The role of competition versus cooperation in microbial community coalescence

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Abstract

Microbial communities are ubiquitous in nature, and rapid advances have been made recently in our understanding of how they assemble and persist. A relatively poorly understood phenomenon is that of "community coalescence", where a new microbial community arises through the encounter and mixing of two or more separately assembled communities. In particular, while recent theoretical work has begun to elucidate the role of competition in coalescence, that of the other key interaction type commonly seen in microbial communities, cooperation, remains unclear. Here, we study the combined effects of competitive and cooperative interactions on the outcome of coalescence events. We simulate communities with varying levels of each type of interaction using a general consumer-resource model where microbial populations can both compete, and cooperate through cross-feeding on metabolic by-products. We perform extensive coalescence simulations of pairs of pre-coalescence communities lying on the spectrum from competition to cooperation, to gain general insights into their relative rolesin determining coalescence success. We find that when both interactions are present in two parent communities, the less competitive one tends to dominate during coalescence, regardless of its cooperativity, suggesting that minimizing competition is the main driving force of this process. When competition in parent communities is weak however, counter-intuitively, more cooperative ones are at a disadvantage in coalescence events because multi-species invasions tend to disrupt established cooperative links. Our results provide new, empirically-relevant predictions about key factors determining microbial community coalescence, and a framework to make new predictions about coalescence based on the interaction structures of coalescing communities.

Introduction

Microbial communities are widespread throughout our planet [1], from the the human gut to the deep ocean, and play a critical role in natural processes ranging from animal development and host health [2, 3] to biogeochemical cycles [4]. These communities are very complex, often harbouring hundreds of species [5], making them hard to characterize. Recently, DNA sequencing has allowed a high-resolution mapping of these consortia, opening a niche for theoreticians and experimentalists to collaboratively decipher the complexity of these systems [6–14]. Despite thorough explorations, the mechanisms responsible for the assembly of microbial communities have only begun to be revealed.

Unlike in the macroscopic world, entire, distinct microbial communities are often displaced over space and come into contact with each other due to physical (e.g., dispersal by wind or water) and biological (e.g., animal-animal interactions or leaves falling to the ground) factors [15–18]. The process by which two or more communities that were previously separated join and reassemble into a new community has been termed community coalescence [19]. Despite the frequency of microbial community coalescence, the outcome of such events in terms of community structure and function remains poorly understood [20].

Early mathematical models of community-community invasion in animals and plants revealed that when two communities merge after barrier removal, asymmetrical dominance of one community over the other one is likely to occur [21, 22]. As an explanation for this observation, it was argued that, because communities have been assembled through a history of competitive exclusion, they are likely to compete with each other as coordinated entities, rather than as a random collection of species. This result has been established more rigorously in recent theoretical work, where consumer-resource models have been used to show that in microbial community coalescence events, the winning community will be that which is capable of simultaneously depleting all resources more efficiently [23, 24]. Overall, these findings suggest that communities arising from competitive species sorting exhibit sufficient "cohesion" to prevent invasions by members of other communities.

However, empirical support for the role of competition alone in coalescence remains circumstantial, and the role of cooperation, which is commonly seen in microbial communities, remains largely unknown. For example, during coalescence in methanogenic communities, cohesive units of taxa from the community with the most efficient resource are co-selected [25], and in aerobic bacterial communities, the invasion success of a given taxon is determined by its community members [26], but neither of these studies was able to establish that competition was the dominant factor shaping cohesiveness and coalescence success. The microbial communities in these experiments presumably display some degree of cooperation through cross-feeding, where leaked metabolic by-products of one species act as substrates for others [27–29]. These cross-feeding networks can vary in their particular link distribution (the architecture of the flow of metabolites shared across species), but also in their link weights (the fraction of consumed resources that is secreted to the environment as metabolic by-products instead of kept for private consumption) [30]. Indeed, several studies have suggested that a combination of competitive and cooperative interactions may determine the outcome of coalescence in microbial communities [31–33].

Here, we focus on the gap in our theoretical understanding of the relative importance of competition and cooperation in community coalescence, which is is largely missing. We use a consumer resource model that includes cross-feeding to assemble complex, cohesive microbial communities spanning a broad range in the competitive-cooperative spectrum. Using novel metrics, we then quantify competition and facilitation levels in the assembled communities, and determine the relative importance of the two types of interactions on success in pairwise coalescence events. We find that when competition and cooperation are present, cohesive communities out-perform competitors in coalescence events, both with and without the effects of leakage. However, when competition is negligible, we find that cohesion is detrimental to to coalescence success.

