.
4. Next, form the matrix M'_{N_i}, whose first column is $H_{i,\text{row}}$ and its remaining columns are the remaining columns of the matrix M_{N_i}. Then, compute its determinant (i.e., $\det(M'_{N_i})$), which has the form $T_{i1}f_1 + T_{i2}f_2 + \dots + T_{in}f_n$ to obtain the ith row of the eliminant matrix. Repeat all previous steps for $i = 1,\dots,n$ to obtain all entries of the eliminant matrix as well as all resultants. Then, obtain the Jacobian of the original polynomial system whose (i,j) entry is $\partial f_i/\partial N_j$. Next, find the determinant of both the eliminant matrix T and the determinant of the Jacobian J.
5. If the determinant of M_{N_i} is 0, use the generalized characteristic polynomial formalism (Canny, 1988) to obtain the resultant. In this case, the resultant is the non-vanishing coefficient of the smallest power of ϵ in $\det(M_{N_i} - \epsilon I)$, where I is the identity matrix of same size as matrix M_{N_i}. To find T_{ij} for $j = 1,\dots,n$, form the matrix M''_{N_i}, whose first column is $H_{i,\text{row}}$ and its remaining columns are the remaining columns of the matrix $M_{N_i} - \epsilon I$. Then, compute its determinant and find the first non-zero coefficient of powers of ϵ in ascending order, which has the form $T_{i1}f_1 + T_{i2}f_2 + \dots + T_{in}f_n$ (see Appendix 5 for an example of this scenario).

6. Expand the generating function $G(f_1(N_1,\dots,N_n),\dots,f_n(N_1,\dots,N_n))$ that is shown below, around $N_1=\infty,\dots,N_n=\infty$ to obtain the Σ's (symmetric sums of the roots).

$$G(f_1,\dots,f_n)=\frac{T(f_1,\dots,f_n)J(f_1,\dots,f_n)}{\prod_{i=1}^{n}\mathrm{Res}_{N_1,\dots,N_{i-1},N_{i+1},\dots,N_n}(f_1,\dots,f_n)}$$
$$=\sum_{m_1=0}^{\infty}\sum_{m_2=0}^{\infty}\cdots\sum_{m_n=0}^{\infty}\frac{\Sigma_{m_1,m_2,\dots,m_n}}{N_1^{m_1+1}N_2^{m_2+1}\dots N_n^{m_n+1}}$$

The expansion of G is done via performing series expansion of the reciprocal of each resultant separately then multiplying them along with T and J. For example, the reciprocal of each resultant can be expanded via MATLAB's "taylor" command after performing change of variables $N_i=1/x_i$ and expanding around $x_i=0$. Alternatively, if the resultant is expressed as $\mathrm{Res}_{N_1,\dots,N_{i-1},N_{i+1},\dots,N_n}(f_1,\dots,f_n)=\sum_{l_i=0}^{K_i}h_{(i,l_i)}N_i^{l_i}$, then

$$\frac{1}{\mathrm{Res}_{N_1,\dots,N_{i-1},N_{i+1},\dots,N_n}}=\frac{1}{N_i^{K_i-1}}\sum_{m_i=1}^{\infty}\frac{p_{(i,m_i)}}{N_i^{m_i}},$$

$$p_{(i,m_i)}=\frac{(-1)^{m_i+1}}{h_{(i,K_i)}^{m_i}}\det(A_i[1:m_i,1:m_i]),$$

$$\text{where } A_i=\begin{bmatrix}1&0&0&0&\dots\\ h_{(i,K_i)}&h_{(i,K_i-1)}&h_{(i,K_i-2)}&h_{(i,K_i-3)}&\dots\\ 0&h_{(i,K_i)}&h_{(i,K_i-1)}&h_{(i,K_i-2)}&\dots\\ 0&0&h_{(i,K_i)}&h_{(i,K_i-1)}&\dots\\ \vdots&\vdots&\vdots&\vdots&\ddots\end{bmatrix},$$

$i=1,\dots,n$.

Finally, denote the roots of $f_i(N_1,\dots,N_n)$ for $i=1,\dots,n$ by $\boldsymbol{\eta_k}=[\eta_{k,1},\eta_{k,2},\dots,\eta_{k,n}]^T$ for $k=1,\dots,\Theta$. The symmetric sum $\Sigma_{m_1,m_2,\dots,m_n}$ is given by $\sum_{k=1}^{\Theta}\eta_{k,1}^{m_1}\eta_{k,2}^{m_2}\dots\eta_{k,n}^{m_n}$. In particular, note that $\Theta=\Sigma_{0,0,\dots,0}$ is the number of complex roots of $f_i(N_1,\dots,N_n)$ for $i=1,\dots,n$ with general coefficients. It is important to record that number.

It is worth mentioning that the previous steps in univariate systems reduce significantly, where the roots of $f(N)$ are considered. The jacobian determinant simply becomes $J=f'(N)$ and the resultant is $f(N)$ itself given that it is the only univariate polynomial in the system. In turn, the eliminant determinant is $T=1$ as the resultant, where written in the form $T_{11}f(N)$ implies $T_{11}=1$. Thus, the generating function reduces to $G=f'(N)/f(N)$ (Appendix 1 illustrates a simplified and detailed methodology for univariate systems). Similarly, in 2-dimensional systems, the two resultants simplify significantly and become determinants of Sylvester matrices involving the coefficients of two polynomial inputs. Then, to find the corresponding eliminant matrix, it is possible to modify a single column in each of the two Sylvester matrices without changing their determinant to write the resultants in the form $T_{i1}f_1+T_{i2}f_2$ (Appendix 2 illustrates a simplified and detailed methodology for 2-species systems). For higher dimensional systems, we need to find the symmetric sums as described above or any other suitable implementation.

