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Benefit Transfer Loops Turn Cheating into a Scaffold for Microbial Diversity

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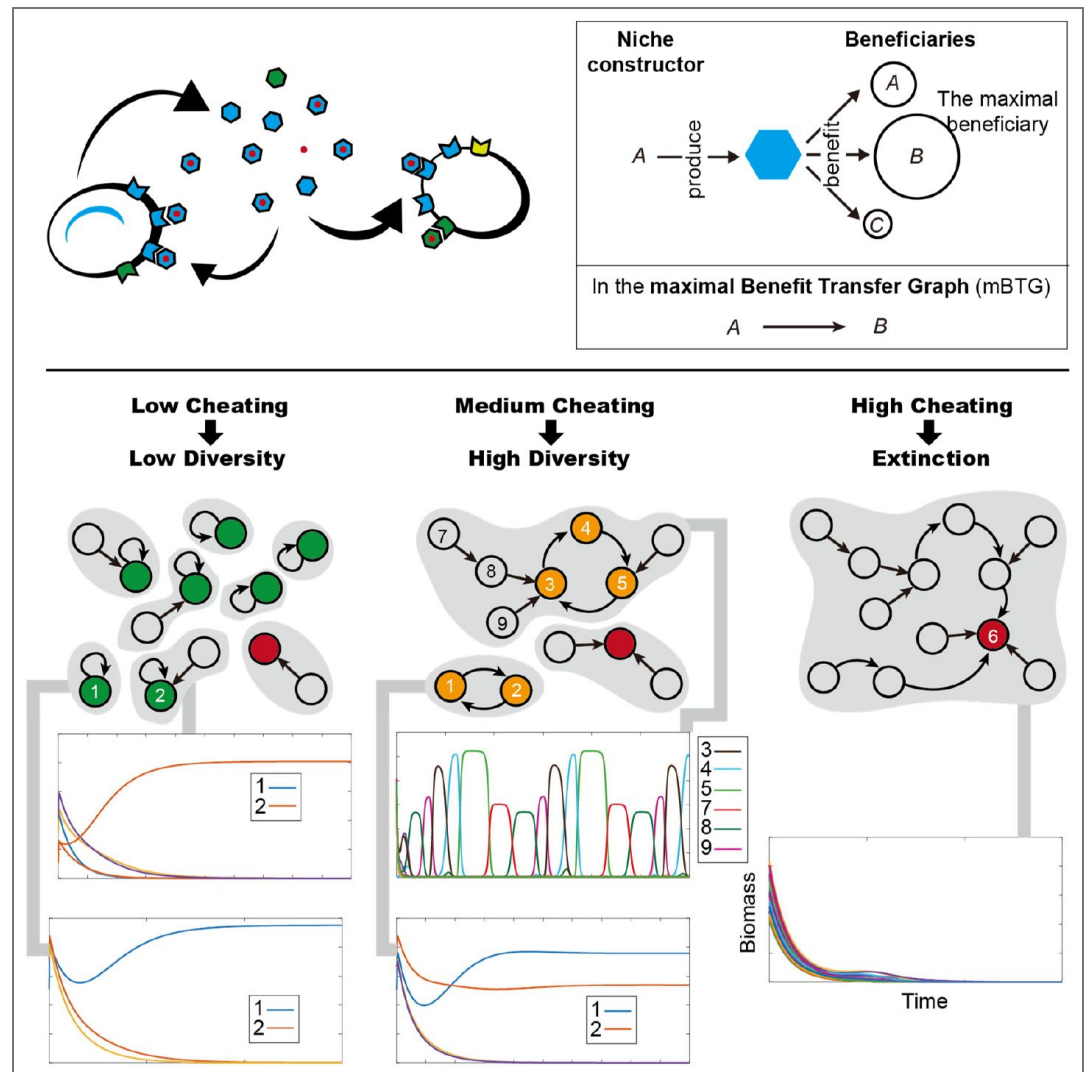
This manuscript provides a **valuable** perspective on microbial community diversity and how this is shaped by the presence of cheaters. The evidence provided is **solid**, and the methods used to assess the research question are **convincing**. However, a major weakness is the general framing (or lack of embedding in recent literature), reducing the usefulness of the paper for a broad audience.

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Abstract

Niche construction drives ecological dynamics, yet the tragedy of the commons predicts that non-contributing cheaters will undermine cooperation. Here, we studied microbial iron competition by combining dynamic modeling with benefit flow graphs, demonstrating that moderate cheating is not merely tolerated but essential for diversity. In small communities, mutual exploitation forms closed loops enabling steady or dynamic coexistence. In larger communities, we uncovered a paradox: increasing cheating breadth promotes community-level extinction, yet fosters higher biodiversity in surviving communities. We resolve this paradox by mapping ecological dynamics onto the topology of the “Maximal Benefit Transfer Graph”, which predicts community fate through its core structure. Broad cheating eliminates the self-loop core that drives competitive exclusion, but increases “terminator” sinks that cause collapse. However, when communities avoid these sinks, cheating aggregates the network and generates cyclic loops to enable coexistence. Thus, structured exploitation acts not as destabilizing vulnerability but as necessary architecture for biodiversity.

Graphical Abstract



How does ‘cheating’ affect microbial biodiversity? By mapping the strongest benefit flows between species, we discovered a topological rule for survival. While too much cheating creates dead-ends that crash the system, moderate cheating connects species into self-sustaining loops. These “exploitation cycles” act as a scaffold, supporting high diversity and complex population.

Introduction

Niche construction drives ecological dynamics[1], yet the “tragedy of the commons” predicts that non-contributing cheaters should undermine cooperative systems[2]. Microbial siderophores represent a classic model of this dilemma: microbes secrete costly iron-scavenging molecules as public goods, which are then uptaken via specific membrane receptors[3]. While functionally straightforward, siderophore systems display remarkable complexity stemming from two key features[4]: (1) extraordinary chemical diversity comprising at least a thousand structures[5]; and (2) high receptor specificity, creating “lock-and-key” patterns where receptors bind only specific siderophore subsets[6]. This specificity generates a rich ecological landscape where microbes possessing matching receptors can exploit “foreign” siderophores[7], forging intricate networks of competition, cooperation, and cheating[8].

This complexity makes siderophore-mediated interactions an ideal system for addressing a central puzzle in ecological theory: how does biodiversity persist in the face of cheating[9-11]? Classical theory suggests cheaters should outcompete producers, yet producers and cheaters coexist

broadly in nature [12]. Observations in the *Pseudomonas* genus further complicate this picture: while pathogenic strains often exhibit extreme strategies with isolated iron-interaction networks, more diverse environmental isolates likely to adopt “partial-producers” strategies that producing siderophores while cheating on others [6]. A fundamental challenge lies in bridging scales: how do fine-grained molecular attributes, including structural diversity and receptor specificity, give rise to macro-scale ecological patterns? While previous studies have explored siderophore dynamics in biofilms or pairwise competitions [13, 14], they often overlook the emergent properties of networks formed by multiple siderophore types [15–17]. Understanding how biodiversity persists in complex communities requires bridging the gap between molecular-level interaction networks and emergent ecosystem dynamics [18].

Here, we develop a general theoretical framework that integrates consumer-resource dynamics with graph-theoretic representation of benefit flows, to systematically address these questions. Through simulations and analytical derivations, we prove that cheating is actually required for stable and oscillatory coexistence in small communities. In large communities, we uncover a paradox: increasing the breadth of cheating heightens the risk of community-level extinction, yet fosters higher biodiversity within surviving communities. By mapping ecological dynamics onto a “maximal Benefit Transfer Graph,” we identify the graph’s core structure as a powerful predictor of ecological outcomes, explaining cheating’s paradoxical role: Increased cheating pervasiveness connects species through network percolation, simultaneously expanding the “terminator” core driving extinction and the cyclic core enabling coexistence. Thus, our findings reveal a universal topological rule: structured exploitation acts not as a destabilizing vulnerability but as a necessary architecture for diversity. This principle extends beyond iron competition to broadly explain persistence in systems governed by directed benefit transfers, from extracellular enzyme hydrolysis to complex metabolic cross-feeding networks.