Consumer-resource-crossfeeding model

We use a consumer-resource model based on Marsland et al [6] for the change in consumer and resource abundance over time:

$$\frac{dn_\alpha}{dt} = g_\alpha n_\alpha \left((1-l) \sum_j c_{\alpha j} R_j - z_\alpha \right), \tag{1}$$

$$\frac{dR_j}{dt} = \kappa_j - \sum_\alpha n_\alpha c_{\alpha j} R_j + l \sum_{\alpha k} n_\alpha D_{kj} c_{\alpha k} R_k. \tag{2}$$

Here, R_j, where $j \in \{1 \dots m\}$, is resource abundance, and n_α, where $\alpha \in \{1 \dots s\}$, is the abundance of bacterial species. κ_j is the supply rate of resource j. The growth of species α is determined by the resources it harvests, which in turn depends on the resource concentration R_j, and whether or not the species α uses resource j ($c_{\alpha j} = 1$ or $c_{\alpha j} = 0$, respectively). Not all the harvested resources contribute to growth, and a fraction, l, leaks back to the environment as metabolic by-products. The matrix element D_{jk} represents the leaked proportion of resource j that is transformed into resource k. Note that, by definition, D is a row stochastic matrix, i.e., its rows sum to 1. Each species's population uses part of its energy intake for maintenance z_α, which we assume is given by:

$$z_\alpha = \chi_0 \sum_j c_{\alpha j} (1 + \epsilon). \tag{3}$$

Here, χ_0 is the average cost of being able to consume a given metabolite, the summation represents the number of resources that species α is able to process, and ϵ is a random fluctuation sampled from a truncated normal distribution (to ensure that $z_\alpha > 0$). Eq 3 ensures that neither generalists nor specialists are systematically favoured during the community assembly (For more information, see Supporting text.). The remaining resources after subtracting leakage and maintenance are transformed into biomass with a proportionality constant of g_α, the value of which does not affect the results presented here. See first vignette in Fig 1 for a graphic representation of the behaviour just described.

The above model entails the following assumptions: (i) all resources contain the same amount of energy (taken to be 1 for simplicity), (ii) a type I functional response, (iii) a binary matrix of consumer preferences, (iv) a shared core metabolism encoded in D, and (v) a complex environment where all resources are externally supplied in equal amount.

Competition and facilitation metrics

In the system described by Eqs 1 and 2, competition for resources exists because of the overlap in metabolic preferences (the $c_{\alpha j}$s) between species. The actual strength of competition between species depends on the resource environment they experience, which is made up of two parts; the externally supplied resources, and the metabolic by-products generated by the community. As such, we calculate individual pairwise competition strength by considering the competition for resources from these two sources. We then measure community-level competition by taking the average competition strengths across all species pairs (see Supporting text for details), that is

$$\mathcal{C} = \langle (C_a)_{\alpha\beta} + (C_b)_{\alpha\beta} \rangle_{\alpha \neq \beta}, \tag{4}$$

where $(C_a)_{\alpha\beta}$ measures the level of competition between species pair (α, β) for externally supplied resources, and $C_b)_{\alpha\beta}$ the level of competition for resources that have been leaked by species across the community

We define the competition for externally supplied resources $(C_a)_{\alpha\beta}$ to be,

$$(C_a)_{\alpha\beta} = (1-l)\sum_k \tilde{\kappa}_k c_{\alpha k} c_{\beta k}. \tag{5}$$

Here, intrinsic competition between the species pair is quantified by their common metabolic preferences through the scalar product of their preference vectors. Interaction strength is determined by the fraction of externally supplied resources that is used for growth, $1-l$ and the factor $\tilde{\kappa}_j$ which accounts for possible differences in the external resource supply rate between metabolites. Competition for resources generated through metabolite leakage (the second term in Eq 4) is defined as,

$$(C_b)_{\alpha\beta} = l\sum_{jk} \tilde{\kappa}_j D_{jk}\left(c_{\alpha j} + c_{\beta j}\right) c_{\alpha k} c_{\beta k}. \tag{6}$$

Here, l is the strength of competition on leaked resources (see Supporting text for details), and the product $D_{jk}(c_{\alpha j} + c_{\beta j})c_{\alpha k}c_{\beta k}$ represents the necessary conditions to have effective competition for the kth leaked resource (see Supporting text for details).

