A general framework for cycles in ecology

Rafael O. Moura[1], Violeta Calleja-Solanas[2] *,
José A. Langa[3], Oscar Godoy[2]

[1]Instituto de Ciências Matemáticas e de Computação Universidade de São Paulo, Brazil.

[2]Estación Biológica de Doñana (EBD-CSIC), Spain.

[3]Dpt. de Ecuaciones Diferenciales y Análisis Numérico, Universidad de Sevilla, Spain.

Abstract

Understanding the mechanisms that promote cyclic dynamics among species is critical for predicting biodiversity patterns and community assembly. Here, we present a general framework for studying cycles in ecological systems. Using invasion graphs derived from the Lotka-Volterra equations, we discovered that cycles are primarily driven by the antisymmetric component of the interaction matrix, which captures directional imbalances in interaction strength and promotes non-hierarchical dynamics. We also generalized the concept of cycles to include multi-species equilibria and transitions between states with varying species compositions. Additionally, we found that intrinsic growth rates modulate the likelihood of cycles: homogeneous growth rates promote cycles, while greater variability, particularly with negative growth rates, inhibits them. Our results suggest that cycles are constrained to ecological systems with pronounced interaction asymmetries and relatively uniform growth rates, providing a theoretical basis for their absence in natural communities.

Keywords: Ecological interactions, intransitive cycles, invasion graphs, ecological assembly

*Corresponding author:violeta.calleja@ebd.csic.es

Introduction

Ecologists continue to debate whether the vast biodiversity we observe in nature is maintained through mechanisms that operate between pairs of species such as differences in phenology, natural enemies, and environmental preferences, or whether additional contributions from indirect effects within ecological networks are necessary [1, 2, 3]. Understanding these different mechanisms is critical for predicting the assembly and dynamics of species within communities [4]. At one extreme, pairwise coexistence mechanisms create a gradient assembly structure containing hierarchically connected states (Fig. 1 A). At the other extreme, chains of indirect interactions lead to cycles as seen in the well-documented case of rock-paper-scissors dynamics [5] (Fig. 1 B).

Although this debate arises primarily from differences in environmental settings, taxa, and methodologies, there is broad consensus on the importance of the structure of species interactions (i.e., the interaction matrix) in determining the relative contributions of direct versus indirect effects to ecological dynamics. However, existing frameworks for predicting the emergence of cycles are limited to specific cases. The study of cycles has primarily focused on scenarios where a single species dominates at any given point in the cycle. In these systems, population dynamics follow a predictable pattern: one species becomes nearly dominant, then declines as another invades, and the sequence repeats without settling into equilibrium. Such cycles often emerge in intransitive communities, where the lack of a clear competitive hierarchy allows species to coexist despite strong competition [6]. This dynamic corresponds to the classic rock-paper-scissors game, where no competitor consistently dominates, maintaining diversity over time [5]. A general framework capable of predicting the presence of cycles of any length, among any subset of species, and across diverse biological systems remains lacking. This framework is paramount to enrich our understanding of the prevalence of cycles in ecology and to predict assembly structures that have not yet been discovered in nature.

To construct this framework, we use one approach borrowed from mathematics, but yet to be exploited in ecology: decomposing the matrix of species interactions into its symmetric and anti-symmetric components. The symmetric component captures the overall baseline strength of interactions within the system and the relative importance of intraspecific interactions compared to interspecific ones. On the other hand, the anti-symmetric component represents the absence of a universal best competitor and indicates the directionality of imbalances in interaction strength. Because both the symmetric and anti-symmetric components of the matrix align well with existing ecological knowledge, they allow making clear predictions about how they contribute to the emergence of cycles. For instance, in ecological

