Coexistence holes characterize the assembly and disassembly of multispecies systems

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A central goal of ecological research has been to understand the limits on the maximum number of species that can coexist under given constraints. However, we know little about the assembly and disassembly processes under which a community can reach such a maximum number, or whether this number is in fact attainable in practice. This limitation is partly due to the challenge of performing experimental work and partly due to the lack of a formalism under which one can systematically study such processes. Here, we introduce a formalism based on algebraic topology and homology theory to study the space of species coexistence formed by a given pool of species. We show that this space is characterized by ubiquitous discontinuities that we call coexistence holes (that is, empty spaces surrounded by filled space). Using theoretical and experimental systems, we provide direct evidence showing that these coexistence holes do not occur arbitrarily—they are constrained by the internal structure of species interactions and their frequency can be explained by the external factors acting on these systems. Our work suggests that the assembly and disassembly of ecological systems is a discontinuous process that tends to obey regularities.

Ecological systems are the product of various assembly and disassembly processes (for example, invasions and habitat fragmentation, respectively) that, together with the underlying ecological dynamics, determine which and how many species we observe in a given place and time. Classic and more recent studies have focused on characterizing the limits on the maximum number of species that can coexist under given constraints. Yet, we know little about the assembly and disassembly processes under which a community can reach such a maximum number, or whether this number is attainable in practice. Specifically, can these assembly and disassembly processes operate smoothly until reaching the limits of coexistence, as assumed in classic coexistence studies? Or is it possible that they find holes where coexistence abruptly breaks before reaching the limits, causing discontinuities in both processes?

Indeed, our current understanding of the assembly and disassembly of ecological systems has two contrasting perspectives. The first perspective, grounded in classic works, suggests that these two processes are predictable following an axis of increasing ecological complexity. This predictability has been echoed by heuristic rules, mathematical formalisms and conceptual frameworks assuming that species coexistence is mostly additive. For instance, the mutual invisibility criterion establishes that, given a pool of species, if all combinations of species coexist, the group of species can also coexist, and vice versa. Consequently, under this first perspective, the assembly and disassembly processes are expected to operate smoothly until reaching the limits of coexistence (that is, reaching the maximum number of species that can coexist). The second perspective originates in evidence showing that the assembly and disassembly of ecological systems are very difficult to predict. This difficulty comes from a complex interplay between many ecological and evolutionary processes, including species interactions, environmental conditions, dispersal, priority effects, phylogenetic relationships and stochasticity. Actually, while the mutual invisibility criterion can be a good rule of thumb, research has shown that it is unlikely to be observed in multispecies systems. Consequently, under this second perspective, it is expected that coexistence breaks before reaching its limits, causing discontinuities in the assembly and disassembly processes. Importantly, the discrepancies between these two perspectives are partly due to the challenges of performing experimental work and partly due to the challenges of developing a formalism under which one can systematically study the multidimensional aspects of species coexistence.

Here, we introduce a new formalism to study the space of species coexistence formed by a given species pool. Our formalism captures coexistence using a hypergraph with vertices corresponding to species and hyperedges corresponding to species collections that coexist (one hyperedge per species collection that coexists). To study the space of species coexistence, we embed such coexistence hypergraphs in the Euclidean space. This embedding consists of associating to each vertex (that is, species) a point in the space and representing each hyperedge as a filled space between the corresponding vertices. In this way, filled spaces represent coexistence relationships between species groups, while empty spaces represent a lack of coexistence. Under this formalism, we show that discontinuities in the assembly and disassembly of ecological systems result in holes (empty spaces surrounded by filled space) of different dimensions in these coexistence hypergraphs, which we call coexistence holes. A coexistence hole occurs during the assembly process when a particular species collection is conceivable from a bottom-up perspective (that is, it can be assembled from sub-collections that coexist), but it is not realized (that is, it does not coexist). In turn, a coexistence hole occurs during the disassembly process when a particular species collection is realized (that is, it does coexist), but it cannot be disassembled into sub-collections.

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(that is, its sub-collections cannot coexist). In this sense, coexistence holes indicate obstructions to assemble or disassemble a system. Detecting coexistence holes in ecological systems can help uncover hidden regularities in their assembly and disassembly, revealing what is possible and what is not.

We have organized this article as follows. First, we introduce formal definitions of coexistence holes, demonstrating their presence in small classic models of competition\cite{21,29,31} and mutualism\cite{31}. Next, we combine our formalism with a structuralist approach\cite{6,29,21,31} to study the emergence of coexistence holes in systems with a larger number of species. Finally, we study coexistence holes in five experimental microbial systems. We conclude by discussing the possible applications and limitations of our formalism.

**Discontinuities in assembly and disassembly processes**

**Coexistence holes.** We consider ecological systems where individuals have been organized into $S$ species (functional groups, taxa or other meaningful organizations). Following previous studies\cite{6,29,31}, we assume that every species collection either coexists or does not coexist (we discuss later how our framework can be adapted when coexistence depends on the initial species abundance). To study coexistence holes during the assembly process, we introduce the assembly hypergraph, $H$. This hypergraph has the isolated species $\{1, 2, \ldots, S\}$ as vertices and it has one hyperedge, $h \subseteq \{1, \ldots, S\}$, for each different species collection that can coexist (Methods and Supplementary Note 1). Here, the dimension of a hyperedge $h \in H$ is $\dim(h) = \text{the number of species in } h - 1$. The maximum $\max_{h \in H} \dim(h) + 1$ characterizes the limits of coexistence. Below such limits, the coexistence hypergraphs can have additional structure, as we discuss below.

We illustrate the concept of coexistence hypergraphs in the toy ecological system of $S = 3$ species of Fig. 1a. In this hypothetical ecological system, species survive in isolation and coexist when assembled in pairs, but species will not coexist when assembled in a trio (Fig. 1b). The corresponding assembly hypergraph is $H = [\{1\}, \{2\}, \{3\}, \{1, 2\}, \{2, 3\}, \{3, 1\}]$ and the limit of coexistence is two species. By embedding the assembly hypergraph into a Euclidean space, discontinuities reveal themselves as holes in the hypergraph, which we call assembly holes. For example, embedding the assembly hypergraph $H$ of the above toy ecological system into the plane reveals a one-dimensional assembly hole (Fig. 1c). The dimension of a hole is defined as the minimum dimension of its boundary. Zero-dimensional holes correspond to connected components of the hypergraph. We say a system has zero-dimensional holes if it contains two or more connected components. In our toy system, the hole's boundary, $\{\{1, 2\}, \{2, 3\}, \{3, 1\}\}$, is one dimensional, making the hole itself one dimensional. A two-dimensional hole would appear, for example, in a hypergraph that looks like a tetrahedron with an empty interior. Thus, assembly holes occur during an assembly process to build a certain species collection (for example, to build $\{1, 2, 3\}$) if coexistence abruptly breaks at the end (Fig. 1d). Assembly holes characterize unexpected obstructions to build larger species collections from smaller ones—species collections that do not coexist, although they can be assembled from sub-collections that coexist.