Facilitation occurs when a species leaks metabolic by-products that are used by another species. Similar to competition, we compute community-level cooperation by calculating the strength of facilitation between individual species pairs and then averaging across the community:

$$\mathcal{F} = \langle F_{\alpha\beta}\rangle_{\alpha\neq\beta}, \tag{7}$$

where the facilitation between the species, $\alpha \to \beta$ is given by :

$$F_{\alpha\beta} = l\sum_{jk} \tilde{\kappa}_j c_{\alpha j} D_{jk} c_{\beta k}, \tag{8}$$

where l is the strenght of cooperative links, and the term $c_{\alpha j} D_{jk} c_{\beta k}$ represents the necessary condition to establish a cooperative link (see Supporting text for further details).

Simulations

Fig 1 presents an overview of our simulation method for analysing coalescence under the mathematical framework presented above (see the matrix implementation used in the simulations in Supporting text. We first assemble cohesive communities. To this end, we sample consumer preferences and metabolic parameters from random distributions, imposing specific constraints in order to modulate the range of competition and facilitation levels achieved in each such community at equilibrium. Once we have assembled communities lying on a spectrum of competition to cooperation, we perform coalescence simulations between random pairs of communities. Finally, we analyse the contribution from each community to the species abundance in the resulting coalesced community, and ask how this contribution depends on the nature of interactions in the ancestral communities. For the parameter values used in the simulations, see Supporting text.

Modulating competition and facilitation levels

We are interested in generating communities spanning a broad range of competition and facilitation levels. These can be modified by sampling $c_{\alpha j}$ and D_{jk} respectively, with specific constraints.

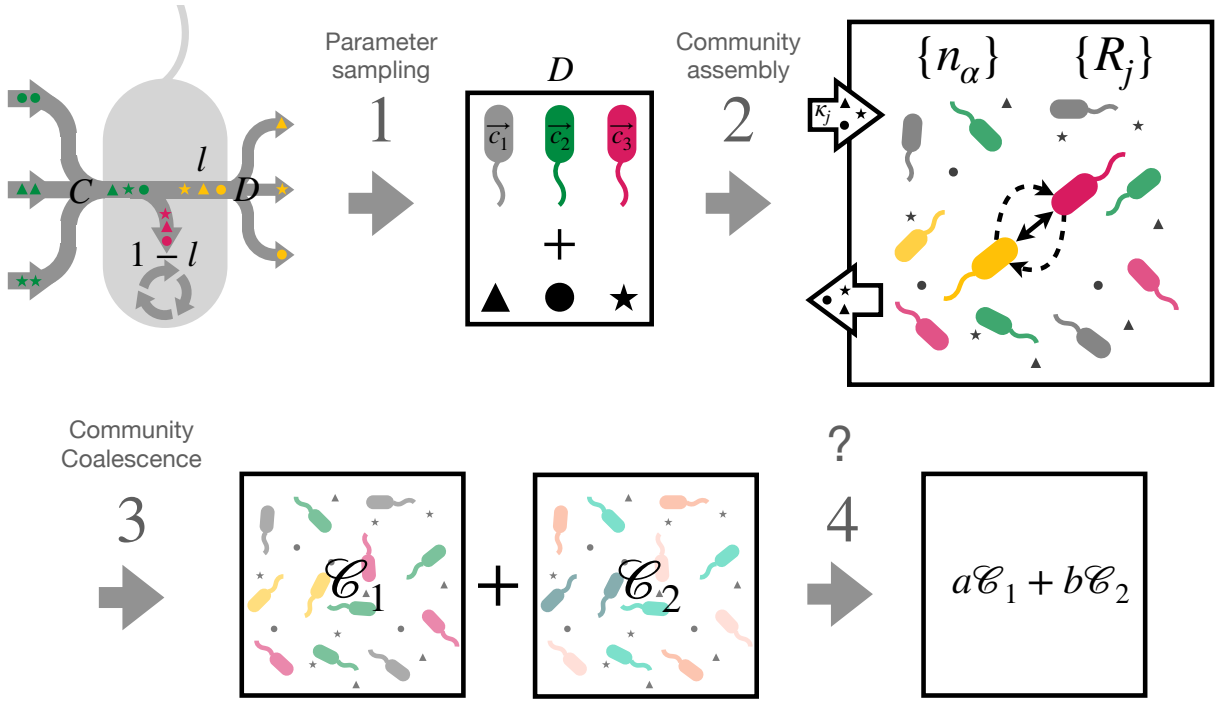

Fig 1. Overview of our coalescence simulations. Step 1 (parameter sampling): the metabolic preferences of 60 bacterial strains ($s = 60$), and the metabolic matrix D, are sampled for each community. This sampling is done either with structure in resource classes, or without it. **Step 2** (assembly): dynamics of the system are allowed to play out in an environment with $m = 60$ resources, according to equations 1 and 2 till the community reaches steady state. **Step 3** (community coalescence): assembled communities are randomly paired up and each hybrid community re-run to steady state in an environment with fresh resources. **Step 4**: the contribution of each community to the final mix is analyzed (Eq 12) as a function of the degree of competitive versus cooperative interactions in the original pair of communities.

