A general framework for assembly cycles in ecology

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Significant statement

Uncertainties of the fundamental blocks that maintain biodiversity hinder our understanding of the dynamics we can observe in ecological communities. By applying a well-developed mathematical approach to studying interactions among species within ecological communities, we discover great potential for observing rock-paper-scissors and more complex cyclic dynamics in nature. However, we predict and confirm analyzing multiple datasets that cyclic dynamics are rare because of two phenomena that pervade ecological communities. These are differences in species´ performance and the dominance of self-limiting effects. Our framework underscores the importance of studying simple properties of biotic interactions to predict complex ecological dynamics.

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Abstract

Theory predicts that indirect interactions embedded in ecological networks maintain species diversity through cycles leading to oscillatory population dynamics. However, a framework that links the structure of species interactions (i.e., the interaction matrix) to the presence, type, and complexity of these cycles remains absent. Here, we first develop an analytical toolbox that combines invasion graphs, a method well-rooted in ecological theory, with mathematical approaches that decompose the species interaction matrix into its symmetric and anti-symmetric components. We discover that assembly cycles — sequences of species invasions forming closed loops in the invasion graph — are suppressed under the dominance of symmetric interactions. This ecological scenario corresponds to the condition where intraspecific competition exceeds interspecific competition. Conversely, cycles such as the classic rock-paper-scissors emerge when the anti-symmetric component dominates, which reflects strong competitive asymmetries between species. As these asymmetries increase, we uncover previously unreported cycles involving both sequential and simultaneous multispecies invasions. Then, applying our analytical toolbox to 21 empirically-determined interaction matrices of plant communities, we find that these natural communities exhibit few cycles because of the prevalence of self-limiting effects. Our work provides a tractable platform for investigating when indirect interactions are tightly linked to the emergence of cycles. This platform underscores that a simple ratio, assessing the relative importance between the symmetric and the anti-symmetric components of an interaction matrix determines the limits to the emergence of cycles in nature and the number of species they can maintain.

Keywords: assembly graphs, asymmetry ratio, biotic interactions, ecological networks, intransitivity, species coexistence.

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, 4, 5, 6, 7]. Understanding these different mechanisms is critical for predicting the assembly and dynamics of species within communities [8]. At one extreme, pairwise mechanisms promote a hierarchical structure of community assembly where species can coexist at fixed equilibrium [9, 10, 11] (Fig. 1A). At the other extreme, chains of indirect interactions break such hierarchy and can lead to the emergence of cycles [12, 13] (Fig. 1B).

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) for modulating contrasted ecological dynamics [1, 5, 14, 15, 16, 17, 4, 6, 7, 18]. However, we still poorly understand how to map the strength and signs of species interactions onto the different kinds of cycles that can occur in nature. This lack of knowledge mostly arises because cycles describing temporal changes in species abundances such as heteroclinic cycles [12, 19, 20], limit cycles [21, 22, 15], and assembly cycles (cycles arising via invasions) [10, 18, 23] have been studied separately. Moreover, the study of cycles has been restricted to the most basic configuration where no universal superior competitor exists in the interaction matrix. This configuration can lead, among other dynamics (see [12]), to the well-studied case of the rock-paper-scissors where one species becomes nearly dominant, then declines as another invades. The sequence repeats without settling into equilibrium [24, 6, 25, 26, 27, 14, 28, 29, 30]. Besides that intransitivity, we do not know which structure of species interactions can lead to other more complex cycles such as multispecies invasions [23, 18]. To address these limitations, we here introduce a framework capable of predicting the presence of assembly cycles with an arbitrary length of transitions, and subsets of species between transitions (i.e., sub-community). We believe this framework is paramount to enriching our understanding of the prevalence of cycles in nature and predicting assembly structures that have not yet been discovered.

To build this framework, we use one approach borrowed from mathematics, yet to be exploited in ecology. That is decomposing the interaction matrix into its symmetric and antisymmetric components [31, 32]. The symmetric component captures the overall strength of interactions within the system, and most importantly, the relative importance of intraspecific interactions compared to interspecific ones. It captures whether community assembly is modulated by self-limiting effects arising from resource requirements or by a competitive