2.2. Assembling the function that counts the number of feasible roots

Once we find the symmetric sums of the roots, we construct an analytical formula of the number of positive roots of the polynomial system of equations—we call that function $F(\boldsymbol{\Psi})$. To derive $F(\boldsymbol{\Psi})$, we apply previous work (Pedersen et al., 1993), which deals with counting real roots in arbitrary domains, to count the number of real roots in an orthotope that lies in the first quadrant (i.e., feasible region), which rests on all the positive axes. Then, we expand the orthotope allowing all non-zero components of all its vertices to go to infinity to cover the entire feasible domain. This can be achieved as follows:

1. Choose a map $m(N_1,N_2,\dots,N_n)$ of length Θ and with independent monomial entries. Typically, the first entry of m is the constant 1. Note that such monomials are chosen so that the coefficients of the characteristic equation shown in the following step do not vanish. Next, let $Q(N_1,N_2,\dots,N_n)=N_1N_2\dots,N_n$ and compute the symmetric matrix $S(s_1,s_2,\dots,s_n)=W\Delta W^t$ where $W_{ij}=m_i(\eta_{j,1},\eta_{j,2},\dots,\eta_{j,n})$ and $\Delta_{ii}=Q(\eta_{i,1}-s_1,\eta_{i,2}-s_2,\dots,\eta_{i,n}-s_n)$ is a diagonal matrix.
2. The next task is to evaluate the determinant of $S(s_1,s_2,\dots,s_n)$ and write it in the form $\det(S(s_1,s_2,\dots,s_n)-\lambda I)=(-1)^{\Theta}\lambda^{\Theta}+v_{\Theta-1}(s_1,s_2,\dots,s_n)\lambda^{\Theta-1}+\dots+v_0(s_1,s_2,\dots,s_n)$. Then, consider the sequence $\mathbf{v}=[v_{\Theta}(s_1,s_2,\dots,s_n)=(-1)^{\Theta},\ v_{\Theta-1}(s_1,s_2,\dots,s_n),\dots,v_0(s_1,s_2,\dots,s_n)]$ and let $V(s_1,s_2,\dots,s_n)$ be the number of consecutive sign changes in $\mathbf{v}$. The formula of $V(s_1,s_2,\dots,s_n)$ is
$$V(s_1,s_2,\dots,s_n)=\sum_{i=0}^{\Theta-1}\frac{1-\mathrm{sign}(v_i(s_1,s_2,\dots,s_n)v_{i+1}(s_1,s_2,\dots,s_n))}{2}. \tag{2}$$
3. Consider the feasibility domain and think about it as a box whose 2^n vertices compose of zeros and infinities. Note that $v_i(m_1,m_2,\dots,m_n)$, where $m_1,m_2,\dots,m_n\in\{0,\infty\}$ is the coefficient of the highest power of $s_1^{k_1}s_2^{k_2}\dots s_n^{k_n}$ in $v_i(s_1,s_2,\dots,s_n)$ where $k_i=0$ if $m_i=0$ and $k_i=1$ if $m_i=\infty$. Finally, let $\#(s_1,s_2,\dots,s_n)$ be the number of infinities that appear in the string $s_1,s_2,\dots,s_n$. The expression of $F(\boldsymbol{\Psi})$ is given by
$$F(\boldsymbol{\Psi})=\frac{1}{2^{n-1}}\sum_{s_1,s_2,\dots,s_n\in\{0,\infty\}}(-1)^{\#(s_1,s_2,\dots,s_n)}V(s_1,s_2,\dots,s_n) \tag{3}$$

2.3. Deducing feasibility conditions and reducing them

The third and last step of our methodology involves deducing feasibility conditions and reducing them. This has the purpose of unveiling the key inequalities that need to be satisfied in order to reach feasibility. This can be achieved as follows:

1. Call $v_i(m_1,m_2,\dots,m_n)$, where $m_1,m_2,\dots,m_n\in\{0,\infty\}$ and $i=0,1,\dots,\Theta-1$ forms the feasibility basis involving $\Theta 2^n$ quantities (feasibility conditions are only dependent on those quantities). Because there are $\Theta 2^n$ quantities and each can take a positive or a negative sign (we neglect the zero case as the values of ecological parameters are never exact), then there are $2^{\Theta 2^n}$ sign combinations. Many of those combinations are impossible to occur (empty) for any choice of real $\boldsymbol{\Psi}$. To detect the non-empty sign combinations, compute the signs of all the v's (the feasibility basis) as well as $F(\boldsymbol{\Psi})$ for a range of parameters $\boldsymbol{\Psi}$, where each component of $\boldsymbol{\Psi}$ varies independently in a large domain (say uniformly between −100 and 100 or in any suitable domain) when parameters are unrestricted. If one or more parameters are restricted, they need to be varied randomly in the domains they are defined at. This operation can be easily computed as it is only necessary to evaluate a few functions without solving systems of equations. Next, extract unique sign combinations of the v's, which yield $F(\boldsymbol{\Psi})\geq 1$. Then, put these sign combinations in a feasibility table (i.e., matrix), whose rows are the signs of the v's and columns are the individual feasibility conditions.
2. After forming the feasibility table, perform a minimization to it. Here, we illustrate a simple minimization technique: If two columns differ by a single sign (in one row), the two columns are combined into one and an X (or 0) is placed in the row where there is a single sign difference. We repeat the same process until no two columns differ by a single sign. Next, we go through a single column at a time and iterate through each quantity in the basis. Then, we compute the conditional probabilities