Competition can be modulated by increasing or decreasing niche similarity between consumers. To this end, we use an iterative procedure to impose a specific level of competition (see Supporting text). In this procedure, metabolic preferences of single species are assigned iteratively by re-evaluating the probability that species α samples resource j, which is given by

$$p_{\alpha j} = (1 - k_c)\frac{1}{m} + k_c \tilde{d}_{\alpha-1 j}, \tag{9}$$

where m is the number of resource types, $\tilde{d}_{\alpha-1j}$ is the normalized cumulative demand of resource j at iteration $\alpha - 1$, and k_c is the competitiveness factor. (see Supporting text for details). In each step of the iteration, the sampling probability of each resource is changed according to the demand on it, such that highly demanded resources are more likely to be sampled in the next step. Note that k_c modulates the intensity with which consumers prefer highly demanded metabolites such that when $k_c = 0$, the sampling is uniformly random (Fig 2A), and as $k_c \to 1$, the sampling becomes increasingly preferential (Fig 2B) .

The facilitation level of the community depends on the metabolic cross-feeding topology. This information is encoded in the community metabolic matrix D (Fig 2D), which is sampled such that it mimics the distribution of resource demands. This effectively results in increasing facilitation levels by causing the community to release large fractions of the resources that are highly demanded (Fig 2E, and see Supporting