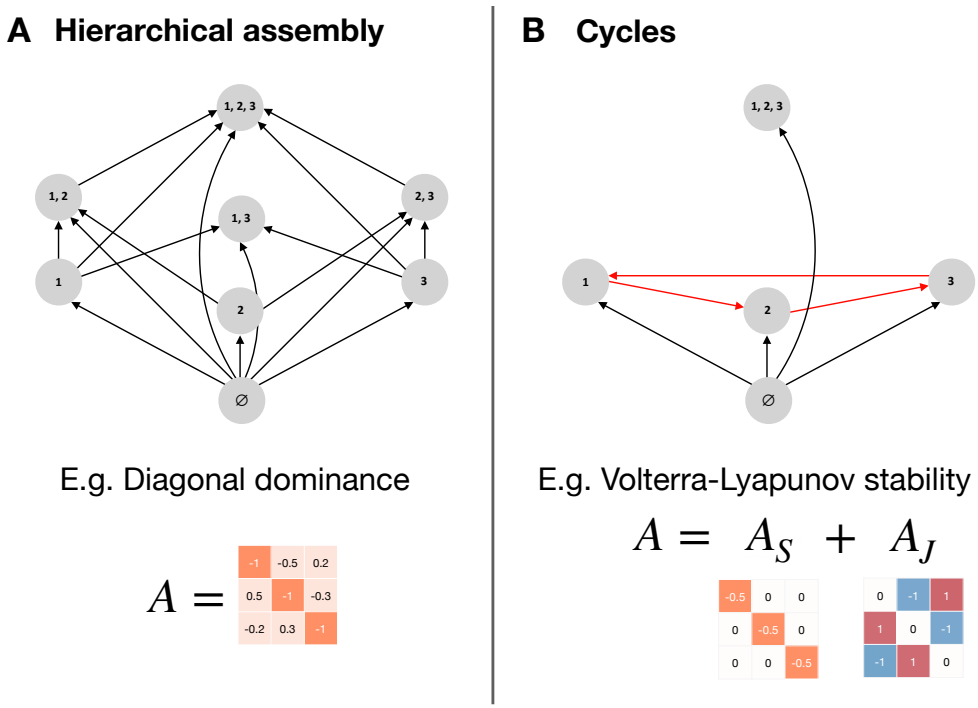

Figure 1: Complete invasions graph of 3-species systems. Nodes' numbers represent species identity within a sub-community, and links represent possible transitions between them. The empty state with no species is denoted by $\varnothing$.(A) A hierarchical assembly structure, where a gradual invasion of one species leads to a final state (equilibrium) of maximum diversity, in this case $(1, 2, 3)$, emerges, for example, from diagonal dominant interaction matrices. (B) Asymmetries in interaction strength among species under Volterra-Lyapunov stability may promote cycles such as the classic rock-paper-scissors game [12]. We predict that the realization of these contrasted invasion graphs depends on the relative importance of the symmetric component of the matrix (A_S) versus the anti-symmetric component (A_J).

hierarchy excluding inferior competitors. On the other hand, the anti-symmetric component captures the asymmetries in interaction strength among species, which may lead to the absence of hierarchy and then of a universal best competitor. Because 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 communities with strong self-limiting effects [3, 29, 33, 34], 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, in ecological communities with weak self-limiting effects, and therefore, low importance of the symmetric component of the interaction matrix, we predict that the emergence of cycles depends on whether species exhibit asymmetries in their interaction strength (i.e., no competitive hierarchy). If species present asymmetries in interaction strength (weak versus strong) and sign (positive and negative), the presence of cycles is widespread. Some examples include marine food webs, insect communities, or plant communities in stressful and productive environments [35, 1, 27, 36, 37, 6].

When studying cycles, it is crucial to recognize that, alongside the interaction matrix, differences in intrinsic growth rates between species are also key to defining the 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 [9, 5]. Most past theoretical work has studied cycles when intrinsic growth rates are alike between species [12, 25] for simplicity reasons. Recent theoretical work and empirical evidence suggest that cycles are more likely to occur when the variability in species' intrinsic growth rates is lower [1, 4, 38, 29, 36, 7], that is when the innate ability of species to produce offspring and survive is similar among species. Together, these previous findings posit that the likelihood of cycles decreases as differences in species' intrinsic growth rates increase. However, an exploration of this prediction in combination with the interaction matrix is currently lacking.

The main body of analyses to illustrate our general framework focuses on the assembly of communities through invasion graphs. This is because an invasion graph incorporates the combined effects of species' intrinsic growth rates and their interaction matrix on community dynamics [13, 10, 39]. Briefly, an invasion graph departs from an empty community and it indicates the different transitions among sub-communities (i.e., subsets of species that can be assembled) until the community reaches its maximum diversity. 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 in the invasion graph. These are: (1) generalizations of the rock-paper-

scissors dynamics for any number of species, (2) cycles involving invasions of more than one species between each sub-community of the invasion graph, and (3) cycles in which these invasions between sub-communities involve different numbers of species, and then cycles are composed of a varying number of species. Beyond these three categories, we found that cycles are more likely to occur when the anti-symmetric component dominates the interaction matrix and species show similar intrinsic growth rates regardless of community richness. To confirm that this combination is rare in nature, we apply our framework to a compilation of existing datasets of interaction matrices in the literature that covers a wide range of species richness and plant communities across contrasted climatic conditions (see [40] for details). As expected, we found low evidence of cycles in such empirical data. This last result opens the discussion of the ecological constraints, both internal (i.e., species interactions) and external (i.e., environmental conditions), to cycles in natural systems.

