

## Review



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# Community coalescence: an eco-evolutionary perspective

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Community coalescence, the mixing of different communities, is widespread throughout microbial ecology. Coalescence can result in approximately equal contributions from the founding communities or dominance of one community over another. These different outcomes have ramifications for community structure and function in natural communities, and the use of microbial communities in biotechnology and medicine. However, we have little understanding of when a particular outcome might be expected. Here, we integrate existing theory and data to speculate on how a crucial characteristic of microbial communities—the type of species interaction that dominates the community—might affect the outcome of microbial community coalescence. Given the often comparable timescales of microbial ecology and microevolution, we explicitly consider ecological and evolutionary dynamics, and their interplay, in determining coalescence outcomes.

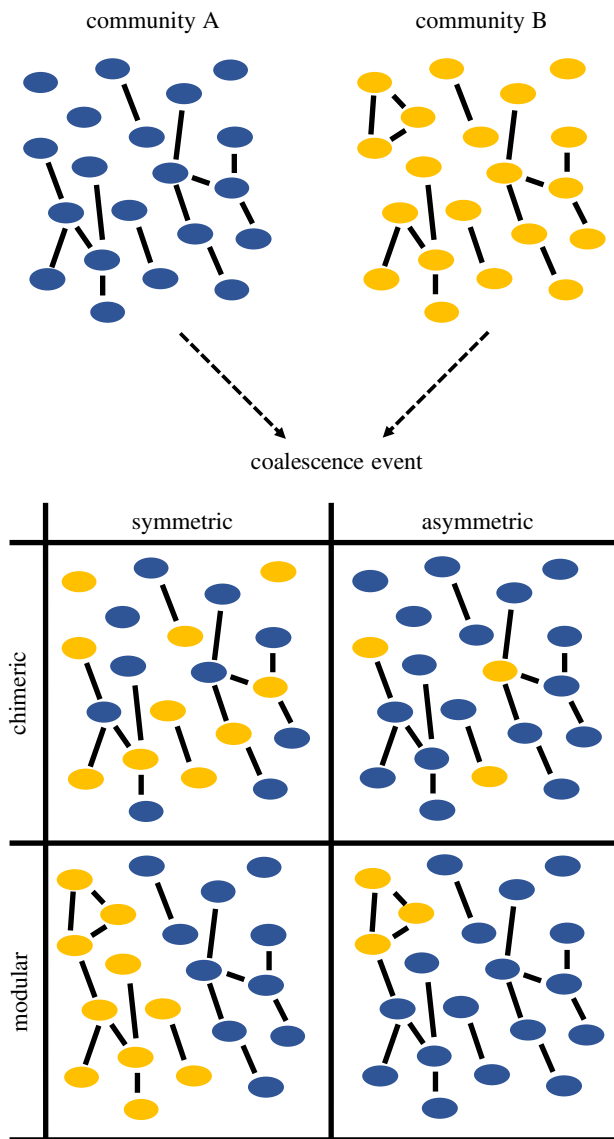
This article is part of the theme issue 'Conceptual challenges in microbial community ecology'.

## 1. Introduction

Community assembly, the process by which species colonise and interact with each other to establish a community, is shaped through ecological and evolutionary selection, drift and immigration [1]. In microbes, however, whole communities often migrate as a unit. The process of more than one community mixing has been termed 'community coalescence' [2]. Natural microbial communities frequently coalesce owing to abiotic (e.g. wind, tides or river flow) and biotic (e.g. animal courtship, parent-offspring interactions or leaves falling) factors [2–6]. Moreover, coalescence occurs owing to human activities such as industrial anaerobic digestion [7], agriculture [8,9] and between-human contact [10,11] (e.g. romantic couples share similar oral microbiota through kissing [12]).

The outcomes of coalescence can be grouped across two main categories (figure 1), which describe the composition and distribution of interactions of the coalesced community. Based on the prevalence of the members of the communities which coalesce, there can be a continuum between symmetric and asymmetric outcomes (equal contribution or dominance of one community). In asymmetrical outcomes, one community can be classed as 'dominant' if the sum of its populations are much greater than the other community and/or if it has more species [7,13–18] (figure 1). In symmetrical outcomes, the initial communities contribute approximately equally to the resultant coalesced community. The outcome of community coalescence can also be described in terms of the interactions between species of the mixed communities: a continuum ranging from chimeric to modular (figure 1). In chimeric coalescence, there is a high number of new interactions between members of different input communities. By contrast, in modular coalescence, interactions within input communities are preserved with fewer new interactions.

The degree of asymmetry and modularity of coalescence outcomes can impact community composition and function. Asymmetrical outcomes are potentially favourable in medicine for treating colonic *Clostridium difficile* infections [19].



**Figure 1.** Different types of coalescence outcomes. Symmetric and asymmetric coalescence shows the extent to which one input community dominates the coalesced community composition. Modular and chimeric coalescence relates to the extent of novel species interactions between the members of both input communities. In chimeric outcomes, new interactions arise more readily, while in modular outcomes, the coalesced community is based on pre-existing interactions between the members of the same input community. Each dot represents a species but, for simplicity, we assume no extinctions post-coalescence and no species appear from rare. Lines represent interactions within input and coalesced communities.

A donor gut microbiome (faecal transplant) is mixed into the patient's gut to displace the resident microbiome, which is facilitating *C. difficile* growth, resulting in patient remission [19]. In novel environments (e.g. industrial fermenters), a chimeric outcome could be favourable if these conditions facilitate the formation of novel interactions that increase community functionality [16,20]. By contrast, if species within coalesced communities are adapted to the environment where mixing occurs, modular outcomes could be beneficial as pre-existing interactions may benefit community function. Despite the potential importance and ubiquity of coalescence, our ability to predict the compositional and functional outcomes of coalescence is underdeveloped.

It will be very hard, if not impossible, to quantitatively predict coalescence outcomes in most cases, as predictions would

require an understanding of established within-community interactions and interactions between species from different communities. Moreover, interspecies interactions can rapidly change due to microevolution [21–24]. Therefore, we discuss how general characteristics of interspecies interactions (competitive, trophic and mutualistic interactions) might affect coalescence outcomes through ecological and microevolutionary processes. First, however, we briefly consider the crucial role played by interactions between members of coalescing communities and the abiotic environment.

## 2. Resident advantage and abiotic adaptation

In nature, most coalescence events occur with one community immigrating into a new environment where there is a resident community present. Here, we would expect asymmetrical coalescence outcomes in favour of the resident versus immigrating community. This resident advantage can arise as a consequence of ecological and evolutionary processes. First, the resident community is likely to be much more abundant and have monopolized available resources, limiting an invader's success (priority effects) [25]. Second, resident species are likely to be locally adapted to the niches present, owing to ecological selection (i.e. species sorting) and evolution, and hence have 'home advantage' over invaders [1,11,26–28].

However, this home advantage could be undermined by the presence, or absence, of evolved biotic interactions, and environmental disturbance [29–31]. For example, invaders can be successful because they are more resistant to predators/parasites affecting the resident species; or invaders can introduce parasites to resident species to which the invaders are more resistant [30,32,33]. The opposite would be expected if residents are more resistant. We explore these ideas in more detail in the 'trophic interactions' section. Moreover, disturbances (notably, non-specific mass mortality events) may reduce resident advantage and promote invasion [34] by increasing resources which open up ecological niches and alter community composition [35]. Furthermore, the invading community may arrive with nutrients which promote the successful establishment of its species.