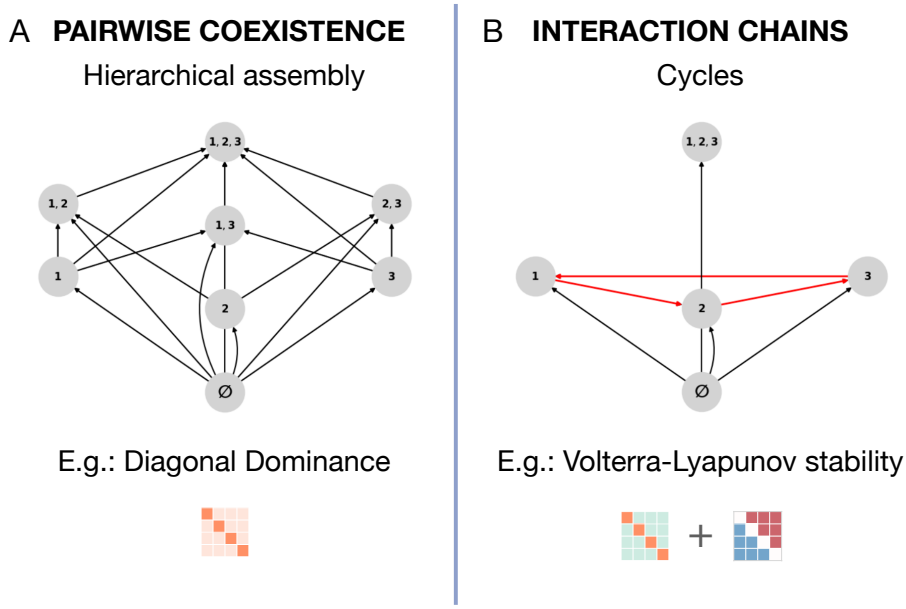

Figure 1: (a) The complete invasion graph of a 3-species system. Nodes' numbers indicate the species that form the subcommunity. The empty state with no species is denoted by ∅. Only pairwise coexistence mechanisms operate, resulting in a hierarchical assembly structure, in the sense that the gradual invasion of one species leads to a final state. We claim that diagonal dominant matrices can only show this kind of invasion graph. (b) An example of an invasion graph with a cycle among three states composed of a single species. We claim that Volterra-Lyapunov stable matrices, which can be decomposed in a symmetric (left matrix) and anti-symmetric (right matrix) components, are a type of matrices that can present cycles.

systems such as forests or perennial grassland communities where strong self-limiting effects are present [3, 7], we predict that the likelihood of cycles is low. This is because the symmetric component of the interaction matrix dominates, while the anti-symmetric component remains negligible. Meanwhile, ecological systems such as marine communities have documented long cycles in weak interaction networks. We predict that this is likely the result of asymmetries in interaction strength, which weakens the symmetric matrix's importance.

When studying cycles, it is crucial to recognize that, alongside the interaction matrix, species's intrinsic growth rates are also key to defining the structure and dynamics of ecological systems. The inherent ability of species to grow significantly influences its ability to recover from low density, withstand environmental variability, and ultimately, the coexistence of entire communities [8]. Past theoretical work has studied cycles when intrinsic growth rates are alike between species [5], and empirical evidence suggests that cycles become more prevalent when the variability in species' intrinsic growth rates is lower. Together, these findings predict that the likelihood of cycles decreases as differences in species' intrinsic

growth rates increase. However, an exploration of this prediction in combination with the species' interaction matrix is currently lacking.

Here, we propose a general framework for studying cycles in ecology. Our main body of analyses focuses on community assembly through invasion graphs, which incorporate the combined effects of species interaction matrices and their intrinsic growth rates [9]. By examining the conditions under which cycles arise —considering the ratio of symmetry to asymmetry in matrices and the variation in intrinsic growth rates— we discover three main groups of cyclic structures. These are: (1) a generalization of the rock-paper-scissors dynamics for any arbitrary odd number of species, (2) cycles involving transitions of more than one species between states, and (3) cycles characterized by varying numbers of species transitioning between states (Fig. 2).

Theoretical Framework

Different assemblage structures and whether they cycle were studied via invasion graphs [9]. Their nodes are subsets of coexisting species (admissible communities), connected by directed links when there is a potential transition due to invasions by missing species (Fig. 1). The main benefit of using invasion graphs is that they define invasions taking both the interaction matrix A and species performance r into account, and thus are a powerful tool to disentangle the role of these parameters in cycle formation.

It is proven that for a particular type of interaction matrices —*Volterra-Lyapunov stable* matrices (VL)— the links in the invasion graph are indeed connections in the phase space of the Lotka-Volterra system [10], and close paths in the invasion graph represent cycles between admissible communities (see Materials and Methods for mathematical details). We based our study on these matrices, which can be conveniently decomposed as the sum of a symmetric A_S and an anti-symmetric matrix A_J (Fig. 1 B). To characterize the interaction matrices, we used the asymmetry ratio (Eq. (4)), defined as the ratio between the norm sum of the anti-symmetric, $\mathrm{Asym}(A_J)$, and symmetric, $\mathrm{Sym}(A_S)$, components of the interaction matrix. The choice is motivated by the fact that systems where intraspecific competition dominates (i.e., large $\mathrm{Sym}(A_S)$ or diagonal-dominant matrices) tend to stabilize communities, whereas systems with greater asymmetry in interactions (i.e., larger $\mathrm{Asym}(A_J)$) create directional imbalances that we predict promote cyclic dynamics. Even though the assumption of working with VL-stable matrices may be restrictive, it allows us to explicitly describe the structure of all connections between equilibria. In contrast, an analytical algorithm to fully reconstruct the dynamics of the Lotka–Volterra model —and actually any high-dimensional system— remains unknown.