Theoretical Framework

The core of our analysis uses invasion graphs to study cycles in different structures of community assembly [13, 10]. The nodes of an invasion graph are subsets of coexisting species, technically known as sub-communities or admissible communities. These nodes are connected by directed links when there is a potential transition due to invasions by missing species (Fig. 1). The links in the invasion graph are indeed connections in the phase space of the Lotka-Volterra system [39] for the broad spectrum of interaction matrices that meet the condition of *Volterra-Lyapunov stable* matrices (VL), (6). The main benefit of using invasion graphs is that they define invasions considering both the interaction matrix A and intrinsic growth rates r into account. Therefore, invasion graphs are a powerful tool for studying the synergies between species interactions and performance in cycle formation.

Within the framework of invasion graphs, a cycle is defined as a closed loop that represents sequences of species invasions that eventually return to the initial sub-community generating oscillations in species abundances. This sequence of invasions is encoded directly in the topology of the invasion graph (red lines in Fig. 1B) and reflects temporal turnover driven by species arrivals. Specifying this definition is important as the term "cycle" refers to different concepts in the ecological literature, particularly in studies of intransitivity and community assembly. Other types of cycles such as limit or heteroclinic cycles also generate oscillatory population dynamics but they are not driven by sequential invasions. They rather emerge from intrinsic population dynamics within a sub-community — for instance, due to predator-prey interactions. These dynamical cycles can also be contained within an invasion graph but they are not represented as a cyclic graph. They "live" inside a single individual node of the assembly graph, and their detection can only be revealed by performing either

direct simulations of population dynamics or mathematical analysis of the sub-community's stability properties [41, 42]. In sum, assembly cycles are the only ones that show a direct correspondence between a cycle in the interaction matrix, a cycle in the invasion graph, and cyclic dynamics in the temporal behavior of a system.

To characterize how an interaction matrix determines an assembly of cycles, we first decompose such matrix as the sum of a symmetric A_S and an anti-symmetric matrix A_J (Fig. 1B) to later compute the asymmetry ratio $\mathrm{Asym}(A)$, (4), defined as the ratio between the magnitude of the entries of the symmetric and anti-symmetric components of the interaction matrix, $\langle|A_S|\rangle$ in (2) and $\langle|A_J|\rangle$ in (3), respectively. Such characterization allows covering a wide range of ecological phenomena. On the one hand, when intraspecific competition dominates, i.e., large $\langle|A_S|\rangle$ as in diagonal-dominant matrices ((7)), communities are stabilized in the absence of cycles. On the other hand systems with greater asymmetry in interactions, i.e., larger $\langle|A_J|\rangle$, create directional imbalances that can promote complex cyclic dynamics. Although our framework is flexible enough to explicitly describe the structure of all connections between equilibria, it might seem restrictive if a matrix is not *Volterra-Lyapunov stable*. Yet, an analytical algorithm to fully reconstruct the dynamics of systems that do not meet this stability condition remains unknown.

To systematically explore the conditions under which cycles emerge, we coupled our theoretical framework with a mathematical algorithm recently developed [32]. This algorithm serves two main goals. First, it generates random VL-stable matrices that allow exploring the invasion graph for an arbitrary number of species. Second, it also generates interaction matrices tailored to include simultaneous invasions of one or more species, which spans beyond the traditional approach of considering cycles between single-species equilibria [12, 15, 5, 23, 18].

Results

We show that the asymmetry ratio of an interaction matrix A determines the presence of cycles in an ecological system. Following our predictions, the dominance of the anti-symmetric component of interactions promotes many different types of cycles, while the dominance of the symmetric component inhibits them (Fig. 2A). Therefore, the probability of cycles is directly proportional to the magnitude of the anti-symmetric matrix $\langle|A_J|\rangle$, (3), and inversely proportional to the magnitude of the symmetric matrix $\langle|A_S|\rangle$, (2). At 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 richness. At the other extreme, such probability goes to