To study coexistence holes during the disassembly process, we introduce the disassembly hypergraph, $D$. By definition, $D$ contains all of the missing boundaries in the hyperedges of $H$, together with all species that survive in isolation (Methods and Supplementary Note 1). Therefore, except for zero-dimensional hyperedges (that is, isolated species), each hyperedge of $D$ is a species collection that does not coexist despite it having been disassembled from a larger species collection that can coexist. To illustrate the disassembly hypergraph in an elementary case, consider the ecological system of $S = 3$ species with coexistence outcomes as in Fig. 1c. Here, the trio of species coexists despite none of its pairs coexist.

The assembly hypergraph for this hypothetical ecological system is $H = [\{1\}, \{1, 2, 3\}]$ (see Fig. 1e). The corresponding disassembly hypergraph is $D = [\{1\}, \{2\}, \{3\}, \{1, 2\}, \{2, 3\}, \{3, 1\}]$. Thus, by embedding the disassembly hypergraph into a Euclidean space, discontinuities in the coexistence reveal themselves as disassembly holes. For example, embedding the disassembly hypergraph of the above toy ecological system into the plane uncovers a one-dimensional disassembly hole (Fig. 1f). Disassembly holes occur during a disassembly process starting at a certain species collection if coexistence abruptly breaks at the start (for example, starting at $\{1, 2, 3\}$ in Fig. 1g). Disassembly holes characterize unexpected obstructions to build smaller species collections from bigger ones—species collections that can be disassembled into sub-collections that do not coexist. In this sense, disassembly holes represent fragile species collections where removing one species will cause secondary extinctions.

**Coexistence holes in small systems with classic dynamics.** We illustrate assembly holes in the classic consumer–resource model of Tilman\cite{21,29}, considering $S = 3$ species that compete for $M = 2$ resources. Assuming that each species can reproduce using at least one resource, it follows that the three species always survive in isolation. An additional consequence of this model is the limits of coexistence: with two resources, at most, two species can coexist (that is, the assembly hypergraph cannot have the interior $\{1, 2, 3\}$ of the triangle). However, the specific shape of the assembly hypergraph will depend on how the species consume the resources (Methods and Supplementary Note 2). If both resources are essential for the three species to grow, but one species is competitively superior to the other two, the assembly hypergraph will have two components characterized by two zero-dimensional assembly holes (Fig. 2a,b). Suppose now that the resources are complementary for one species (that is, species 2 has a positive reproductive rate even if one resource is absent; Fig. 2c). In that case, the assembly hypergraph has only one zero-dimensional assembly hole (Fig. 2d). Finally, suppose that species 1 consumes only resource 1, species 2 consumes both resources in a complementary way and species 3 consumes only resource 2 (Fig. 2e). Then, the assembly hypergraph has one one-dimensional assembly hole (Fig. 2f).

Disassembly holes occur, for example, in systems with mutualism or special types of competition between species (Methods). Specifically, two zero-dimensional disassembly holes occur when $S = 2$ species survive through obligate mutualism only\cite{31} (Fig. 2g,h). A one-dimensional disassembly hole occurs for $S = 3$ species engaged in cyclic competition\cite{31}, where only species in isolation or in the trio coexist (Fig. 2i,j).

**Uncovering coexistence holes via homology theory.** In general, characterizing all discontinuities in the assembly and disassembly processes requires identifying all of the coexistence holes of different dimensions in the assembly and disassembly hypergraphs (see Methods for the formal definition of assembly and disassembly holes of arbitrary dimension). Identifying coexistence holes in systems with more than three species is challenging because their assembly/disassembly hypergraphs may not be adequately embedded into a two- or three-dimensional space. Consider the assembly hypergraph of Fig. 3a. In this example, the assembly holes are evident from the embedding into the plane. Figure 3b shows its associated disassembly hypergraph embedded in the plane. From this embedding, it is not evident that the species collection $\{5, 6, 7, 8, 9\}$ is a two-dimensional disassembly hole.

To overcome the above challenge, we constructed a novel homology theory to calculate the so-called Betti numbers of arbitrary hypergraphs (Methods and Supplementary Note 3). The Betti numbers are the vector $\beta = [\beta_0, \beta_1, \ldots]$, where $\beta_k$ ($k \geq 0$) counts the number of $k$-dimensional holes in the hypergraph. For example,
The Betti numbers for the assembly hypergraph of Fig. 3a are $\beta(H) = [2, 3, 0, 0, \ldots]$. The Betti numbers for the disassembly hypergraph of Fig. 3c are $\beta(D) = [4, 1, 1, 0, \ldots]$. The Betti numbers distil the essential form of assembly/disassembly hypergraphs into their (homotopic) assembly/disassembly skeletons—namely, a minimal hypergraph with the same Betti numbers (Fig. 3b,d).

**Results**

**A structuralist approach to explain coexistence holes.** To study how coexistence holes emerge in ecological systems with a larger number of species, we adopt a structuralist approach1,2,3 (Methods). We make this approach concrete by leveraging the mathematical tractability of the Lotka–Volterra model. Following previous works1,2,3, we assume that the system’s structure is phenomenologically captured by the interaction matrix $A = \{a_{ij}\}_{i,j=1}^{S}$, with $a_{ij}$ representing the effect of species $j$ on the per-capita growth rate of species $i$. In turn, the context is phenomenologically captured by the intrinsic growth rates $r = \{r_{i}\}_{i=1}^{S}$, with $r_{i}$ representing how species $i$ grows in isolation under given factors. We assume the context can change uniformly at random over the positive section of the unit sphere.