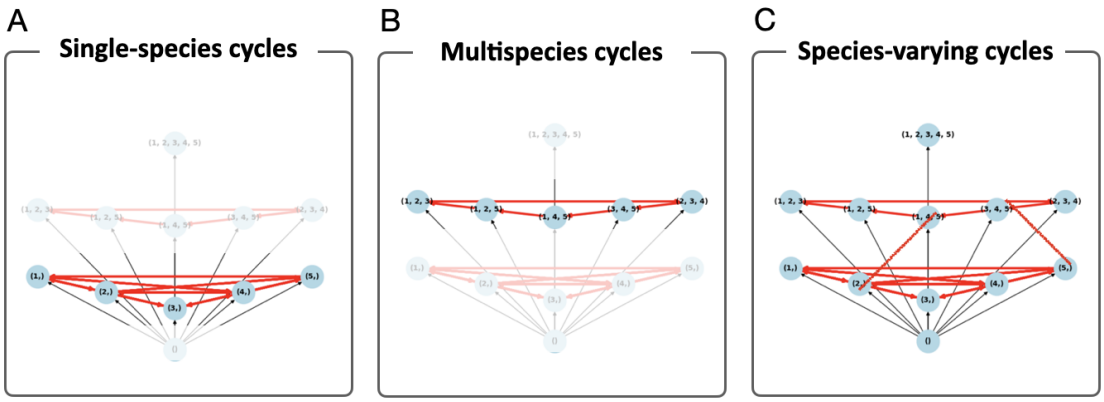

Figure 2: Types of cycles that can emerge in the invasion graph: (a) cycles among subcommunities of one single species. In the panel, it is highlighted the single-species cycle of the rock-paper-scissors-lizard-Spock 5-species system. Since cycles are intransitive, they are contained to any arbitrary odd number of species. (b) Cycles involving transitions of more than one species between states. In the panel, it is highlighted the 3-species cycle of the previous system. (c) Cycles among subcommunities of a heterogeneous number of species. In the panel, a toy example involving a cycle among nodes with 3 and 1 species.

Next, to systematically explore the conditions under which cycles emerge, we developed an algorithm to generate random VL-stable matrices, something that had not been previously achieved. Additionally, we constructed another novel method to generate interaction matrices tailored to include cycles between equilibria with multiple species, including cases where one or more species invade the community simultaneously. For each matrix, we computed the associated invasion graph, which maps the transitions between community states and allows us to identify the conditions under which cycles occur.

Our study first uncovers how the probability of cycles depends on the asymmetry ratio, the number of potential species, and the variability in species performances. Secondly, we investigated how the asymmetry ratio influences the likelihood of cycles involving equilibria composed of different numbers of species (e.g. the three-species cycles in Fig. 2 B). As a third step, we analyzed how the interplay between the asymmetry ratio and growth rate variability shapes both the probability of cycles and the structural complexity of the invasion graph, as reflected in its expected number of nodes (admissible subcommunities). These analyses reveal how the interaction between species performances and the structure of interactions governs the emergence of cycles, offering new insights into the dynamics of ecological communities.

Results

We observed that the presence of cycles in an ecological system that satisfies the Lotka-Volterra equations depends on the ratio of asymmetry of its interaction matrix A. In particular, the dominance of the anti-symmetric component of interactions facilitates the existence of cycles, while major importance of the symmetric component inhibits them, Fig 3. The probability of cycles is directly proportional to the sum norm of the anti-symmetric matrix A_J, Eq. (3), and inversely proportional to the sum norm of the symmetric matrix A_S, Eq. (2). Then, on one extreme, an ecological system has a high probability of containing cycles when the symmetric component is weak compared with the anti-symmetric component, especially for systems with a large number of species. On the other extreme, the cycle's probability goes to zero when the anti-symmetric component tends to zero, and the interaction's matrix becomes symmetric, in agreement with the fact that symmetric Lotka-Volterra systems are gradient [11]. This probability decreases sharply at a ratio that we have computationally found to be $\mathrm{Asym}(A_J)/\mathrm{Sym}(A_S) < 1$. We found diagonal dominant matrices among the matrices with zero cycle probability. This is explained because the self-regulation rates A_{ii} are in the symmetric component of A (the diagonal of A_S is the diagonal of A, and the diagonal of A_J is zero), and then when A is diagonal dominant, its symmetric component is always larger than its anti-symmetric component, so the diagonally dominant matrices are located before the region where the asymmetry ratio equals one, i.e. $\mathrm{Asym}(A_J)/\mathrm{Sym}(A_S) = 1$.