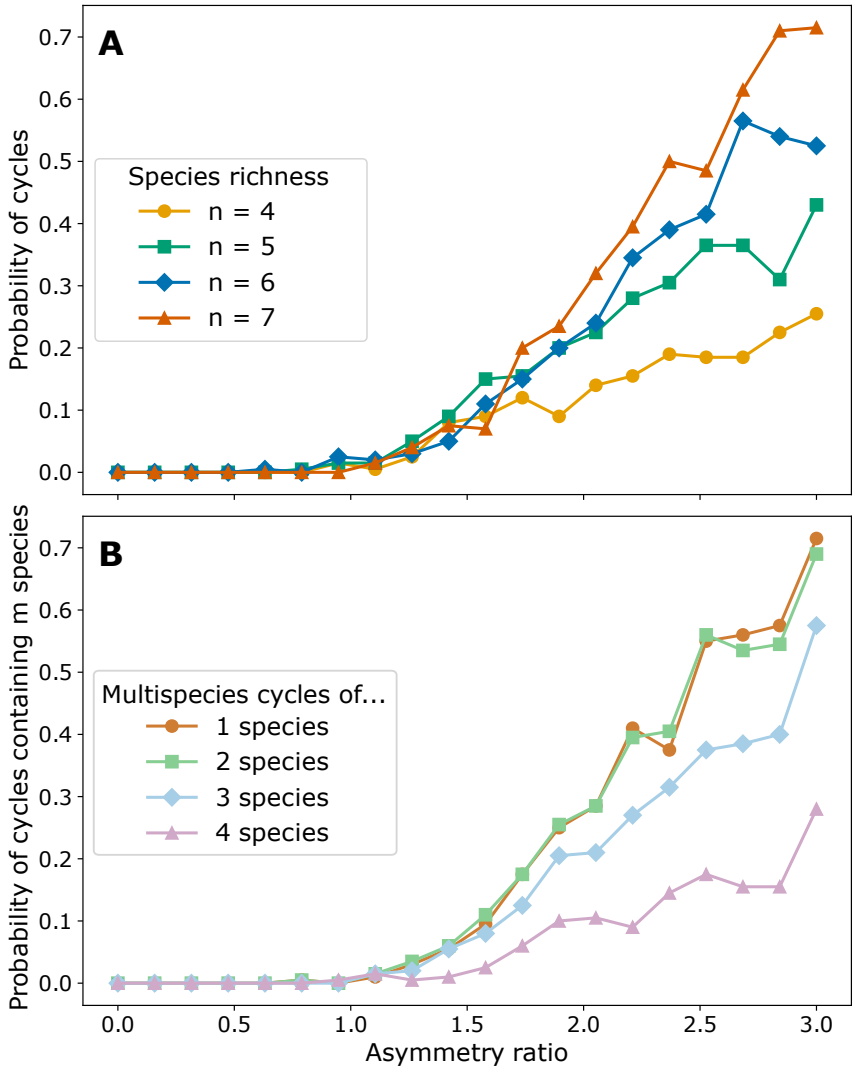

Figure 2: The influence of the asymmetry ratio on the probability of cycles. For twenty values of the asymmetry ratio, defined in (4), with a range in species richness between 4 and 7, we sampled randomly 200 matrices A and calculated the associated invasion graphs for a total of $16,000$ matrices. (A) The probability of an invasion graph containing any type of cycle increases non-linearly with the asymmetry ratio and with the species richness within the community. That is, the greater the asymmetry ratio the more likely to find a cycle, and for a fixed asymmetry ratio value the more species the more likely also to find a cycle. (B) The probability of an invasion graph containing any type of cycle with sequential invasions (class A in Fig. 3) or multispecies invasions (class B in Fig. 3) increases also non-linearly with the asymmetry ratio. That is, the greater the asymmetry ratio the more likely to find a cycle of sequential invasion of one species, but overall cycles of sequential invasion are more likely to occur than cycles of multispecies invasions (i.e., cycles containing 2, 3, or 4 species between each sub-community). For both panels, species intrinsic growth rates are all equal (r=1).

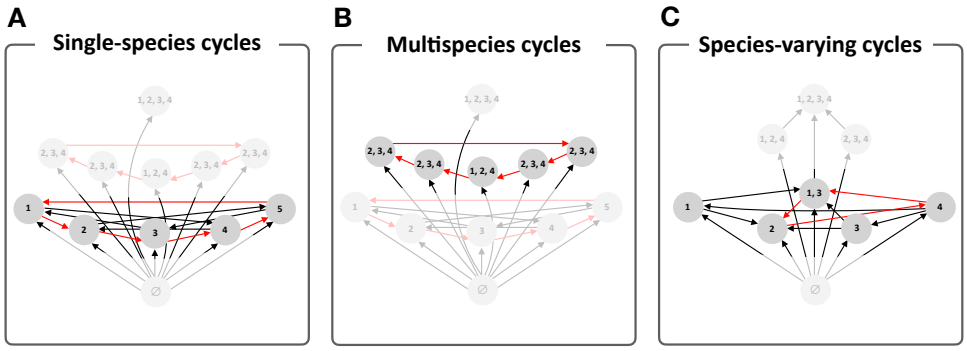

Figure 3: Categories of cycles: (A) cycles among sub-communities of one single species, which can be seen as generalizations of the rock-paper-scissors dynamics. Here is the case of rock-paper-scissors-lizard-Spock, which involves sequential invasions of five species. (B) Cycles involving multispecies sub-communities. (C) Cycles with a heterogeneous number of species among sub-communities. We illustrate here a particular case of sequential invasions of one species and a simultaneous invasion of two species (from sub-community (4) to $(1, 3)$). These three cycles, highlighted in red, have been built with an algorithm of cycles *à la carte*. See material and methods for details.

zero when the anti-symmetric component tends to zero, and therefore the interaction matrix becomes symmetric. There is a special case in which this probability decreases sharply at a ratio that we have computationally found to be $\langle |A_J| \rangle / \langle |A_S| \rangle = 1$. This particular case includes diagonal dominant matrices. This limit to cycles 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). In other words, when A is diagonally 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. The mathematical proof describing why diagonal dominant matrices do not contain any type of cycle is not trivial; worse, it is currently unknown, except in particular cases, for instance when cycles are among sub-communities of one single species [32]. However, we believe our result is robust. We sampled millions of diagonally dominant matrices coupled in the LV model to positive and negative intrinsic growth rates and no cyclic invasion graph was found. In conclusion, our results suggest that diagonal dominant matrices are incompatible with the presence of any kind of cycle.