The relationship between abiotic adaptation and coalescence outcomes could be influenced by environmental spatial structure. In homogeneous (and disturbed) environments, species which monopolize resources fastest will probably dominate, resulting in a chimeric outcome composed of the most competitive species from input communities [25,26]. By contrast, more structured environments can promote coexistence between species by limiting interaction intensity as niche boundaries are greater [36,37]. In these environments, coalescence outcomes are expected to be more modular as mixing between communities is limited and interactions become more localized. Soils, for instance, show spatial structuring with clustering of microbial communities [38,39] which may be observed during coalescence of a leaf into a soil microbiome. Gradual leaf litter decomposition into the soil creates nutrient gradients and slows coalescence by temporarily maintaining physical barriers. In this way, spatial structuring can limit interactions between input communities, potentially resulting in modular coexistence.

In contrast with natural scenarios, coalescence during human activities often occurs in novel environments (e.g. bioreactors)

to which the mixed communities are naive. In novel environments, which community dominates is probably determined by existing abiotic adaptations linked to the evolutionary history of the communities. Abiotic adaptations are shaped within a species' local environment so the community which previously developed in an environment most similar to the novel environment would probably dominate during coalescence. For instance, in *de novo* mouse gut colonization experiments, colonization success of diverse microbiota (originated from, e.g. soil, human and zebrafish) was highest for vertebrate microbiota and correlated with their ability to metabolize host resources [40].

### 3. Interactions, evolution and coalescence

Communities consist of a diverse range of interactions, including competition, trophic interactions and mutualisms. The relative strength and diversity of these interactions varies between communities, owing to differences in ecological and (co)evolutionary histories [1]. In this section, we discuss how the 'dominant' interaction type within a community might affect coalescence outcomes.

#### (a) Competition

Competition probably dominates interactions between community members in many microbial communities [41]. During coalescence, species from different communities compete for available niches. The simplest coalescence outcomes would be one community asymmetrically dominating if a large proportion of its constituent species' populations are better adapted to the abiotic environment, and hence monopolize resources faster than the ecologically equivalent populations within other communities [13,26]. Recent theory has shown that more diverse communities are more likely to asymmetrically dominate because they have a higher chance of containing better adapted populations (selection effects) [42]; a result consistent with previous empirical work [17,43].

However, this simple prediction does not take into account structural differences between communities' species interaction networks. Diversifying selection can reduce competition between co-occurring species by favouring resource specialization [44,45]. Consequently, competition (on average) may be lower between species from the same versus different communities. In this way, the success of one species can indirectly benefit members of the same community during coalescence (co-selection) [7,17,43,46]. By minimizing competition through resource specialization, communities become more 'niche-packed' and are expected to monopolize total resources more efficiently; the dominant community following coalescence should be the most productive of the input communities [13]. Moreover, weaker competitive interactions may promote the community's structural stability: the breadth of ecological interactions under which species can coexist [47,48]. This stability arises from greater within- versus between-species competition, meaning that if species reach a low frequency, they will experience relatively little competition and consequently increase in frequency (negative frequency dependent selection [49]). Taken together, for communities dominated by competitive interactions, longer coevolution within a community is expected to promote dominance during coalescence.

Mechanistically, niche partitioning can arise through ecological and evolutionary processes. During community assembly of bacterial communities, ecological species sorting

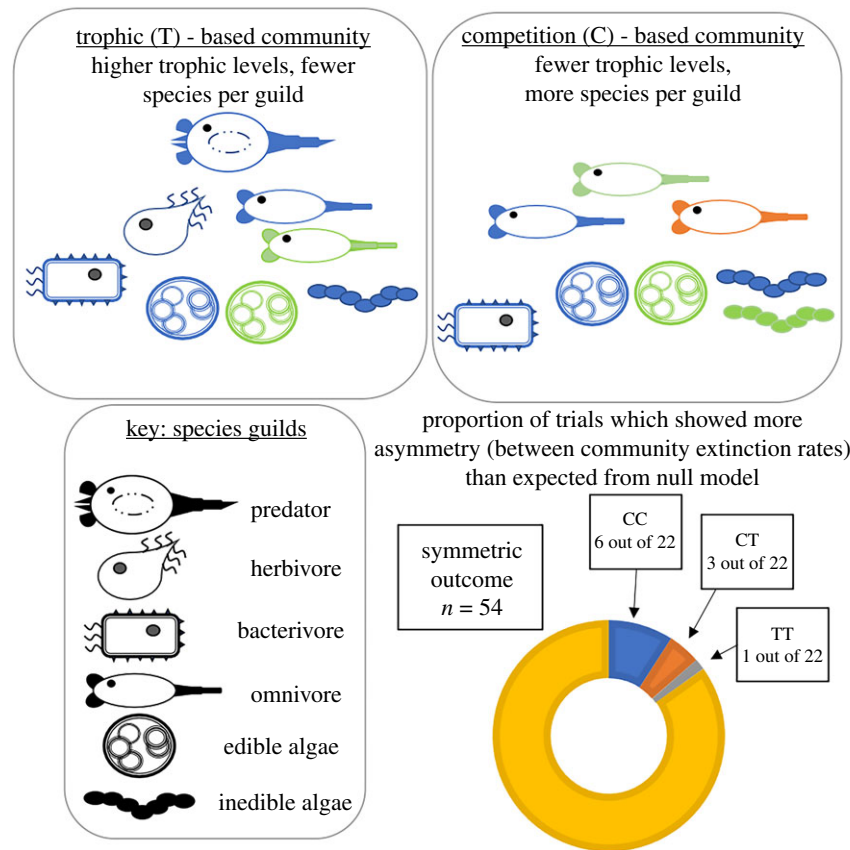
results in competitive exclusion of species whose niches overlap or are absent [40,50,51]. Simulation studies are consistent with this finding as symmetric outcomes were more probable in random community assemblages compared to those where species sorting occurred [18]. Additionally, evolution can reduce interspecies competition by selecting for traits which increase niche separation (character displacement) [45]. This evolutionary process is perhaps most clearly demonstrated in experimental evolution of 'adaptive radiations' of initially clonal bacteria that diversify to occupy distinct niches [44]. For example, in static tubes of nutrient rich media, *Pseudomonas fluorescens* diversifies into genetically distinct mat-forming variants which coexist with broth-inhabiting colonies [52].

What little empirical evidence exists largely supports the expectation of asymmetric outcomes when communities are competitive. For example, mixing established aquatic communities dominated by competitive, versus trophic, interactions resulted in more asymmetries in coalescence (figure 2) [15]. In biomethane-producing communities, the highest producing and more 'niche-packed' community dominated during coalescence, with indirect evidence for co-selection (figure 3*b,c*) [7]; although mutualistic interactions are also important in these communities (figure 3*a*). Therefore, owing to the complexity of competitive communities, direct evidence for a role of competition in determining coalescence outcomes is lacking.