The values of the intrinsic growth rates in Fig. 3 were all taken equal to one, to study antisymmetries in isolation. Fig. 4 shows how the probability of finding a cycle in the invasion graph (represented as the red gradient) also depends on the heterogeneity of intrinsic growth rates. We found that cycles' probability is inversely proportional to the variability of r, meaning that when they are all equal, there are more cycles; and when they are more widely distributed (even assuming negative values) the probability of finding cycles reduces. Additionally, we sampled millions of diagonal dominant matrices, allowing now positive and negative r, and no cyclic invasion graph was found. This strongly suggests that diagonal dominant interaction matrices eliminate the possibility of intransitive cycles, and importantly, the absence of cycles is not the consequence of diagonal dominance, but more generally, it is caused by the relative strength of symmetric interactions.

Our framework has also allowed us to discover and characterize more complex cycles than cycles between single-species subcommunities (such as in the rock-paper-scissors system, Fig. 1 B). We found cycles with multi-species equilibria, i.e. between equilibria with more than one species (such as between 3 species in the rock-paper-scissors-lizard-Spock system, Fig. 2 B), and cycles involving states with a varying number of species (Fig. 2 C). Regarding

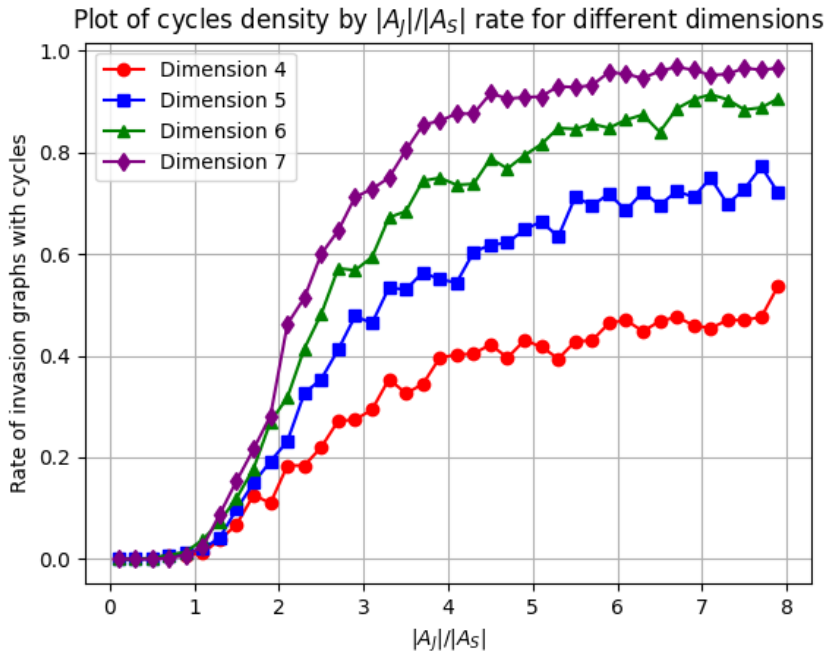

Figure 3: Probability of cycles vs. Asymmetry Ratio, defined in Eq. (4). We randomly sampled 200 matrices A for each given ratio and dimension, and calculated the associated invasion graphs. The y-axis represents the rate of those 200 invasion graphs that contained cycles.

multi-species cycles, we found that when asymmetries grow, cycles between subcommunities with a larger number of species are more and more probable, Fig. 5.

Additionally, high asymmetries also cause the complexity of the invasion graph to decline, Fig. 6, in the sense that the number of nodes in the invasion graph decreases with the asymmetry ratio $\mathrm{Asym}(A_J)/\mathrm{Sym}(A_S)$. This means that more symmetric interactions produce a larger number of equilibria in the invasion graph, and potentially more possible invasion paths to coexistence. A more frondose IG structure implies a greater probability of the addition of new species in existing ecosystems and reduces the probability of substitutions that lead to extinctions. Besides, the number of equilibria also decreases when the intrinsic growth rates vary more and can assume negative values.