Our results also show that when the anti-symmetric component of the matrix dominates, we obtain three distinct classes of cycles: single-species, multispecies, and species-varying cycles (Fig. 3). The first category encompasses a generalization of the rock-paper-scissors to any number of species. This generalization means that cyclic dynamics following the May-Leonard case of sequential transitions of single species between sub-communities can be

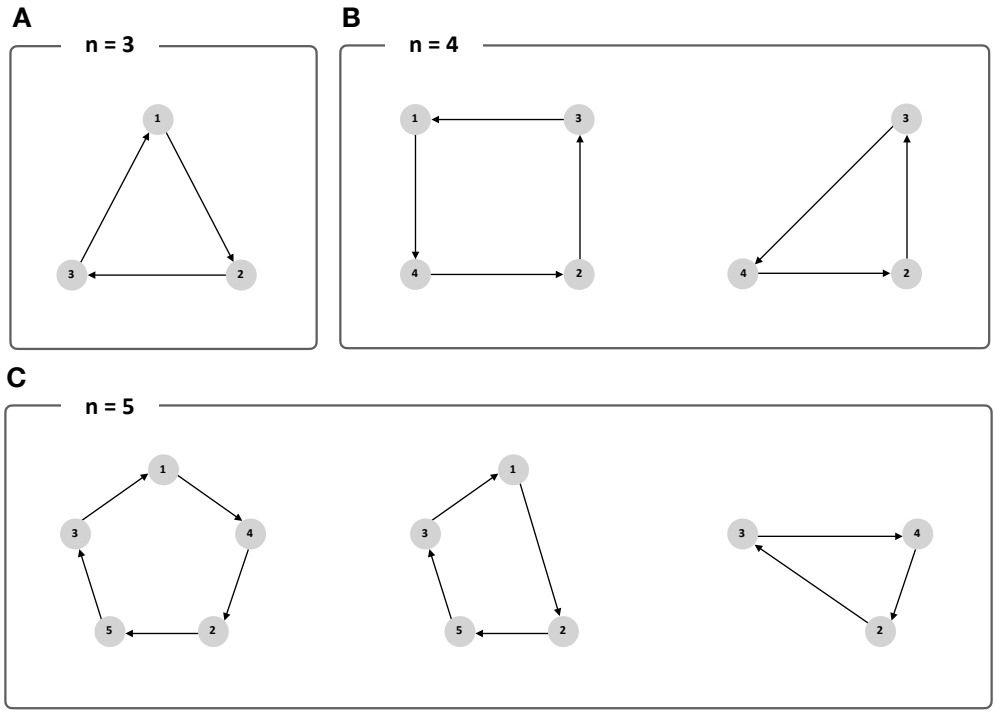

Figure 4: Examples of generalizations of the rock-paper-scissors system (A) to four (B) and five (C) species, where single-species cycles of an arbitrary number of species can emerge. In the panels, the invasion graphs are not depicted but some of the present cycles.

described for assemblages of any odd number, including 3, and also 5, 7, 9 species (Fig. 3A) as previous work suggested [24, 43]. Nevertheless, this generalization also encompasses cycles with an even number of species (e.g. 4, 6, 8 species), which has been much less studied before. Overall, this first category includes any assemblage of species that contains an assembly cycle of sequential invasions of an arbitrary number of species length. Such cycles can contain all species within the assemblage or only a subset of them (Fig. 4). The other two categories correspond to cycles with more complex transitions beyond the traditional single-species sub-communities. In more detail, the second category (*multispecies cycles*) corresponds to cycles between states with more than one species. Fig. 3B shows the rock-paper-scissors-lizard-Spock system, where each sub-community has three species sequentially invaded by one species at a time. Finally, the cycles in the third category (*species-varying* cycles) can involve not only sequential but also simultaneous multispecies invasions, transitioning between sub-communities of a varying number of species. Fig. 3C shows an example of a cycle transitioning between sub-communities composed of either one or two species. Finally, we also found that cycles composed solely of one-species equilibria (the first category) are more common than cycles containing at least a sub-community of $m < n$ species, which correspond to the latter categories (Fig. 2B).

To study the effect of the anti-symmetric component of the matrix in isolation, the values of the intrinsic growth rates in Fig. 2 were taken all equal to one. Nevertheless, as theoretical and experimental work has shown before, the probability of finding a cycle in the invasion graph also depends on the variation of the intrinsic growth rates (r). For our study, and in agreement with previous findings, we found that the probability of cycles is inversely proportional to the variability of r (Fig. 5A). This means that cycles are more frequent when variation in intrinsic growth rates is minimal, conversely, there are fewer cycles in an invasion graph when intrinsic growth rates are more variable, including both positive and negative values. When combining the effect of both the asymmetry ratio and the variation in intrinsic growth rates, we discovered that the highest probability of finding a cycle in an invasion graph corresponds to a low variation in intrinsic growth rates and a high asymmetry ratio. If we focus now on the complexity of the invasion graph, understood as the number of sub-communities involved in the cycle, we find an opposite pattern for the asymmetry ratio $\langle|A_J|\rangle/\langle|A_S|\rangle$. This means that more symmetric interactions produce a larger number of sub-communities at equilibrium in the invasion graph, and therefore, enlarge the number of possible invasion paths to coexistence (Fig. 5B). For intrinsic growth rates, lower variation also promotes more complexity of the invasion graph. Therefore, the invasion graphs with more frondosity (i.e., transitions between sub-communities) emerge under the combination of low asymmetry ratio and low variation in intrinsic growth rates.