Results

A Generalized Framework for Siderophore-mediated Interactions

To link molecular specificity with ecological dynamics, we developed an integrated framework coupling dynamic modeling with network topology (Fig. 1 [↗](#), SI Appendix, Section 1 [↗](#)). Our dynamic model extends classical chemostat equations by incorporating diverse siderophore-receptor pairs, where growth depends on both iron uptake and primary metabolism (Fig. 1A [↗](#)). The model incorporates two key biological constraints: (1) a metabolic trade-off (parameter α), where species i allocate limited resources between growth (α_{i0}) and siderophore production (α_{ij} for siderophore type j , under the constrain $\alpha_{i0} + \sum_{j=1}^{N_{\text{sid}}} \alpha_{ij} = 1$); and (2) a receptor profile (parameter v), which dictates the specificity of iron uptake (v_{ij} represents the fraction of receptors dedicated to siderophore type j in species i , under the constrain $\sum_{j=1}^{N_{\text{sid}}} v_{ij} = 1$).

The dynamic model tracks three sets of variables: (1) Microbial biomass concentration M_i for each species $i = 1, 2, \dots, N_{\text{spe}}$; (2) concentrations of each siderophore type R_j ($j = 1, 2, \dots, N_{\text{sid}}$); (3) Free iron concentration R_{iron} :

$$\frac{dM_i}{dt} = M_i \cdot \left(\gamma \cdot \alpha_{i0} \cdot \sum_j v_{ij} \cdot J_j - d \right) + \sigma, \quad (1)$$

where $i = 1, \dots, N_{\text{spe}}$.

$$\frac{dR_j}{dt} = \sum_i M_i \cdot \alpha_{ij} \cdot \epsilon_j - d \cdot R_j, \quad \text{where } j = 1, \dots, N_{\text{sid}}. \quad (2)$$

$$\frac{dR_{\text{iron}}}{dt} = d \cdot (R_{\text{supply}} - R_{\text{iron}}) - \sum_{i,j} M_i \cdot v_{ij} \cdot J_j. \quad (3)$$

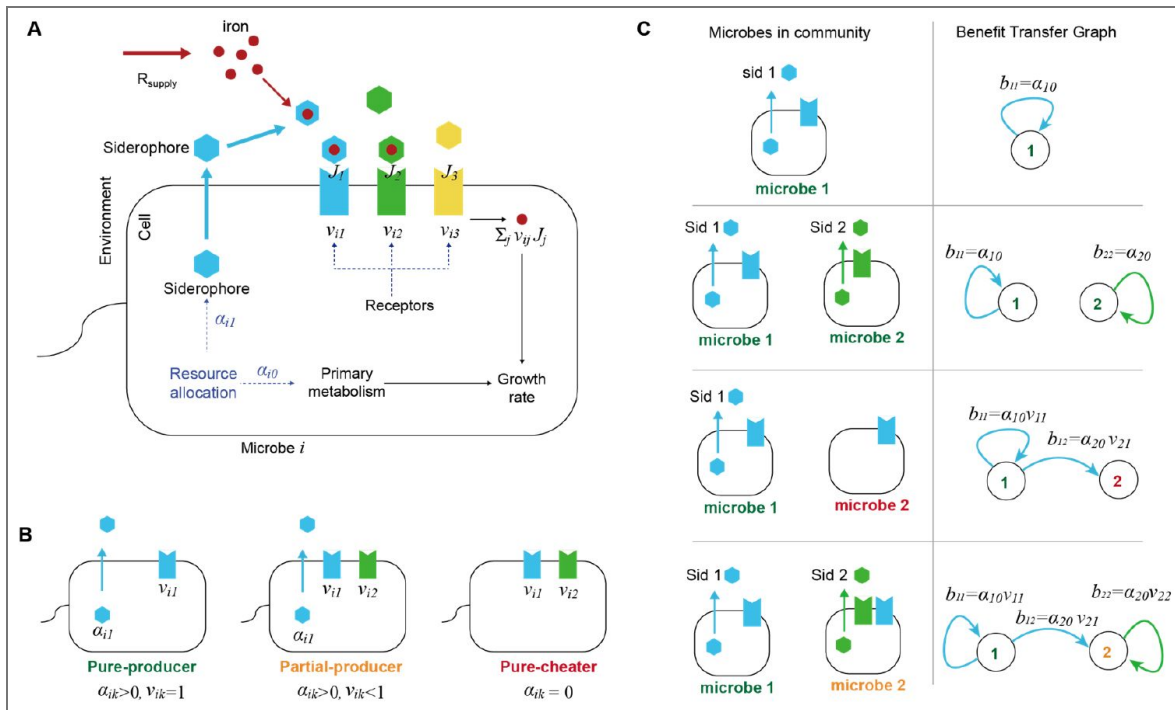


Figure 1. Framework for modeling siderophore-mediated interaction and benefit transfer in microbial communities.

(A) Overview of the siderophore-mediated iron uptake. Microbes allocate internal resources between growth (α_{i0}) and the production of siderophores (α_{ij} for $j > 0$). Secreted siderophores form siderophore-iron complexes, which are taken up via type-specific receptors with allocation fractions v_{ij} . Different types of siderophores with their matching receptors are distinguished by colors. (B) Microbial iron-scavenging strategies. Microbes are categorized into three major classes by siderophore production and uptake patterns: (i) “Pure-producers,” which produce and exclusively utilize their own siderophores; (ii) “Partial-producers,” which produce/utilize their own siderophores and also exploit foreign siderophores; (iii) “Pure-cheaters,” which rely entirely on siderophores produced by others. (C) Benefit Transfer Graph (BTG). Left panels illustrate example siderophore-mediated interactions; right panels show their BTG representations: Nodes denote species, and directed edges represent benefit transfer from siderophore producers to beneficiaries. Edge colors correspond to siderophore types.

Varying parameters α and v generates a continuum of strategies, from “pure-producers” (exclusively utilizing their own siderophores) to “pure-cheaters” (no production) and “partial producers” (producing one siderophore while exploiting several other types) (Fig. 1B [↗](#)).

Crucially, we mapped these biochemical interactions onto a “Benefit Transfer Graph” (BTG) to quantify ecological dependencies (Fig. 1C [↗](#)). In this directed graph, nodes represent species, and edges represent the flow of growth benefits from a siderophore producer to its beneficiaries. An edge exists if a species possesses receptors matching another’s siderophore, with the weight $b_{m1,m2}$ quantifying the specific growth gain species $m2$ derives from species $m1$ ’s production:

$$b_{m1,m2} = \begin{cases} 0, & \text{if } \alpha_{m1,j} = 0 \text{ for all } j \\ \alpha_{m2,0} \cdot v_{m2,j}, & \text{if } \alpha_{m1,j} > 0 \end{cases} \quad (4)$$

This abstraction allows us to translate complex kinetic systems into topological structures, analyzing how benefit transfers drive community assembly.

Closed Benefit Loops Drive Transitions from Exclusion to Coexistence and Chaos

We first analyzed minimal community motifs to dissect the topological rules of coexistence. In single-species systems with only one producer (Fig. 2A [↗](#)), the Benefit Transfer Graph only consists of self-loops. Dynamic modeling reveals that siderophore-mediated positive feedback creates an Allee effect [19], leading to bistability where survival depends on initial biomass thresholds (Fig. 2B [↗](#); SI Appendix, Section 2 [↗](#)). Consequently, when two pure-producers compete, they are driven to competitive exclusion: either one species becomes completely dominant, or the system exhibits priority effects in which the final winner is determined by who is initially more abundant (SI Appendix, Section 3 [↗](#)).