These results are complementary and reveal the general behavior of the invasion graphs at each combination of asymmetry ratio and intrinsic growth rate variability. When the anti-symmetric component of the interaction matrix dominates, cycles appear with high probability if $r = \{r_i\}$ are positive and homogeneous (Fig. 4). Cycles are inhibited when growth rates are more heterogeneous and potentially negative. When the interaction matrix is mostly symmetric, cycles are less probable. Their probability does not significantly change

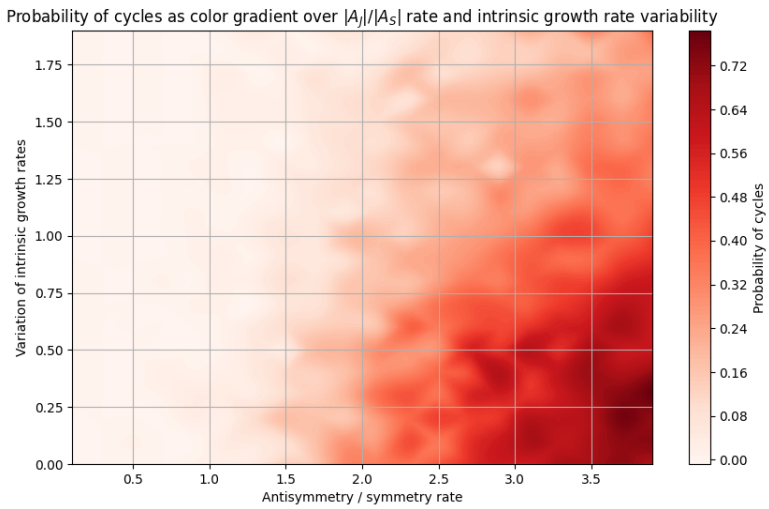

Figure 4: The color gradient captures the probability of finding cycles in the invasion graph, given the asymmetry ratio and variation of intrinsic growth rates. The y-axis represents the variation limit of the intrinsic growth rates, centered on the value of 1. For example, if the y value is 0.4, the intrinsic growth rates are sampled uniformly at random between 0.6 and 1.4. Notice that high values of variation (larger than 1 in our case) allow negative growth rates.

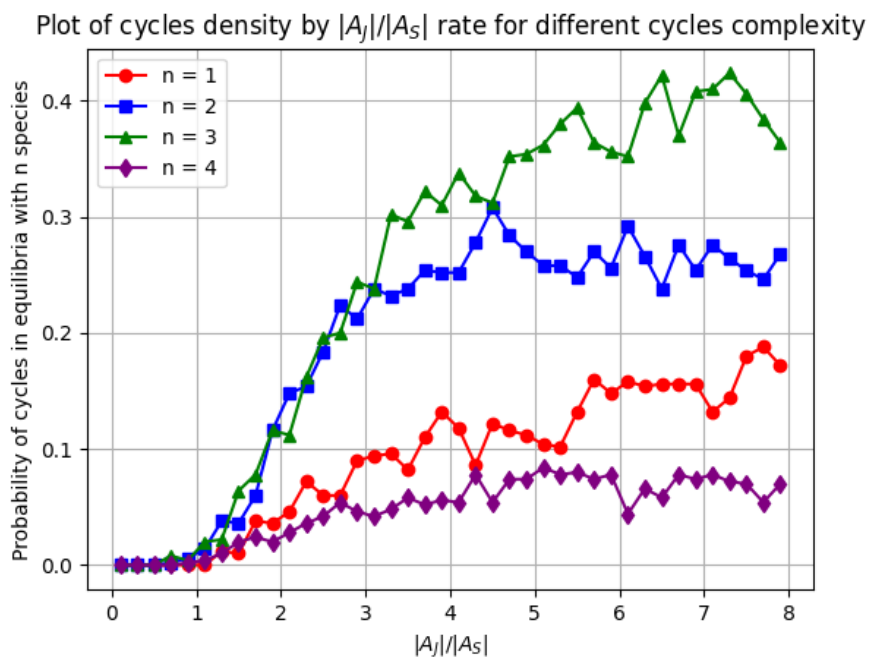

Figure 5: For each asymmetry ratio, this plot shows the probability of finding a cycle in the invasion graph involving equilibria between subcommunities composed all by 1, 2, 3, or 4 species in coexistence.

