Siderophore Piracy Promotes Dynamical Coexistence in Microbial Community

Jiqi Shao[1,#], Yinxiang Li[2,#], Jingyuan Lu[1], Shaohua Gu[1,3]and Zhiyuan Li[1,3,4,*]

[1]Center for Quantitative Biology, Academy for Advanced Interdisciplinary Studies, Peking University, Beijing, 100871, China

[2]School of Physics, Peking University, Beijing, 100871, China

[3]Peking-Tsinghua Center for Life Sciences, Academy for Advanced Interdisciplinary Studies, Peking University, Beijing, 100871, China

[4]Lead contact

[#]These authors contributed equally

[*]Correspondence: zhiyuanli@pku.edu.cn

Abstract

The game between cooperation and cheating in the microbial world is captivating. Microbes that acquire essential iron through the secretion of siderophores face the public good dilemma. In this game of iron, the specific recognition of different types of siderophores by corresponding receptors adds more complexity. Despite the prevalence of siderophore synthesis and piracy among microbes, the ecological consequences of siderophore-mediated interactions remain largely underexplored. This study introduced the framework of resource partition model for siderophore-mediated interactions, revealing conditions for stable coexistence in dual-species scenarios and uncovering surprising oscillatory and chaotic coexistence in systems with three or more species. Intriguingly, analytical analysis and simulations highlight the how 'cheating' promotes biodiversity, emphasizing the non-monotonic changes in biodiversity as the level of siderophore piracy increases in producers. This work sheds light on the complex dynamics introduced by resource partition in microbial communities, elucidating the intricate balance between cooperation and cheating.

Keywords: resource partition, chemical innovation, siderophore piracy, cheating, microbes

Highlights:

(1) Resource partition introduce complex dynamics
(2) Cheating play a main force in promoting coexistence
(3) Increased proportion of cheating prefers dynamical behaviors

Introduction

In the diverse microbial world, the interplay between cheating and cooperation has been a fascinating topic. By secreting a wide range of secondary metabolites to accomplish biofilm formation, toxin degradation, and nutrient acquisition, microbes shape their niches to survive and thrive[1,2]. Nevertheless, these secreted molecules, while conferring benefits to the microbial community as a whole, become susceptible to exploitation by non-producers[3,4]. The piracy of public goods within microbial communities poses potential threat to entire community, a microbial parallel to the "tragedies of the commons" elucidated in classical game theory[5]. Recognizing the prevalence of both cooperative and cheating traits among microorganisms, scholars have dedicated considerable effort to investigating mechanisms that to suppress cheaters, including but not limited to, the study of spatial dynamics, kin selection, and the imposition of punitive measures[6-11]. Despite these strides, ongoing investigations persist, propelled by the continuous influx of discoveries in the complex microbial world about cooperation and cheating.

Siderophores are recognized as one of the fascinating microbial “public goods” [1,12]. Although iron is abundant on Earth, its bioavailability is significantly lower than what microbes need for survival[13,14]. In response to this iron deficiency, microbes produce and secrete siderophores, which are small molecules with a high affinity for iron. These siderophores bind to iron and are then taken up by membrane receptors[12,15].There exists a diverse range of siderophores[16]. Interestingly, specific types of membrane receptors demonstrate selective recognition and uptake for particular types of siderophores[17,18], similar to a lock-key system[19]. Thus, only bacteria possessing receptors that match the structure of a specific siderophore can utilize these iron-loaded compounds. By this siderophore selectivity of receptors, while microbes compete for the same iron, the diverse siderophores they produce partition this resource into various types of siderophore-iron complexes[20,21]. This specialization introduces additional resource dimensions and constitutes a form of resource partition[15]. Furthermore, siderophores act as exploitable "public goods" by any species who possess the right receptors to utilize siderophores. If a species utilizes a type of siderophore without producing it, it can gain a growth advantage by saving the energy and resources that would otherwise be used in siderophore synthesis[1,15]. Such “siderophore piracy” has been frequently observed among microorganisms[22-24].

Siderophores, therefore, exhibit two key characteristics: first, they serve as self-produced resource dimensions under the resource partition mechanism[17]; second, they function as environmental public goods only for these with the corresponding receptors[25]. The interplay between siderophores and receptors introduces an added layer of complexity: producing one type of siderophore while exploiting multiple types through the possession of several types of receptors[19,24]. Given these complexities, despite the widespread prevalence of siderophore production and receptors in microbial communities, this specific form of resource partition remains underexplored. This oversight leaves gaps in

our understanding of how siderophore-mediated resource partition affects the stability and interactions within coexisting microbial populations. For instance, how should microbes strategically allocate their siderophore receptors, and how many types are required for survival across diverse ecological niches? Moreover, do different microbial communities exhibit variations in interaction structures, siderophore production, and absorption based on their environmental context? Lastly, what roles do cheating and cooperation play in shaping these complex interactions?

In this study, we constructed a resource competition model within a resource partition framework. We considered both the production of siderophores and the distribution of various siderophore receptors. Applied to dual-species scenarios, our model pinpointed the conditions necessary for stable coexistence, echoing findings in Tilman's classical model[26]. In these scenarios, species allocated more resources to "cheating" receptors to achieve mutual invasion and stable coexistence. Surprisingly, when applied to systems of three or more species, our model observed oscillatory coexistence and various bifurcation phenomena, including infinite period and Hopf bifurcations. In a system with five species, we even observed the emergence of chaotic behaviors. Our statistical analyses revealed that cheating promotes biodiversity when it is within an appropriate level. Moreover, this piracy-fostered diversity is contributed by producers who are capable of cheating, but not of pure cheaters. Our findings illuminated the complex dynamics that resource partition introduced at the microbial community level and emphasized the role of siderophore-mediated 'cheating' as a pivotal force in microbial coexistence.

Result

The generalized resource partition model for siderophore-mediated interactions

To model siderophore-mediated interactions, we developed a comprehensive framework rooted in the principle of resource partitioning. This framework represents an extension of classical resource-consumer models that are widely employed to simulate interactions between organisms mediated by environmental resources. Traditionally, these models focus primarily on externally supplied resources or by-products resulting from cross-feeding [27,28]. However, in conditions where iron is scarce, microorganisms actively allocate a significant portion of resources to produce a diverse array of siderophores (see Figure 1). This unique characteristic transforms them into not only consumers but also producers of environmental chemicals. Moreover, diverse siderophores are synthesized, leading to the partitioning of the limited iron resource into distinct "parts" represented by unique Fe-siderophore complexes. Each type of complex is exclusively accessible through its corresponding receptors, governed by the Lock-Key principle.

The generalized ODE equations to model such resource partition are listed below:

$$\frac{dM_i}{dt} = \sigma + M_i\left(\gamma\alpha_{i,0}\sum_j v_{ij}J_j - d\right), \text{ where } i = 1, \cdots, N_{\text{spe}} \ . \tag{1}$$

$$\frac{dR_j}{dt} = \sum_i M_i\alpha_{i,j}\epsilon_j - d \cdot R_j, \text{ where } j = 1, \cdots, N_{\text{sid}} \ . \tag{2}$$

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

This model contains three classes of variables: (1) populations of the i-th microbial species, quantified by their biomass M_i; (2) concentrations of the j-th type of siderophores, designated as R_j; and (3) concentration of the limiting resource iron, labeled R_{iron}.