There are caveats to these arguments regarding the role of competition in coalescence. First, the 'resident advantage' outlined in §2 as the experimental studies aforementioned in this section coalesced communities into a common garden environment [7,15,54]. When coalescence occurs as invasion, the non-resident community is likely to be less successful as the niches present are occupied and potentially different from that which species are adapted [17,25,26]. Experimentally, local adaptation to the environment gave resident bacterioplankton communities a competitive advantage, and naive communities a disadvantage, in coalescence [55,56]. In these studies, the naive community only had an impact on final community assembly when the naive community was allowed to occupy niches first (priority effect) [55,56]. However, local adaptation can override priority effects, as suggested by one study where human microbiota inhabiting a mouse gut was displaced by invading mouse microbiota [40]. The interacting role of priority effects and local adaptation in competition has been supported by mathematical models [57].

Second, how a community partitions resources is an essential consideration for predicting coalescence outcomes. Increased niche separation is not an inevitable outcome of competition, with work on rapidly growing aquatic plants suggesting selection for trait convergence [58]. Moreover, in another study, niche differentiation between bacterial morphotypes occurred in parallel across 'communities', resulting in a symmetric and chimeric coalescence outcome as competitors from different communities coexisted [54]. Therefore, where communities are equally adapted to the abiotic environment, we would expect to observe symmetric and chimeric outcomes. Although untested, we would not expect modular outcomes as species tend to compete with many others for limited resources.

Finally, competition can also lead to exploitative interactions, where individuals benefit from 'public goods' produced by other species, such as antibiotic degrading enzymes [59] and siderophores that remediate toxic heavy metals [60]. How cheats impact coalescence outcomes is



**Figure 2.** Livingston *et al.* [15] coalesced eight-species communities varying in competitive (C) and trophic (T) interactions (22 replicates per coalescence combination). Asymmetry (extinction rates between coalesced communities) were significant in 10 out of 66 pairs, with most coming from CC trials.

unclear and may depend on whether cheats are better at exploiting species from their own community or others. Conceptually, interspecific cooperator–cheat relationships can best be viewed in the context of trophic interactions.

### (b) Trophic interactions

Trophic interactions, where a species' growth rate is increased by antagonistically feeding on another species, may play a key role in coalescence outcomes because of their importance in structuring communities. For instance, bacteria–virus interactions are thought to drive community structure in marine microbial communities [61]. These trophic interactions can be categorized as predator–prey and host–parasite (including cheating) dynamics.

Trophic interactions often result in high structural stability (i.e. they promote species coexistence within a community) [47,62]. This stability arises because an increase in density of a given prey (or host) species results in an increase in the associated (parasite) species. In turn, this results in density reductions of the prey and, subsequently, the predator. Rare prey species, and their associated predators, have a fitness advantage if we assume trade-offs between resistance and competitiveness [63], specialism of predators on different prey species [64], or facultative switching of predators to common hosts/prey [65,66]. If communities differ in stability, an asymmetrical coalescence outcome of trophic communities may be expected with the more stable community dominating. Consistent with this prediction, a simulation study suggests that trophic interactions versus purely competitive interactions increased the likelihood of asymmetric coalescence outcomes [67].

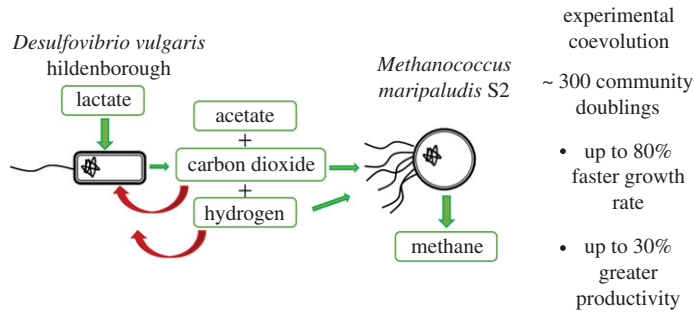
An asymmetric outcome of coalescence in trophic communities will probably be dependent on one community having

less negative intra-community interactions than it does with members of the other community. If a species experiences high parasitism/predation within its own community, then new trophic interactions (from the other input community) will have an additive negative effect. However, it is unclear how frequently trophic interactions will extend from one community to another. If taxa between communities are sufficiently distinct, host/prey species may have an intrinsic defence against allopatric enemies (termed 'non-host resistance' in the context of host–parasite interactions [68]). As such, there may be greater parasite/predation and apparent competition (from other taxa sharing parasites/predators) within communities than between communities. A predominance of such antagonistic interactions within communities would probably increase the likelihood of symmetric outcomes because of the absence of positive co-selection. Moreover, trophic interaction specialization would be expected to increase modularity, as has been observed in macrobes [69]. For bacteria–virus interactions, modularity does not seem to be ubiquitous, but this effect may be present because studies are carried out at variable taxonomic scales [70]. Phages (bacteria infecting viruses) typically show a high degree of taxa specificity [71], hence it is likely that modular interactions would dominate within most natural microbial communities. Consequently, we suggest the resultant communities will on average be modular.

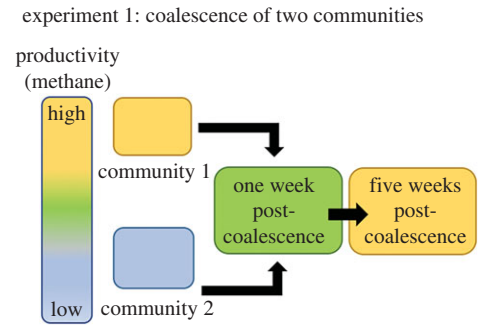
Microevolution plays a key role in shaping the interaction specificity. Trophic interactions place selection pressures on hosts/prey to evolve defensive mechanisms, while antagonists coevolve to overcome these barriers [23,72]. Consequently, the extent to which community members are coevolved may play a lesser role for trophic communities than competitive communities. While species can evolve to be less competitive by



(a) background: mutualistic coevolution: modelled by two anaerobic digesting bacteria Hillesland & Stahl [53]

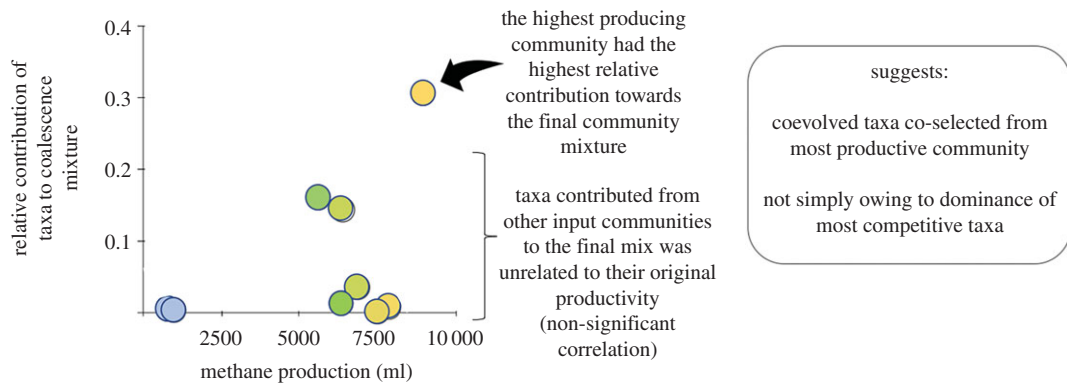


(b) coalescence of complex methanogenic communities Sierocinski *et al.* [7]



(c) experiment 2: coalescence of many communities

productivity converged on highest producing community (consistent with experiment 1).