Stable coexistence emerges only when species adopt “partial-producer” strategies, forming a closed mutual cheating loop in the BTG (Fig. 2C–D [↗](#)). Analytically, we derived that each species must deliver greater growth benefits to its competitor than to itself ($b_{2,1} > b_{2,2}$, $b_{1,2} > b_{1,1}$, SI Appendix, Section 4 [↗](#)). Strikingly, this mutual exploitation generates a synergistic rescue effect: in parameter regimes where single species would collapse, the combined siderophore pool allows the mutualistic pair to survive (Fig. 2E–G [↗](#)).

Expanding these loops to multi-species motifs identifies key topologies that enable dynamic coexistence. In three-species systems, an intransitive “rock–paper–scissors” BTG loop (Fig. 2H [↗](#)) generates sustained population oscillations (Fig. 2I [↗](#)). Bifurcation analysis demonstrates that increasing self-reliance drives a transition from oscillatory coexistence to competitive exclusion via Heteroclinic bifurcation [20], while balanced benefit flows favor stable coexistence over limit cycles (SI Appendix, Section 5 [↗](#)).

As the interaction network grows more complex, such as in five-species motifs with overlapping loops (Fig. 2J [↗](#)), coupled feedback can drive the system into deterministic chaos (Fig. 2K [↗](#)). Similarly, increasing self-reliance progressively drives transition from chaotic dynamics to stable periodic cycles and, eventually, to exclusion. Collectively, these results demonstrate that closed benefit-transfer loops serve as the structural scaffold for diversity: short mutual loops support stable coexistence, while longer cycles enable dynamic fluctuations.

The Paradox of Cheating in Large Communities

We extended our framework to complex ecosystems by simulating $1.5 \cdot 10^6$ communities ($N_{\text{spe}} = 50$) with varying “cheating breadth” (the average number of foreign siderophores a species can exploit) and fractions of “pure-cheaters” (Fig. 3A [↗](#)). Simulation outcomes reveal an unintuitive paradox. On one hand, broad cheating and high pure-cheater ratio act as destabilizing forces, monotonically increasing the probability of community-wide extinction (Fig. 3B [↗](#)).

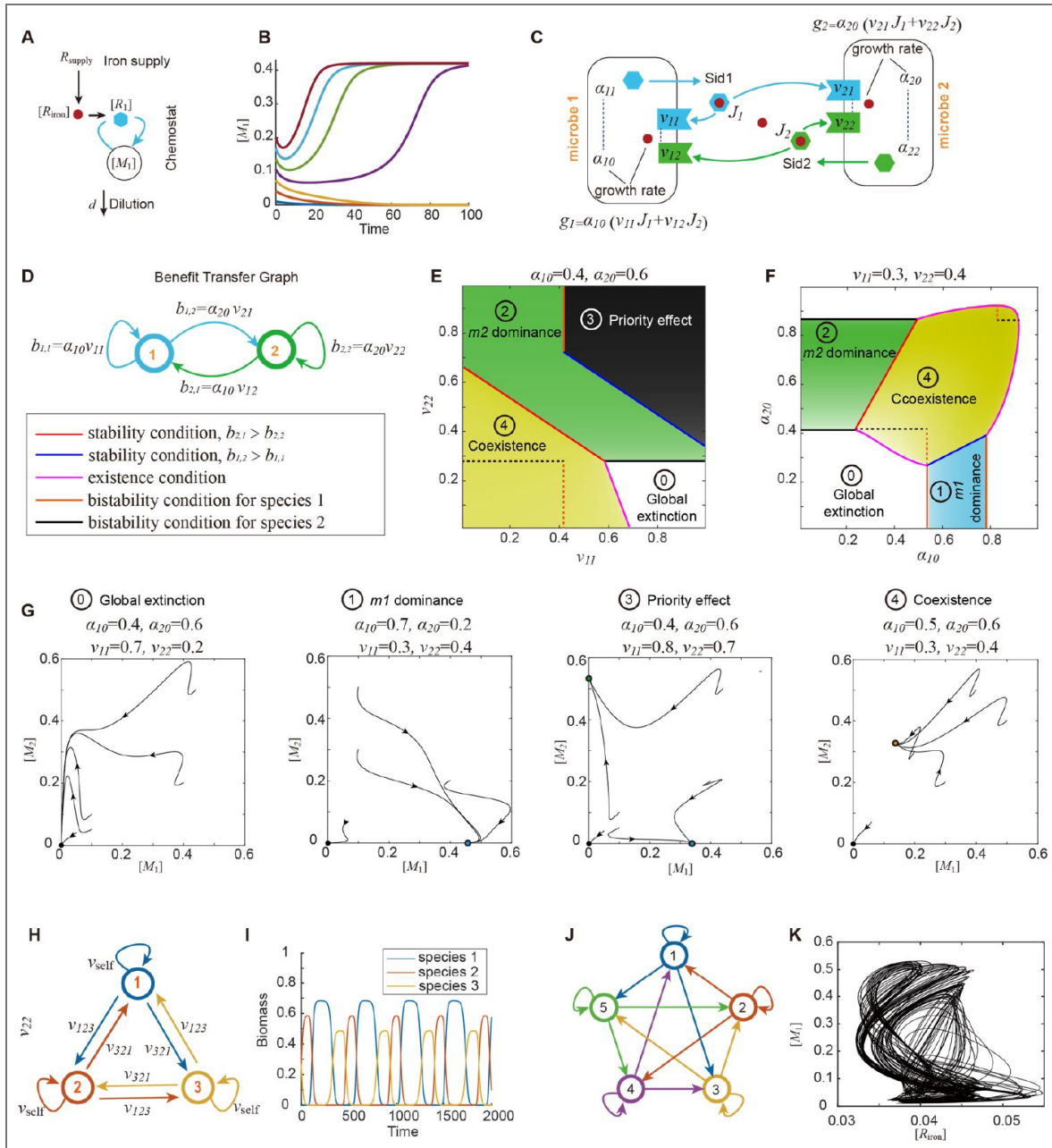


Figure 2. Rules governing siderophore-mediated iron interactions in single- and two-species models.

A. Schematic of the single-species chemostat model with iron supply R_{supply} and dilution rate d . Variables $[R_{\text{iron}}]$, $[M_1]$, $[R_1]$ denote the concentration of free iron, microbial biomass, and siderophore, respectively. B. Time courses of biomass (M_1) starting from different initial inoculations, illustrating the threshold-dependent survival. C. Schematic of a two-species system where two pure-producers compete. Each species secretes and exclusively utilizes its own siderophore type (blue for species 1, green for species 2). D. The Benefit Transfer Graph (BTG) corresponding to (C). Nodes represent species; edges represent the benefit flow. This graph features self-loops ($b_{1,1}$, $b_{2,2}$) and cross-species benefit transfers ($b_{1,2}$, $b_{2,1}$). E-F. Phase diagram spanning the receptor profile (v_{11} - v_{22} for E) and growth allocation (α_{10} - α_{20} for F). Distinct ecological outcomes are color-coded and numbered. Color intensity is proportional to the total steady-state biomass. G. Representative state-space simulation projected onto the M_1 - M_2 plane, parameters are from four different regimes in (E)-(F). Arrows denote the directionality of trajectories. Solid circles indicate stable fixed points. H. BTG of a three-species system. Blue, orange, and yellow arrows represent benefit transfers mediated by different siderophores produced by species 1, 2, and 3, respectively. Two rock-paper-scissors loops emerge: clockwise (characterized by v_{321}) and counterclockwise (characterized by v_{123}). Self-loops indicate self-utilization (v_{self}). I. Representative time courses showing sustained oscillations in the system of (H). J. BTG of a five-species system. K. State-space projection onto the R_{iron} - M_1 plane showing a chaotic trajectory.