This modeling framework is under the following assumptions:
(1) Two levels of resource allocation trade-offs: first, given a finite total energy and protein budget for microbial growth, we coarsely partition the budget in each species i into two functions: the fraction allocated to growth, $\alpha_{i,0}$, and the fraction allocated to producing the j-th type of siderophore, $\alpha_{i,j}$. We set:

$$\alpha_{i,0} + \sum_{i=1}^{N_{\text{sid}}} \alpha_{i,j} = 1 \tag{4}$$

Second, given the limited membrane surface and the cost of transportation, we posit that the total number of membrane-bound siderophore receptors is restricted. The fraction of receptors in species i allocated to absorb the j-th type of siderophore is v_{ij}, which satisfies:

$$\sum_{i=0}^{N_{\text{sid}}} v_{ij} = 1 \ . \tag{5}$$

v_{ij} can also be interpreted as the "preference" of species i on the type j siderophore.

(2) Iron as the sole limiting resource: for simplification, we only consider iron competition in this framework. For each species, the iron flux contributed by type j siderophore, per receptor, is described by J_j, framed in the context of the law of mass action for simplification:

$$J_j = u_j \ R_j \ R_{\text{iron}}, \tag{6}$$

where u_j indicates iron affinity for iron for the type j siderophores.

To promote iron uptake, microbial species can allocate some resources to produce siderophores (represented by $\alpha_{i,j}$, $j > 0$). We assume the production rate is proportional to the resource allocated in production, and the parameter ϵ_j represents the efficacy of

resource transformation into siderophore j concentration (Eq. 3).

For the species i, the total iron influx is $\sum_j v_{ij}J_j$. For simplicity, we assume that the growth rate is linearly proportional to the total amount of iron uptake, as well as the fraction of resource it allocated to growth $\alpha_{i,0}$:

$$\text{growthrate} = \gamma\alpha_{i,0}\sum_j v_{ij}J_j. \tag{7}$$

Here γ denotes the efficiency of microbial resource-to-growth conversion.

(3) Chemostat-styled environment: In this model, the external influx is balanced by the dilution rate d, ensuring a constant overall volume for microbial community interactions. This allows for a focused examination of steady-state dynamics under microbial growth. In this environment, microbes grow and undergo dilution according to Equation 1, with a small migration rate σ. Siderophores produced by microbes serve as resource dimensions within the system by offering iron supply (Eq. 2). Iron is supplied at concentration R_{supply} from the influx, uptake by microbes in complex with siderophores, and diluted at the rate of d (Eq. 3).

By adopting these assumptions, our model offers a concise representation of microbial interactions under iron deficiency. Within this framework, different species in the model can employ various iron-scavenging strategies, as denoted by distinct parameter choices in growth resource allocation $\alpha_{i,j}$ and receptor allocation v_{ij}. For example, a species i that produces siderophore of type j ($\alpha_{i,j} > 0$) and only uptake this specific type of siderophores ($v_{ij} = 1$) conforms to the classical concept of producers in game theory[2], which we term as "pure producers". (Figure 1B, left panel). Those that do not produce siderophores ($\alpha_{i,0} = 1$) align with the classical cheaters in game theory, and we term them "pure cheaters"(Figure 1B, middle panel). Meanwhile, it has been observed that many producer strains, in addition to having their own siderophore synthetase and corresponding receptors, can also harbor multiple receptors capable of uptaking siderophores of other types [19]. These strains are represented by $\alpha_{i,j} > 0$ and $v_{ij} < 1$, which we termed “partial producers” (Figure 1B, right panel). Here, we emphasize the notion of 'cheating' in partial producers. In these strains, receptors that bind to non-self siderophores are termed “cheating-receptors”, as opposed to “self-receptors”, which engage with the organism's endogenous siderophores (Figure 1).

Building upon the aforementioned framework, our goal is to comprehend the distinct roles that various strategies play within microbial interactions during iron deficiency, with a specific focus on the role of "cheating."

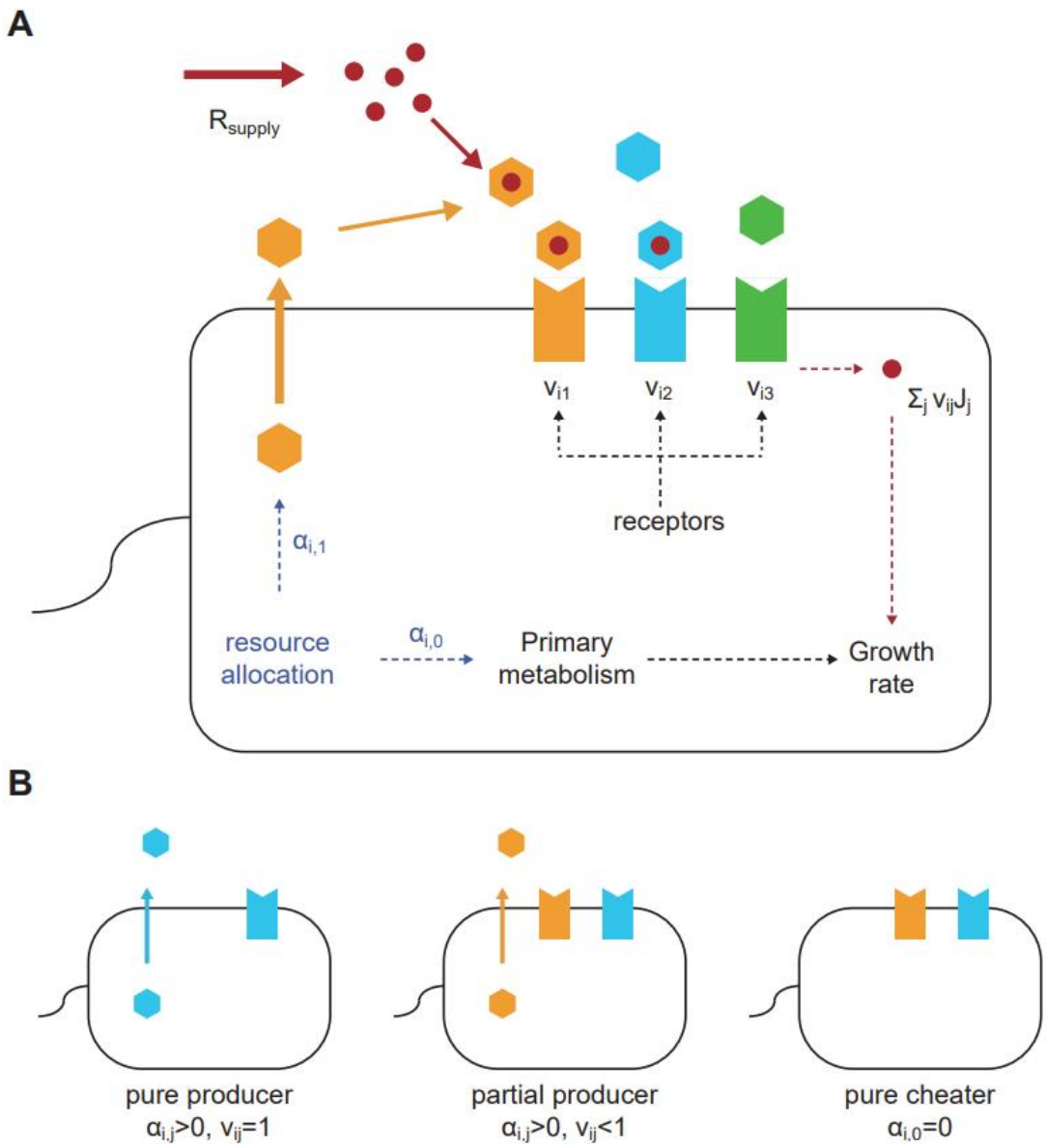

Figure 1. Schematic diagram of the resource partition model and three classes of iron-scavenging strategies.