where the quantity takes its correspondent sign given that all remaining quantities have their correspondent signs. If one or more conditional probabilities are 1, the sign of one of those quantities may be replaced by **X** in the table. We then repeat computing the same conditional probabilities, which were 1 but without the **X**'ed quantity being part of the calculation. We repeat the process until no conditional probability is one. We then go through all columns and repeat the same process until it terminates. It is worth noting that these are not the only minimization approaches. For instance, comparing signs of v's with $F(\boldsymbol{\Psi})$ may reveal to us redundant quantities in the system (see the examples in Appendices 3–6).

2.4. Illustrative example

We illustrate the methodology above using the following univariate system:

$$\frac{dN}{dt} = N(aN^2 + bN + c). \tag{4}$$

First, we find the symmetric sums of roots. For this purpose, let us focus on the quadratic polynomial $f(N) = aN^2 + bN + c$ of the equation above with model parameters $\boldsymbol{\Psi} = (a, b, c)$. This example has the same mathematical form of a population model with an Allee effect (Case, 2000; Sun, 2016). Denote the two roots of $f(N)$ by η_1 and η_2. Let $m(N) = [1, N]$ be a monomial map of length $n = 2$ and $Q(N) = N$. Now, we can compute the matrix $S(s_1) = W \Delta W^t$, where $W_{ij} = m_i(\eta_j)$ and $\Delta_{ii} = Q(\eta_i - s_1)$ is the diagonal matrix

$$S(r) = \begin{bmatrix} 1 & 1 \\ \eta_1 & \eta_2 \end{bmatrix} \begin{bmatrix} \eta_1 - s_1 & 0 \\ 0 & \eta_2 - s_1 \end{bmatrix} \begin{bmatrix} 1 & \eta_1 \\ 1 & \eta_2 \end{bmatrix} = \begin{bmatrix} \eta_1 + \eta_2 - 2s_1 & \eta_1^2 + \eta_2^2 - s_1(\eta_1 + \eta_2) \\ \eta_1^2 + \eta_2^2 - s_1(\eta_1 + \eta_2) & \eta_1^3 + \eta_2^3 - s_1(\eta_1^2 + \eta_2^2) \end{bmatrix}.$$

Note that we only have symmetric sums of η's up to the power of $2n - 1 = 3$ (i.e., $\eta_1^k + \eta_2^k$ where $k = 1, 2, 3$). Second, we need to assemble the function that counts the number of feasible roots. Thus, to evaluate these symmetric sums, we need to evaluate the Laurent series of the generating function $G(N) = f'(N)/f(N)$ at $N = \infty$ up to the order $O(N^{-5})$ as shown below

$$G(N) = \frac{2aN + b}{aN^2 + bN + c} = \frac{2}{N} + \frac{-b}{aN^2} + \frac{b^2 - 2ac}{a^2N^3} + \frac{-b^3 + 3abc}{a^3N^4} + O(N^{-5}).$$

Hence, $\eta_1 + \eta_2 = -b/a$, $\eta_1^2 + \eta_2^2 = (b^2 - 2ac)/a^2$, and $\eta_1^3 + \eta_2^3 = (-b^3 + 3abc)/a^3$. Let us denote these sums by Σ_1, Σ_2 and Σ_3 respectively. Now, the characteristic equation of $S(s_1)$ is

$$\det(S(s_1) - \lambda I) = \lambda^2 + \lambda[-\Sigma_1 - \Sigma_3 + s_1(2 + \Sigma_2)] + [\Sigma_1\Sigma_3 - \Sigma_2^2 + s_1(\Sigma_1\Sigma_2 - 2\Sigma_3) + s_1^2(2\Sigma_2 - \Sigma_1^2)].$$

Next, we can construct the characteristic equation whose coefficients are $[v_2(s_1) = 1, v_1(s_1), v_0(s_1)]$ and evaluate the signs of v's at both $s_1 = 0$ and $s_1 = \infty$. That is,

$$\begin{cases} \text{sign}(v_2(0)) = 1, \quad \text{sign}(v_1(0)) = \text{sign}(-\Sigma_1 - \Sigma_3), \\ \text{sign}(v_0(0)) = \text{sign}(\Sigma_1\Sigma_3 - \Sigma_2^2) \\ \text{sign}(v_2(\infty)) = 1, \quad \text{sign}(v_1(\infty)) = \text{sign}(2 + \Sigma_2), \\ \text{sign}(v_0(\infty)) = \text{sign}(2\Sigma_2 - \Sigma_1^2), \end{cases}$$

where $v_i(0)$ and $v_i(\infty)$ are the coefficient of the trailing (constant) and leading term of $v_i(s_1)$ respectively. Now, we compute $V(0)$ and $V(\infty)$ to have

$$V(0) = \frac{1 - \text{sign}(-\Sigma_1 - \Sigma_3)}{2} + \frac{1 - \text{sign}(-\Sigma_1 - \Sigma_3)\text{sign}(\Sigma_1\Sigma_3 - \Sigma_2^2)}{2}$$

$$V(\infty) = \frac{1 - \text{sign}(2 + \Sigma_2)}{2} + \frac{1 - \text{sign}(2 + \Sigma_2)\text{sign}(2\Sigma_2 - \Sigma_1^2)}{2}.$$