**Figure 3.** Methanogenic community coalescence. (a) Methanogenic bacteria can coevolve within an obligate mutualism: *Desulfovibrio vulgaris* Hildenborough benefits *Methanococcus maripaludis* S2 by producing carbon dioxide (CO<sub>2</sub>) and hydrogen (H<sub>2</sub>) (green/straight arrows show metabolic pathways); CO<sub>2</sub> and H<sub>2</sub> inhibit *D. vulgaris* growth (red/curved arrows) but *M. maripaludis* S2 removes them [53]. (b) In methanogenic communities, productivity becomes indistinguishable from the most productive input community after five weeks [7]. (c) In a second experiment, the most productive community had the highest relative contribution towards the final community mixture. Whereas taxa contributed from other communities were unrelated to their original productivity. This evidence supports that mutualistic co-selection led to community cohesion and asymmetrical dominance of the highest producing community [7]. Adapted from Sierocinski *et al.* [7].

occupying distinct ecological niches, coevolution in trophic interactions is often characterized by the long-term fluctuating selection, where there is a non-directional change in defence and counter-defence [73,74].

While evolutionary change can be non-directional in trophic interactions, species' population traits can result in local adaptation [72] which will probably impact a species' fitness in coalescence. As local adaptation can depend upon population size, generation time and migration, it seems unlikely that generalizations can be made as to whether host or parasite (or predator or prey) should become locally adapted [72]. For example, for the same bacteria–virus combination, bacteria became locally adapted in nutrient media [75] while the virus became locally adapted in soil [76]. One outcome of bacteria becoming locally adapted are 'weaponized' prophage which are integrated into host genomes and prevented from killing their local hosts [32,77]. When the resistant bacteria are coalesced with a susceptible population, the prophage kill susceptible bacteria, allowing the resistant population to colonize their niches [32,77]. Where there are no consistent patterns of local (mal)adaptation across trophic interactions, we might expect symmetric outcomes. There may be a tendency towards chimeric over modular communities, as original modules break down in favour of new interactions between different community members.

Any intrinsic advantage of a resident community over invading communities may be altered in the context of trophic

interactions. Resident advantage may be diminished because encounter rates between trophic levels will be density- and environmentally dependent. In a coalescence context, an invading community becomes diluted by resident community members and as such, the invading species may have a relative growth rate advantage as trophic encounter rates are reduced. However, the abiotic environment might alter whether trophic communities have a resident advantage. For example, environments differing in nutrient availability can alter densities and encounter rates of hosts and parasites, and predator and prey [75,76]. In turn, encounter rates can determine whether enemies stably coexist and the investment into, often costly, defence and counter-defences [23,78]. Consequently, communities from low-nutrient environments with less trophic selection may be decimated in a nutrient rich environment under stronger trophic interactions. Reciprocally, highly defended species may face a growth rate cost in nutrient poor environments where there are fewer enemies [33].

Unfortunately, evidence for the importance of trophic interactions in determining coalescence outcomes is limited. Studies usually examine communities consisting of one antagonist pair, which probably tell us little about coalescence in natural microbial communities. To our knowledge, only one study has addressed this question and the findings are consistent with our ad-hoc reasoning. Mixing of synthetic aquatic microbial communities with strong trophic interactions (which had equilibrated) resulted in more

symmetric outcomes than when interactions are purely competitive (figure 2) [15].

### (c) Mutualisms

Many microbial interactions result in a net benefit to the interacting partners, such as where microbes benefit from secreted metabolites of other species. Mutualistic interactions can be two-sided (+/+) mutualisms, where both species directly benefit from a good or service (e.g. cross-feeding [79], cross-protection [80]) provided by the other species; or can be one-sided (+/0), with a species indirectly benefiting another species without benefit to itself (commensalism) [47]. The latter is not a true mutualism, but similarly increases interspecies dependencies which may have similar effects in determining coalescence outcomes.

Multiple models have considered the implications of mutualisms on community dynamics, with evidence that positive interspecies interactions can reduce stability [47,62,81]. Positive fitness interactions can result in positive feedbacks, where the reduction of one species fitness causes others to decline [11,47]. At its extreme, these feedbacks end with co-extinctions or ecosystem breakdowns [47,81]. In coalescence, communities may become destabilized as species loss has knock-on effects across co-dependents. However, we would expect destabilization during coalescence to be asymmetrical with the relatively more stable community dominating. Mutualistic networks are often characterized by nested interactions, with some taxa interacting with many species, and others interacting within specialized subsets [82]. Consequently, if broadly interacting taxa have a relative advantage, they may positively co-select other community members. For instance, in stressful environments, we may expect co-selection where mutualists facilitate resource uptake in anaerobic and low-nutrient conditions [82,83]. Conversely, selection against broadly interacting mutualists will probably play a disproportionate role in community destabilization. Therefore, we might expect asymmetric outcomes to be common when mutualistic interactions predominate coalesced communities. Where there are symmetrical outcomes, it would seem likely that mutualistic interactions have been destabilized in all communities, and hence more chimeric outcomes may be more probable.

There is good evidence that the ecological effects of mutualisms on community stability can be established and enhanced via (co)evolution. For example, coevolution between a plasmid and bacteria resulted in an initially antagonistic interaction becoming mutualistic [84]. Moreover, recent work shows that initially competitive communities become increasingly mutualistic as a result of evolved cross-feeding [79,85]. ‘Policing’ mechanisms can subsequently evolve to reinforce mutualism strength and increase the cost of either exploiting or existing without the other species [86]. By these mechanisms, evolution can increase species co-dependency, and hence the strength of co-selection, while at the same time destabilizing communities. These evolutionary processes are thought to increase the degree of symmetry in coalesced communities.

Mutualisms are highly contingent on the abiotic environment [81,87,88], and hence the resident advantage is likely to be a particularly important impact on the outcome of coalescence of mutualistic communities. For example, nutrient exchange that maximize fitness for mutualistic algae (*Chlorella* sp.) and *Paramecium bursaria* are highly contingent on light levels, which often vary between environments [88]. Moreover,

the recent theory suggests mutualistic interactions are particularly vulnerable to novel environments because a mismatch in adaptation, and hence species’ growth rates, can rapidly destabilize mutualisms [89]. Finally, because of positive feedbacks and dilution effects, mutualists invading from rare are not likely to become established.

Empirical studies on coalescence are broadly consistent with these predictions. Dominance of one community can arise where mutualistic species are positively co-selected during coalescence [7,13,43]. Microbes in biomethane communities form mutualistic interactions where carbon sources are digested and metabolites are cross-fed between community members [53,90]. Mutualistic coevolution has been shown between two species, including a methanogen, where one species’ waste products (which inhibit its growth) are metabolized by the other species (figure 3a) [53]. In coalescence of complex biomethane communities, consistent taxonomic dominance of the most productive community suggests that mutualists are co-selected and cohesively compete for resources (figure 3b,c) [7]. As mentioned previously, competitive interactions also exist in these complex communities and thus the relative importance of mutualisms and competition in this coalescence example is unclear. Additionally, diseased gut microbiomes have been successfully cured using faecal transplants but not with probiotics [16,19]. Functioning gut microbiomes rely on diverse species and network interactions, especially mutualisms, which are provided by faecal transplants as network interactions can be retained to facilitate an asymmetric treatment outcome [16,19,91]. Further support comes from an *in vitro* study which established and coalesced communities in single-resource environments [46]; a context where mutualistic interactions become particularly important for efficient resource uptake [79]. Here, the importance of interspecific interactions was found as community success increased through bottom-up (rare species) and top-down (dominant species) interactions [46].