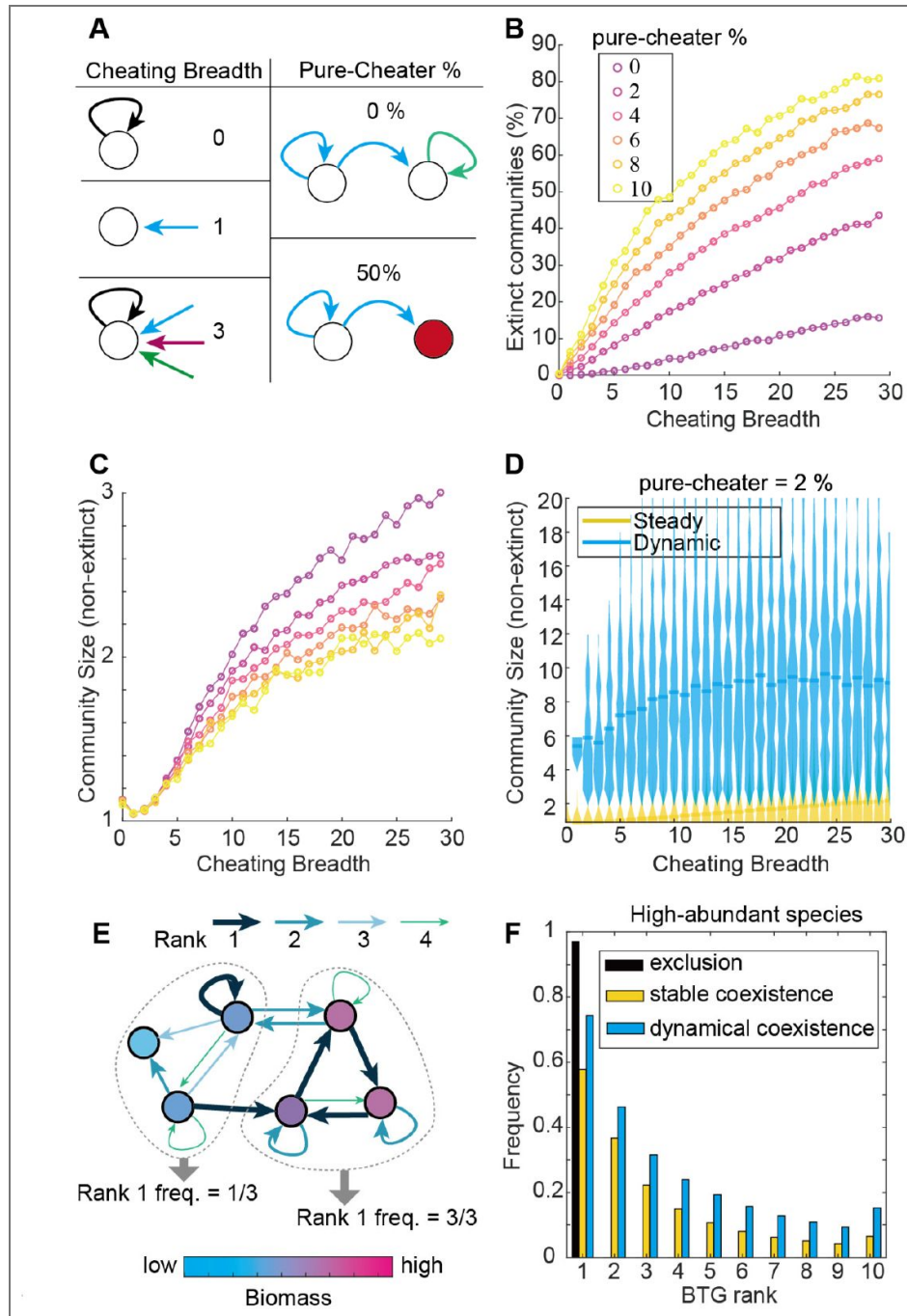


Figure 3. Cheating breadth elevates both extinction risk and community diversity

A. Definitions of cheating breadth (number of exploitable foreign siderophore types) and pure-cheater ratio. B. Probability of community-level extinction increases with both cheating breadth and pure-cheater ratio (ratio is color-coded; consistent across panels B–C). C. In non-extinct communities, species richness increases with cheating breadth but decreases with pure-cheater ratio. D. Violin plots showing non-extinct community size distributions for steady (yellow) versus dynamic (green) outcomes (pure-cheater ratio = 2%), under different cheating breadth. Dynamic communities consistently support higher biodiversity. E. Schematic illustrating edge ranking in BTGs, where edges from producers i are ranked by their weights b_{ij} . Two subgraphs formed by low-biomass species (left) and high-biomass species (right) are bracketed by dashed lines, with the relative frequency of Rank-1 incoming edges shown below. F. Rank frequency distribution of benefit transfer edges in BTGs. Top-ranked edges were enriched in subgraphs formed by high-abundance species (biomass $> 10^{-3}$)

On the other hand, within non-extinct communities (having at least one surviving species), cheating promotes biodiversity. Species richness increases monotonically with cheating breadth (Fig. 3C), and these diverse communities are more likely to exhibit dynamic behaviors (oscillations or chaos) (SI Appendix, Section 6). Notably, dynamic communities consistently support larger populations than stable ones, suggesting that temporal fluctuations create niches for species maintenance (Fig. 3D).

The paradox of cheating breadth implies that surviving communities must harbor non-random interaction structures that enable persistence. To identify these structures, we analyzed the Benefit Transfer Graph within each non-extinct community. For every siderophore producer i , we ranked all its outgoing benefit edges (b_{ij}) by magnitude, designating the single strongest flow as the “Rank-1 edge” (Fig. 3E). Notably, we found that the subgraph formed by surviving species is overwhelmingly dominated by these Rank-1 incoming edges (Fig. 3F), far exceeding their frequency in randomly assembled subgraphs (SI Appendix, Section 6). This finding suggests that community fate is not determined by average interaction strengths, but by a specific topological backbone formed by maximal benefit flows.

The Maximal Benefit Transfer Graph Resolves the Cheating Paradox

To decode the structural basis of the cheating paradox, we formalized the “Rank-1” backbone as a maximal Benefit Transfer Graph (mBTG). By retaining only the strongest outgoing benefit edge for each producer, the mBTG assumes the topology of a directed pseudoforest, a graph class where every node has at most one outgoing edge (Fig. 4A). A central feature of such graphs is their decomposition into Weakly Connected Components (WCCs), which are groups of nodes connected by paths regardless of direction. In directed pseudoforests, benefit flows within each WCC inevitably converge to a unique “Core”: the minimal subset of nodes with no outgoing edges to the rest of the graph (Fig. 4B).

We discovered that the topology of this Core serves as a potent predictor of community fate, achieving around 80% classification accuracy. Irrespective of initial conditions, asymptotic biomass consistently concentrates within a single WCC, and specifically within its core (SI Appendix, Section 7). This indicates that each WCC represents a distinct basin of attraction, with the core acting as the structural and dynamic nucleus. Characterizing these cores by their “loop length” (the number of edges forming the core) reveals three distinct architectures that dictate ecological outcomes (Fig. 4B):

1. Sink Core (Loop length 0, W_0 in Fig. 4B): A core consisting of a single pure-cheater acts as a resource “black hole,” absorbing benefits without reciprocation. This topology leads to community extinction with 97% probability.
2. Self-loop Core (Loop length 1, W_1 in Fig. 4B): A core formed by a producer benefiting maximally from itself leads to a steady state (Fig. 4C) where the core species survives alone, driving all others to exclusion (Fig. 4D).
3. Cyclic Core (Loop length ≥ 2 , W_2 and W_3 in Fig. 4B): A closed loop of two or more species supports coexistence. Notably, as the loop length reaches three, the probability of entering oscillatory or chaotic attractors increases sharply (Fig. 4C). While species richness in steady-state systems plateaus at short loop lengths, dynamic systems continuously support higher diversity (Fig. 4D). These dynamic communities often harbor twice as many total survivors (biomass $> 10^{-6}$) as high-abundance species (biomass $> 10^{-3}$), suggesting that oscillatory dynamics enable rare species to persist by intermittently accessing benefits from abundant ones (Fig. 4D).