A. Schematic diagram of the resource partition model. The diagram shows that species i can acquire iron by absorbing three types of siderophore-iron complexes (siderophore type indicated by colors). The growth rate is linearly proportional to the total amount of iron absorbed, and also proportional to the fraction of resources that species i allocates for autotrophic growth $\alpha_{i,0}$. $\alpha_{i,j}$ represents the resource allocation for siderophore j synthesis, and v_{ij} indicates the proportions of receptors allocated to uptake the i-th type of siderophore.

B. Schematic diagram of the three classes of strategies in the iron game. From left to right are: “pure producer”, “partial producer” and “pure cheater”, according to whether they produce siderophores and whether they harbors cheating-receptors.

Appropriate mutual piracy enables stable coexistence in the two-species system

We began by investigating the most basic two-species ecological network. We proved that each species must significantly "cheat" on the other to coexist. Here, we designated $N_{\mathrm{spe}} = N_{\mathrm{sid}} = 2$, indicating two species and two types of siderophores. We set that species 1 exclusively generates siderophore type 1 ($\alpha_{1,1} > 0, \alpha_{1,2} = 0$), and species 2 solely manufactures siderophore type 2($\alpha_{2,1} = 0, \alpha_{2,2} > 0$). Remarkably, both species possess two types of receptors (for all i and j, $v_{ij} > 0$)(Figure2 A). In this sense, both species belong to the “partial producers”, who are able to produce and ready to cheat.

Now we are going to derive analytically the conditions for stable coexistence. When two species coexist, the fixed point of the resource partition model (Eq 1-3) satisfies:

$$\begin{aligned}
J_1^* &= \frac{d \cdot (\alpha_{2,0} v_{22} - \alpha_{1,0} v_{12})}{\gamma \alpha_{1,0} \alpha_{2,0} (v_{11} + v_{22} - 1)}, \\
J_2^* &= \frac{d \cdot (\alpha_{1,0} v_{11} - \alpha_{2,0} v_{21})}{\gamma \alpha_{1,0} \alpha_{2,0} (v_{11} + v_{22} - 1)}, \\
R_{sid,1}^* &= \frac{d \cdot (\alpha_{2,0} v_{22} - \alpha_{1,0} v_{12})}{u_1 \gamma R_{iron}^* \alpha_{1,0} \alpha_{2,0} (v_{11} + v_{22} - 1)}, \\
R_{\mathrm{sid},2}^* &= \frac{\mathrm{d} \cdot (\alpha_{1,0} \mathrm{v}_{11} - \alpha_{2,0} \mathrm{v}_{21})}{\mathrm{u}_2 \gamma \mathrm{R}_{\mathrm{iron}}^* \alpha_{1,0} \alpha_{2,0} (\mathrm{v}_{11} + \mathrm{v}_{22} - 1)}, \\
M_1^* &= \frac{d^2 \cdot (\alpha_{2,0} v_{22} - \alpha_{1,0} v_{12})}{\gamma R_{iron}^* \alpha_{1,0} \alpha_{2,0} (1 - \alpha_{1,0}) \epsilon_1 u_1 (v_{11} + v_{22} - 1)}, \\
M_2^* &= \frac{d^2 \cdot (\alpha_{1,0} v_{11} - \alpha_{2,0} v_{21})}{\gamma R_{iron}^* \alpha_{1,0} \alpha_{2,0} (1 - \alpha_{2,0}) \epsilon_2 u_2 (v_{11} + v_{22} - 1)}, \\
R_{supply} &- R_{iron}^* \\
&= \frac{d^2}{\gamma^2 R_{iron}^* \alpha_{1,0} \alpha_{2,0} (v_{11} + v_{22} - 1)} \left[\frac{\alpha_{2,0} v_{22} - \alpha_{1,0} v_{12}}{\alpha_{1,0} (1 - \alpha_{1,0}) \epsilon_1 u_1} \right. \\
&\left. + \frac{\alpha_{1,0} v_{11} - \alpha_{2,0} v_{21}}{\alpha_{2,0} (1 - \alpha_{2,0}) \epsilon_2 u_2} \right].
\end{aligned} \tag{8}$$

The superscript “*” denotes the value at the fixed point.

The concentrations at the fixed point must be positive, which requires $\alpha_{1,0} v_{11} - \alpha_{2,0} v_{21}$, $\alpha_{2,0} v_{22} - \alpha_{1,0} v_{12}$, and $v_{11} + v_{22} - 1$ have the same sign. It can also be derived that $R_{iron}^* < R_{supply}$. In addition, the last equation of Eq. 8 is a quadratic equation of R_{iron}^*, and the existence of a real solution requires the determinant to be non-negative:

$$\begin{aligned}
R_{supply}^2 - \frac{4d^2}{\gamma^2 \alpha_{1,0} \alpha_{2,0} (v_{11} + v_{22} - 1)} \left[\frac{\alpha_{2,0} v_{22} - \alpha_{1,0} v_{12}}{\alpha_{1,0} (1 - \alpha_{1,0}) \epsilon_1 u_1} \right. \\
\left. + \frac{\alpha_{1,0} v_{11} - \alpha_{2,0} v_{21}}{\alpha_{2,0} (1 - \alpha_{2,0}) \epsilon_2 u_2} \right] \geq 0
\end{aligned} \tag{9}$$

At this fixed point, the Jacobian matrix can be derived as:

$$Jacobian = \begin{pmatrix} 0 & 0 & \gamma\alpha_{1,0}c_{11} & \gamma\alpha_{1,0}c_{12} & \gamma\alpha_{1,0}c_{10} \\ 0 & 0 & \gamma\alpha_{2,0}c_{21} & \gamma\alpha_{2,0}c_{22} & \gamma\alpha_{2,0}c_{20} \\ (1-\alpha_{1,0})\epsilon_1 & 0 & -d & 0 & 0 \\ 0 & (1-\alpha_{2,0})\epsilon_2 & 0 & -d & 0 \\ -\sum_j v_{1j}J_j^* & -\sum_j v_{2j}J_j^* & -\sum_i c_{i1} & -\sum_i c_{i2} & -d-\sum_i c_{i} \end{pmatrix} \quad (10)$$

For simplicity, we introduce abbreviations:

$$c_{i0} = M_i^* \sum_{\mathrm{j}} v_{ij}\left(\frac{\partial J_j}{\partial R_{iron}}\right)^*$$

$$c_{ij} = M_i^* v_{ij}(\frac{\partial J_j}{\partial R_j})^* \ \ (\text{for } j = 1,2)$$

If the fixed point is stable, all the coefficients must be positive. If we set the characteristic equation to the form:

$$a_0\lambda^5 + a_1\lambda^4 + \cdots + a_5 = 0,$$

we can put the fixed point values and Eq.(4) to Eq.(7) into Jacobian matrix and get:

$$a_5 = -\,\mathrm{d}M_1^*M_2^*\gamma^2\alpha_{1,0}(1-\alpha_{1,0})\epsilon_1 u_1\alpha_{2,0}(1-\alpha_{2,0})\epsilon_2 u_2(v_{11}+v_{22} - 1)R_{iron}^*(R_{supply} - 2R_{iron}^*),$$

$$\mathrm{a}_4 = \left[\frac{\mathrm{d}^4}{\mathrm{R}_{\mathrm{iron}}^*} + 2\mathrm{R}_{\mathrm{iron}}^*\frac{\mathrm{R}_{\mathrm{supply}} - \mathrm{R}_{\mathrm{iron}}^*}{\mathrm{d}\left(\mathrm{R}_{\mathrm{supply}} - 2\mathrm{R}_{\mathrm{iron}}^*\right)^2}\mathrm{a}_5\right]\left(R_{supply} - 2R_{iron}^*\right), \quad (11)$$