Using the formula $F(a, b, c) = V(0) - V(\infty)$ together with two basic properties of sign functions (namely $\text{sign}(xy) = \text{sign}(x)\text{sign}(y)$ and $\text{sign}(y) = 1/\text{sign}(y)$ for any non-zero real numbers x and y), we obtain the expression of $F(a, b, c)$:

$$F(a, b, c) = -\frac{\text{sign}(ab(a^2 + b^2 - 3ac))[1 + \text{sign}(ac(b^2 - 4ac))]}{2} + \frac{\text{sign}(2a^2 + b^2 - 2ac)[1 + \text{sign}(b^2 - 4ac)]}{2}.$$

The feasibility basis in this case is given by $v_0(0), v_1(0), v_0(\infty), v_1(\infty)$. We use the factors shown in the expression of $F(a, b, c)$ as our basis in the feasibility table. The five quantities that constitute the basis are $Q_1 = ab, Q_2 = a^2 + b^2 - 3ac, Q_3 = ac, Q_4 = b^2 - 4ac, Q_5 = 2a^2 + b^2 - 2ac$. Next, we randomize a, b and c uniformly between -100 to 100 and evaluate the signs of the Q_i's as well as $F(a, b, c)$. We find that there are only 3 sign combinations that yield $F(a, b, c) \geq 1$ and are given by the feasibility conditions C_1, C_2 and C_3 shown below

	C_1	C_2	C_3
ab	+	−	−
$a^2 + b^2 - 3ac$	+	+	+
ac	−	−	+
$b^2 - 4ac$	+	+	+
$2a^2 + b^2 - 2ac$	+	+	+
$F(a, b, c)$	1	1	2

Once the table is obtained, we start the minimization process of the number of feasibility conditions. It is clear from columns 1 and 2 above that the sign of Q_1 does not matter and can be replaced by an X symbol. This concludes the first minimization step as no two columns differ by a single sign and we end up with the feasibility conditions $C_{1+2} = \{Q_2 > 0, Q_3 < 0, Q_4 > 0, Q_5 > 0\}$ and $C_3 = \{Q_1 < 0, Q_2 > 0, Q_3 > 0, Q_4 > 0, Q_5 > 0\}$. For the second minimization step, we focus on column C_{1+2}. We find that the conditional probabilities $P(Q_2 > 0 | Q_3 < 0, Q_4 > 0, Q_5 > 0) = 1$, $P(Q_3 < 0 | Q_2 > 0, Q_4 > 0, Q_5 > 0) \neq 1$, $P(Q_4 > 0 | Q_2 > 0, Q_3 < 0, Q_5 > 0) = 1$ and $P(Q_5 > 0 | Q_2 > 0, Q_3 < 0, Q_4 > 0) = 1$, which implies that the sign of Q_2, Q_4, or Q_5 can be replaced by **X** in that column. Then, let us replace the sign of Q_2 by **X**. Next, we continue computing the conditional properties that were one but without the condition $Q_2 > 0$. We find that $P(Q_4 > 0 | Q_3 < 0, Q_5 > 0) = 1$ and $P(Q_5 > 0 | Q_3 < 0, Q_4 > 0) = 1$. This implies that we can replace the sign of Q_4 or Q_5 by **X**. Now, let us replace the sign of Q_4 by **X** and eliminate it from the latter conditional probability to find that $P(Q_5 > 0 | Q_3 < 0) = 1$. This time, the sign of Q_4 can be replaced by **X** in column C_{1+2}. We repeat the same process with the column C_3 and obtain the feasibility table including the 2-step minimization shown below

	C_1	C_2	C_3		C_{1+2}	C_3		C_{1+2}	C_3
ab	+	−	−		X	−		X	−
$a^2 + b^2 - 3ac$	+	+	+		+	+		**X**	**X**
ac	−	−	+	⟶	−	+	⟶	−	+
$b^2 - 4ac$	+	+	+		+	+		**X**	+
$2a^2 + b^2 - 2ac$	+	+	+		+	+		**X**	**X**
$F(a, b, c)$	1	1	2		1	2		1	2

From the last step, we conclude that the condition $ac < 0$ guarantees exactly one feasible equilibrium point (i.e., $F(a, b, c) = 1$), while the condition $ab < 0, ac > 0, b^2 - 4ac > 0$ guarantees exactly 2 feasible equilibrium points (i.e., $F(a, b, c) = 2$). Note that a special case of this is the Allee effect model that has the following form (Sun, 2016):

$$\frac{dN}{dt} = N\left(\frac{N}{A} - 1\right)\left(1 - \frac{N}{K}\right) = N\left(\left(\frac{-1}{AK}\right)N^2 + \left(\frac{1}{K} + \frac{1}{A}\right)N - 1\right), \quad 0 < A < N < K \tag{5}$$

where $a = -1/AK$, $b = 1/A + 1/K$ and $c = -1$. It is clear that the second feasibility condition is satisfied as $ab < 0$, $ac > 0$ and $b^2 - 4ac = (A - K)^2/(A^2K^2) > 0$ (see Appendix 3 for a minimized feasibility table of a 2-species system with higher-order terms).