## 4. Discussion

Here, we tentatively suggest that different interaction types, and the extent to which they have been shaped by coevolution, lead to different coalescence outcomes. We considered numerous related community properties: structural stability (conditions under which species in a community coexist and there are few extinctions), strength and sign of co-selection and the network structure; in addition to the relative importance of resident advantage.

However, both theoretical and empirical research is greatly lacking, meaning many of these predictions are highly speculative. To date, theory of competition in coalescence is the most developed [13,43,54–57] but more attention is warranted to trophic and mutualistic interactions (table 1) [7,15]. Experiments with synthetic systems can be used to understand the mechanisms underlying coalescence [92,93], while natural communities address whether results are ecologically relevant [7,8,55,56,94]. Some microbial systems have been studied in the context of hosts, such as locusts [95] or plant species [28,96], to examine between-microbiome dynamics and implications on host health. Owing to the complexity of microbial communities, we would encourage future research to explore a breadth of interaction types which could influence coalescence outcomes.

**Table 1.** Ecological interactions, how evolution can impact them, and how eco-evolutionary processes may impact community coalescence outcomes.

interaction	eco-evolution	coalescence	evidence
competition	<ul style="list-style-type: none"> <li>— eco-evolutionary processes lower interspecific competition within community</li> <li>— species locally adapt to environmental resources</li> </ul>	<i>asymmetric:</i> <ul style="list-style-type: none"> <li>— competition is stronger between than within communities</li> <li>— community which monopolizes resources most efficiently dominates</li> </ul> <i>symmetric, chimeric:</i> <ul style="list-style-type: none"> <li>— niche competition equal between input communities (trait convergence, parallel evolution)</li> </ul>	<ul style="list-style-type: none"> <li>— [7]: biomethane communities</li> <li>— [13]: theory</li> <li>— [15]: protists, rotifers, algae</li> <li>— [43,54]: bacteria</li> <li>— [55,56]: bacterioplankton</li> </ul>
trophic	<ul style="list-style-type: none"> <li>— promote stability negative feedbacks, weakening competition</li> <li>— coevolution characterized by non-directional change in overall resistance/infectivity</li> <li>— specialized interactions can lead to local adaptation</li> </ul>	<i>symmetric, modular:</i> <ul style="list-style-type: none"> <li>— dilution may limit antagonists' impact in coalescence</li> <li>— specialized interactions promote modularity in heterogeneous environments</li> </ul>	<ul style="list-style-type: none"> <li>— [15]: protists, rotifers, algae</li> </ul>
mutualism	<ul style="list-style-type: none"> <li>— mutualisms risk co-dependency</li> <li>— (co)evolution can reinforce co-dependencies</li> </ul>	<i>asymmetric, modular:</i> <ul style="list-style-type: none"> <li>— broadly interacting mutualists can lead to co-selection across coevolved taxa</li> </ul> <i>symmetric, chimeric:</i> <ul style="list-style-type: none"> <li>— mutualistic destabilization in both input communities</li> </ul>	<ul style="list-style-type: none"> <li>— [7]: biomethane communities</li> <li>— [46]: mixed soil/plant microbiomes</li> </ul>

The implications of coalescence for natural community structure and function is unclear, but could be particularly important in the context of environmental change [97]. Temperature changes alter eco-evolutionary dynamics, and could impact coalescence through range shifts, altering species interactions, and changing weather patterns [97–100]. Additionally, antibiotics and environmental pollutants disturb gut, soil and aquatic microbiomes with associated disease outbreaks and biodiversity loss [101–103]. Although untested, disturbance histories could impact coalescence outcomes by affecting 'niche-packing', through biodiversity loss, and by selecting for stress-resistant species. Considering abiotic variation may be particularly important for predicting ecological coalescence outcomes as species in nature are likely to be exposed to diverse conditions over spatial and temporal scales.

By contrast, there is a clear relevance of microbial community coalescence to biotechnology and medicine. Microbiomes may be 'engineered' through coalescence to optimize biomethane production in industry by combining diversities of input communities [20]. In agriculture, coalescence can aid in helping crops obtain nutrients and resist disease, with one study demonstrating how engineered soil communities can be used to restore disturbed microbiomes [8]. Similarly, gut

microbiome recovery in medicine relies on successful displacements of diseased microbiomes through dominance of a healthy donor community [16,19]. That said, our ability to predict whether the functional coalescence outcomes will be beneficial (from an anthropocentric perspective) is limited. In some cases, dominance following coalescence equates to beneficial functions [7,13], in which case mixing a large number of communities may be useful. However, beneficial outcomes from mixing many communities may not always be the case if function is reduced below that of the original communities. By exploring a diverse range of eco-evolutionary interactions and environmental factors using model and natural communities, we may begin to untangle how coalescence can be used as a tool to efficiently optimize community functions.

**Data accessibility.** This article has no additional data.

**Authors' contributions.** M.C. and A.B. planned and drafted the review. M.C., P.S. and D.P. produced figures. All authors edited and approved the final manuscript.

**Competing interests.** We have no competing interests

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## References

- Nemergut DR *et al.* 2013 Patterns and processes of microbial community assembly. *Microbiol. Mol. Biol. Rev.* **77**, 342–356. (doi:10.1128/MMBR.00051-12)
- Rillig MC, Antonovics J, Caruso T, Lehmann A, Powell JR, Veresoglou SD, Verbruggen E. 2015 Interchange of entire communities: microbial community coalescence. *Trends Ecol. Evol.* **30**, 470–476. (doi:10.1016/j.tree.2015.06.004)