$a_5 > 0$ requires $v_{11} + v_{22} - 1$ and $R_{supply} - 2R_{iron}^*$ have opposite signs, while given $a_4, a_5 > 0$, $R_{supply} - 2R_{iron}^*$ must be positive because at the fixed point the iron concentration must be less than R_{supply} and therefore the factor in the square brackets in the a_4 formula must be positive. Now we get a necessary condition for stability of fixed points in Eq. (1) to Eq. (3):

$$v_{12} + v_{21} > 1. \quad (12)$$

Combining it with the requirement of positivity, we can get a stronger condition:

$$\frac{v_{22}}{v_{12}} < \frac{\alpha_{1,0}}{\alpha_{2,0}} < \frac{v_{21}}{v_{11}} \quad (13)$$

Equations 12-13 constitute the necessary conditions for two partial producers to stably coexist. According to Equation 12, the whole system should prefer the two cheating-receptors ($v_{12} + v_{21}$) more than the two self-receptors ($v_{11} + v_{22}$). Meanwhile, Equation 13 establishes the species' self-investment range ($\alpha_{1,0}/\alpha_{2,0}$) based on the preferences for siderophores by their own producers versus the cheater (v_{22}/v_{12} , v_{21}/v_{11}). To illustrate, if the type 2 siderophore gets more favored by its own producers than by the cheater (v_{22}/v_{12} increases), it implies that either the producer (species 2) should allocate less to growth (resulting in a smaller $\alpha_{2,0}$) or the cheater (species 1) should increase its investment in self-growth (resulting in a larger $\alpha_{1,0}$).

Similarly, it can be proven that the necessary condition for species 1 to exclude species 2 ($M_1^* > 0, M_2^* = 0$) is:

$$\alpha_{1,0} v_{11} - \alpha_{2,0} v_{21} > 0 \tag{14}$$

Aligned with the analytical derivation, simulation of the ODE model delineates a phase diagram that categorizes the ecosystem into four distinct regions (Figure2 B), based on preference of receptors. In simulation, we assigned species 1 to allocate more resources for self-investment ($a_{1,0} = 0.8$ and $a_{2,0} = 0.4$). In the phase diagram, coexistence locates in the lower-left region, where species exhibit a stronger preference for cheating-receptors over self-receptors. This is analogous to the mutual invasion in the resource-consumer model[26,29]. Conversely, a bistable zone emerges when both species strongly favor their respective self-receptors.

Due to that species 1 invest more on growth and less on siderophore production, species 1 excludes species 2 when species 1 prefers its self-receptors and species 2 also prefers siderophore 1. Conversely, extinction zones manifest when species 1 benefits from pirating species 2's siderophores, while species 2 prefers to utilize its own siderophores. This is similar to the situation where a cheater invades and causes a population collapse: species 1 easily invades species 2, leading to its extinction, yet species 1 is ineffective in utilizing its own siderophores.

Under this straightforward two-species model, the preceding analysis and simulation highlight the essential criteria for coexistence, underscoring the significance of maintaining an appropriate level of siderophore piracy among interacting species. This prompts us to delve deeper into the dynamics of interactions, particularly under multi-species conditions.

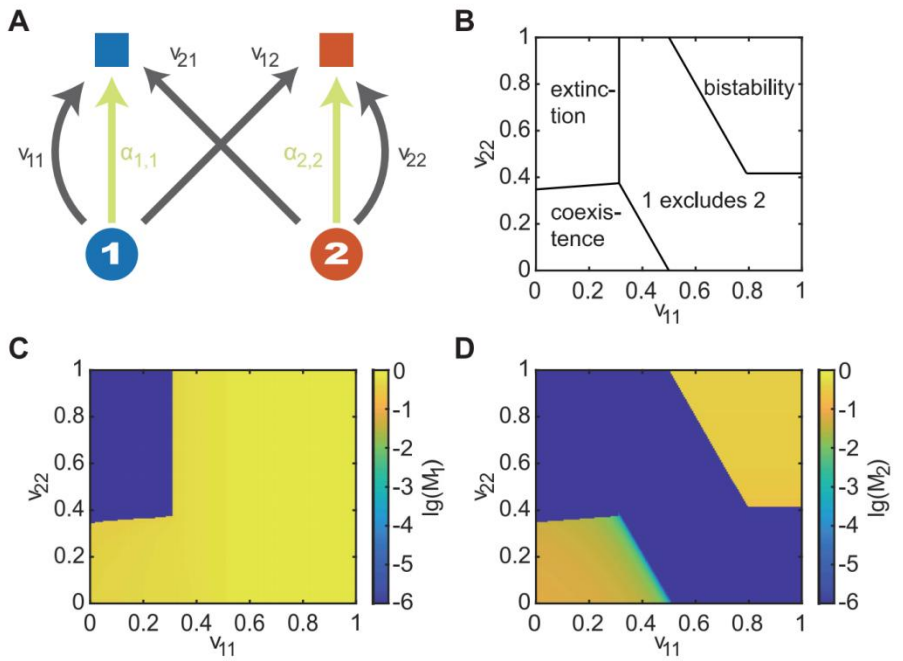

Figure 2. Phase diagram for the two-species ecosystem

(A) Schematic diagram of the two species Interactions: Circles denote species; squares symbolize siderophores; different colors indicate different types of siderophores. Yellow arrows represent production processes, and gray arrows signify utilization.
(B) Phase diagram of the system outcomes depending on receptor preferences. In the 'coexistence' region, both species can coexist stably; the '1 excludes 2' region indicates that species 2 is outcompeted by species 1; in the 'bistability' region, each species has the potential to exclude the other based on the initial conditions, offering two single-species equilibrium states; the 'extinction' region indicates that neither species can maintain stable existence, with the only stable point being total extinction.
(C-D) Biomass of species 1 (C) and species 2 (D) at equilibrium under different receptor preferences, by simulation. In (C), the biomass of species 1 is 100 times that of species 2 in the initial condition. In (D), the biomass of species 2 is 100 times that of species 1.

Multi-species interactions lead to oscillation and chaos

Oscillation can emerge in a three-species community. We initiate our exploration with a tri-species system (Figure 3A). Each species produces one type of siderophores, and has the potential to uptake three types of siderophores. Proportions of the self-receptors (v_{ii}) in all species are set to the same parameter, v_{self}. In additional to the allocation to self-receptors, If species 1 can uptake the siderophore of type 2 ($v_{12} > 0$), species 2 can uptake the siderophore of species 3 ($v_{23} > 0$), and species 3 can uptake the siderophore of type 1 ($v_{31} > 0$), then the system forms a clock-wise rock-paper-scissor ring, and we set the parameter v_{123} that $v_{12} = v_{23} = v_{31} = v_{123}$. Similar, a counter-clock-wise rock-paper-scissor ring can be characterized by $v_{32} = v_{21} = v_{13} = v_{321}$. The two parameters v_{123} and v_{321} symbolizing the strength of the clock-wise and counter-clock-wise cheating respectively. There are constraints that $v_{\text{self}} + v_{321} + v_{123} = 1$.