3. Unfolding links between model parameters

To illustrate additional applications of our methodology, we study the mathematical relationships between model parameters while satisfying feasibility conditions in models that are impossible to solve via isocline approaches. First, let us consider the simplest 2-species LV model with type III functional responses (Turchin, 2003) that is impossible to solve for the location of the equilibrium points analytically.

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 + a_{11}N_1 + a_{12}\frac{N_1N_2}{1+hN_1^2})\\ \frac{dN_2}{dt} &= N_2(r_2 + a_{21}\frac{N_1^2}{1+hN_1^2} + a_{22}N_2).\end{aligned} \tag{6}$$

Here, the set of model parameters is given by $\boldsymbol{\Psi} = (r_1, r_2, a_{11}, a_{12}, a_{21}, a_{22}, h)$. The common numerators of the RHS of the system above, after deleting N_1 and N_2 outside the brackets, are given by

$$\begin{aligned}f_1(N_1,N_2) &= r_1 + a_{11}N_1 + a_{12}N_1N_2 + r_1hN_1^2 + a_{11}hN_1^3\\ f_2(N_1,N_2) &= r_2 + a_{22}N_2 + (a_{21}+r_2h)N_1^2 + a_{22}hN_1^2N_2.\end{aligned}$$

Upon eliminating N_1 from both $f_1(N_1,N_2)$ and $f_2(N_1,N_2)$, we obtain $\text{Res}_{N_1}(f_1,f_2)$ which is a polynomial of degree 5 in N_2 and cannot be solved analytically in closed-form (Abel, 1826). Similarly, upon eliminating N_2 from both $f_1(N_1,N_2)$ and $f_2(N_1,N_2)$, we obtain $\text{Res}_{N_2}(f_1,f_2)$ that is a polynomial of degree 5 in N_1 as shown below:

$$\begin{aligned}\text{Res}_{N_2}(f_1,f_2) =&(-a_{11}a_{22}h^2)N_1^5 + (-a_{22}h^2r_1)N_1^4\\ &+(a_{12}a_{21} - 2a_{11}a_{22}h + a_{12}hr_2)N_1^3\\ &+(-2a_{22}hr_1)N_1^2 + (a_{12}r_2 - a_{11}a_{22})N_1 + (-a_{22}r_1)\end{aligned}$$

$$\begin{aligned}\text{Res}_{N_1}(f_1,f_2) =&(a_{12}^2a_{22}^3h^2)N_2^5 + (3r_2a_{12}^2a_{22}^2h^2 + 2a_{21}a_{12}^2a_{22}^2h)N_2^4\\ &+(a_{12}^2a_{21}^2a_{22} + 4a_{12}^2a_{21}a_{22}hr_2\\ &+3a_{12}^2a_{22}h^2r_2^2 + 2a_{11}a_{12}a_{21}a_{22}^2h)N_2^3\\ &+(a_{12}^2a_{21}^2r_2 + 2a_{12}^2a_{21}hr_2^2 + a_{12}^2h^2r_2^3\\ &+2a_{11}a_{22}a_{12}a_{21}^2 + 4a_{11}a_{22}a_{12}a_{21}hr_2)N_2^2\\ &+(a_{22}a_{11}^2a_{21}^2 + 2a_{12}a_{11}a_{21}^2r_2\\ &+2a_{12}ha_{11}a_{21}r_2^2 + a_{22}ha_{21}^2r_1^2)N_2\\ &+(r_2a_{11}^2a_{21}^2 + a_{21}^3r_1^2 + hr_2a_{21}^2r_1^2).\end{aligned}$$

In other words, the number of roots of $f_1(N_1,N_2)$ and $f_2(N_1,N_2)$ is 5. Note that the roots of the univariate polynomials $\text{Res}_{N_1}(f_1,f_2)$ and $\text{Res}_{N_2}(f_1,f_2)$, upon appropriate pairing of roots of the first polynomial with the second, are the roots of the system $f_1(N_1,N_2) = 0$ and $f_2(N_1,N_2) = 0$. Since the roots of either $\text{Res}_{N_1}(f_1,f_2)$ or $\text{Res}_{N_2}(f_1,f_2)$ are unattainable analytically, then the system $f_1(N_1,N_2) = 0$ and $f_2(N_1,N_2) = 0$ is unsolvable analytically.

Next, to find relationships between model parameters, for illustration purposes, let us consider the parameters $\boldsymbol{\Psi} = (r_1, r_2, a_{11}, a_{12}, a_{22}) = (0.5, -1.5, 1, -1.5, 1)$, and the parameters $a_{21} \in [-6,-1]$ and $h \in [0.5, 4]$. In this special case, we find that feasibility (i.e., $F(\boldsymbol{\Psi}) \geq 1$) can only be satisfied under the single condition $\upsilon_0(0,0) < 0$. See Appendix 4 for the expression of $\upsilon_0(0,0)$ written as symmetric sums (i.e., sigmas), along with closed forms of the sigmas and derivations. We find that the feasibility domain generated via solving numerically (using the software tool PHCLab) the isocline equations (i.e., $f_1(N_1,N_2) = 0, f_2(N_1,N_2) = 0$) and checking for the feasibility of roots matches the domain generated by the inequality $\upsilon_0(0,0) < 0$ (see Fig. 1A–B). Note that a_{21} and h are independent in the model, yet they are bounded by feasibility.