Finally, to explore our general framework beyond simulations, we evaluated the potential emergence of cycles in 21 empirically determined matrices that account for a wide variety of terrestrial plant communities with varying levels of species richness [40]. We found that only 8 (38%) of these matrices are diagonally dominant either in a row or column sense (that is, the strength of intraspecific interactions is stronger than interspecific interactions, (7)). Moreover, a greater proportion of them (14 matrices, 66%) also meet the more strict conditions of Volterra-Lyapunov stability, (6). In contrast, the remaining third of the matrices could not be classified as VL-stable (33%). Once their stability was assessed, we tested for the presence of cycles following two complementary approaches. These approaches cope with the fact that information on the variation in intrinsic growth rates between species is missing. On the one hand, we built invasion graphs considering all intrinsic growth rates between species equal to one. We found no cycles for any community, instead, 5 of them (24%) presented full frondosity, allowing the existence of any possible sub-community. On the other hand, we sampled a thousand random vectors of intrinsic growth rate vectors within the interval $(-1, 1)$ for each of the empirical matrices. We found that the occurrence of cycles in invasion graphs was associated with only 2 of the 21 total communities (9%) for some values of intrinsic growth rates. This negligible proportion agrees with the fact that the average asymmetry ratio across communities across the 21 communities is low, with an

average of 0.41 and variance of 0.06.

Taken together, the combination of results obtained from simulations and their application to empirical interaction matrices indicates that there is, in principle, a strong potential for the emergence of assembly cycles in ecological systems. These cycles can involve the well-documented rock-paper-scissors but there is also potential for much more complex assembly dynamics. However, the realization of these cycles seems unlikely in nature, at least for the dataset analyzed. This is because of the restriction imposed by the biotic interactions among species, in which the relative importance of self-limiting effects compared to interspecific effects (i.e., a tendency towards diagonal dominant matrices) reduces the anti-symmetric component of the matrix, and hence the presence of cycles.

Discussion

Despite decades of research, ecologists still strongly debate the prevalence and mechanisms of cycles in nature [25, 14, 5, 4, 40, 6]. This debate is more broadly linked to the importance of mechanisms of biodiversity maintenance that operate between pairs of species versus indirect chains of interspecific interactions [12, 9, 2, 5]. Here, we present a general framework that captures the essence of this discussion and shows with an associated mathematical toolbox a metric that predicts the presence or absence of assembly cycles for any given ecological community composed of an arbitrary number of species. This metric, called asymmetry ratio, summarizes the balance between the symmetric and the anti-symmetric components of a matrix containing the interaction strength and sign within and between species. In more detail, our framework expects the presence of cycles when the anti-symmetric component in the interaction matrix dominates, $\langle|A_J|\rangle/\langle|A_S|\rangle > 1$, but restricts them when the symmetric component dominates, $\langle|A_J|\rangle/\langle|A_S|\rangle < 1$. In ecological terms, this means that cycles are absent when the assembly of a community is governed by stronger intraspecific than interspecific interactions. Alternatively, cycles are present when intraspecific interactions are overall weak and there are strong asymmetries in interspecific interactions. Overall, our framework shows that the complexity of biotic interactions we observe in ecological communities can be summarized in a simple asymmetry ratio that predicts the presence of cycles in nature.

The study of cycles in ecology has always dealt with sequential changes in species dominance and hence in their abundance. Our study enlarges this current view showing that these sequential dynamics are only a small part of the picture. With larger species pools, assembly cycles can be much more complex, including cycles with multispecies invasions or cycles with varying species invasions. Whether this occurs in nature remains to be empirically described. Initial explorations could include systems with microorganisms, where it has