Akin to those observed in the two-species systems, simulation unveils that coexistence is more likely when cheating receptors are favored over self-receptors (Figure 3B): as v_{self} increases, the system can transit from stable coexistence into oscillatory coexistence, and then competitive exclusion.

Various parameter changes can induce different bifurcation types. To explore dynamic behaviors in the coexistence zone and understand changes at behavior boundaries in Figure 3B, we systematically increased the v_{123} parameter while reducing v_{self}. This led to a transition from single-species survival to oscillatory coexistence of all three species, featuring period-doubling bifurcation (Figure 3C). This bifurcation occurs precisely on the boundary between the exclusion and oscillation regions in Figure 3B. Furthermore, by increasing v_{123} while reducing v_{321} (v_{self} maintains constant), we observed a Hopf bifurcation, shifting from stable to oscillatory coexistence among the three species. These findings suggest potential intricate dynamical behaviors within the system.

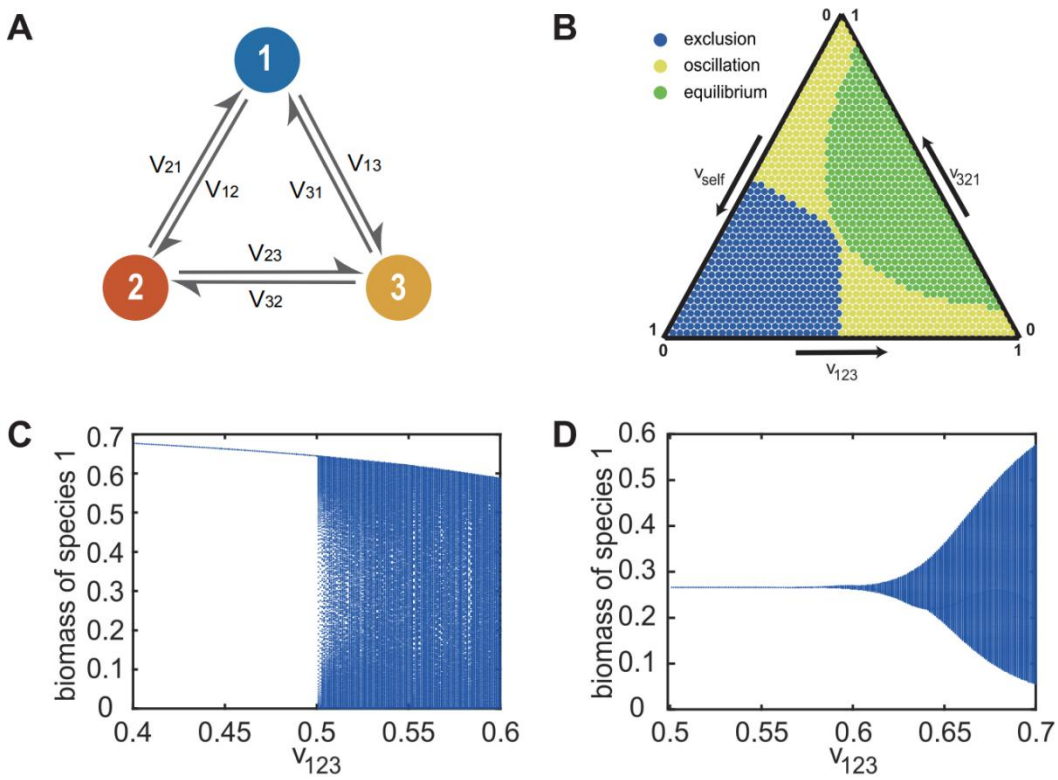

Figure 3. Dynamics and bifurcations in a tri-species system

(A) Simplified three-species interaction network. The diagram illustrates two cycle where three species utilize siderophores produced by other species, where v_{ij} indicates the preference of species i pirating the siderophore produced by species j.

(B) Phase diagram of the system in (A).

(C) Infinite-period bifurcation leading to oscillations, observed as the cheating strength increases.

(D) Hopf bifurcation leading to oscillation, observed with an increasing difference in the cheating strengths between the clock- and counterclockwise rings

In a five-species interaction network (Figure 4A), chaos has emerged (Figure 4B). To elucidate how network properties impact the system's dynamics, we introduce two independent parameters: 1. v_{self}, the fraction of self-receptors, and 2. δv, the variance between fractions different cheating edges. We observed that, as the self-utilization strength (v_{self}) increases, the system transit from chaotic region into stable oscillations, then exclusion (Figure 4C). Also, when the variance in cheating strength (δv) increases, the system enters chaotic region through period-doubling bifurcation (Figure 4D).

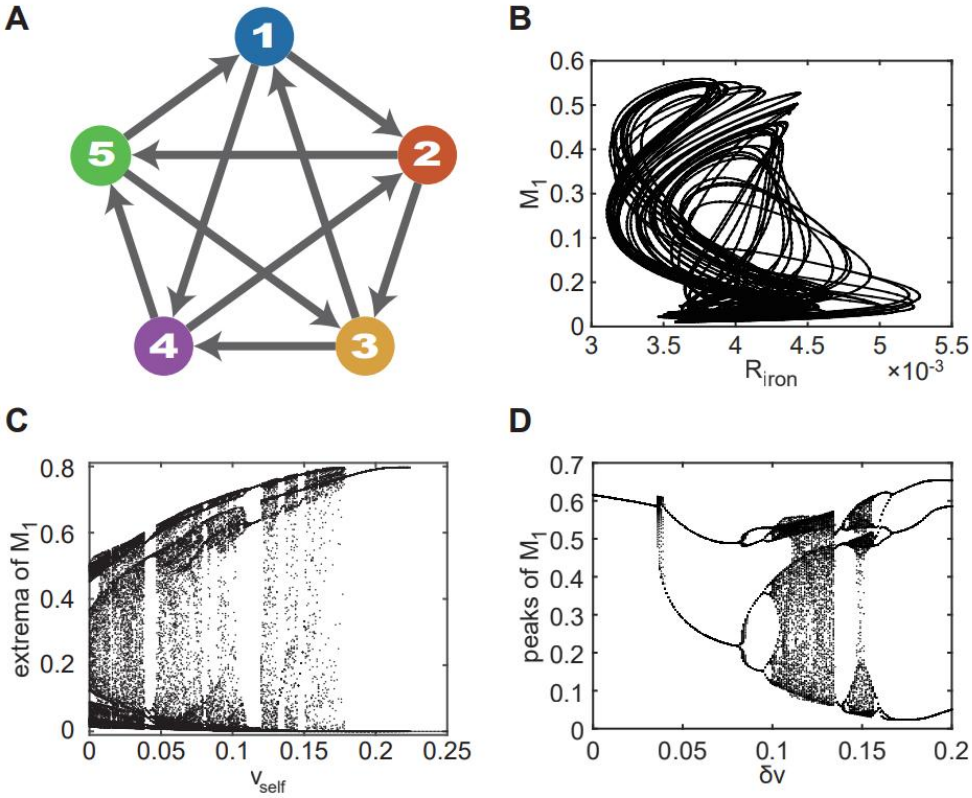

Figure 4 Chaotic dynamics in a pentadic-species system

(A) Simplified five-species interaction network. In the diagram, the gray arrows represent the utilization of siderophores produced by other species. The arrows point from the cheating species to the exploited species. For any species i,$v_{ii} = v_{\text{self}}$, $v_{12} = v_{51} = 1/2\,(1 - v_{\text{self}} + 3v_{\text{diff}})$, $v_{14} = v_{53} = 1/2\,(1 - v_{\text{self}} - 3v_{\text{diff}})$,$v_{23} = v_{31} = v_{45} = 1/2\,(1 - v_{\text{self}} + v_{\text{diff}})$,$v_{25} = v_{34} = v_{42} = 1/2\,(1 - v_{\text{self}} - v_{\text{diff}})$

(B) A representative trajectory depicting chaotic dynamics. In addition to iron concentration on the x-axis, the biomass of species 1 is also utilized as a representation of the system dynamics on the y-axis.