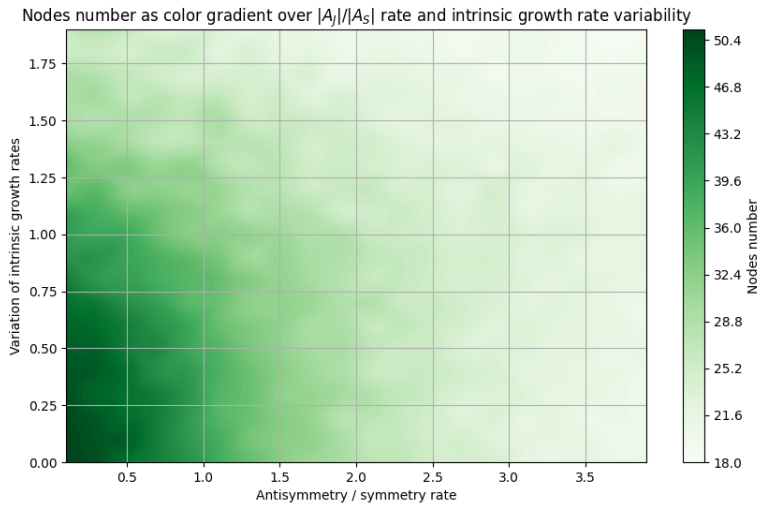

Figure 6: The color gradient represents the expected number of nodes of the invasion graph (i.e. of equilibria of the system), given the asymmetry ratio and the variation of intrinsic growth rates. The system in which the simulations were performed had 5 different species.

either with positive (and consequently an IG with many nodes) or heterogeneous r (and consequently an IG with fewer nodes)(Fig. 6). Then, our results suggest that the presence of cycles is restrained to a very particular interaction scheme, and align well with the lack of cycles in natural communities.

Discussion

Our findings provide a robust framework for understanding the presence of cycles in ecological systems, integrating the role of asymmetries in species interactions and the variability of intrinsic growth rates. The results demonstrate that asymmetry in interactions, captured by the anti-symmetric component of the interaction matrix, plays a key role in facilitating cycles. Conversely, a prevalence of symmetric interactions strongly inhibits cycles' occurrence, particularly when the ratio of the anti-symmetric to symmetric components falls below a critical threshold, $\mathrm{Asym}(A_J)/\mathrm{Sym}(A_S) < 1$. Importantly, diagonal dominance in interaction matrices —a property commonly theorized in natural systems [12]— ensures the suppression of cycles, emphasizing the ecological relevance of self-regulation in maintaining stable community structures.

Our exploration of multi-species cycles reveals that as interaction asymmetries grow, cycles become increasingly complex, involving transitions among equilibria with varying numbers of coexisting species. Moreover, we studied how a strong symmetric part of the interactions ma-

trix, aligned with homogeneous intrinsic growth rates, implies more frondosity in the invasion graphs. We conclude that these results refine the classification of coexistence mechanisms beyond the classic dichotomy of intransitive single-species cycles and pairwise interactions. Focusing on the ratio of interactions' asymmetries, coexistence can be maintained by (1) the dominance of the anti-symmetric component through cycles of varying complexity, or by (2) the dominance of the symmetric component that increases the admissible equilibria in the system.

Finally, the interplay between interaction asymmetries and intrinsic growth rate variability further refines our understanding of cycle dynamics. Our results show that a great variability of intrinsic growth rates decreases the likelihood of cycles. This dual dependence stresses how community dynamics are shaped not only by the structure of interaction networks but also by the individual performance of species. Our results indicate that communities with strong intrinsic growth differences are less likely to exhibit intransitive cycles as a coexistence mechanism, a finding that aligns with empirical observations in forest and perennial grassland ecosystems, where self-limiting effects and asymmetric competition are prominent [7]. Collectively, our findings suggest that cycles are constrained to specific ecological conditions characterized by high interaction asymmetries and low variability in growth rates. This may explain the relative scarcity of cycles observed in natural communities, where stabilizing mechanisms such as self-regulation and heterogeneous responses often dominate.