This topological framework resolves the paradox of cheating breadth. The mBTG is composed of four functional node types, whose abundance changes by cheating breadth (Fig. 4E, SI Appendix, Section 8):

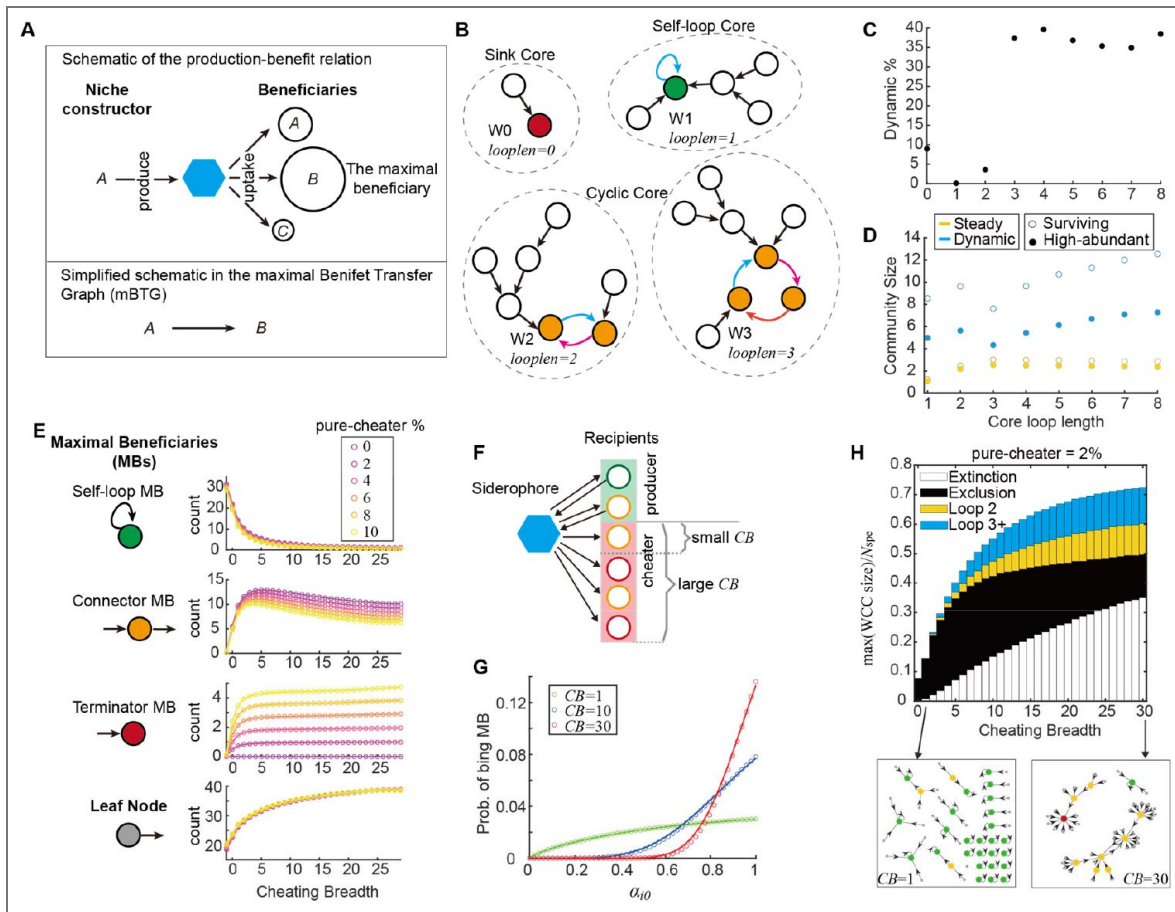


Figure 4. Core loops of the maximal Benefit Transfer Graph (mBTG) predicts community fate and resolves the cheating paradox

A. Construction of the mBTG. For each producer, the single strongest outgoing benefit flow defines the “maximal beneficiary,” forming a rank-1 directed edge. B. Topology of the mBTG decomposes into Weakly Connected Components (WCCs), each containing exactly one “Core” (colored nodes and edges). Four WCCs are separated by dashed circles. Core classes (Sink, Self-loop, Cyclic) are marked on each top. C. Scatter plots showing the probability of entering dynamic attractors leaps at core loop length of three. D. Scatter plot showing how community size increases with core loop length, for steady-state (yellow) and dynamic (blue) communities. Filled and open circles indicate high-abundance and surviving species (biomass threshold 10^{-3} and 10^{-6}), respectively. E. Node classifications in mBTG (left) and how their counts change with cheating breadth (right). Self-loop maximal beneficiaries (MBs) have edges directed to itself; Connector MBs possess both incoming and outgoing edges; Terminator MBs have only incoming edges and no outgoing edges; Leaf nodes have no incoming edges. F. Probabilistic explanation that increasing cheating breadth expands the pool of potential recipients, diluting the producer’s chance of retaining its own siderophore (Self-loop MBs decline). G. Broader cheating amplifies MB selection bias toward high- α_0 species, creating heavy-tailed in-degree distributions and promoting Terminator MBs (CB is abbreviation for cheating breadth). H. The percolation transition. The curve shows the fraction of nodes occupied by the largest WCC, which grows with cheating breadth. Colors under the curve indicate the proportion of WCCs governed by different core lengths. The system transitions from fragmented Self-loop Cores (exclusion) to giant components dominated by either Terminators (extinction) or Cyclic Cores (coexistence), with examples shown in bottom insets.

1. “Self-loop” Maximal Beneficiaries (MBs): Producers that gain the highest benefit from their own siderophores. These form Self-loop Cores, driving exclusion. However, increasing cheating breadth expands the pool of potential recipients, “diluting” a producer’s probability of retaining its own siderophore as the maximal benefit (Fig. 4F). This causes a monotonic decline in exclusion-driving Self-loops.
2. “Connector” MBs: Partial-producers possessing both incoming edges and an outgoing edge. This type benefits most from foreign siderophores while producing a siderophore whose maximal beneficiary is not itself. They are the essential “glue” for Cyclic Cores, linking species into loops that support stable or dynamic coexistence.
3. “Terminator” MBs: Nodes with incoming edges but no outgoing edges, corresponding exclusively to pure-cheaters. They form Sink Cores. Selection of maximal beneficiaries probabilistically favors species with higher growth allocation (like pure-cheaters with $\alpha_0 = 1$), and broader cheating amplifies this bias (Fig. 4G), causing a surge in Terminator MBs.
4. “Leaf” Nodes: Species with no incoming edges. The number of Leaf nodes increases as cheating breadth expands, indicating that incoming edges concentrate disproportionately on a small subset of species. This trend can also be explained by the increased bias towards high- α_0 species, which leads to a heavy-tailed in-degree distribution in which a small set of “super-beneficiaries” capture maximal benefits from many sources whereas most species get none.

Taken together, as cheating breadth increases, the mBTG undergoes a percolation-like transition. The suppression of Self-loops releases outgoing edges, while the concentration of edges toward “super-beneficiaries” promotes the coalescence of fragmented components into a giant connected cluster (Fig. 4H). This reduces multi-stability, forcing the community into few dominant attractors. Thus, while broad cheating eliminates the self-loops that trigger exclusion, it forces the community to “gamble”: it either collapses into a Terminator Sink or stabilizes into a complex, high-diversity Cyclic Core. Cheating therefore does not always act as a destabilizing vulnerability, but can also provide the necessary architectural scaffold for biodiversity.