(C) Bifurcation diagram illustrating the system's response to an increase in self-utilization strength.

(D) Bifurcation diagram illustrating the systems' response to an increase in the cheating strength difference.

Collectively, our case observations on the tri- and pentadic- species models unveil intriguing and complex dynamical behaviors within the iron interaction system. In both instances, the inclination of species towards cheating appears to foster dynamic coexistence. While these two models leverage specialized interaction frameworks to illustrate transitions between exclusion, coexistence, oscillation, and chaos, extrapolations from more expansive community models indicate that this trend is not an isolated occurrence but rather a generalized phenomenon.

Cheating in partial producers, but not pure cheaters, promotes more surviving species in large species pool

Expanding on the previous section, we transitioned into a generalized exploration of diverse species and siderophores within natural ecosystems. Through simulations, we modeled communities comprising 100 species ($N_{\mathrm{spe}} = 100$) and 50 siderophores ($N_{\mathrm{sid}} = 50$) with randomized $\alpha_{i,j}$ and v_{ij} matrices. Our observations focused on key metrics such as species survival rates and oscillatory coexistence patterns, as we change two parameters related to cheating behavior: the weight of self-receptors relative to cheating receptors $w_{self} = \sum_{\alpha_{ij}>0} v_{ij} / \sum_{\alpha_{ij}=0} v_{ij}$, and the average number of cheating receptors per species $D_{cheat} = \sum_{\alpha_{ij}=0,\, v_{ij}>0} 1/N_{spe}$.

We observed that, within a certain range, increasing the average number of cheating receptors enhances coexistence. As D_{cheat} gradually increases, a transition takes place near the mean cheating type of 10, shifting the system from single-species exclusion to multi-species coexistence (Figure 5A). Concurrently, the proportion of communities exhibiting fluctuating dynamics also undergoes a significant elevation. This trend of heightened species diversity with increased cheating types holds true across varying relative weights of self-receptors (w_{self}). Notably, a smaller weight of self-receptors can amplify this trend, supporting the notion that cheating can indeed foster species diversity.

To discern whether stable fixed points or dynamical attractors predominantly contribute to the rise in species diversity, we calculated the average number of surviving species in both stable and dynamical (including both oscillatory and chaotic) attractors (Figure 5C). The results clearly indicate that communities in stable points typically exhibit only one or two species coexistence, whereas in dynamical communities, a more diverse array of species coexists. Hence, the elevation in the average number of surviving species primarily stems from an increase in the proportion of communities displaying dynamical coexistence, consequently accommodating a greater number of species.

We also observed that fluctuating communities exhibit distinct biomass distribution patterns compared to equilibrium ones. As indicated by the study by Dalmedigos et.al, in the stable communities, some species have relatively high biomass and most species go extinct(exactly speaking, at the ’migration floor’, which means the biomass is mostly maintained by migration) [30]. In our simulation, only a limited number of species maintain intermediate biomass levels. Conversely, in fluctuating communities, a significant number of species exhibit intermediate biomass and constitute a substantial portion of the surviving species (Figure 5D). Typically, a species may have high biomass at times and be near the 'migration floor' at other times. The mean biomass over a specific time window is roughly proportional to the duration during which the species maintains relatively high biomass (Figure5 D). Consequently, the abundance of species with intermediate biomass

implies significant variability in the widths of biomass peaks among different species.

To ensure that the observed phenomena in this section are not artifacts resulting from specific parameter choices, we conducted additional investigations to assess the impact of varying other parameters (Details in Supplementary Information), including initial growth resource allocation ($\alpha_{i,0}$) and intake rate constants (u_j). Our findings suggest that, with the exception of a substantial reduction in intake rate constants u_j, the majority of examined parameters have no qualitative effects on the outcomes depicted in Figure 5. This lends support to our initial hypothesis that the properties of cheating play a significant role in shaping community outcomes.

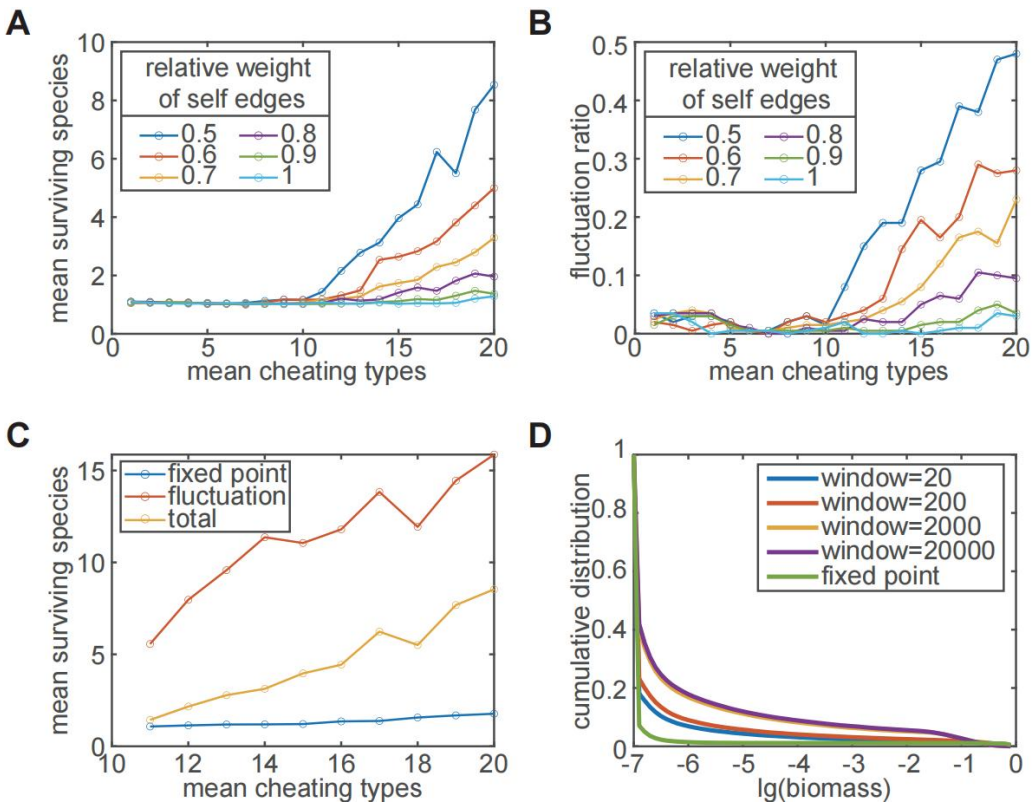

Figure 5. Statistical properties of large microbial community in iron interactions

(A) How the average number of surviving species in a community (y-axis) increase with the number of cheating receptors each species can utilize (x-axis, D_{cheat}). Different relative strengths of self-receptor (w_{self}) are indicated by different colors.