Under the above assumptions, from the universe of all possible assembly and disassembly skeletons, the interaction matrix $A$ constrains which ones can be realized given the system’s structure. From the set of all skeletons that can be realized, the intrinsic growth rates $r$ determine which assembly and disassembly skeletons will be observed for that particular context. For example, consider the hypothetical system of $S = 6$ species interacting as described by the interaction matrix $A$ of Fig. 4a. From this interaction matrix, a fixed and finite set of possible assembly and disassembly skeletons emerge (Fig. 4b). Each one of these skeletons is compatible with a specific range of directions of $r$, implying that each assembly and disassembly skeleton will be selected from the set of possible skeletons with a different probability. A large probability associated with a skeleton implies a larger fraction of external conditions (intrinsic growth rates) compatible with such a skeleton. Thus, the higher the probability of being selected, the higher the chances that a given skeleton occurs due to internal constraints (species interactions) alone. In our example, we have 4 possible assembly skeletons and 14 possible disassembly skeletons (Fig. 4c). Skeletons with assembly and disassembly holes are possible (white bars in Fig. 4c). Ecological systems with a higher strength or number of interspecific interactions can adopt a larger number of skeletons (Supplementary Note 5.1 and Supplementary Fig. 5).

**Coexistence holes in random Lotka–Volterra systems.** Figures 2i,j and 4a–c show that assembly and disassembly holes emerge in simple population dynamics, without sophisticated mechanisms such as
Fig. 2 | Assembly and disassembly holes in classic ecological models. a-f. Coexistence outcomes for $S = 3$ species and $M = 2$ resources using Tilman’s consumer–resource model\(^5\) under different conditions. In this model, the limit of coexistence implies that, at most, $M = 2$ species can coexist. a, Top: impact matrix specifying how each species consumes the resources. In this example, all resources are (perfectly) essential for all species. b, One zero-dimensional assembly hole. c, Two zero-dimensional assembly holes. d, One one-dimensional assembly hole. e, One-dimensional assembly skeleton. f, All pairs coexist. g, Mutualism. h, Obligate mutualism. i, Cyclic competition. j, Only solos and the trio coexist. k, No collector coexists. l, All collectors coexist. m, Only solos coexist. n, Only solos and trio coexist.

as complex functional responses\(^6\) or higher-order interactions\(^7\). To investigate how general this conclusion is, we systematically analysed an ensemble of systems governed by Lotka–Volterra dynamics with random interaction matrices $A$ (Methods and Supplementary Note 5.2). Two parameters of the interaction matrix characterize the ensemble: the connectance, $C_A \in [0, 1]$, describing the probability that two species interact, and the typical interspecific interaction strength, $\sigma_i > 0$. We found that as soon as the interaction matrix exceeds a small complexity threshold measured by $\sigma_i C_A$, the presence of assembly and disassembly holes is unavoidable (Fig. 4d and Supplementary Note 5.3). This result implies that discontinuities are the norm rather than the exception in the assembly and disassembly of random (unstructured) Lotka–Volterra systems.

We also found that coexistence holes in random Lotka–Volterra systems obey two general patterns. First, knowledge of the disassembly skeleton strongly determines which assembly skeleton the system can adopt, but not vice versa (Supplementary Note 5.4 and Supplementary Fig. 6). That is, there is an asymmetry in the information contained in the assembly and disassembly skeletons. Second, low-dimensional and high-dimensional assembly/disassembly holes are unlikely to co-occur. That is, when the numbers of low-dimensional (that is, one- or two-dimensional) and high-dimensional (that is, three- or four-dimensional) holes are used as coordinates in a plane, the assembly and disassembly skeletons generated by random Lotka–Volterra models avoid the upper-right corner (Fig. 4e). This pattern arises because the likelihood of observing assembly or disassembly holes depends on their dimensions and the particular interaction matrix (Supplementary Note 5.5 and Supplementary Fig. 7). Specifically, high-dimensional assembly holes are more likely at weak interspecific interactions, whereas low-dimensional holes are more likely at strong interspecific interactions. We also observe that the probability of finding an assembly or disassembly hole decreases with the hole’s dimension, and that systems tend to generate more disassembly skeletons than assembly skeletons (Supplementary Fig. 7). Mathematically, it is possible to conceive hypergraphs that simultaneously have many
coexistence holes in empirical ecological systems. To study whether coexistence holes occur in empirical ecological systems, we analysed five experimental microbial communities: Vandermeer (S = 4), Friedman (S = 8), Stein (S = 12), Venturelli (S = 14) and MDSINE (S = 16). In each of these studies, a Lotka–Volterra model was parameterized and systematically validated using high-resolution experimental data, resulting in empirical estimations of the parameters A and r (Methods and Supplementary Note 6).

All five empirical interaction matrices can generate assembly and disassembly hypergraphs (Supplementary Fig. 8a–e). The numbers of possible assembly and disassembly skeletons differ across ecological systems, but most skeletons contain assembly and disassembly holes. In the two systems with smaller species pools, the empirical interaction matrices generate more assembly skeletons than disassembly skeletons (1.8 and 1.55 times more for Vandermeer’s and Friedman’s, respectively). The small number of disassembly skeletons in these systems could be explained by their size and simple assembly rules. For the systems with larger species pools, the empirical interaction matrices generate between 2.14 (Venturelli’s) and 221.5 (MDSINE) times more assembly skeletons than disassembly skeletons (1.8 and 1.55 times more for Vandermeer’s and Friedman’s, respectively). The small number of disassembly skeletons could be explained by their size and simple assembly rules.

The role of internal and external constraints. Next, we focus on the five empirical assembly and disassembly hypergraphs obtained from the experimentally parameterized (A, r) (Fig. 5a–e). For Vandermeer’s and Friedman’s, we find that their assembly hypergraphs are a simplicial complex. A simplicial complex is a particular hypergraph where each hyperedge has all of its boundaries (Fig. 5a,b). Notice that this occurs if and only if the associated disassembly hypergraph consists only of the isolated vertices. A system whose assembly hypergraph is a simplicial complex follows the sim-
ple closed-under-inclusion assembly rule: a species collection coexists if all of its sub-collections coexist. For Friedman’s system, this result agrees with the existence of a simple assembly rule derived in their original work\(^2\). There is a large probability of observing such a simple assembly rule for Vandermeer’s system due to internal constraints alone (among the random disassembly skeletons, the probability is \(P = 0.82\) for observing the empirical disassembly skeleton with only isolated vertices). For Friedman’s system, such probability is lower (\(P = 0.25\)), indicating that external factors (intrinsic growth rates) also play a role. Interestingly, it is possible to explain the lack of holes of dimension 1 or higher in Vandermeer’s system by internal constraints alone (\(P = 0.48\)). In contrast, explaining the presence of the two one-dimensional assembly holes in Friedman’s system also requires considering external factors (\(P = 0.08\) for internal constraints alone).