Discussion

In this study, we introduce an integrated framework that bridges molecular specificity, ecological dynamics, and network topology to resolve the “cheating paradox” in microbial communities. By mapping siderophore-mediated interaction dynamics to a maximal Benefit Transfer Graph (mBTG), we demonstrate that community fate, whether extinction, exclusion, or coexistence, is encoded in the core topology of benefit flows. Our findings challenge the classical view that cheating is purely detrimental. While unchecked cheating (Sink Cores) indeed drives collapse, structured exploitation (Cyclic Cores) acts as a necessary architectural scaffold for biodiversity.

The concept of niche construction traditionally emphasizes how organisms modify environments to their benefit, but it also creates vulnerabilities to exploitation[21]. While mechanisms such as spatial segregation[22], metabolic cross-feeding[23], and kin selection[24] have been proposed to resolve this dilemma, our model demonstrates that cheating itself can be transformed into an organizing force. This can be analogous to the central tenet of Modern Coexistence Theory, which posits that stable coexistence arise from either niche differentiation or fitness equivalence [25, 26]. Similarly, when microbes create multiple “chemical niches” by diverse siderophore types, partial-producers emerge as essential “loop connectors,” linking distinct niches through their dual capacity to produce and exploit. This aligns with empirical observations in *Pseudomonas*, where partial-producers are associated with diverse, non-pathogenic communities, whereas pure strategies are linked to low diversity and pathogenicity[6].

This graph-theoretic framework bridges experiments, bioinformatics, and ecological theories. While kinetic parameters are often elusive in wild communities, the structure of the Benefit Transfer Graph can be inferred from genomic analysis[4] or cross-feeding assays[27]. By coarse-graining molecular specificity into topological motifs (WCCs and Cores), the mBTG approach can


forecast community fate not only in systems governed by siderophore-mediated interactions, but also in other systems driven by shared chemical resources, such as extracellular enzyme hydrolysis[28], antibiotic degradation[29], or metabolic cross-feeding networks[30].

Percolation theory describes abrupt transitions from local connectivity to global connectivity [31]. Previously applied to physical connectivity like fragmented habitats [32, 33], percolation concepts now extend to abstract interaction networks [34]. Our Maximal Benefit Transfer Graph (mBTG) exhibits distinctive percolation behavior shaped by its pseudoforest topology: increasing cheating breadth rapidly merges Weakly Connected Components into a giant component, while Strongly Connected Components (formed the cores) approach but never reach the percolation threshold. Under evolutionary dynamics, this structure self-organizes further. Pure-cheaters face extinction, driving the network toward self-sustaining structures composed by either Self-loops or Connector-based cycles. This mirrors autocatalytic set emergence, where mutually reinforcing cycles evolve spontaneously from random networks [35]. Biologically, this suggests that ecosystems operate near a critical point. Bacteria generally possess multiple siderophore receptors, ranging from 1–4 in *E. coli* to 20–30 in *Pseudomonas* and other environmental strains [7, 36–38]. This range corresponds to the “near-critical spot” in our simulations—high enough to ensure global connectivity and diversity, yet structured enough to maintain stability.

Our work provides a mechanistic foundation that grounds abstract ecological theory in molecular specificity. We show that siderophore-mediated interactions generate rich phenomena, ranging from synergistic rescue and priority effects to heteroclinic bifurcations. While phenomenological models highlight the role of intransitive interactions in maintaining diversity[39], our work identifies a concrete chemical basis for such dynamics. Furthermore, the emergence of oscillation and chaos supports theoretical predictions that non-equilibrium dynamics promote diversity through temporal niche partitioning[40].

Our current framework relies on simplified assumptions to ensure analytical tractability, such as well-mixed environments and single-siderophore production. These simplifications point toward fruitful avenues for future exploration. For instance, incorporating spatial structure could reveal how biofilm stabilize or fragment large interaction loops [41], and integrating more interactions like nutrient competition and antibiotic antagonism would offer a more holistic ecological picture [42]. Additionally, incorporating evolutionary dynamics will be crucial to understand the selective origins of these topological motifs [8, 43]. Ultimately, these future complexities will build upon the fundamental principle established here: molecular specificity transforms the social dilemma of public goods, recasting cheating from a destabilizing threat into the structural scaffold of diverse ecosystems.

Data availability

All computer code and scripts used for the simulations, analysis, and figure generation in this study have been deposited in the Zenodo repository: (<https://zenodo.org/records/18158439> ) . This study is a theoretical work and did not generate new biological materials or empirical datasets; all data supporting the findings are derived from the model simulations and are available within the article and its Supplementary Information.

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Additional files

[SI Appendix](#) 

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Peer reviews

Reviewer #1 (Public review):

In this work, Jiqi Shao and colleagues evaluate the microbial iron competition and siderophore-mediated interactions combining (a) a dynamic modeling framework based on the consumer-resource model, including multiple siderophore and siderophore-receptor types, and (b) a graph-theory framework based on directed graphs to quantify the ecological dependencies of the community (referred to as Benefit Transfer Graph). Through a plethora of simulation experiments, by changing the number of species in the community, the ratio of pure-cheaters, and the number of foreign siderophores a partial-producers can utilize (referred to in this study as 'Cheating Breadth'), the authors found:

(1) Using simulations of small communities of 5 or fewer members, they observe that closed benefit-transfer loops (commensalism/mutualism loops) serve as the structural scaffold for

diversity, observing coexistence, dominance, or dynamic fluctuations in function of the fraction of receptors in species and the number of community members.

(2) Using simulations of large communities of 50 members, they observed a paradox on the capacity of partial producers to utilize different foreign siderophores (referred to in this study as 'The Paradox of Cheating'). They observed that broad 'Cheating Breadth' of partial-producer members increases the probability of community-wide extinction and can act as destabilizing forces. However, at the same time, 'Cheating Breadth' of partial-producer members promotes species richness and community biodiversity.

(3) The application of graph-theory framework helps to unveil ecological complexities of small and large microbial communities, explaining the aforementioned Paradox of Cheating.

As major strengths of this work, the authors present a novel modeling framework considering the ecological complexity of siderophore-mediated interactions by differentiating types of community members (pure-producers, partial-producers, and pure-cheaters), siderophore/receptor pairs, and exploring a wide range of situations (such as the number of community members, the ratio of pure-cheaters, or the siderophore breadth of partial-producers). Moreover, the discussion and conclusions of this study are mechanistically well-founded with a graph-theory framework (Benefit Transfer Graph). All computer code and scripts to replicate the simulations, analysis, and figure generation are public in the Zenodo repository.

However, this study still has some work to do before it meets the expected standards, presenting some weaknesses to be addressed. Please regard the following paragraph as constructive feedback aimed at improving your work. The main weakness of the actual version is the Abstract, the missing Methods section, the structure of the Results section, and the results displaying (i.e., Figures), and how partial-producers are considered as cheaters (including how they referred to the capacity of partial-producers to use different siderophores as 'Cheating Breadth'). The Abstract could be significantly improved with a better introduction of the system (cooperators and cheaters, and the concept of the 'Tragedy of Commons'), a better description of the modeling framework, and other details included in 'Recommendations for the authors'. The current version of the manuscript misses a proper 'Methods' section.