Materials and Methods

Dynamical setting. We model the population of n species through the generalized Lotka-Volterra equations, where each species interacts positively or negatively with themselves and all the others. This set of nonlinear differential equations describes the changes in the density x_i of species i over time as:

$$\frac{dx_i}{dt} = x_i \left(r_i + \sum_j A_{ij} x_j \right) \tag{1}$$

In this idealized dynamics, the vector or intrinsic growth rates $r = \{r_i\}$ denotes species performance, i.e. how species would grow isolated under given abiotic conditions. In turn, interactions among species are phenomenologically captured by the $n \times n$ interaction matrix A. Its diagonal elements A_{ii} represent intraspecific interactions, that is, how a species limits itself. Interspecific competition is captured in A_{ij}, the per-capita effect of species j on the per-capita growth rate of species i. The interaction matrix can be expressed as $A = A_S + A_J$, the sum of a symmetric A_S, $A_S = A_S^\top$, and anti-symmetric A_J, $A_J = -A_J^\top$, components. If

we define

$$\mathrm{Sym}(A_S) = \frac{\sum_{i,j} |[A_S]_{ij}|}{n^2} \tag{2}$$

and

$$\mathrm{Asym}(A_J) = \frac{\sum_{i,j} |[A_J]_{ij}|}{n^2} \tag{3}$$

then the asymmetry ratio is

$$\mathrm{Ratio}(A) = \frac{\mathrm{Asym}(A)}{\mathrm{Sym}(A)} \tag{4}$$

Invasion graphs. The analytical study of Eq. (1) is generally hard, especially for systems with many species. However, we can use a simpler algebraic approach to detect the possible solutions and their cycles in the system's dynamics. This approach is the *Invasion Graph* (IG) [9], which connects all possible solutions via invasions. By a solution, we mean a state of the system where some $m < n$ species coexist, a subcommunity. Mathematically, a subcommunity is defined as a set $I \subset \{1, \ldots, n\}$ for which it exists a non-negative equilibrium $x^I = (x_1^*, \ldots, x_n^*)$ in Eq. (1) with $x_i^* > 0$ if and only if $i \in I$.

To construct an IG, we start by searching all potential subcommunities, that will be the nodes of the graph. Note that the potential subcommunities are all the possible combinations of our species, but a certain combination will only become a node if it is connected with other subcommunities. For example, all possible subcommunities for $n = 3$ species appear in the IG of Fig. 1 A, but only a subset appears in Fig. 1 B. Then, the connections among the nodes are established via invasions. Namely, species' abilities to invade (or fail to invade) under the ecological conditions of the current community establish the links. To do so, the invasion rate of the species i on the community I is the average species per-capita growth rate when rare, which is defined as:

$$R_i(I) = r_i + \sum_{j \in I} A_{ij} x_j^* \tag{5}$$

If the subcommunity is empty $I = \emptyset$, we use the convention $R_i(\emptyset) = r_i$ [9]. The graph contains a link from subcommunities I to J if, and only if, $I \neq J$, and $R_j(I) > 0$ for every species j that is in J but not in I, and $R_i(J) < 0$ for every species i that is in I but not in J. This indicates that the conditions in I allow the invading species i to establish and persist. Conversely, for the transition to occur, any species that was in the initial subcommunity I but not in the new one J cannot invade it. Note that invasions are not limited to single species. For example, in Fig. 1 A, the subcommunity composed solely of species 1 can be simultaneously invaded by species 2 and 3 to form the new state where all three species coexist. To detect cycles, we note that the IG is a directed network, and then there is a

cycle if a path of directed links starts and ends at the same node.

Algorithm for generating Volterra-Lyapunov stable matrices. Recent work by Almaraz et al. [10] demonstrated that for Lotka–Volterra systems with Volterra–Lyapunov (VL) stable interaction matrices, the invasion graph is equivalent to the graph that represents the connections between the system's equilibria. Building on this result, we restricted our study to systems with VL stable matrices, as they provide a clear mathematical framework for analyzing cycles. Since our primary goal is to explore the conditions under which cycles emerge, we needed an efficient way to generate a large number of VL stable matrices. To address this, we redefined VL stability using an equivalent formulation that enables the random generation of VL stable matrices or their construction according to specific research objectives. In particular, we found that a matrix A is *Volterra-Lyapunov* stable if it can be written in the form:

$$A = H\,(S + J) \tag{6}$$

where S is a symmetric and stable matrix (i.e. all its eigenvalues are strictly negative), $H = diag(h_i)$ with all $h_i > 0$, and J is an arbitrary anti-symmetric matrix. To generate VL stable matrices, we first draw a random positive diagonal matrix H. Next, we create a random anti-symmetric matrix J by starting with a random matrix F and taking $J = K - K^T$. Finally, we construct a random symmetric stable matrix S by generating another random matrix F and calculating $S = F + F^T - \alpha * I$, where $\alpha \geq 0$ is chosen to be sufficiently large so that all eigenvalues of are strictly negative, and I is the identity matrix. This procedure guarantees that the resulting matrix A meets the mathematical criteria for VL stability. With this procedure, we can tune the ratio of asymmetry to explore a broad range of interaction structures.