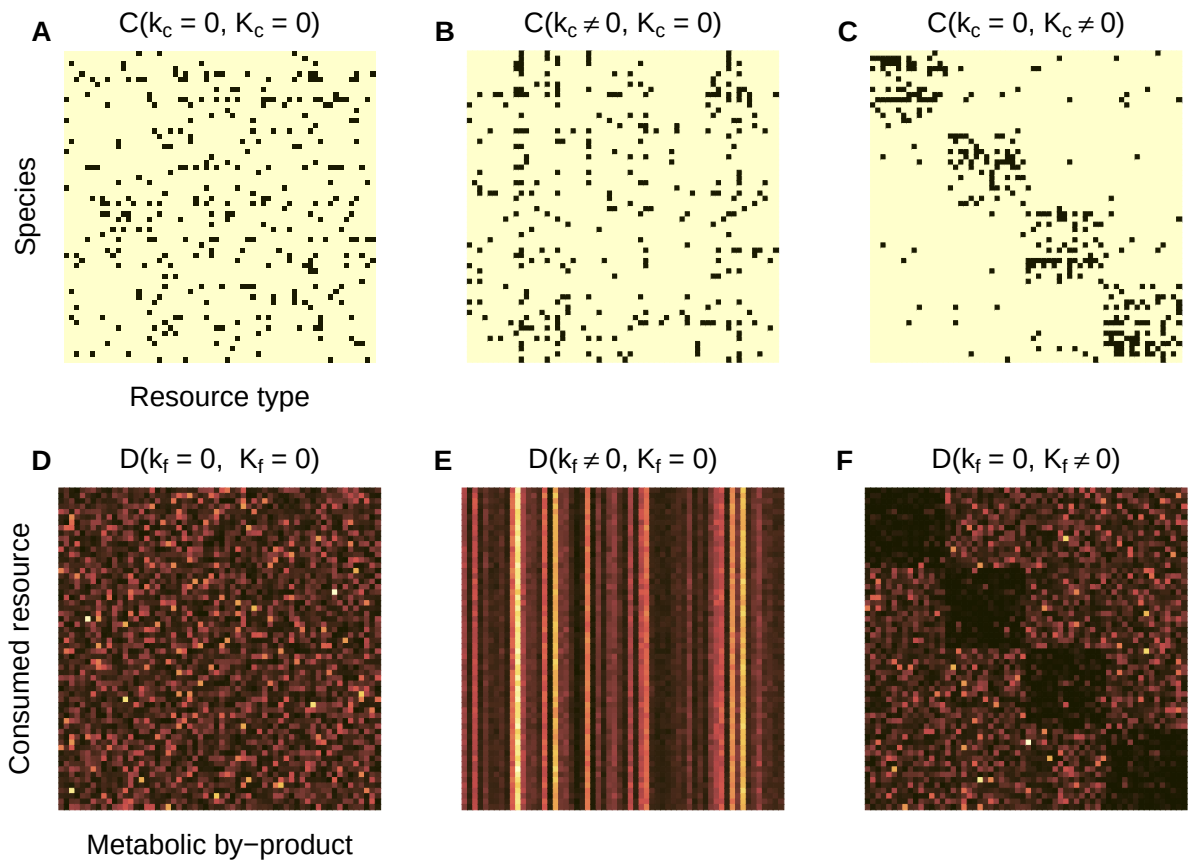

Fig 2. Examples of the preference (C) and metabolic (D) matrices for different combinations of the competition and facilitation parameters k_c, K_c, k_f, and K_f in a system of 60 resource types and 60 consumer species. Figures A and D represent purely random matrices, where all the four parameters are 0. As k_c and k_f are increased (B and E) the regime moves towards greater preferential sampling, where more demanded resources are more likely to be sampled (increase of k_c), but also secreted at higher fractions (increase of k_f). Instead, if K_c and K_f are increased (C and F), the regime moves towards greater metabolic and taxonomic structure where species are more likeley to sample resources from their metabolic class (increase in K_c), and leak a higher fraction of energy in the form of resources that don't belong to their taxonomic class (increase in K_f).

text for details).

Decoupling facilitation from competition on leaked resources

In the previous section we imposed a preferential structure in the sampling of the community's metabolic properties that allowed us to modulate the levels of competition and facilitation. However, increasing levels of facilitation by greater leaking of more demanded metabolites only decreases competition for externally supplied resources, leaving competition for leaked resources unchanged. In order to decouple facilitation from competition on leaked resources, we need to ensure that the resources species consume are not the same as those which they leak. To this end, we add further structure to the matrices C and D by partitioning the resources into different resource classes, and imposing an additional constraint on consumers meaning they tend to feed on a preferred class, but leak to any other.

Incorporating this structure yields two levels of cooperation; coarse structure with

inter-guild facilitation due to the existence of distinct resource classes, and a fine structure with intra-guild facilitation due to the previously imposed preferential sampling

In this case, we sample the metabolic preferences analogously to the previous section. The only difference is that the probability $p_{\alpha j}$ that species α is assigned resource j as one of its preferences has the form (this is derived in Supporting text)

$$p_{\alpha j} = \begin{cases} \frac{1}{\mathcal{A}}\left(1 + K_c(N_c - 1)\right)\left(\frac{1}{m}\left(1 - k_c\right) + \tilde{d}_{\alpha-1j} k_c\right) & \text{if } C(j) \in T \\ \frac{1}{m}(1 - K_c) & \text{otherwise,} \end{cases} \tag{10}$$

where $\mathcal{A}$ is a normalization constant ensuring that probabilities sum to 1. Each of the two pieces of this function is weighted up or down depending on whether resource j belongs in the preferred class of species α or not, respectively (Fig 2C). The magnitude of this effect is given by the heterogeneity constant K_c, which controls the amount of guild structure in the preferences matrix.

The metabolic matrix D is also constructed with the two levels of structure imposed on C. Specifically, we use a two-tier secretion model, where the first tier contains by-products that are not in the resource class of the substrate (off block-diagonals of D), and the second contains by-products that share resource class with their substrates (block-diagonals of D). The flux of resource k leaked to each tier is lower if that resource belongs to the same class as its substrate j, and higher, otherwise (Fig 2F). The amount of heterogeneity in the matrix is given by the inter-guild facilitation factor K_f (see Supporting text for details).

Community coalescence

Previous theoretical and experimental work in coalescence suggests that during these events, microbial communities exhibit an emergent cohesiveness where multiple taxa from the same community act as cohesive units and are selected together (ecological co-selection) [21–23, 25, 26]. Here, we quantitatively estimate the community cohesion (denoted as Θ), by considering the pairwise interactions between the species in the community. Generally, more cohesive communities will be those where competition is minimized and facilitation is maximized, such that

$$\Theta = \mathcal{F} - \mathcal{C}, \tag{11}$$

where $\mathcal{F}$ and $\mathcal{C}$ are the measures of competition and facilitation presented previously, Eqs 4 and 8.