Stein’s and Venturelli’s systems contain higher-dimensional assembly and disassembly holes (Fig. 5c,d). The empirical assembly and disassembly skeletons of Stein’s system cannot be explained by internal constraints alone (\(P = 6.66 \times 10^{-4}\) and \(P < 3.33 \times 10^{-4}\), respectively). A similar situation occurs for Venturelli’s (\(P = 0.13\) and \(P = 0.01\) for the empirical assembly and disassembly skeletons). For MDSINE (the system with the largest species pool), the dimension of its assembly and disassembly hypergraphs only allowed us to compute its assembly and disassembly holes up to dimension 2. This empirical assembly skeleton consists of a single connected component without holes, and internal constraints alone can explain it (\(P = 0.999\)). However, its empirical disassembly skeleton has holes, and it is unlikely by internal constraints alone (\(P = 6 \times 10^{-3}\)). These results confirm that internal constraints (species interactions) play an important role in the emergence of coexistence holes.

Finally, to understand what properties render an empirical skeleton more or less likely to be observed, we compared the number of empirical coexistence holes of different dimensions with their randomizations (Fig. 5f–j). We find cases of depletion or (strong) enrichment in the number of coexistence holes, depending on the particular system and the hole’s dimension. In all empirical assembly and disassembly skeletons, low- and high-dimensional holes do not co-occur (colours in Supplementary Fig. 8), supporting our finding that coexistence holes obey general patterns. These results indicate that coexistence holes occur in empirical systems at specific dimensions due to a combination of internal constraints and external factors.

**Discussion**

Coexistence in multispecies systems has ubiquitous discontinuities or obstructions characterized by coexistence holes. Assembly holes do not exist if and only if \(\delta (H) = \{1, 0, \cdots, 0\}\). In this particular case, it is possible to build each species collection that coexists from its sub-collections (that is, assembled from the bottom up), and an invasion analysis\(^3\) can be applied with confidence. Our analysis of random (unstructured) and empirical ecological systems based on the Lotka–Volterra model suggests that the absence of coexistence holes is the exception rather than the norm. In particular, with random interactions, coexistence holes are more likely to occur when their complexity increases. This result aligns with May’s complexity–stability trade-off\(^3\), indicating that stability loss contributes

**Fig. 4 | A structuralist approach to understanding the emergence of coexistence holes in the Lotka–Volterra model.** a. A hypothetical interaction matrix, \(A\), describing the interactions between \(S = 6\) species (see values in Supplementary Equation (4)). b. Possible assembly and disassembly skeletons generated by the interaction matrix of a. c. By choosing \(r\) uniformly at random over the positive section of the unit 2-norm sphere \(\{r \in \mathbb{R}^6_+ | r_1^2 + \cdots + r_6^2 = 1\}\) (left), some assembly/disassembly skeletons are more likely to occur (right). Note that the unit sphere is illustrated in three dimensions, although in reality it is a unit sphere of dimension \(S = 6\). Here, solid bars denote skeletons without holes and hollow bars denote skeletons with at least one hole. d. Expected probability of finding at least one assembly (blue) or disassembly hole (pink) in the ensemble of Lotka–Volterra models with random parameters and \(S = 8\) species. e. Not all possible assembly/disassembly skeletons are possible in ensembles of Lotka–Volterra models with random parameters. Namely, note that skeletons that simultaneously have a large number of low-dimensional holes (that is, one- or two-dimensional holes) and high-dimensional holes (that is, three- and four-dimensional holes), which occupy the top-right corners of the panels, are very unlikely.
to generating discontinuities in the assembly and disassembly of ecological systems. It remains open to understand the prevalence of coexistence holes in more realistic situations, such as when species have specific interaction types or when species interact non-randomly organized or when abiotic conditions affect species interactions.

Our analysis also suggests that coexistence holes obey general patterns. Knowing the disassembly skeleton of a system also informs about the assembly skeleton, but not vice versa. This result suggests that, in multispecies experiments, focusing on characterizing their disassembly is better as it contains more information about both processes. Understanding which ecological properties lead to this pattern is an important open question for future research. We also find that low- and high-dimensional coexistence holes are unlikely to co-occur. This result is expected for random systems. For example, high-dimensional assembly holes need larger species collections to coexist to form the hole’s boundary. For random systems, this is more likely with weak interspecies interactions. In contrast, low-dimensional assembly holes can occur even when small species collections coexist, allowing for stronger interspecies interactions. Our analysis of empirically parametrized Lotka–Volterra models supports the hypothesis that species interactions play a crucial role in the emergence of coexistence holes.

Additional theoretical work is needed to understand the conditions leading to coexistence holes. Rough conditions can be derived from existing work. For example, additive coexistence guarantees that the system’s assembly is a complete hypergraph between all species that survive in isolation. In general, additive coexistence occurs if species occupy sufficiently different ecological niches. In the Lotka–Volterra model, some particular system structures, such as...
as food chains, imply the absence of coexistence holes\(^3\) (see also refs.\(^{20,25,50}\)). Our formalism can be adapted to cases when coexistence depends on the initial species abundance. Using a probability distribution for the initial species abundance, it is possible to calculate the corresponding Betti numbers' statistics.

One limitation of our study is that we calculated assembly hypergraphs using mathematical models. Ideally, assembly hypergraphs should be entirely constructed by experimentally testing each species collection's coexistence. This task is feasible for systems with a few species\(^4\) or systems where massive automated co-culture experiments are possible\(^5\). We followed this approach to construct the assembly hypergraph of \(S = 5\) bacterial species in \(Drosophila melanogaster\) gut microbiota from in vivo experimental data\(^6\) (Supplementary Note 7). The assembly hypergraph we obtained has one connected component and two one-dimensional assembly holes, supporting our hypothesis that coexistence holes are ubiquitous in ecological systems. In general, for systems with many species, the combinatorial explosion \(2^{|S|} - 1\) in the number of different species collections makes it impossible to rely on experiments only. Circumventing this limitation requires parameterizing population dynamics models to predict the coexistence of some species collections (Supplementary Note 4.3). Future work should not overlook the limitations of the Lotka–Volterra model\(^7\). In general, we expect that coexistence cases become more likely in more detailed ecological models\(^6\).