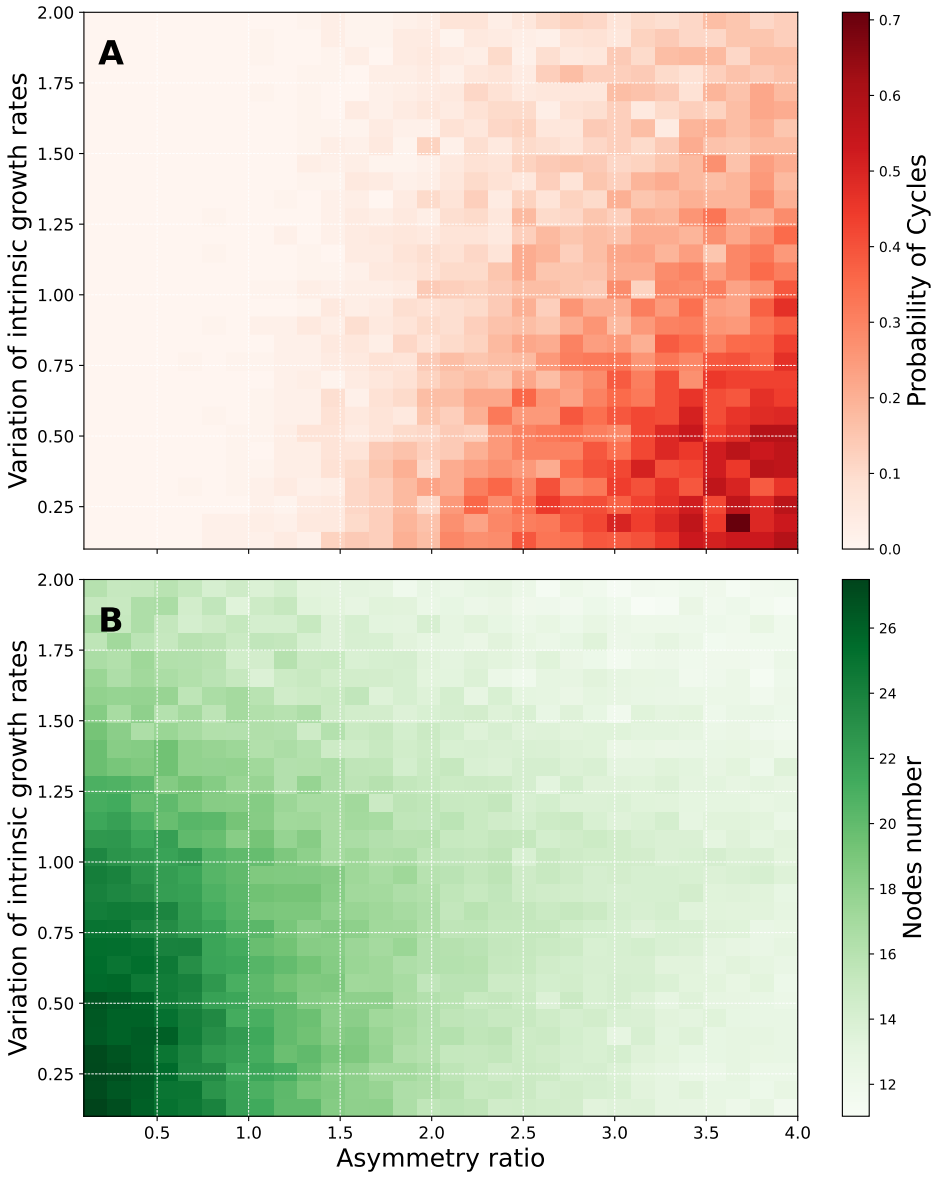

Figure 5: Probability of finding a complex cycle. (A) The color gradient captures the probability of finding cycles in the invasion graph, given both the variation in the asymmetry ratio and species´ intrinsic growth rates. The y-axis represents the variation limit of the intrinsic growth rates, centered on the value of 1. Then, for a value of 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. (B) The color gradient represents the mean number of sub-communities of the invasion graphs. The number of invasion graphs tested for each combination of parameters was 100 and had a maximum of 5 species.

been very recently suggested that these complex cyclic assembly dynamics might occur [18]. If our predictions hold, we envision that they would also advance our understanding of the relationship between multi-species assembly cycles and coalescence, a process in which entire microbial communities are replaced by others [44, 45].

At a more macroscopic level, our findings explain the rarity of cycles in nature, at least for the empirical plant communities analyzed, based on two features commonly observed in ecological communities that often are coupled: intraspecific competition stronger than interspecific competition [46, 40], and differences in species' intrinsic growth rates [4, 7]. Seeing it from the opposite perspective, this coupling indicates that the presence of cycles and their frondosity (i.e., the number of nodes contained in the invasion graph) are constrained to ecological configurations governed by high interaction asymmetries and low variability in intrinsic growth rates. Our results therefore go beyond the classic dichotomy of absence/presence of cycles based on no universal best competitor. Assembly cycles are related to a more nuanced perspective of complementarity of processes governing species population dynamics.

The term "cycle" has encompassed a broad range of perspectives and dynamics in the ecological literature. Many empirical approaches have documented cycles (also referred to as intransitivity) in the interaction matrix but these are not linked to oscillatory dynamics in species abundances [4, 29, 5]. Others have studied such oscillatory dynamics but in tournaments [25, 1, 24]. The connection between cycles in the interaction matrix with oscillatory dynamics has been done through the study of heteroclinic and limited cycles [12, 15, 21, 19], but such studies have excluded assembly cycles occurring via successful invasions. Our work of studying cycles through the lens of invasion graphs should not be viewed as another independent approach. Instead, it groups all these previous cycles' perspectives as different elements of an assembly graph. That is, it can contain internal oscillatory dynamics in a single sub-community as well as cyclic connections between sub-communities through invasions due to the lack of a universal best competitor. Therefore, we here present a general framework for cycles in ecology. This framework provides clear expectations of when cycles should be common in nature and the associated consequences for the assembly and dynamics of ecological communities.