3. Mansour I, Heppell CM, Ryo M, Rillig MC. 2018 Application of the microbial community coalescence concept to riverine networks: riverine microbial community coalescence. *Biol. Rev.* **93**, 1832–1845. (doi:10.1111/brv.12422)
4. Röhl O, Graupner N, Peršoh D, Kemler M, Mittelbach M, Boenigk J, Begerow D. 2018 Flooding duration affects the structure of terrestrial and aquatic microbial eukaryotic communities. *Microb. Ecol.* **75**, 875–887. (doi:10.1007/s00248-017-1085-9)
5. Vandegrift R, Fahimipour AK, Muscarella M, Bateman AC, Van Den Wymelenberg K, Bohannan BJM. 2019 Moving microbes: the dynamics of transient microbial residence on human skin. *bioRxiv* 586008. (doi:10.1101/586008)
6. Moeller AH, Suzuki TA, Lin D, Lacey EA, Wasser SK, Nachman MW. 2017 Dispersal limitation promotes the diversification of the mammalian gut microbiota. *Proc. Natl Acad. Sci. USA* **114**, 13 768–13 773. (doi:10.1073/pnas.1700122114)
7. Sierocinski P *et al.* 2017 A single community dominates structure and function of a mixture of multiple methanogenic communities. *Curr. Biol.* **27**, 3390–3395.e4. (doi:10.1016/j.cub.2017.09.056)
8. Calderón K, Spor A, Breuil M-C, Bru D, Bizouard F, Violle C, Barnard RL, Philippot L. 2017 Effectiveness of ecological rescue for altered soil microbial communities and functions. *ISME J.* **11**, 272–283. (doi:10.1038/ismej.2016.86)
9. Rillig MC *et al.* 2016 Soil microbes and community coalescence. *Pedobiologia* **59**, 37–40. (doi:10.1016/j.pedobi.2016.01.001)
10. Meadow JF, Bateman AC, Herkert KM, O'Connor TK, Green JL. 2013 Significant changes in the skin microbiome mediated by the sport of roller derby. *PeerJ* **1**, e53. (doi:10.7717/peerj.53)
11. Sprockett D, Fukami T, Relman DA. 2018 Role of priority effects in the early-life assembly of the gut microbiota. *Nat. Rev. Gastroenterol. Hepatol.* **15**, 197–205. (doi:10.1038/nrgastro.2017.173)
12. Kort R, Caspers M, van de Graaf A, van Egmond W, Keijser B, Roeselers G. 2014 Shaping the oral microbiota through intimate kissing. *Microbiome* **2**, 41. (doi:10.1186/2049-2618-2-41)
13. Tikhonov M. 2016 Community-level cohesion without cooperation. *eLife* **5**, e15747. (doi:10.7554/eLife.15747)
14. Antonovics J, Veresoglou SD, Rillig MC. 2019 Species diversity in a metacommunity with patches connected by periodic coalescence: a neutral model. *arXiv* 1905.03669.
15. Livingston G, Jiang Y, Fox JW, Leibold MA. 2013 The dynamics of community assembly under sudden mixing in experimental microcosms. *Ecology* **94**, 2898–2906. (doi:10.1890/12-1993.1)
16. Wilson BC, Vatanen T, Cutfield WS, O'Sullivan JM. 2019 The super-donor phenomenon in fecal microbiota transplantation. *Front. Cell. Infect. Microbiol.* **9**, 2. (doi:10.3389/fcimb.2019.00002)
17. Rocca JD, Simonin M, Wright JP, Washburne A, Bernhardt ES. 2019 Rare microbial taxa emerge when communities collide: freshwater and marine microbiome responses to experimental seawater intrusion. *bioRxiv* 550756. (doi:10.1101/550756)
18. Gilpin, M. 1994 Community-level competition: asymmetrical dominance. *Proc. Natl Acad. Sci. USA* **91**, 3252–3254.
19. Wang J-W *et al.* 2019 Fecal microbiota transplantation: review and update. *J. Formos. Med. Assoc.* **118**, S23–S31. (doi:10.1016/j.jfma.2018.08.011)
20. Rillig MC, Tsang A, Roy J. 2016 Microbial community coalescence for microbiome engineering. *Front. Microbiol.* **7**, 1967. (doi:10.3389/fmicb.2016.01967)
21. Barraclough TG. 2015 How do species interactions affect evolutionary dynamics across whole communities? *Annu. Rev. Ecol. Evol. Syst.* **46**, 25–48. (doi:10.1146/annurev-ecolsys-112414-054030)
22. Johnson MTJ, Stinchcombe JR. 2007 An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.* **22**, 250–257. (doi:10.1016/j.tree.2007.01.014)
23. Brockhurst MA, Koskella B. 2013 Experimental coevolution of species interactions. *Trends Ecol. Evol.* **28**, 367–375. (doi:10.1016/j.tree.2013.02.009)
24. Koskella B, Hall LJ, Metcalf CJE. 2017 The microbiome beyond the horizon of ecological and evolutionary theory. *Nat. Ecol. Evol.* **1**, 1606–1615. (doi:10.1038/s41559-017-0340-2)
25. De Meester L, Vanoverbeke J, Kilsdonk LJ, Urban MC. 2016 Evolving perspectives on monopolization and priority effects. *Trends Ecol. Evol.* **31**, 136–146. (doi:10.1016/j.tree.2015.12.009)
26. Vanoverbeke J, Urban MC, De Meester L. 2016 Community assembly is a race between immigration and adaptation: eco-evolutionary interactions across spatial scales. *Ecography* **39**, 858–870. (doi:10.1111/ecog.01394)
27. Pantel JH, Duvivier C, Meester LD. 2015 Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms. *Ecol. Lett.* **18**, 992–1000. (doi:10.1111/ele.12480)
28. Morella NM, Weng FC-H, Joubert PM, Metcalf CJE, Lindow S, Koskella B. 2019 Successive passaging of a plant-associated microbiome reveals robust habitat and host genotype-dependent selection. *bioRxiv* 627794. (doi:10.1101/627794)
29. Thompson JN. 2002 Coevolution and maladaptation. *Integr. Comp. Biol.* **42**, 381–387. (doi:10.1093/icb/42.2.381)
30. Green PT, O'Dowd DJ, Abbott KL, Jeffery M, Retallick K, Mac Nally R. 2011 Invasional meltdown: invader–invader mutualism facilitates a secondary invasion. *Ecology* **92**, 1758–1768. (doi:10.1890/11-0050.1)
31. Farkas TE, Hendry AP, Nosil P, Beckerman AP. 2015 How maladaptation can structure biodiversity: eco-evolutionary island biogeography. *Trends Ecol. Evol.* **30**, 154–160. (doi:10.1016/j.tree.2015.01.002)
32. Brown SP, Le Chat L, De Paepe M, Taddei F. 2006 Ecology of microbial invasions: amplification allows virus carriers to invade more rapidly when rare. *Curr. Biol.* **16**, 2048–2052. (doi:10.1016/j.cub.2006.08.089)
33. Zhang Q-G, Buckling A. 2016 Migration highways and migration barriers created by host–parasite interactions. *Ecol. Lett.* **19**, 1479–1485. (doi:10.1111/ele.12700)
34. Pickett STA, White PS. 1985 *The ecology of natural disturbance and patch dynamics*. Amsterdam, The Netherlands: Elsevier.
35. Lear L, Hesse E, Shea K, Buckling A. 2020 Disentangling the mechanisms underpinning disturbance-mediated invasion. *Proc. R. Soc. B* **287**, 20192415. (doi:10.1098/rspb.2019.2415)
36. Vallespir Lowery N, Ursell T. 2019 Structured environments fundamentally alter dynamics and stability of ecological communities. *Proc. Natl Acad. Sci. USA* **116**, 379–388. (doi:10.1073/pnas.1811887116)
37. Tamme R, Hiiesalu I, Laanisto L, Szava-Kovats R, Pärtel M. 2010 Environmental heterogeneity, species diversity and co-existence at different spatial scales. *J. Veg. Sci.* **21**, 796–801. (doi:10.1111/j.1654-1103.2010.01185.x)
38. Ettema C. 2002 Spatial soil ecology. *Trends Ecol. Evol.* **17**, 177–183. (doi:10.1016/S0169-5347(02)02496-5)
39. Rillig MC, Muller LA, Lehmann A. 2017 Soil aggregates as massively concurrent evolutionary incubators. *ISME J.* **11**, 1943–1948. (doi:10.1038/ismej.2017.56)
40. Seedorf H *et al.* 2014 Bacteria from diverse habitats colonize and compete in the mouse gut. *Cell* **159**, 253–266. (doi:10.1016/j.cell.2014.09.008)
41. Ghou M, Mitri S. 2016 The ecology and evolution of microbial competition. *Trends Microbiol.* **24**, 833–845. (doi:10.1016/j.tim.2016.06.011)
42. Vila JCC, Jones ML, Patel M, Bell T, Rosindell J. 2019 Uncovering the rules of microbial community invasions. *Nat. Ecol. Evol.* **3**, 1162–1171. (doi:10.1038/s41559-019-0952-9)
43. Rivett DW, Jones ML, Ramoneda J, Mombrikotb SB, Ransome E, Bell T. 2018 Elevated success of multispecies bacterial invasions impacts community composition during ecological succession. *Ecol. Lett.* **21**, 516–524. (doi:10.1111/ele.12916)
44. Stroud JT, Losos JB. 2016 Ecological opportunity and adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.* **47**, 507–532. (doi:10.1146/annurev-ecolsys-121415-032254)
45. Schluter D. 2000 Ecological character displacement in adaptive radiation. *Am. Nat.* **156**, S4–S16. (doi:10.1086/303412)
46. Lu N, Sanchez-Gorostiaga A, Tikhonov M, Sanchez A. 2018 Cohesiveness in microbial community coalescence. *bioRxiv* 282723. (doi:10.1101/282723)
47. Coyte KZ, Schluter J, Foster KR. 2015 The ecology of the microbiome: networks, competition, and stability. *Science* **350**, 663–666. (doi:10.1126/science.aad2602)
48. Edwards KF, Kremer CT, Miller ET, Osmond MM, Litchman E, Klausmeier CA. 2018 Evolutionarily stable communities: a framework for understanding the role of trait evolution in the maintenance of diversity. *Ecol. Lett.* **21**, 1853–1868. (doi:10.1111/ele.13142)
49. Chesson P. 2018 Updates on mechanisms of maintenance of species diversity. *J. Ecol.* **106**, 1773–1794. (doi:10.1111/1365-2745.13035)