Our formalism allows comparing the assembly and disassembly of ecological systems using the corresponding hypergraphs' skeletons even if they have a different number of species. For example, regardless of its number of species or dynamics, a system follows the simple closed-under-inclusion assembly rule if and only if \(\beta(D) = [0, 0, 0, \ldots, 0]\). Indeed, comparing objects through the lenses of holes is far from a novel idea. Algebraic topology—the branch of mathematics roughly described as the study of holes—originated in the work of the great mathematician Henri Poincaré in the nineteenth century\(^8\). A discovery of algebraic topologists is that, even in low dimensions, holes can appear in many non-evident ways, such as in the infamous Klein bottle (the bottle has two holes, one of which disappears if traversed twice). Recently, algebraic topology is finding more applications across the sciences\(^9\).

Unfortunately, with the notable exception of Sugihara's work in the 1980s\(^{10}\), algebraic topology has been an underused tool in ecology.

Our work shows how species coexistence is a complex interplay between filled spaces (that is, species collections that coexist) and empty spaces (that is, species collections that do not coexist). Some empty spaces give rise to assembly and disassembly holes that characterize cases when coexistence abruptly breaks, implying that coexistence (or biodiversity) is a discontinuous process\(^11\). Identifying these discontinuities can improve our understanding of which processes in nature are driven by internal constraints of design and not merely by randomness, as it can be naively perceived.

Methods

Definition of assembly and disassembly hypergraphs. Denote by \(V = \{1, 2, \ldots, S\}\) the species pool and by \(2^V\) its power set (that is, the collection of all subsets of \(V\)). We adopt as convention that sets do not contain repeated elements. Given a species collection \(\Sigma \subseteq 2^V\), we assume its coexistence is a dichotomy. Thus, we formalize species coexistence as a function \(c : 2^V \to \{0, 1\}\). For any species collection \(\Sigma \subseteq 2^V\), we interpret the condition \(c(\Sigma) = 1\) as 'species in \(\Sigma\) coexist' and \(c(\Sigma) = 0\) as 'species in \(\Sigma\) do not coexist'. If \(\Sigma\) contains a single species, coexistence is interpreted as surviving in isolation. For mathematical completeness, for the empty set \(\emptyset \subseteq 2^V\), we define \(c(\emptyset) = 0\).

To describe species coexistence in an ecological system, we need to encode all coexistence relationships that one species has with any other species collection. These relationships can be encoded using a hypergraph (Supplementary Note 1).

Specifically, the assembly hypergraph \(H = (V, H)\) captures all coexistence relationships, where \(V\) is its vertex set and \(H \subseteq 2^V\) is its hyperedges given by:

\[
H := \{\Sigma \subseteq 2^V | c(\Sigma) = 1\}.
\]

Note that in this hypergraph, a successful assembly process adding one species at a time consists of moving from an initial hyperedge of dimension \(d\) (representing an initial species collection that coexists) to some adjacent hyperedge of dimension \(d + 1\) (for example, moving from \(\{1\}\) to \(\{1, 2\}\) in Fig. 1a).

Next, we introduce the notion of disassembly hypergraph \(D(H)\). For a hypergraph \(H\), denote by \(K(H) = \{c | V \not\in c \text{ for some } c \in H\}\) the minimal simplicial complex containing it. Recall that a simplicial complex is a hypergraph \(H\) such that if \(h \in H\) is a hyperedge then \(\forall c \in H\) for all \(c < h\). In words, in a simplicial complex, each hyperedge contains all of its boundaries. Define the missing boundary of a hypergraph \(H\) as \(M(H) = K(H)\). Then, the disassembly hypergraph \(D(H)\) of the hypergraph \(H = (V, H)\) is \(D(V, D(H))\), where:

\[
D(H) = M(H) \cup \{h \in H \text{ such that cardinality } (h) = 1\}.
\]

Assembly holes in Tilman’s consumer–resource model. This classic model considers \(S\) species indirectly interacting by consuming \(M\) resources that are supplied to the system\(^7\). Denoting by \(x_i(h)\) and \(f_i(h)\) the abundance of the \(i\)th species and \(j\)th resource at time \(t\) \(\geq 0\), the model takes the form:

\[
x_i = x_i \{f_i(R_1, \ldots, R_M) - m_i\}, \quad i = 1, \ldots, S,
\]

\[
R_j = (R_j^0 - R_j) - \sum_{k \in S} h_{jk} x_k f_k(R_1, \ldots, R_M), \quad j = 1, \ldots, M.
\]

Above, the symbol \(\cdot\) denotes a derivative with respect to time. The parameters for some models are the mortality rate \(m_i > 0\) of the \(i\)th species, the functional relationship \(f_j : \mathbb{R}^M \to \mathbb{R}\) between the availability of resources and the per-capita growth rate of species \(i\), the supply rate \(R_j^0 \geq 0\) of the \(j\)th resource and the impact vector \(h_i = (h_{i1}, \ldots, h_{iM})\) of the \(i\)th species (with \(h_{ij} \geq 0\) describing the amount of resource \(j\) required to produce an individual of species \(i\)). The impact matrix is \(H = (h_{ij}) \in \mathbb{R}^{S \times M}\). Recall that, in this model, a feasible interior equilibrium exists for some species collection only if the supply rate \(R^* = (R_1^*, \ldots, R_M^*)\) lies in the cone spanned by their impact vectors\(^7\). If a feasible equilibrium exists, the species collection coexists if such equilibrium is stable.