First, we simulate coalescence between pairs of communities assembled under the preferential sampling scenario (Fig 3 A). Here, such events are performed by mixing in fresh media (all resources are set to the initial concentrations before assembly) a randomly picked pair of previously assembled communities (see Supporting text for further details on assembly), and letting the combined system relax to a new equilibrium state. For each value of leakage, we perform $2 \cdot 10^4$ coalescence instances. We then analyse the species abundances in the mixed community at equilibrium to understand how the interactions between species in the ancestral communities affects the outcome of the coalescence process. To this end, the cohesion values of each community Θ_1 and Θ_2 are recorded before coalescence, and the species abundance of the mix at equilibrium is analyzed in order to compute the similarity of the outcome community to each of their parent communities. This measure (see Eq 12) specifies the identity of the post-coalescence community in the basis of the parent communities C_1

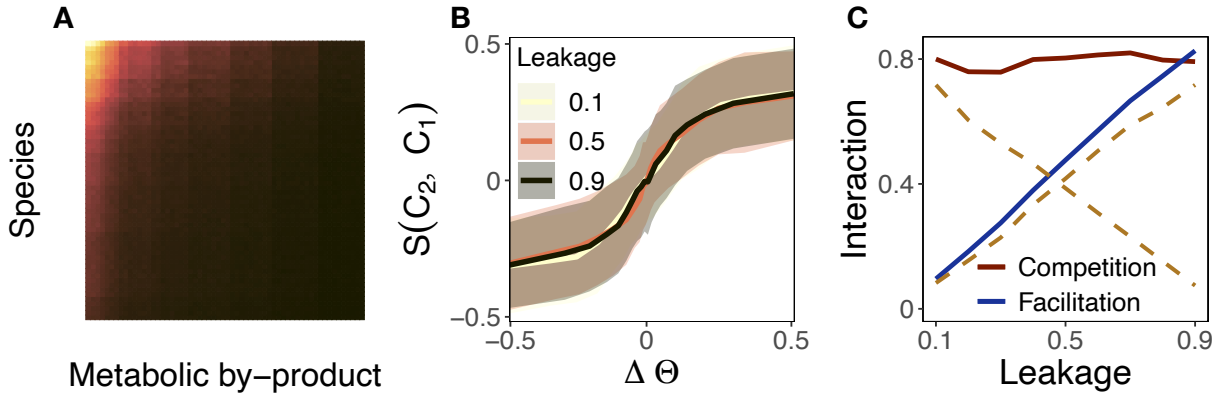

Fig 3. Coalescence results assuming preferential sampling. Figure A shows one example of the matrix of secretions $(CD)_{\alpha k}$, which represent the total leakage of metabolite k by an individual of species α. Columns and rows have been reordered according to the dominant eigenvectors of CD and $(CD)^T$, respectively. This reveals a nested structure where a portion of species (lighter top rows) leak the majority of the more demanded metabolites (lighter left columns). Figure B shows that community coalescence success is positively correlated with community-level cohesion. The composition of the post-coalescence community on the basis community 1 ($S = 1$) - community 2 ($S = -1$), $S(C_2, C_1)$ is plotted as a function of the community cohesion difference $\Delta\Theta = \Theta_1 - \Theta_2$ between them. Shown is binned mean (20 bins) over communities with similar $\Delta\Theta$ (solid line) $\pm\sigma$ (shaded). Figure C shows community-level competition $\mathcal{C}$ (dark red) and facilitation $\mathcal{F}$ (blue) averaged across simulations for each levels of leakage. When $l << 1$, abiotic competition (dashed decreasing line) dominates over biotic competition, $C_a >> C_b$ (dashed increasing), but this relation inverts as leakage increases, so that total competition C_T remains consistently high across all values of leakage. Facilitation increases linearly with l.

and C_2 and it is calculated as

$$S(C_2, C_1) = \frac{1}{r_1}\sum_{i=1}^{r_1} b_i - \frac{1}{r_2}\sum_{i=r_1}^{r_2} b_i, \tag{12}$$

where b_i represents presence (1) or absence (0) of species i in the post-coalescence community C_P, and r_1 and r_2 represent the species richness of communities 1 and 2, respectively. Note that if $S = 1$, then $C_P = C_1$, and if $S = -1$, then $C_P = C_2$. Also note that this measure is richness independent, allowing us to mix communities with different richness without introducing a bias in the similarity towards the richer community. Once the community composition of the mix is measured, we plot it against the difference in cohesion of the parent communities $\Delta\Theta = \Theta_1 - \Theta_2$ (see Fig 3B), finding that the resulting community is similar to its more cohesive parent. In the case of low leakage, facilitation is negligible (blue line in Fig 3C), and competition is mainly for abiotic resources (dashed line in Fig 3C). Thus, in this regime, being more cohesive is equivalent to being less competitive. Therefore, in the low leakage regime, communities that minimize competition succeed in coalescence events. Surprisingly, this trend is consistent even for high values of leakage, where facilitation is slightly larger than competition (now mainly for leaked resources) on average. This suggests that when competition is not negligible, it drives the outcome of community coalescence, overriding any effects that facilitation may have.