(B) Same as (A), except that the y-axis is the fraction of simulations exhibiting fluctuating dynamics (not distinguishing chaos or oscillation)

(C) Comparison of the average numbers of surviving species in the stable (blue color) and fluctuating (red color) communities. Here, the relative self-receptor strength w_{self} is set at 0.5.

(D) Biomass cumulative distribution in fluctuating communities and stable communities, over different time windows. Here, the relative self-receptor strength w_{self} is set at 0.5. The cumulative distribution defined as $\mathcal{F}(M) = \sum_{M_i > M} 1/N_{\text{spe}}$, is essentially the integral of the single-species biomass probability distribution.

However, the phenomenon of increasing cheating enhancing coexistence only occurs within a certain range—namely, for cheating receptor types smaller than 20. As we further increase the number of cheating receptors from 20 to 50, the diversity and fluctuation ratio in communities begin to decrease after surpassing a certain maximum level (Figure 6 A-B). This outcome indicates that only an optimal number of cheating receptor types promotes the coexistence of numerous species.

We also noted that elevating the ratio of pure cheaters in the species pool leads to a suppression of diversity and fluctuation. It is worth emphasizing that the decline in diversity due to an increase in cheating types occurs relatively late if there are no pure cheaters in the species pool (Figure 6C). As the ratio of pure cheaters increases (Figure 6D), the probability of extinction rises, contributing to the decline in diversity. In summary, biodiversity follows a non-monotonic trend concerning the types of cheating receptors per species, indicating an "optimal level" of cheating that maximizes the survival of species in a dynamic manner. Importantly, this optimal cheating is contributed by partial producers, as cheating in pure producers is detrimental to the community.

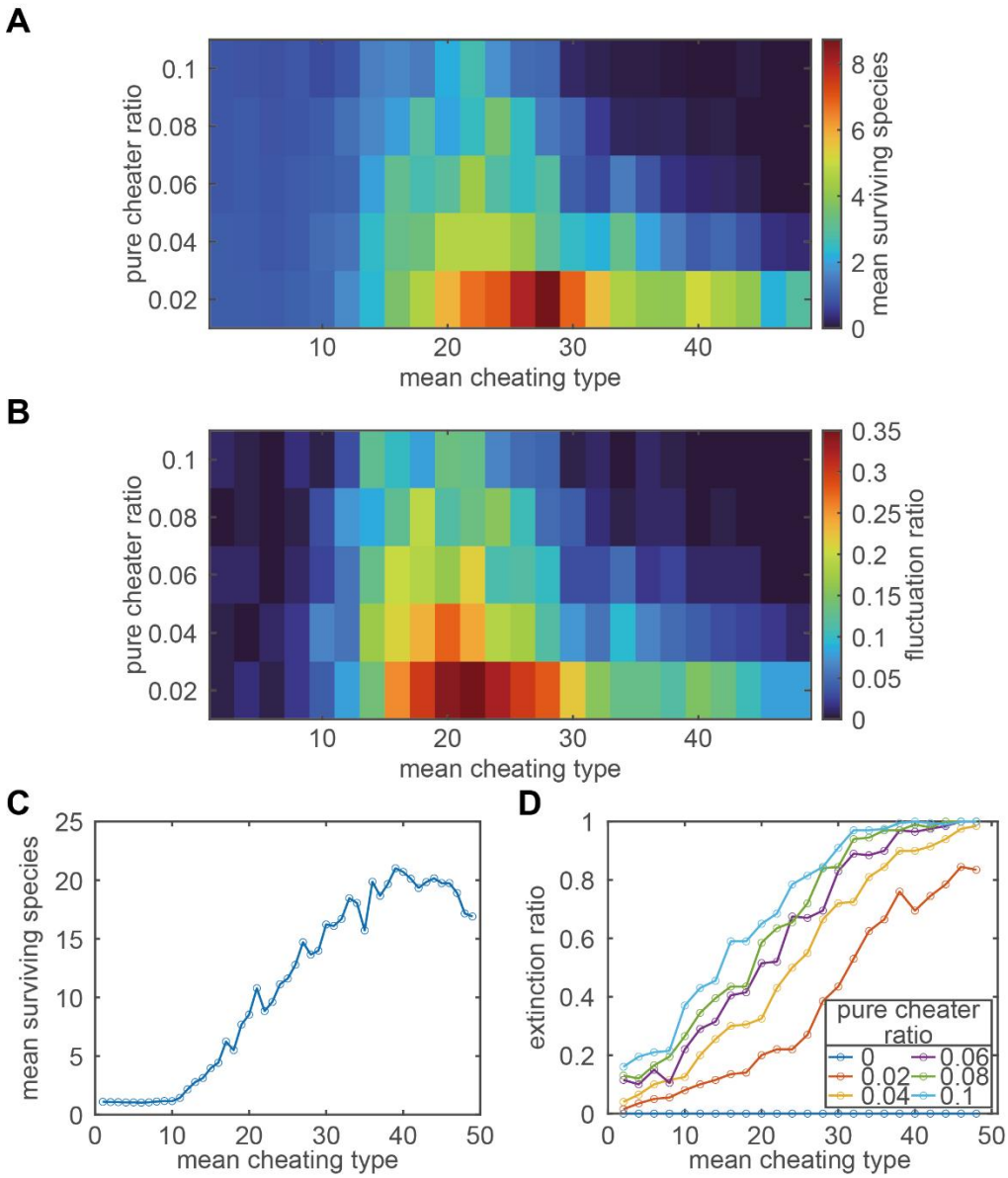

Figure 6. Dependence of biodiversity on the average number of cheating receptors and the ratio of pure cheaters.

In this figure $w_{self} = 0.5$.

(A) Heatmap illustrating the mean surviving species under varying numbers of cheating receptors (x-axis) and ratios of pure cheaters in the community (y-axis).

(B) Same as (A), except that the heatmap color represents the fraction of simulations exhibiting fluctuating dynamics (not distinguishing chaos or oscillation)

(C) Mean surviving species with increasing mean cheating types, for communities with no pure cheater.

(D) Extinction ratio with increasing mean cheating types, with varying ratios of pure cheaters.

Discussion

The exploration of microbial community diversity has long been a central focus in theoretical ecology, with resource dynamics playing a crucial role. In this study, we investigated the impact of resource partitioning on community dynamics, leveraging the widespread presence of siderophores in microbial systems. Our generalized resource partition model, distinct from traditional approaches, incorporates the active production of diverse siderophores by microbes to partition iron resources, introducing new resource dimensions. In assessing the general properties of resource partition model, we found that self-generated resource dimensions can give rise to complex dynamics, especially the emergence of oscillatory or chaotic dynamics with various types of bifurcations. Notably, coexistence in the community, stable or dynamical, is closely related to siderophore piracy. Specifically, cheating promotes biodiversity when it is within an appropriate level, contributed by partial producers instead of pure producers. In other words, in siderophore-mediated microbial interactions, cheating serves as the primary driving force for coexistence.

The role of cheating in microbial interaction and coexistence

The interplay between cheating and cooperation has long been a focal point in microbiology[31]. Classical game theory traditionally views "cheaters" as agents of destruction, resulting in suboptimal outcomes for all parties involved[32]. Similarly, in the biological world where social interactions are intensive, traits associated with cheating are often considered disruptive, posing a potential threat to the survival of the entire community[33]. Therefore, researchers have dedicated efforts to unravel the mechanisms that uphold cooperation, employing strategies such as introducing spatial heterogeneity, kin selection, and implementing punishments[6-9]. Conversely, cheating has been proposed as a catalyst for promoting diversity. For example, relationships of mutual inhibition or cheating similar to "rock-paper-scissors" can promote species coexistence in homogeneous environment[34,35]. Furthermore, theoretical explorations in eco-evolutionary games have unveiled intriguing phenomena, highlighting instances where mutualism arises from cheating[36-39].