Diagonal dominant matrices. An ecologically relevant subset of VL stable matrices are *Diagonal Dominant* matrices (DD), defined by:

$$DD = \frac{1}{n}\sum_{i}\left(|A_{ii}| - \sum_{j\neq i}|A_{ij}|\right) > 0 \tag{7}$$

This condition reflects systems where self-regulation plays a stronger role than competitive exclusion by other species. For example, in ecological networks dominated by species that specialize in distinct nutrient niches, higher diagonal dominance can lead to more even and stable community structures [13]. This is closely tied to competition asymmetry, as species with stronger self-limitation are less likely to exclude others, promoting coexistence and reducing the dominance of a single fast-growing competitor [14].

Algorithm for generating Volterra-Lyapunov stable matrices containing *à la carte* cyclic behavior. We first present our algorithm for the example of the extension to five dimensions of the classic three competing species community of May and Leonard 1975 [5], generating an invasion graph containing a cycle with five transitions that behaves like the rock-paper-scissors-lizard-Spock (RSPLS) game. To create this invasion graph, we take advantage of the definition of a Volterra-Lyapunov stable matrix as in Eq. (6), setting H equal to the identity matrix I. We can then write a matrix as $A = A_S(d) + A_J$, where $d < 0$ and the symmetric and anti-symmetric components are given by:

$$A_S(d) = \begin{pmatrix} d & 0 & 0 & 0 & 0 \\ 0 & d & 0 & 0 & 0 \\ 0 & 0 & d & 0 & 0 \\ 0 & 0 & 0 & d & 0 \\ 0 & 0 & 0 & 0 & d \end{pmatrix} \qquad A_J = \begin{pmatrix} 0 & -1 & 1 & -1 & 1 \\ 1 & 0 & -1 & 1 & -1 \\ -1 & 1 & 0 & -1 & 1 \\ 1 & -1 & 1 & 0 & -1 \\ -1 & 1 & -1 & 1 & 0 \end{pmatrix}$$

The anti-symmetric matrix A_J was constructed to represent the positive and negative interactions in an RSPLS game, the matrix $A_S(d)$ was chosen to be stable, and intrinsic growth rates were all chosen to be 1. The increase of the absolute value of d makes the system more symmetric, as the species interact more with themselves than with the others and we expect to have the inhibition of the cycle behavior. Then, we chose d to be small, so that the symmetry of the matrix does not inhibit the cyclic behavior. In this example, cycles exist in the invasion graph when $d \in (-1, 0)$, they cease to exist when $d = -1$, and when $d < -1$, we have observed by simulation that the invasion graph determined by matrix A is the same as the invasion graph determined by the diagonal matrix $A_S(d)$, which does not have any cycles. The IG when $d < -1$ contains all possible subcommunities and has a gradient structure.

We can create interesting cyclic behavior for any dimension using these previous ideas (if we restrict the intrinsic growth rates to be equal). The idea is to sum a diagonal stable matrix like $A_S(d)$ with an anti-symmetric matrix A_J containing the cyclic interactions between the species. When the diagonal terms of $A_S(d)$ are small in absolute values, we have a small symmetric part and the cycles emerge in the invasion graph.

Finally, it is also possible to construct cycles involving equilibria with several species with one or more invading species at a time, (third cyclic category, Fig. 2 C). Suppose we want a cycle where species 3 beats species 1 and 2, then species 4 beats 3, and species 1 and 2 beat

4. This behavior is present in the dynamics of the system with the matrix:

$$A_{double} = \begin{pmatrix} d & 0 & -1 & 0.5 \\ 0 & d & -1 & 0.5 \\ 1 & 1 & d & -1 \\ -0.5 & -0.5 & 1 & d \end{pmatrix}$$

The matrix A_{double} is Volterra-Lyapunov stable, and its anti-symmetric component represents the cyclic dynamics we want to create (cycles between one-species and two-species subcommunities). When $d \in (-1, 0)$, we have the cycle $(1, 2) \to (3) \to (4) \to (1, 2)$ in the invasion graph of the system. When $d = -1$ the cycle breaks, and when $d < -1$ the invasion graph of the system becomes identical to the invasion graph of the decoupled symmetric system with matrix $d \cdot I$.

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