As a second example, let us consider the LV model with higher-order interactions that is shown below. This example is the simplest ecological 3-species model whose isocline equations are impossible to be solved analytically as it has five roots (see Appendix 6).

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(r_1 + a_{11}N_1 + a_{12}N_2 + a_{13}N_3 + b_1N_2N_3),\\ \frac{dN_2}{dt} &= N_2(r_2 + a_{21}N_1 + a_{22}N_2 + a_{23}N_3 + b_2N_1N_3),\\ \frac{dN_3}{dt} &= N_3(r_3 + a_{31}N_1 + a_{32}N_2 + a_{33}N_3 + b_3N_1N_2).\end{aligned} \tag{7}$$

To study the feasibility conditions of this model, we need to consider the three polynomials inside the brackets. The resultants are shown in Appendix 6. Let us consider

$$\boldsymbol{\Psi} = (r_1, r_2, r_3, a_{11}, a_{12}, a_{13}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}, b_1, b_2) = (1.5, -1.5, -1.5, 2, -1.5, -1.5, 2, -1.5, -1.5, -1, 1, 1, -1),$$

where the parameters $a_{21} \in [1,6]$ (pairwise effect of species 1 on 2) and $b_3 \in [2,5]$ (higher-order effect on species 3) are restricted. We find that feasibility (i.e., $F(\boldsymbol{\Psi}) \geq 1$) is satisfied when $\upsilon_0(0,\infty,0) > 0$ (see Appendix 6 for more details). Again, for confirmation purposes, the feasibility domain generated by solving numerically the isocline equations (i.e., $f_i(N_1,N_2,N_3) = 0$ for $i = 1,2,3$) using the software tool PHCLab and checking for the feasibility of roots matches the domain generated by the inequality $\upsilon_0(0,\infty,0) > 0$ (see Fig. 1C–D). This illustrates that pairwise and higher-order interactions can be non-trivially linked and their incorporation into ecological models must be done with caution.

4. Discussion

Feasibility conditions can be obtained analytically by solving the isocline equations for species abundances $\boldsymbol{N}^* = (N_1^*, N_2^*, \ldots, N_n^*)^T$ before imposing the positivity condition $\boldsymbol{N}^* > \boldsymbol{0}$. This approach works well for LV model, whose isocline equations is the linear system $\boldsymbol{r} + \boldsymbol{A}\boldsymbol{N}^* = \boldsymbol{0}$ and whose feasibility conditions are given by $\boldsymbol{N}^* = -\boldsymbol{A}^{-1}\boldsymbol{r} > \boldsymbol{0}$ (Goh, 1976; Volterra and Brelot, 1931; Saavedra et al., 2020). However, when the isocline equations have five or more complex roots, the system of polynomial equations cannot be solved analytically. This is a consequence of Grobner elimination theorem combined with Abel's impossibility theorem (Adams et al., 1994; Abel, 1824, 1826). Specifically, from the elimination theorem, in any system of polynomial equations which has Θ complex roots and n variables, any $n-1$ variables can be eliminated from the system to obtain a univariate polynomial with the remaining variable of degree at least Θ. The roots of this univariate polynomial are all the correspondent coordinates of the roots of the isocline equations (Adams et al., 1994). This is a generalization of Gaussian elimination, which can eliminate any $n-1$ variables from the system leaving a single linear univariate polynomial in the remaining variable to be solved (Lazard, 1983). However, from Abel's impossibility theorem, it is impossible to solve a univariate polynomial in terms of radicals (i.e., analytically) (Abel, 1824, 1826) if this polynomial has five or more roots. For instance, this number of roots is quickly reached by adding Type III functional responses to a 2-species LV model or adding higher-order interactions to a 3-species LV model (AlAdwani and Saavedra, 2019).

In this work, we have proposed a general formalism to analytically obtain the feasibility conditions for any multivariate, polynomial, population, dynamics model of any dimensions without the need to solve for the equilibrium locations. We found that feasibility conditions are entirely functions of symmetric sums of the roots of the isocline equations. Unlike the location of the roots, which cannot be obtained analytically, symmetric sums of the roots can be obtained for any polynomial system regardless of order and dimension. We have also created an analytical formula of the number of feasible roots in the system, which are functions of signs of $\Theta 2^n$ quantities (i.e., the υ's evaluated at the feasibility box whose coordinates compose of zeros and infinities). We have shown how to create a feasibility table (i.e., matrix) whose columns are the individual feasibility conditions of the model. We have then provided