To uncover the effects of facilitation in the community we need to switch off competition for a range of leakage values where facilitation is not negligible. To this end we perform a second set of community coalescence simulations between pairs of communities assembled under the general sampling scenario (Fig 4A). This sampling method allows us to substantially lower the term C_b in Eq 4, bringing out a new regime at high l values where $\mathcal{C} << \mathcal{F}$ (see Fig 4C). The simulation pipeline detailed above is

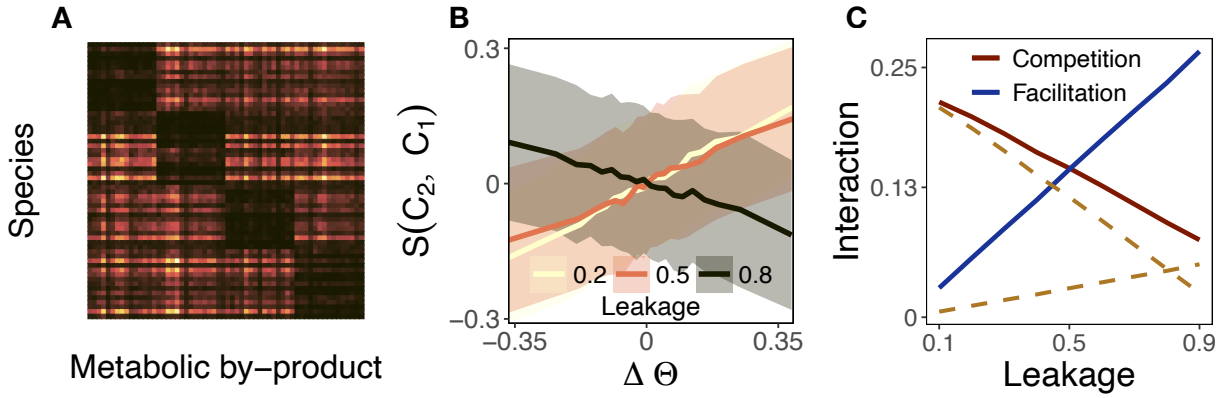

Fig 4. Coalescence results assuming different resource classes . Figure A shows an example of the secretion matrix with added structure in resource classes. Figure B shows that success of community coalescence is positively correlated with $\Delta\Theta$ for low values of leakage, when $\mathcal{C} > \mathcal{F}$; but negatively correlated with $\Delta\Theta$ for high values of leakage, when $\mathcal{C} < \mathcal{F}$. Figure C shows community-level competition ($\mathcal{C}$) and facilitation ($\mathcal{F}$) averaged across simulations for different levels of leakage. For low values of leakage, abiotic competition C_a (dashed decreasing line) dominates, and for high values of leakage facilitation F is the important term. Biotic competition C_b (dashed increasing line) is consistently low due to the imposed class structure.

now run on these communities. In the low leakage regime, where competition is present, we recover the previous result. In the high leakage regime, competition is negligible, so being more cohesive is equivalent to having higher levels of facilitation. We find that cohesion is negatively correlated with coalescence success, that is, more facilitative communities perform poorly in coalescence events (see Fig 4B).

Discussion

New microbial communities often emerge through community coalescence [19]. Previous studies have focused on coalescence as an outcome of competition between two communities behaving as coherent wholes [21–26, 31, 34]. Our findings generalize these results to include facilitation arising from metabolic cross-feeding. In particular, we find that the balance between competition and facilitation can substantially change the outcome of coalescence events [32].

In the work of [23], the cohesiveness displayed by coalescing communities in the absence of cooperative interactions resulted in effective resource depletion. This allowed the winning community to engineer an environment more favorable for itself than for the losing community, which was partially or completely displaced. The latter theoretical prediction has been experimentally verified in methanogenic communities [25], which are characterized by a dense metabolic cross-feeding network. However, we cannot help to question this claim: how is it possible that a minimal theoretical setting built exclusively around competition can explain the complex reality of coalescence events in the presence of syntrophy?

In this work we presented a theoretical framework that incorporates the intricate cross-feeding topology displayed by microbial communities and more realistically reconciles theory with observations. The previous theoretical result suggesting that in a coalescent event, "the winning [more cohesive] community is the one that is most efficient at depleting all substrates simultaneously", appears here as a particular case of a more general description. In this work cohesiveness is not defined in terms of resource depletion efficacy, but rather in terms of minimizing competition and maximizing cooperation. Reassuringly, the emerging pattern at $l \approx 0$, obtained here through our

interaction-dependent cohesion measure (yellow line in figure 3B), parallels that emerging in [23] through the resource-depletion-dependent cohesion measure. We find this pattern to be surprisingly consistent across all values of leakage. Thus, considering also that in the purely competitive regime, our model collapses to the one presented in [23] (see Supporting text), it appears that resource use efficiency is a consequence of minimizing of competition.