For our analysis, we studied \(S = 3\) species, \(M = 2\) resources and three different forms in which species compete for resources. First, in the system of Fig. 2a,b, both resources are essential for the three species (that is, the species' reproductive rate is zero if any resource is absent). This is modelled using:

\[
f_j(R_1, R_2) = \min \left( \mu_j, \frac{R_1}{R_1 + K} , \frac{R_2}{R_2 + K} \right)
\]

and the impact matrix:

\[
H = \begin{pmatrix}
2.49771 & 0.889986 & 1.959 \\
2.04922 & 3.22467 & 2.46907
\end{pmatrix}
\]

We use the parameters \(K = 1\), \(m_i = 0.15\), \(m_3 = 0.6\), \(m_3 = 0.08\), \(\mu_2 = 0.5\), \(\mu_1 = 2.5\) and \(\mu_1 = 1\) and the supply rate \(R^* = (0.6, 0.8)\). The bottom panel of Fig. 2a displays the zero net growth isoclines (ZNGLs) in the resource plane where the species' population does not change. The species collection \(\{1, 2\}\) coexists since it has a feasible equilibrium (the supply rate is the cone spanned by the impact vectors). Furthermore, this equilibrium is stable (Supplementary Fig. 1a). The ZNGL for species 3 is below the ZNGLs of the other two species, indicating that species 3 is competitively superior and it cannot coexist with the other two species. Therefore, the assembly hypergraph has two zero-dimensional assembly holes represented by two connected components (Fig 2b). More broadly, for essential resources, we find that at most one pair of species will coexist, even if the ZNGL of species 3 intersects the ZNGLs of species 1 and 2. Hence, the assembly hypergraph of the system always contains at least two zero-dimensional holes. Note that zero-dimensional assembly holes characterize groups where species coexist with some species of the same group, but they do not coexist with any species of other groups.

Second, in the system of Fig. 2c,d, resources are essential for species 1 and 2 but complementary for species 2 (that is, species 2 has a positive reproductive rate even if one resource is absent). Specifically, we keep the same \(f_j(R_1, R_2)\) and \(f_j(R_1, R_2)\) as in the first system, but for species 2 we use:

\[
f_j(R_1, R_2) = \frac{R_1}{R_1 + K} + 0.8 \frac{R_2}{R_2 + K},
\]

with \(K = 1\). The impact matrix is chosen as:

\[
H = \begin{pmatrix}
1.49084 & 1.63284 & 0.531918 \\
0.96024 & 0.35632 & 1.69407
\end{pmatrix}
\]

and the supply rates are \(R^* = (0.9, 0.7)\). Geometrically, these choices result in a curved ZNGL for species 2 that intersects the ZNGLs of the other two species (bottom panel of Fig. 2c). For this particular example, a feasible equilibrium...
exists for all pairs of species. However, only two of these three equilibria are stable (Supplementary Fig. 1b). Consequently, the assembly hypergraph looks like a broken triangle and consists of one connected component (Fig. 3d).

Finally, in the system of Fig. 2e, species 1, species 2 consumes both resources in a complementary way and species 3 consumes only resource 2. We model this case using:

\[ f_1(R_1, R_2) = 0.5 \frac{R_1}{R_1 + K}, \quad f_2(R_1, R_2) = \frac{R_1}{R_1 + R_2 + K}. \]

In this sense, resource 1 is essential for species 1 and resource 2 is essential for species 3. Furthermore, we assume that species 2 consumes both resources, and that for this species both resources are complementary:

\[ f_2(R_1, R_2) = \frac{R_1}{R_1 + K} + \frac{R_2}{R_2 + K}. \]

For the results of the text, we choose \( K = 1 \) and the mortality rates \( m_1 = 0.15, m_2 = 0.4 \) and \( m_3 = 0.3 \). The impact matrix is:

\[ H = \begin{bmatrix} 3.93957 & 1.0809 & 0 \\ 0 & 0.86745 & 3.33962 \end{bmatrix}. \]

The supply rate is \( R^T = (0.8, 0.8) \). Under these conditions, a stable interior equilibrium exists for all pairs of species (Supplementary Fig. 1c). However, since the triangle's interior cannot be realized due to the limits of coexistence, the assembly hypergraph has one one-dimensional assembly hole (Fig. 2f).

Disassembly holes in classic models of mutualism and cyclic competition. We study disassembly holes in a classic phenomenological model of mutualism for \( S = 2 \) species\(^1\). Denoting by \( x_i(t) \) the abundance of the \( i \)-th species at time \( t \), the model takes the form:

\[ \dot{x}_1 = x_1 \left( r_1 - \frac{r_1}{a_1 x_2} x_1 \right), \]
\[ \dot{x}_2 = x_2 \left( r_2 - \frac{r_2}{a_2 x_1} x_2 \right), \]

with \( r_i > 0 \) the intrinsic growth rate of species \( i \) and \( K(xc) = k_0 \left( 1 - \exp \left( -\frac{x}{a_i} \right) \right) \). The mutualistic interaction strength of species 2 on species 1 (respectively species 1 on species 2) is described by the parameter \( a_1 > 0 \) (respectively \( b_1 > 0 \)) (see Fig. 2g). In this model, species cannot survive in isolation, but the two species can coexist if the mutualistic interaction strengths are large enough (\( a_1 b_1 > 1 \)). The parameter plane \((a, b)\) has an obligate mutualism region where both species coexist (bottom panel of Fig. 2g). In this region, the coexistence hypergraph is \( H = \{ [1, 2], [2, 1] \} \) producing a disassembly hypergraph \( D = \{ [1, 2], [2, 1] \} \) with two zero-dimensional disassembly holes (Fig. 2h). Higher-dimensional disassembly holes can appear in systems involving many species that coexist through obligate mutualism only. For the results presented in the main text, we choose \( r_i = r, a_1 = 1 \) and \( k_0 = 1 \).

We also study disassembly holes in the May–Leonard classic model of cyclic competition between \( S = 3 \) species\(^1\). In this model, species directly compete with each other according to the Lotka–Volterra equations with the interaction matrix shown in Fig. 2i and equations given by:

\[ \dot{x}_1 = x_1 \left( r_1 - x_1 - \frac{r_1}{a_1 x_2} x_1 \right), \]
\[ \dot{x}_2 = x_2 \left( r_2 - \frac{r_2}{a_2 x_1} x_2 - \frac{r_2}{a_2 x_3} x_2 \right), \]
\[ \dot{x}_3 = x_3 \left( r_3 - \frac{r_3}{a_3 x_1} x_3 - \frac{r_3}{a_3 x_2} x_3 \right). \]

The parameters \( a_i > 0 \) and \( \beta > 0 \) describe the competitive strength between species. Species always survive in isolation, but their coexistence in pairs and the trio depend on the competition parameters (bottom panel of Fig. 2j). When the competition parameters are asymmetrical, only isolated species and the trio of species coexist, producing one one-dimensional disassembly hole (Fig. 2j).