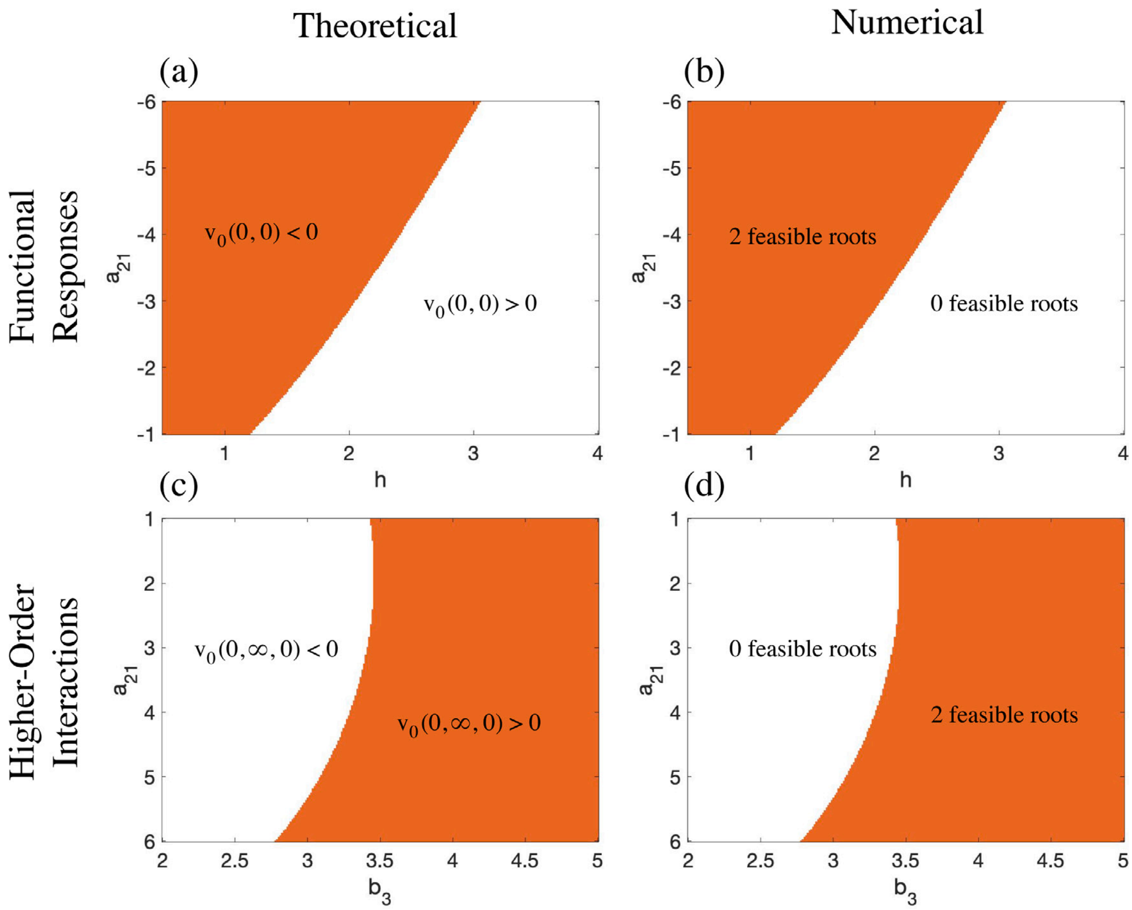

Fig. 1. Unfolding mathematical links between model parameters. Panels A–B show the mathematical link between a pairwise interaction a_{21} and the constant h while maintaining feasibility in a modified Lotka–Volterra model with type III functional responses (see main text), where $(r_1, r_2, a_{11}, a_{12}, a_{22}) = (0.5, -1.5, 1, -1.5, 1)$, $a_{21} \in [-6, -1]$ and $h \in [0.5, 4]$. The panels show the sign of $v_0(0,0)$ and the number of feasible roots. Note that $v_0(0,0)$ is the constant or trailing term of the characteristic equation (i.e., coefficient of λ^0) evaluated at $s_1 = 0$ and $s_2 = 0$ (the s's are the variables in the symmetric matrix $S = W \Delta W^t$, see Methodology). The number of feasible roots is obtained by solving the isocline equations numerically using the software package PHCLab and checking for the feasibility of roots. Both panels confirm that the number of feasible roots is greater than zero when $v_0(0,0) < 0$. Hence, the theoretical relationship is given by $F(\boldsymbol{\Psi}) = -2 * \text{sign}(v_0(0,0))$. Panels C–D show the mathematical link between a pairwise interaction a_{21} and a higher-order interaction b_3 while maintaining feasibility in a modified Lotka–Volterra model with higher-order interactions (see main text), where $(r_1, r_2, r_3, a_{11}, a_{12}, a_{13}, a_{22}, a_{23}, a_{31}, a_{32}, a_{33}, b_1, b_2)$ $= (1.5, -1.5, -1.5, 2, -1.5, -1.5, 2, -1.5, -1.5, -1, 1, 1, -1)$, $a_{21} \in [1, 6]$ and $b_3 \in [2, 5]$. The panels show the sign of $v_0(0, \infty, 0)$ and the number of feasible roots. Note that $v_0(0, \infty, 0)$ is the coefficient of the highest power in s_2 in the trailing term of the characteristic equation (see Methodology). Again, the number of feasible roots is obtained by solving the isocline equations numerically using the software package PHCLab and checking for the feasibility of roots. Both panels confirm that the number of feasible roots is positive when $v_0(0, \infty, 0) > 0$. Hence, the theoretical relationship is given by $F(\boldsymbol{\Psi}) = 2 * \text{sign}(v_0(0, \infty, 0))$.

a minimization process that can combine feasibility conditions into fewer ones and remove redundant quantities. Of course, the expressions involved in the inequality are complicated, nevertheless, they can be significantly simplified by sophisticated factorization.