Moreover, the authors could include (1) a section with the simulated systems and parameter choices of simulation experiments, (2) the key model assumptions, and (3) a separate (and more detailed) section explaining the graph-theory framework applied in this study (Benefit Transfer Graph). Most of this information is included in Supporting Information, but including it in the main text will facilitate the comprehension of the work. The structure of the results displayed (i.e., Figures) is quite confusing, especially in the section 'Closed Benefit Loops Drive Transitions from Exclusion to Coexistence and Chaos'. Moreover, important results are included in Supportive Information when they should be in the main text. Also, the lack of a proper Method section makes it harder to follow the Results sections. I have included some recommendations/suggestions to improve the Results structure. This study reveals an interesting ecological dynamic in siderophore-mediated interactions. The authors suggest the existence (and further explanation) of the 'Paradox of Cheating'. However, this paradox (and their discussion) may come from a misunderstanding of concepts and/or terminologies used by the authors applied here (and maybe widely applied in cooperator-cheaters systems). The authors refer to the capacity of 'partial-producers' to utilize foreign siderophores (i.e., siderophores of other species) as cheating. Also, they refer to the number of foreign siderophores that a 'partial-producer' can utilize as 'Cheating Breadth'. A microbial cheater is one that has receptors for siderophore uptake but does not pay the cost of producing siderophore themselves. Because 'partial-producers' are generating at least one type of siderophore, these are not technically cheaters (although they may act as 'pure-cheaters', changing their gene expression and do not synthesize any siderophore for the

community). All this may entail a misleading of the results and a potentially overstated title and conclusions of this work. Community members 'pure-producers', 'partial-producers' cheaters may be called in a different way, e.g., 'single-receptor producer', 'multiple-receptor producers' and 'nonproducers', respectively [Gu. et al. (2025), doi: 10.1126/sciadv.adq5038]. A better terminology for 'the number of foreign siderophores that a partial-producer can utilize' could be 'Siderophore Breadth', and instead of stating a 'Paradox of Cheating', it can be a 'Paradox of Multiple-receptor Producers'. The discussion of the authors aligns better with the presented results if the proposed terms 'single-receptor producer/multiple-receptor producer and cheater' are used, considering multiple-receptor producers as cooperative members rather than 'moderate cheating'. On the other hand, the Paradox of Multiple-receptor Producers (or Paradox of Cheating by the authors) could be a modeling artifact. Although some species possess multiple siderophore receptors in their genome (some studies suggest that *Pseudomonas* species and other environmental strains' genomes can have up to 20-30 siderophore receptors), that does not mean that they are all expressed simultaneously.

Regardless of the weaknesses and the major points to be improved, the findings presented in this work substantially advance our understanding of complex ecological interactions between cooperators and cheaters mediated by siderophore and siderophore-receptor syntheses, especially when multiple-receptor producers are present. Moreover, the modeling and graph-theory frameworks presented by the authors can be applied in other microbial systems, such as collaboration/competition/cheating for substrates or nutrients. Fundamental modeling exercises are indispensable to unveil ground ecological rules of complex microbial communities, accelerating the advances in ecology by developing theory-based hypotheses for future experimental and environmental studies.

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Reviewer #2 (Public review):

Summary:

This study investigates how cheating affects microbial diversity, using a chemostat model of a microbial community in which species compete for a shared iron pool through siderophore-mediated uptake. After analyzing minimal communities, the study simulates large randomly generated communities in which species either produce no siderophore or produce a single siderophore type. Producers can differ in siderophore type and production level, while all species can differ in the siderophore-specific receptor types they express. Siderophore production trades off with resource allocation to growth. Total receptor expression is normalized, so increasing expression of one receptor type reduces expression of other receptor types. A key parameter in these simulations is the average number of "cheating receptor types," i.e., receptor types that allow a species to use siderophores it does not produce itself. The authors use this parameter as one axis for characterizing cheating behavior and term it "cheating breadth." The results reveal a statistical pattern the authors report as a "paradox": increasing cheating breadth increases the frequency of whole-community extinction, but also increases the mean number of surviving species per non-extinct community. To explain this pattern, the study reduces a community's producer-receiver network into components by retaining only the link from each producer to its maximal beneficiary, i.e., the species receiving the largest growth benefit from that producer. The study finds that the core topology of such a component predicts the community's ecological fate, namely, extinction, single-species survival, or multi-species coexistence, when biomass is concentrated in that component. The study argues that increasing cheating breadth reduces the probability that a community contains components predicting single-species survival, while increasing the probabilities that it contains components predicting extinction or multi-species coexistence. This argument is used to explain why greater cheating breadth increases both community extinction risk and diversity. Based on these

results, the study concludes that microbial diversity not only tolerates but requires moderate cheating.

Strengths:

The major strengths of this study are that it presents an interesting mathematical model of microbial interactions mediated by diverse siderophores and that it reduces simulation results to simple predictive patterns by focusing on one primary beneficiary per producer, as summarized above.

Weaknesses:

The study also has two major weaknesses. First, the observed diversity is not shown to be evolutionarily stable, which limits the biological relevance of the findings. The cycle structure that supports this diversity may be vulnerable to invasion by mutants that disrupt this structure and can thereby drive many species, or even the whole community, extinct. This concern is suggested by previous studies on the hypercycle, which is analogous to the cycle structure found in this study (Eigen and Schuster, *The Hypercycle*, Springer-Verlag, pages 32-57, 1979 <https://doi.org/10.1007/978-3-642-67247-7>). For example, a community with a cyclic network may be invaded by mutants that increase growth allocation at the cost of siderophore production (Maynard Smith, *Nature* 280:445-446, 1979 <https://doi.org/10.1038/280445a0>). It may also be destabilized by mutants that increase the expression of the "self-receptor," the receptor for the siderophore they produce themselves. Another possibility is a "short-circuit mutant" that expresses receptors in a way that bypasses intermediate species in a cycle (Bresch et al., *Journal of Theoretical Biology* 85:399-405, 1980 [https://doi.org/10.1016/0022-5193\(80\)90314-8](https://doi.org/10.1016/0022-5193(80)90314-8)). Cyclic networks may remain evolutionarily unstable even when spatial self-organization is considered (Hogeweg and Takeuchi, *Origins of Life and Evolution of the Biosphere* 33:375-403, 2003 <https://doi.org/10.1023/A:1025754907141>). Without demonstrating robustness to these plausible evolutionary hazards, the study's coexistence results may have limited biological relevance.

The second weakness is that the study treats cheating breadth as if it were a pure measure of increased cheating, framing the observed pattern as a paradox that increasing cheating breadth increases diversity within surviving communities while also increasing community extinction risk. However, increasing cheating breadth decreases the mean expression level of all expressed receptors, a confounding effect that arises from the normalization of total receptor expression. Consequently, increasing cheating breadth also reduces the mean benefit a producer gains from its own siderophore production. In other words, increasing cheating breadth spreads each producer's dependence across diverse siderophores at the cost of a reduced return on the self-produced siderophore. Once these coupled effects are recognized, the reported pattern is less paradoxical: increasing cheating breadth might be expected to increase diversity within surviving communities by distributing dependence, while also increasing extinction risk by reducing self-reliance. Therefore, the apparent paradox may arise from the way cheating behavior is parameterized rather than from a direct effect of increased cheating alone.

Additional context:

The present study can be considered alongside previous studies proposing that cheating can, in some contexts, promote microbial diversity by generating ecological dependencies. The Black Queen hypothesis proposes that such dependencies can be created by adaptive gene loss and reliance on functions performed by other community members (Morris et al., *mBio* 3:e00036-12, 2012, <https://doi.org/10.1128/mbio.00036-12>). A related study by Fullmer et al. discusses how mutual cheating can contribute to microbial diversity (*Frontiers in Microbiology* 6:728, 2015, <https://doi.org/10.3389/fmicb.2015.00728>).