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 itself and all the others. This set of nonlinear differential equations describes the changes in the density x_i of species i over time as:

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

In these 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, where n denotes the total number of species. Its diagonal elements A_{ii} represent intraspecific interactions, that is, how a species limits itself. Interspecific competition is captured in A_{ij}, the 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 and anti-symmetric A_J components, where $A_S = \frac{A+A^T}{2}$ and $A_S = A_S^\top$, $A_J = \frac{A-A^T}{2}$ and $A_J = -A_J^\top$.

If we define the matrix norms:

$$\langle |A_S| \rangle = \sum_{i,j} |[A_S]_{ij}| \tag{2}$$

and

$$\langle |A_J| \rangle = \sum_{i,j} |[A_J]_{ij}|, \tag{3}$$

the asymmetry ratio is then:

$$\mathrm{Asym}(A) = \frac{\langle |A_J| \rangle}{\langle |A_S| \rangle} \tag{4}$$

Invasion graphs

The analytical study of (1) is generally hard [42], 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) [10], which connects all possible solutions via invasions. By a solution, we mean a state of the system where some $m < n$ species coexist, a sub-community. Mathematically, a sub-community 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 (1) with $x_i^* > 0$ if and only if $i \in I$.

To construct an IG, we start by searching all potential sub-communities, which will be the nodes of the graph. Note that the potential sub-communities are all the possible combinations of our species, but a certain combination will only become a node if it is connected with other sub-communities. For example, all possible sub-communities for $n = 3$ species appear in the IG of Fig. 1A, but only a subset appears in Fig. 1B. Then, the connections among the nodes are established via successful invasions. 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 sub-community is empty $I = \emptyset$, we use the convention $R_i(\emptyset) = r_i$ [10]. The graph contains a link from sub-communities 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 sub-community I but not in the new one J cannot invade it. Because the IG is a directed network, cycles emerge when a path of directed links starts and ends at the same node.

Algorithm for generating Volterra-Lyapunov stable matrices

Recent work [39] 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 parallelism, our study focuses on 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 [32]. 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 any 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 K 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 S are strictly negative, and I is the identity matrix. This procedure guarantees that we can obtain a wide range of matrices A with varying asymmetry ratios, and all of them meet the mathematical criteria for VL stability.

Diagonal dominant matrices

An ecologically relevant subset of VL stable matrices are *Diagonal Dominant* matrices (DD), which satisfy the following condition:

$$|A_{ii}| - \sum_{j \neq i} |A_{ij}| > 0, \ \forall i \tag{7}$$

Diagonal dominant matrices always have an asymmetry ratio of less than one by definition. In a DD matrix self-regulation plays a stronger role than interspecific competition, which might reflect differences in resource use among species [47]. Mathematically, diagonal dominance can also be defined by columns:

$$|A_{ii}| - \sum_{j \neq i} |A_{ji}| > 0, \ \forall i \tag{8}$$

Both definitions are 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 [46, 48].

Algorithm for generating Volterra-Lyapunov stable matrices containing *à la carte* cyclic behavior

For illustrative purposes of our main findings, it is useful to create an interaction matrix with a desired cyclic behavior (see Figs. 1, 3 and 4). We here introduce an algorithm capable of doing this by extending the classic three-species competitive community of May and Leonard (1975) [12] into five dimensions. This extension generates an invasion graph with a cycle of five single-species nodes known as 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 (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:

$$A_S(d) = \begin{pmatrix} d & 0 & 0 & 0 & 0 \\ 0 & d & 0 & 0 & 0 \\ 0 & 0 & d & 0 & 0 \\ 0 & 0 & 0 & d & 0 \\ 0 & 0 & 0 & 0 & d \end{pmatrix},$$

$$A_J = \begin{pmatrix} 0 & -1 & 1 & -1 & 1 \\ 1 & 0 & -1 & 1 & -1 \\ -1 & 1 & 0 & -1 & 1 \\ 1 & -1 & 1 & 0 & -1 \\ -1 & 1 & -1 & 1 & 0 \end{pmatrix}$$

The anti-symmetric matrix A_J represents the positive and negative interactions in an RSPLS game 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. Since we have predicted that a diagonal dominant matrix inhibits cycles, which occur when $d < -4$, 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 $d \in (-1, 0)$, but they disappear when $d = -1$.

Extending the ideas of this previous example, we can create interesting cyclic behavior for any dimension. The core of the approach 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, for species-varying cycles (the third category in Fig. 3 C), suppose we want a cycle where species 3 beats species 1 and 4 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 sub-communities). 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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Contributions

All authors conceptualized the ideas of the study. ROM led the data analysis with input from VC-S and FS. VC-S and OG drafted the manuscript with contributions from all the other authors.

Declaration

The authors declare no conflict of interest

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