Our research reveals that, on an ecological scale, iron piracy in partial producer can promote dynamical coexistence, without relying on specifically designed interaction structures. Within a larger microbial community, cheating-receptors serve as pivotal nodes connecting different species, and the overall coexistence is heavily influenced by the diversity of siderophores each species can absorb. Within a certain range, an increase in cheating-receptor types correlates with higher average species diversity. This diversity arises because species can more effectively utilize siderophores produced by others, reducing the likelihood of a few species excluding all others. Importantly, it's worth noting that pure cheaters, devoid of any cooperative aspects, still exhibit purely destructive behaviors. Interestingly, empirical observations corroborate with the role of partial

489 producers, revealing microbes capable of producing just one siderophore type but
490 possessing receptors for multiple others[40-42].
491
492 Yet, the benefits of expanding cheating-receptor diversity promote coexistence only within
493 appropriate limits. Using the average number of community-surviving species as a metric,
494 our results indicate that an excessive proliferation of siderophore receptors does not
495 necessarily elevate community robustness—in fact, it may diminish diversity after certain
496 threshold, especially when there are pure cheaters (see Figure 6A and Supplementary
497 Information). Biologically, expanding the range of siderophore receptors excessively
498 incurs significant metabolic costs, which may negate any potential benefits. Furthermore,
499 the presence of even a small number of 'pure cheaters' intensifies this issue. With too
500 many receptor types, the likelihood of complete species extinction increases. This is
501 because, if every species is capable of uptaking most siderophore types, it becomes
502 improbable for a subset of surviving species to effectively exclude all 'pure cheaters,'
503 especially if they are unable to produce siderophores that these cheaters cannot uptake.
504 Conceptually, although cheating serves as a potent strategy for undermining interspecies
505 fitness, it inadvertently fosters broader dynamic coexistence, even if such an outcome is
506 not an intentional objective from the microbial standpoint.
507

508 **Public vs private siderophores**

509 We expand upon the concepts of "public" and "private" siderophores as a continuum
510 rather than binary categories. Public siderophores are those that can be utilized by a
511 broad array of microbial species, whereas private siderophores are specialized forms
512 accessible only to specific microbial classes[17,18]. Our recent work indicated not only
513 amazing diversities in siderophore[43] but also the pervasive “Lock-Key” relationship
514 between siderophore and receptors[19]. Microbes frequently require specialized
515 cheating-receptors to safeguard these common iron resources from competitive
516 exploitation[44], adding complexities into the interplay between cheating and cooperation.
517 Cooperative actions often exhibit a 'private' characteristic, limited to either the organism
518 itself or its phylogenetically related counterparts. Such private siderophores could function
519 as key factors in enhancing individual fitness. On the other hand, public siderophores,
520 particularly high-affinity variants like Enterobactin, act as a sort of 'universal currency' for
521 iron[22,45]. Cheating and cooperation thus act as antagonistic forces: one diminishing the
522 fitness of competing species while the other elevates individual adaptability. Intriguingly,
523 our model suggests that undermining the fitness of competitors via cheating mechanisms
524 might be more pivotal for sustaining community coexistence than merely boosting one's
525 own adaptive advantages in producing and utilizing siderophores.

526 **Regulation and absorption**

527 There are several factors not yet incorporated into our current model framework. For
528 simplicity, we did not consider microbial regulatory mechanisms for receptor expression.

One immediate limitation stems from the model assumption that microbes constantly express all available receptors, an approach that is neither energy-efficient nor optimal for maximizing iron absorption. Experimental studies have shown that microbes can sense siderophores in their environment and adjust the expression of corresponding receptors[24]. This implies a more nuanced level of environmental sensing and adaptability, suggesting that receptor expression in microbes is dynamically regulated rather than a fixed attribute. Additionally, our model makes assumptions about the forms of growth dependence on resources, absorption kinetics of siderophore receptors, and chelation kinetics of siderophores. In the Supplementary Information (see section 'The generalized community model for siderophore-mediated interaction'), we discuss a generalized model with saturated kinetics and find that the model is robust to slight deviations from these assumptions, although results can vary significantly when these factors are substantially altered. In summary, the current simplified model serves as a starting point; future modifications can be made based on specific needs and circumstances.

Coexistence in fluctuations

Understanding biodiversity is a central focus in theoretical ecology[46]. Microbes vary in their capabilities for nutrient uptake, necessitating a well-balanced environmental fitness for stable coexistence[26]. This balance entails resource competition and subsequent alterations to the environmental chemical landscape. Classical resource competition models stipulate the Competitive Exclusion Principle (CEP), stating that the number of stable coexisting species cannot exceed the number of resources they compete for[47]. However, real-world observations frequently contradict this theory, as microbial diversity often exceeds these theoretical limitations. Various theories seek to bridge this gap[28,48-51], with one prevailing notion suggesting that microbes bypass the CEP by expanding resource dimensions through metabolic activities. For example, a singular carbon source can generate multiple byproducts via microbial metabolism, facilitating cross-feeding and stable coexistence[52]

Among many theories to overcome CEP, it has been suggested that fluctuating dynamics promote biodiversity[53]. In the seminal work by Huisman et.al[48], oscillatory and chaotic dynamics were found in consumer-resource model under mismatched nutrient dependence and preference, which exceed the limits of the CEP to allow for a more diverse assemblage of coexisting species. In a recent work, Hu et. al showed oscillatory dynamics emerges under large pooling size and strong interactions, which also coincides with an increase in diversity[54]. Adding to these discourses, our prior investigation posited that self-generated dimensions within resource partition schemes are capable of inducing oscillatory dynamics in community ecosystems[17]. In the current study, our observations at the community scale unveil a prevalent form of dynamic coexistence that accommodates a broader spectrum of species than stable coexistence, yet remains within the confines set forth by the CEP. Nevertheless, the production of various siderophores increases the nutrient dimensions in the microenvironment, elevating the upper boundaries of the CEP.

Intriguingly, the induction of fluctuating dynamics is attributed to cheating, a phenomenon widespread in microbial iron utilizations and possibly evolutionarily favored.

It has been observed microbes in their natural habitants exhibit oscillatory dynamics [55,56]. However, verifying dynamical coexistence in the wild is challenging, as external periodic factors may interrupt observations, such as day and night cycles, temperature variations, and seasonal changes [57]. Recent works have observed oscillations in lab experiments[54,58], providing valuable insights for further exploration. Understanding how these findings translate to natural settings remains an exciting avenue for future research.

In summary, our study offers a novel computational model that illuminates the complex interplay of resource partition and cheating mechanisms in shaping microbial community dynamics. Leveraging the role of siderophores as key agents, we elucidate how cheating operates as a pivotal driver for community coexistence. Despite that the model's current form is highly simplified, warranting future exploration, these insights not only enrich our understanding of microbial community resilience and diversity but also offer valuable implications for future biotechnological applications.

Author contributions

Conceptualization, Z.L., J.S..; Methodology, J.S., and Y.L.; Formal Analysis Y.L., J.S.; Writing – Original Draft, J.S., Y.L., Z.L.; Funding Acquisition, Z.L., S.G.; Supervision, Z.L.

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Declaration of Interests

The authors declare no competing interests.

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