When leakage was present, we found that reducing competition was still the main force driving the outcome of community coalescence. The difference being that now competition was taking place in another environment; the one engineered by a community that both used and created resources. Ultimately, competition in the for leaked resources exists because bacteria are secreting resources necessary for their own growth. While this might seem disadvantageous, and thus unrealistic at first, leaking essential metabolites is an observed phenomenon in many microbial systems [35, 36], and may be advantageous as a "flux control" mechanism employed by individual cells to promote growth in crowded environments [37, 38]. Overall, this finding extends the results of previous theoretical studies to accommodate metabolic interdependence; an essential feature of microbial communities, thus constituting a more robust result supporting experimental findings [25] and hypotheses [39].

To further disentangle the effects of facilitation, we introduced functional classes that confined each consumer to obtain its energy from a subset of resources. We then paired the taxonomic structure with metabolic structure, such that species from a taxonomic class leaked energy in the form of resources that belonged to a different class than their preferred one. These two constraints allowed us to survey a regime of communities with very low competition and high facilitation levels. Performing a second round of coalescence simulations revealed that cohesion was detrimental for coalescence success in cooperative communities, that is, those communities where facilitation was high and competition was negligible were easily displaced by an invading community. This finding is experimentally supported by several studies [40–42] which recognize that strong cooperative links are susceptible to be intercepted by invading species. Nonetheless, recent *in-silico* results of single species invasions on microbial communities have found that cooperative communities are more resistant to invasions than their competitive counterparts [43]. The apparent contradiction between this finding and our own suggests that community invasion ecology cannot simply be extrapolated from our understanding of single species invasions [44].

The pairs of coalescing communities in this work were drawn with no richness restrictions, that is, communities with different species richness were allowed to compete. Consequently, the results reported here are independent of the species richness of the mixed communities. Interestingly, several works have pointed to microbial community diversity as an important factor driving resource use efficiency and, therefore, determining community resistance against biotic and abiotic perturbations [45–47]. These observations do not necessarily contradict the results reported here. Instead, our findings suggest that community interactions may be a more fundamental mechanism explaining the response of communities to environmental and biotic perturbations, and that biodiversity is rather a consequence of the underlying community interaction network. It is not surprising that experiments have come across biodiversity's influence in community resilience before the effect of community interactions, since the latter is much harder to measure than the former. Understanding biodiversity as an emergent property of the interaction network topology in a microbial community is a promising line of research [48].

The only interactions considered here were facilitation and competition. However, microbial inter-relations are more complex than just a binary classification [49], often involving the release of antimicrobial compounds, end-product inhibition, predation, or

interactions with spatial dependencies, an aspect that was also omitted here.

Throughout this work, we assumed absence of environmental fluctuations, since the supply rate of all resources was kept fixed. Considering only biotic perturbations allowed us to pinpoint the effect of each interaction separately. While this assumption may be sensible in some cases [50], it surely is oversimplifying in others [33]. When two communities collide, the process will entail, in general, a mixture of biotic and abiotic perturbations. Laying down a theoretical framework to understand the effect of abiotic perturbations, and the interplay between the two, in multi-species microbial invasions is an exciting direction for future research.

Encounters between microbial communities are becoming increasingly frequent across the globe [51]. Moreover, *in-vitro/in-vivo* mixing of whole microbial communities is gaining popularity for bio-engineering [52], soil restoration [53], faecal microbiota transplantation [54, 55], and the use of probiotics [56]. In the absence of robust theory that complements these observations and experiments, we present a framework which ties multiple interactions in microbial communities to the outcome of community coalescence events. Although more work is required so to bridge the gap between theory and experiments, this study constitutes a first step in that direction.

Supporting information

Supporting text. In the supporting text the reader will find several sections dealing with the equivalence of the model with other consumer-resource models, notes about the cost function, and detailed derivations of the used metrics, sampling preferences methods, matrix representations of some equations, and other tests.

Author Contributions

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Formal Analysis: Pablo Lechón

Methodology Pablo Lechón

Software Pablo Lechón

Visualization: Pablo Lechón

Writing – Original Draft Preparation: Pablo Lechón

Writing – Review & Editing: Pablo Lechón, Jacob Cook, Thomas P. Smith, Tom Clegg, Samraat Pawar.

Funding Acquisition: Samraat Pawar

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