Additionally, we have shown how to provide feasibility conditions under parameter restrictions. We have shown that by restricting parameters, the feasibility domain can be described by a single inequality only. In recent years, the topic of feasibility has been focused on relationships between parameters while maintaining feasibility (Saavedra et al., 2017). Using simulations (i.e., solving for the location of the isocline equations numerically then checking for the feasibility of roots) one can plot the feasibility domain for one, two, or three parameters at most while fixing the remaining ones. However, it is impossible to generate a four-dimensional plot that the human eye can capture. Also, it is impossible to find an analytical expression of the feasibility domain using numerical simulations. Of course, someone can find an approximate formula of the feasibility domain, nevertheless, there is no unique formula and different approximations may lead to different interpretations of how parameters are linked while maintaining feasibility. Following our proposed methodology, we can determine mathematically how any number of parameters are linked by describing polynomial inequalities that are functions of those free-parameters while maintaining feasibility: a task that is impossible to perform with simulations. This is an important property to consider in ecological modeling given that mathematical expressions are frequently formed assuming that parameters are independent of each other. However, once one imposes mechanisms or constraints, such as feasibility, these parameters can be linked and break the conclusions based on independent parameters (Song et al., 2019).

Our methodology provides a fast method for plotting feasibility domains, computing the number of feasible roots, and displaying feasibility conditions. For example, for our 3-species example with higher-order interactions, plotting the feasibility domain by solving the isocline equations numerically using the software package PHCLab (Guan and Verschelde, 2008) took more than 1.5 h to compute the number of feasible points with 2^{16} trials. Instead, using our methodology (and code which involves a naive implementation of our methodology without parallelization), it took less than 11.5 min to run the analysis, and a few seconds to plot the feasibility domain for different ranges of the free parameters using the same number of trials. Moreover, when we change the ranges of our free parameters a_{21} and b_3, we only need a few seconds to run our code, whereas we need to repeat the entire 1.5 h with the traditional numerical technique. With a clever implementation of the methodology and parallelizing the code (since the entire methodology can be parallelized), a faster computation of the feasibility domain/conditions and links between parameters can be achieved.

One significant drawback of the methodology is that it requires the handling of large symbolic expressions. Thus, careful implementation is required to run a successful code using the presented methodology. For example, when we created the generating function G, we did not multiply the determinant of the eliminant T and the determinant of the Jacobian of the isocline equations J, divided them by the product of all resultants, and took the series expansion of the final polynomial quotient. Instead, we took the series expansion of each resultant reciprocal separately, wrote TJ as multivariate polynomial in species abundances, found the coefficients of each term, and multiplied it by a single appropriate term in the series expansion of each resultant reciprocal to find the Σ's. However, it is always possible to handle such large expressions as the entire methodology can be parallelized. The second drawback of the methodology is its susceptibility to numerical errors. In our 3-species application example, our code gives as output non-integer values of the number of feasible roots in the system. Nevertheless, in our example we rectified it quickly by assigning non-integer values to their closest integers (see Appendix 6). Remember that the methodology requires only checking signs of large symbolic expressions, and we do not need them to be computed accurately. Nevertheless, such quantities can be computed more accurately by following several techniques such as increasing precision of numeric calculations. Similarly, cancellation errors can be reduced by combining positive numbers and negative ones together, and then performing a single subtraction. Round-off and truncation errors can also be avoided when ratios are computed. For example, instead of computing $(10^{90} - 10^{91})/10^{90}$ by computing $(10^{90} - 10^{91})$ then dividing the result by 10^{90}, it is better to add $10^{90}/10^{90} = 1$ with $-10^{91}/10^{90} = -10$ as the latter reduces round-off errors in large computations (Trefethen and Bau III, 1997). Of course, there are other techniques to reduce such errors, nevertheless, it is important to think about numerical errors in the implementation process.

Previous work has already provided foundational knowledge on species coexistence from microbial to plant–pollinator systems by focusing on how the behavior of such systems change as a function of both model choice and parameter values (Fort, 2018; Deng et al., 2021; Yacine and Loeuille, 2022; Aliyu and Mohd, 2022). However, this work has had to rely either on relatively simple models or numerical solutions, limiting our understanding of how the behavior of these systems will be affected by adding much more complex dynamics, increasing the dimension of the systems, or taking into account the entire parameter space. In this line, our work has unlocked the opportunity to increase our systematic understanding of how more complex models and the full set of parameters affect our conclusions of species coexistence. Indeed, it has been shown that the existence of a feasible solution is a necessary condition for persistence and permanence under equilibrium dynamics in models of the form $dN_i/dt = N_i f_i(\boldsymbol{N})/q_i(\boldsymbol{N})$ (Hofbauer and Sigmund, 1998; Stadler and Happel, 1993). Similarly, it has been proved that this type of models cannot have bounded orbits in the feasibility domain without a feasible free-equilibrium point (Hofbauer and Sigmund, 1998). In fact, we cannot talk about asymptotic or local stability without the existence of a feasible equilibrium point (AlAdwani and Saavedra, 2020). Hence, coexistence, stability, or permanence domains are subsets of the feasibility domain and their conditions are effectively part of the feasibility conditions obtained in this work.

CRediT authorship contribution statement

Mohammad AlAdwani: Designed the study, Performed the study, Derivations and code, Formal analysis, Writing – original draft. **Serguei Saavedra:** Designed the study, Supervision, Formal analysis, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data sharing

The code supporting the results can be found at https://github.com/MITEcology/Feasibility_AlAdwani_2021.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecolmodel.2022.109900.

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