A homology theory for hypergraphs. Here, we present a summary of our methods, referring to the Supplementary Notes for details and examples. Our formalism considers arbitrary hypergraphs \( H \) over the set of vertices \( V = \{1, 2, \ldots, S\} \). By construction, hypergraphs are combinatoric objects (that is, collections of subsets of \( V \)). To study their structure, and in particular to identify their holes, we need to endow hypergraphs with the structure of a topological space. We do this as usual by embedding the hypergraph into an \( S \)-dimensional Euclidean space \( \mathbb{R}^S \). First, we associate to each vertex \( v \in V \) the \( v \)-th unit vector of \( \mathbb{R}^S \). Second, a hyperedge \( h \in H \) is associated to the relative interior of the simplex spanned by the unit vectors associated to the vertices it contains—a process we denote as relint(h). In this form, the embedding or geometric realization \( |H| \subseteq \mathbb{R}^S \) of the hypergraph \( H \) is:

\[ |H| := \bigcup_{h \in H} \text{relint}(h). \]

Note that the location of the vertices in the space is arbitrary. Therefore, we focus only on the topological properties of the geometric realization of hypergraphs—that is, properties that remain invariant when the geometric realization of a hypergraph is transformed without gluing or cutting it (that is, invariant to homeomorphisms).

Since in principle the dimension \( S \) can be arbitrarily large, we study the topological properties of hypergraphs using algebraic topology. From a mathematical viewpoint, analysing the topological space generated by the geometric realization of a hypergraph is difficult because it is neither open nor closed in \( \mathbb{R}^S \). Specifically, calculating the holes of \( |H| \) requires using the notion of singular homology, which is in general very challenging to calculate. Indeed, there only exists a mature theory with efficient algorithms to analyse the topological properties of the special class of hypergraphs known as simplicial complexes—hypergraphs where each hyperedge contains all of its boundaries\(^2\). To the best of our knowledge, there is no efficient algorithm to calculate the homology (Betti numbers) for arbitrary hypergraphs.

To circumvent the above challenge, we built a homology theory for hypergraphs analogous to that for simplicial complexes. We build our homology by imagining we explode the hypergraph into its hyperedges (see illustration of Supplementary Fig. 1b,c). We will now connect back these hyperedges ensuring that we keep the original structure of the hypergraph. To characterize those connections that are allowed, we define the notion of \( k \)-simplex:

**Definition 1.** A \( k \)-simplex \( \sigma \) of a hypergraph \( H \) is a collection \( \sigma = \{ (i_1, i_2, \ldots, i_k) \} \) of \( k \)-dimensional hyperedges \( h_i \in H \) such that \( h_i \subseteq h_j \) for all \( i \). We can put together connections between groups of \( k \)-hyperedges by adding together different \( k \)-simplices. This idea is formalized in the notion of a \( k \)-chain of the hypergraph. A \( k \)-chain is the formal sum

\[ c = \sum_q n_q \sigma_q, \]

where each \( \sigma_q \) is a \( k \)-simplex of \( H \), and the coefficients satisfy \( n_q \in [0, 1) \) with addition defined modulo 2 (that is, \( 1 + 1 = 0 \)). In words, a modulo 2 sum means that repeated hyperedges cancel each other out. From the above definition, we can construct the \( k \)-th chain group of the hypergraph \( H \) denoted by \( C_k(H, \mathbb{Z}) \). This is the group of all \( k \)-chains, with \(' + \)' denoting addition modulo 2.

The final notion that we need is that of boundary, defined as follows:

**Definition 2.** The boundary of a \( k \)-simplex \( \sigma = \{ (i_1, i_2, \ldots, i_k) \} \) of \( H \) is the \((k-1)\)-th chain

\[ \partial_k \sigma = \sum_{q=1}^{k+1} \sigma \setminus h_q = \sum_{q=1}^{k+1} \{ h_1, h_2, \ldots, h_{k+1} \} \setminus h_q, \quad k \geq 0. \]

Note that this definition is not unique and that different cycles may encircle the same hole. Therefore, to count the number of different holes using cycles, it is necessary to construct an equivalence class of cycles encircling the same hole. These ideas are made operable by characterizing two key subgroups of the \( k \)-th chain group \( C_k(H) \) of a hypergraph \( H \):

**Definition 3.**

1. The \( k \)-th boundary group \( B_k \) is:

\[ B_k = \text{im} \partial_{k+1} := \{ c \in C_{k+1} \mid 3d \in C_{k+1} \text{ such that } c = \partial_{k+1} d \}. \]

A chain \( c \in B_k \) is the boundary of some higher-dimensional chain \( d \in C_{k+1} \). Therefore, such a \( k \)-chain \( c \) is a \( k \)-boundary or a bounding cycle. Cycles that are not in \( B_k \) are non-bounding cycles. Therefore, bounding cycles bound higher-dimensional chains so that they are filled cycles. Non-bounding cycles are empty cycles.

It turns out that both subgroups \( Z_k \) and \( B_k \) are normal (because they are abelian), allowing the construction of quotient spaces. To illustrate the implications of this fact, consider the hypergraph of Supplementary Fig. 1b. Let \( B \subseteq B_1 \) and...
Articles

Our homology theory for defining assembly and disassembly holes.

Definition of assembly and disassembly holes. Our homology theory for hypergraphs allows us to rigorously define assembly and disassembly holes as follows. Let \( H(\mathcal{D}) \) denote the hypergraph and \( \mathcal{D} \) the assembly graph of the assembly and disassembly hypergraph, respectively. Then, a \( k \)-dimensional assembly is a chain \( c \in \mathcal{H}(\mathcal{D}) \), and a \( k \)-dimensional disassembly hole is a chain \( c \in \mathcal{H}(\mathcal{D}) \).

Identifying coexistence holes by computing Betti numbers. To efficiently calculate the Betti numbers, we showed that they can be calculated by first building an inclusion graph between the hyperedges of the hypergraph and then measuring the Betti numbers of hyperedges. We proved that the constructed homology exactly captures all holes of the geometric realization of a hypergraph.

Definition of assembly and disassembly holes. Our homology theory for hypergraphs allows us to rigorously define assembly and disassembly holes as follows. Let \( H(\mathcal{D}) \) denote the hypergraph and \( \mathcal{D} \) the assembly graph of the assembly and disassembly hypergraph, respectively. Then, a \( k \)-dimensional assembly is a chain \( c \in \mathcal{H}(\mathcal{D}) \), and a \( k \)-dimensional disassembly hole is a chain \( c \in \mathcal{H}(\mathcal{D}) \).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All of the data analysed in this study are publicly available.