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Author response:

We would like to express our sincere gratitude for your time and constructive feedback. We are highly encouraged by the positive assessment highlighting the solid evidence and convincing methods of our study. We also deeply value the insightful and constructive comments regarding our conceptual framing, the integration with established ecological theories, and the underlying dynamic mechanisms. We believe that incorporating these excellent suggestions will substantially enhance the conceptual clarity and theoretical depth of our manuscript. To achieve this, we are fully committed to conducting a comprehensive revision to address all the points raised. Below, we outline our main strategies for the forthcoming revision:

(1) Structural Reorganization

We fully agree with the reviewers and the Editor that the manuscript's structure requires improvement. We are especially grateful to Reviewer 1 for providing such a detailed and constructive roadmap for the revision. We will adopt all of the suggested changes. Specifically, in the revised manuscript, we will:

(1.1) Rewrite the Abstract: provide a clearer introduction to the "Tragedy of the Commons" and a more accessible description of our modeling framework.

(1.2) Establish a dedicated Methods section: move the core model equations, key assumptions, parameter choices, and the detailed explanation of our graph-theoretic framework (the Benefit Transfer Graph) from the Supplementary Information (SI) into the main text.

(1.3) Restructure results and figures: We will reorganize the Results section to improve the logical flow. As suggested, we will split the current Figure 2, move critical diagrams from the SI into the main text, and expand our figure captions to ensure all data representations are immediately clear.

(2) Reframing the Conceptual Framework and Terminology

We thank Reviewer 1 for the insightful critique regarding the use of the term "cheating." We have reflected on our previous phrasing and fully agree that "cheating" introduces an unnecessarily humanized judgment and conflates pure exploitation with metabolic generalism. To ensure mechanistic accuracy and alignment with recent ecological literature, we will systematically update our terminology throughout the text, from title to supplement:

(2.1) Species strategies: "Pure-producers," "partial-producers," and "pure-cheaters" will be redefined as "single-receptor producers," "multi-receptor producers," and "non-producers," respectively.

(2.2) Receptor types: "Cheating-receptors" will be renamed to "exogenous-receptors" (or foreign-receptors, exploitative-receptors) to objectively describe the uptake of siderophore types that are not produced by the focal microbe.

(2.3) Updating the key parameter: To avoid ambiguity regarding synthesis versus uptake, we will rename "Cheating Breadth (CB)" to "Siderophore Exploitative Breadth (SEB)," defined strictly as the number of distinct exogenous-receptors expressed by a species.

(2.3) Updating the core paradigm: We will reframe "The Paradox of Cheating" to "The Paradox of Siderophore Exploitation." We will clarify that the transition to high-diversity coexistence is not driven by "cheating", but by the topological connectivity of the mBTG.

(3) Contextualizing within BQH and Hypercycles

We sincerely thank the Editor and Reviewer 2 for highlighting the connections between our work, the Black Queen Hypothesis (BQH), and Hypercycle theory. We will dedicate a new section in the Discussion to thoroughly compare our siderophore-mediated network with these established frameworks.

We will explicitly discuss the key similarities and differences. While the exploitation of siderophores in our model resembles the producer-beneficiary dependency described in BQH, the evolutionary drivers are distinct, in that BQH is primarily driven by the adaptive loss of costly genes (reductive evolution), whereas siderophore exploitation is driven by the acquisition of exogenous-receptors (e.g., via horizontal gene transfer). More importantly, the high diversity and lock-and-key specificity of siderophore-receptor interactions, renders each siderophore a "mixed good." This dynamic can actually drive the community into a Red Queen-like arms race, as suggested by the high probability of oscillatory dynamics observed in our simulations. Although we did not explicitly consider genetic mutations in the current ecological framework, unidirectional exploitation typically drives the involved species to extinction; consequently, the system naturally selects for communities where exploitation is reciprocated, organically giving rise to closed, distributed loops of benefit transfer.

In the revised text, we will cite recent theoretical progress on structured and multi-goods BQH networks. We will also discuss how our topological loops link to Eigen's Hypercycle theory by illustrating how specific structures of exploitative interactions foster community diversity.

(4) Addressing Siderophore Exploitative Breadth (SEB) Interpretations

(4.1) The biological realism of the SEB range

Both reviewers raised insightful questions regarding the settings and impacts of SEB (previously "CB"). While some of these questions will be addressed through new control simulations, we would like to immediately clarify the biological realism of the SEB parameter, particularly addressing Reviewer 1's concern about the simultaneous expression of multiple receptors.

We completely agree that possessing a vast genomic repertoire of siderophore receptors does not mean a microbe expresses all of them simultaneously. Receptor expression in nature is a highly regulated and substrate-specific process. In Gram-negative bacteria like *Pseudomonas*, the expression of exogenous-receptors is tightly regulated by cell-surface signaling pathways (e.g., ECF sigma/anti-sigma factor systems). Under iron-limited conditions, a specific receptor is upregulated only when it detects its corresponding siderophore in the environment. Based on our literature review, while a bacterium may not express 30 receptors at once, expressing a substantial subset (e.g., 5–15) is biologically realistic. Therefore, in our model, SEB does not represent a static genomic capacity, but rather the number of active receptors that actually have corresponding siderophore producers present within the local community. We extended the SEB axis up to 30 in our initial figures primarily to capture the complete theoretical phase transition. However, following the reviewer's excellent suggestion, we will adjust the x-axis in our primary revised figures to highlight the more realistic regime (e.g., SEB 0–15) and add a dedicated paragraph detailing these biological regulatory mechanisms, with appropriate citations.

(4.2) Disentangling the receptor allocation trade-off

We highly appreciate Reviewer 2's perceptive insight regarding the confounding effect: under a normalized allocation scheme, increasing SEB inevitably decreases the expression level of

the self-receptor, thereby reducing self-reliance. We completely agree that explicitly addressing this trade-off is crucial.

Biologically, this strong trade-off is realistic: receptor operations are energetically costly, and the initiation of their expression requires competing for a finite pool of RNA polymerase core enzymes. Therefore, investing in the capacity to exploit heterologous siderophores inherently incurs a cost to self-reliance. To rigorously test whether our central paradox is merely an artifact of this specific trade-off, we immediately initiated a series of control simulations. In these new models, we mathematically decoupled the variables by fixing the allocation fraction of the self-receptor as a constant.

We are encouraged to report that our preliminary results support the core of the original paradox. Even when self-reliance is mathematically maintained, community-level extinction risk and the biodiversity of surviving communities remain positively linked. Interestingly, these controlled simulations exhibit an even clearer non-monotonic pattern, where both diversity and extinction risk peak at a biologically realistic SEB of approximately 5. This suggests that the paradox is fundamentally driven by network topology changes rather than the allocation trade-off alone: Viewed through our maximal Benefit Transfer Graph (mBTG) framework, a higher probability of non-self-directed edges in the mBTG forces the community to "gamble" between collapsing into a Sink Core or surviving in a high-diversity Cyclic Core. We are currently performing exhaustive simulations to gather detailed statistics on this decoupled model, particularly the non-monotonic behavior, which will be prominently featured in the revised manuscript.

(5) Evolutionary Stability and Topological Resilience

We also deeply appreciate Reviewer 2's insightful critique regarding the evolutionary stability of our proposed cyclic networks, particularly their potential vulnerability to self-serving or short-circuit mutants that bypass intermediate species in a loop.

To rigorously address this, we are currently conducting invasion simulations in which established communities are challenged by randomly generated mutant species. While the exhaustive computational analysis is ongoing, our preliminary results suggest the absence of a strict, static Evolutionarily Stable Strategy (ESS). Instead, the topological space fosters complex, intransitive competition. Intriguingly, these early data suggest that communities exhibiting oscillatory dynamics are actually more robust against invaders than those at a stable equilibrium. We intend to explore this phenomenon fully.

Furthermore, we will expand our Discussion to address the implications of longer evolutionary timescales. When true structural mutations occur (e.g., the appearance of novel siderophore-receptor pairs to evade existing exploitation), the system will likely transition into a continuous Red Queen regime of ongoing molecular arms races. We will thoroughly discuss these evolutionary horizons and present our complete invasion simulation data in the revised manuscript.

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