50. Soininen J. 2014 A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* **95**, 3284–3292. (doi:10.1890/13-2228.1)
51. Staley C, Gould TJ, Wang P, Phillips J, Cotner JB, Sadowsky MJ. 2015 Species sorting and seasonal dynamics primarily shape bacterial communities in the Upper Mississippi River. *Sci. Total Environ.* **505**, 435–445. (doi:10.1016/j.scitotenv.2014.10.012)
52. Rainey PB, Travisano M. 1998 Adaptive radiation in a heterogeneous environment. *Nature* **394**, 69–72. (doi:10.1038/27900)
53. Hillesland KL, Stahl DA. 2010 Rapid evolution of stability and productivity at the origin of a microbial mutualism. *Proc. Natl Acad. Sci. USA* **107**, 2124–2129. (doi:10.1073/pnas.0908456107)
54. Castledine M, Buckling A, Padfield D. 2019 A shared coevolutionary history does not alter the outcome of coalescence in experimental populations of *Pseudomonas fluorescens*. *J. Evol. Biol.* **32**, 58–65. (doi:10.1111/jeb.13394)
55. Rummens K, De Meester L, Souffreau C. 2018 Inoculation history affects community composition in experimental freshwater bacterioplankton communities: experimental priority effects in bacterioplankton. *Environ. Microbiol.* **20**, 1120–1133. (doi:10.1111/1462-2920.14053)
56. Svoboda P, Lindström ES, Ahmed Osman O, Langenheder S. 2018 Dispersal timing determines the importance of priority effects in bacterial communities. *ISME J.* **12**, 644–646. (doi:10.1038/ismej.2017.180)
57. Fukami T. 2015 Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Syst.* **46**, 1–23. (doi:10.1146/annurev-ecolsys-110411-160340)
58. Hart SP, Turcotte MM, Levine JM. 2019 Effects of rapid evolution on species coexistence. *Proc. Natl Acad. Sci. USA* **116**, 2112–2117. (doi:10.1073/pnas.1816298116)
59. Frost I, Smith WPJ, Mitri S, Millan AS, Davit Y, Osborne JM, Pitt-Francis JM, MacLean RC, Foster KR. 2018 Cooperation, competition and antibiotic resistance in bacterial colonies. *ISME J.* **12**, 1582–1593. (doi:10.1038/s41396-018-0090-4)
60. Hesse E, Padfield D, Bayer F, van Veen EM, Bryan CG, Buckling A. 2019 Anthropogenic remediation of heavy metals selects against natural microbial remediation. *Proc. R. Soc. B* **286**, 20190804. (doi:10.1098/rspb.2019.0804)
61. Suttle CA. 2007 Marine viruses: major players in the global ecosystem. *Nat. Rev. Microbiol.* **5**, 801–812. (doi:10.1038/nrmicro1750)
62. Loeuille N. 2010 Influence of evolution on the stability of ecological communities: evolution and stability of communities. *Ecol. Lett.* **13**, 1536–1545. (doi:10.1111/j.1461-0248.2010.01545.x)
63. Winter C, Bouvier T, Weinbauer MG, Thingstad TF. 2010 Trade-offs between competition and defense specialists among unicellular planktonic organisms: the ‘killing the winner’ hypothesis revisited. *Microbiol. Mol. Biol. Rev.* **74**, 42–57. (doi:10.1128/MMBR.00034-09)
64. Hamilton WD, Axelrod R, Tanese R. 1990 Sexual reproduction as an adaptation to resist parasites (a review). *Proc. Natl Acad. Sci. USA* **87**, 3566–3573. (doi:10.1073/pnas.87.9.3566)
65. McCann K, Hastings A, Huxel GR. 1998 Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798. (doi:10.1038/27427)
66. Rooney N, McCann K, Gellner G, Moore JC. 2006 Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269. (doi:10.1038/nature04887)
67. Wright CK. 2008 Ecological community integration increases with added trophic complexity. *Ecol. Complex.* **5**, 140–145. (doi:10.1016/j.ecocom.2007.10.004)
68. Gill US, Lee S, Mysore KS. 2015 Host versus nonhost resistance: distinct wars with similar arsenals. *Phytopathology* **105**, 580–587. (doi:10.1094/PHYTO-11-14-0298-RVW)
69. Fortuna MA, Stouffer DB, Olesen JM, Jordano P, Mouillot D, Krasnov BR, Poulin R, Bascompte J. 2010 Nestedness versus modularity in ecological networks: two sides of the same coin? *J. Anim. Ecol.* **79**, 811–817. (doi:10.1111/j.1365-2656.2010.01688.x)
70. Flores CO, Valverde S, Weitz JS. 2013 Multi-scale structure and geographic drivers of cross-infection within marine bacteria and phages. *ISME J.* **7**, 520–532. (doi:10.1038/ismej.2012.135)
71. Koskella B, Meaden S. 2013 Understanding bacteriophage specificity in natural microbial communities. *Viruses* **5**, 806–823. (doi:10.3390/v5030806)
72. Greischar MA, Koskella B. 2007 A synthesis of experimental work on parasite local adaptation. *Ecol. Lett.* **10**, 418–434. (doi:10.1111/j.1461-0248.2007.01028.x)
73. Brockhurst MA, Chapman T, King KC, Mank JE, Paterson S, Hurst GDD. 2014 Running with the Red Queen: the role of biotic conflicts in evolution. *Proc. R. Soc. B* **281**, 20141382. (doi:10.1098/rspb.2014.1382)
74. Hall AR, Scanlan PD, Morgan AD, Buckling A. 2011 Host-parasite coevolutionary arms races give way to fluctuating selection: bacteria-phage coevolutionary dynamics. *Ecol. Lett.* **14**, 635–642. (doi:10.1111/j.1461-0248.2011.01624.x)
75. Morgan AD, Gandon S, Buckling A. 2005 The effect of migration on local adaptation in a coevolving host-parasite system. *Nature* **437**, 253–256. (doi:10.1038/nature03913)
76. Gomez P, Buckling A. 2011 Bacteria-phage antagonistic coevolution in soil. *Science* **332**, 106–109. (doi:10.1126/science.1198767)
77. Joo J, Gunny M, Cases M, Hudson P, Albert R, Harvill E. 2006 Bacteriophage-mediated competition in *Bordetella* bacteria. *Proc. R. Soc. B* **273**, 1843–1848. (doi:10.1098/rspb.2006.3512)
78. Thompson RM, Townsend CR. 2005 Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* **108**, 137–148. (doi:10.1111/j.0030-1299.2005.11600.x)
79. D’Souza G, Shitut S, Preussger D, Yousif G, Waschina S, Kost C. 2018 Ecology and evolution of metabolic cross-feeding interactions in bacteria. *Nat. Prod. Rep.* **35**, 455–488. (doi:10.1039/C8NP00009C)
80. Estrela S, Brown SP. 2018 Community interactions and spatial structure shape selection on antibiotic resistant lineages. *PLoS Comput. Biol.* **14**, e1006179. (doi:10.1371/journal.pcbi.1006179)
81. Toby Kiers E, Palmer TM, Ives AR, Bruno JF, Bronstein JL. 2010 Mutualisms in a changing world: an evolutionary perspective. *Ecol. Lett.* **13**, 1459–1474. (doi:10.1111/j.1461-0248.2010.01538.x)
82. Rohr RP, Saavedra S, Bascompte J. 2014 On the structural stability of mutualistic systems. *Science* **345**, 1253497. (doi:10.1126/science.1253497)
83. Stachowicz JJ. 2001 Mutualism, facilitation, and the structure of ecological communities: positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. *BioScience* **51**, 235. (doi:10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2)
84. Modi RI, Adams J. 1991 Coevolution in bacterial-plasmid populations. *Evolution* **45**, 656–667. (doi:10.1111/j.1558-5646.1991.tb04336.x)
85. Lawrence D, Fiegna F, Behrends V, Bundy JG, Phillimore AB, Bell T, Barraclough TG. 2012 Species interactions alter evolutionary responses to a novel environment. *PLoS Biol.* **10**, e1001330. (doi:10.1371/journal.pbio.1001330)
86. El Mouden C, West SA, Gardner A. 2010 The enforcement of cooperation by policing. *Evolution* **64**, 2139–2152. (doi:10.1111/j.1558-5646.2010.00963.x)
87. Piccardi P, Vessman B, Mitri S. 2019 Toxicity drives facilitation between 4 bacterial species. *Proc. Natl Acad. Sci. USA* **16**, 15 979–15 984. (doi:10.1073/pnas.1906172116)
88. Lowe CD, Minter EJ, Cameron DD, Brockhurst MA. 2016 Shining a light on exploitative host control in a photosynthetic endosymbiosis. *Curr. Biol.* **26**, 207–211. (doi:10.1016/j.cub.2015.11.052)
89. Northfield TD, Ives AR. 2013 Coevolution and the effects of climate change on interacting species. *PLoS Biol.* **11**, e1001685. (doi:10.1371/journal.pbio.1001685)
90. Schink B. 1997 Energetics of syntrophic cooperation in methanogenic degradation. *Microbiol. Mol. Biol. Rev.* **61**, 262–280. (doi:10.1128/61.2.262-280.1997)
91. Lloyd-Price J, Abu-Ali G, Huttenhower C. 2016 The healthy human microbiome. *Genome Med.* **8**, 51. (doi:10.1186/s13073-016-0307-y)
92. O’Malley MA, Travisano M, Velicer GJ, Bolker JA. 2015 How do microbial populations and communities function as model systems? *Q. Rev. Biol.* **90**, 269–293. (doi:10.1086/682588)
93. Bell T. 2019 Next-generation experiments linking community structure and ecosystem functioning. *Environ. Microbiol. Rep.* **11**, 20–22. (doi:10.1111/1758-2229.12711)