Code availability

The code supporting the results is archived in the GitHub repository at https://syntheticdynamics.github.io/CoexistenceHoles.jl.

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References

1. Fukami, T. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annu. Rev. Ecol. Evol. Syst. 46, 1–23 (2015).
2. Tylianakis, J. M., Martinez-Garcia, L. B., Richardson, S. J., Pelzler, D. A. & Dicke, I. A. Symmetric assembly and disassembly processes in an ecological network. Ecol. Lett. 21, 896–904 (2018).
3. Checchi, J. M., Blows, S. A., Wright, T. M., Gerstein, K. & May, F. Ecosystem decay outperforms biodeterioration loss with habitat loss. Nature 584, 238–243 (2020).
4. Vellend, M. The Theory of Ecological Communities (MPB-57) (Princeton Univ. Press, 2016).
5. Hutchinson, G. E. Homage to Santa Rosalia or why there are so many kinds of animals? Am. Nat. 93, 145–159 (1959).
6. Tilman, D. Resource Competition and Community Structure (Princeton Univ. Press, 1982).
7. Barbier, M., Arnoldi, J.-F., Bunin, G. & Loreau, M. Generic assembly patterns in complex ecological communities. Proc. Natl Acad. Sci. USA 115, 2156–2161 (2018).
8. Serván, C. A., Capitán, J. A., Grilli, J., Morrison, K. E. & Allesina, S. Coexistence of many species in random ecosystems. Nat. Ecol. Evol. 2, 1237–1248 (2018).
9. MacArthur, R. Species packing and competitive equilibrium for many species. Theor. Popul. Biol. 1, 1–11 (1970).
10. Medeiros, L. P., Boege, K., del Val, E., Zaldívar-Riverón, A. & Saavedra, V. Observed ecological communities are formed by species combinations that are among the most likely to persist under changing environments. Anm. Nat. https://doi.org/10.1086/711663 (2020).
11. Barabási, A.-L. & Stumpf, M. M. Chesson’s coexistence theory. Ecol. Monogr. 88, 277–303 (2018).
12. Grainger, T. N. & Gilbert, J. M. L. B. The invasion criterion: a common currency for ecological research. Trends Ecol. Evol. 34, 925–935 (2019).
13. Alberch, P. The logic of monsters: evidence for internal constraint in development and evolution. Geobios 22, 21–57 (1989).
14. Clements, F. E. Nature and structure of the climax. J. Ecol. 24, 252–284 (1936).
15. Odum, E. P. & Barrett, G. W. Fundamentals of Ecology 5th edn (Thomson Brooks/Cole, 2005).

confirmation of the ecological system’s capacity to maintain species diversity in the face of changing environmental conditions. This hypothesis is tested in dynamical systems theory to confirm the conditions under which species diversity can be maintained. The results of these simulations indicate that the Lotka–Volterra model provides a robust framework for predicting the outcomes of species interactions in complex ecological systems. This model can be used to understand the dynamics of species diversity in ecosystems and to design strategies for conservation and management.
16. Friedman, J., Higgins, L. M. & Gore, J. Community structure follows simple assembly rules in microbial microcosms. Nat. Ecol. Evol. 1, 0109 (2017).
17. Chesson, P. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Evol. Syst. 31, 343–366 (2000).
18. Drake, J. A. Community-assembly mechanics and the structure of an experimental species ensemble. Am. Nat. 137, 1–26 (1991).
19. Warren, P. H., Law, R. & Weatherly, A. J. Mapping the assembly of protist communities in microcosms. Ecology 84, 1001–1011 (2003).
20. Bucci, V. et al. MDSINE: Microbial Dynamical Systems Inference Engine for ecology. Nat. Commun. 8, 2042 (2017).
21. Case, T. J. & Leibold, M. A. Simple model of mutualism. Evol. Popul. Biol. 8, 762–775 (1996).
22. Stein, R. R. et al. Ecological modeling from time-series inference: insight into interspecific interactions from experiments with perennial crop mixtures to predict optimal combinations. Ecol. Appl. 27, 2277–2289 (2017).
23. Chase, J. M. & Leibold, M. A. Contemporary Approaches to Ecological Communities. Springer, 105 (2003).
24. Dean, A. M. A simple model of mutualism. Am. Nat. 116, 362–393 (1981).
25. May, R. M. & Leonard, W. J. Nonlinear aspects of competition between three species. SIAM J. Appl. Math. 29, 243–253 (1975).
26. Assaf, A. K. and Allesina, S. Tractable models of ecological assembly. Nat. Commun. 10, 349–358 (2019).
27. Allesina, S. & Tang, S. The stability–complexity relationship at age 40: a reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity. Theor. Popul. Biol. 13, 244–267 (1978).
28. Saavedra, S. et al. A structural approach for understanding multispecies diversity in a model ecosystem. Phys. Rev. Lett. 118, 028103 (2017).
29. Broadley, M. E., Aerts, J. & Verheyen, K. Plants, soils and sustainability: an interdisciplinary perspective. Trends Ecol. Evol. 35, 384–396 (2020).
30. Sugihara, G. Graph theory, homology and food webs. In Proc. Symposia in Applied Mathematics 30, 83–101 (American Mathematical Society, 1984).
31. Law, R. & Morton, R. D. Permanence and the assembly of ecological communities. J. R. Soc. Interface 14, 20160966 (2020).
32. Turelli, M. A reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity. Theor. Popul. Biol. 13, 244–267 (1978).
33. Case, T. J. & Leibold, M. A. Simple model of mutualism. Am. Nat. 116, 362–393 (1981).
34. Law, R. & Blackford, J. C. Self-assembling food webs: a global viewpoint of coexistence of species in Lotka–Volterra communities. Ecology 73, 567–578 (1992).
35. Allesina, S. & Tang, S. The stability–complexity relationship at age 40: a reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity. Theor. Popul. Biol. 13, 244–267 (1978).
36. Posfai, A., Taillefumer, T. & Wingreen, N. S. Metabolic trade-offs promote diversity in a model ecosystem. Phys. Rev. Lett. 118, 028103 (2017).
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