94. Ridaura VK *et al.* 2013 Gut microbiota from twins discordant for obesity modulate metabolism in mice. *Science* **341**, 1241214. (doi:10.1126/science.1241214)
95. Dillon RJ, Vennard CT, Buckling A, Charnley AK. 2005 Diversity of locust gut bacteria protects against pathogen invasion. *Ecol. Lett.* **8**, 1291–1298. (doi:10.1111/j.1461-0248.2005.00828.x)
96. Rodriguez PA, Rothballer M, Chowdhury SP, Nussbaumer T, Gutjahr C, Falter-Braun P. 2019 Systems biology of plant-microbiome interactions. *Mol. Plant* **12**, 804–821. (doi:10.1016/j.molp.2019.05.006)
97. Heal G, Park J. 2016 Reflections—temperature stress and the direct impact of climate change: a review of an emerging literature. *Rev. Environ. Econ. Policy* **10**, 347–362. (doi:10.1093/reep/rew007)
98. O’Gorman EJ *et al.* 2012 Impacts of warming on the structure and functioning of aquatic communities. In *Advances in ecological research* (eds G Woodward, U Jacob, EJ O’Gorman), pp. 81–176. Amsterdam, The Netherlands: Elsevier.
99. Plebani M, Fussmann KE, Hansen DM, O’Gorman EJ, Stewart RIA, Woodward G, Petchey OL. 2015 Substratum-dependent responses of ciliate assemblages to temperature: a natural experiment in Icelandic streams. *Freshw. Biol.* **60**, 1561–1570. (doi:10.1111/fwb.12588)
100. Jiang L, Morin PJ. 2004 Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *J. Anim. Ecol.* **73**, 569–576. (doi:10.1111/j.0021-8790.2004.00830.x)
101. Shreiner AB, Kao JY, Young VB. 2015 The gut microbiome in health and in disease. *Curr. Opin. Gastroenterol.* **31**, 69–75. (doi:10.1097/MOG.0000000000000139)
102. Barra Caracciolo A, Topp E, Grenni P. 2015 Pharmaceuticals in the environment: biodegradation and effects on natural microbial communities. A review. *J. Pharm. Biomed. Anal.* **106**, 25–36. (doi:10.1016/j.jpba.2014.11.040)
103. Simonin M, Richaume A. 2015 Impact of engineered nanoparticles on the activity, abundance, and diversity of soil microbial communities: a review. *Environ. Sci. Pollut. Res.* **22**, 13 710–13 723. (doi:10.1007/s11356-015-4171-x)