

# Interchange of entire communities: microbial community coalescence

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**Microbial communities are enigmatically diverse. We propose a novel view of processes likely affecting microbial assemblages, which could be viewed as the Great American Interchange *en miniature*: the wholesale exchange among microbial communities resulting from moving pieces of the environment containing entire assemblages. Incidental evidence for such 'community coalescence' is accumulating, but such processes are rarely studied, likely because of the absence of suitable terminology or a conceptual framework. We provide the nucleus for such a conceptual foundation for the study of community coalescence, examining factors shaping these events, links to bodies of ecological theory, and we suggest modeling approaches for understanding coalescent communities. We argue for the systematic study of community coalescence because of important functional and applied consequences.**

## Great American Interchange *en miniature*?

Alfred Russell Wallace [1] was perhaps one of the first to consider what would happen when previously separated communities meet – in his case at a very large spatial and temporal scale, in what has become known as the Great American Interchange: the linking of North and South America by the appearance of the Isthmus of Panama. The result of such wholesale migration, mixing and joining of communities was likely a multifold of establishments, species exchanges and extinctions; massive effects at any rate. What if community encounter events like these were not exceptional singularities, but were to occur very frequently, at timescales relevant to understanding community structure? Here, we develop the idea that events reminiscent of the Great American Interchange could be common in microbial systems, and with potentially even greater degrees of mixing. We think this is the case because in nature, pieces of the environment much larger and more

persistent than an individual microbe, and indeed containing entire local microbial communities, are routinely moved (Figure 1 and Box 1). Forces that move pieces of the environment containing entire microbial assemblages include gravity (falling leaves), animals (e.g., burrows and casts), growth of macroorganisms (plant roots encountering each other in the soil), wind (dust movement), flow in liquids (natural or industrial water bodies mixing, movement inside the human body), or human activities (horticultural outplanting, ploughing, or movement of wood). We propose the term community coalescence (see Glossary) to describe such community interchange events (Box 1).

While the literature is replete with studies on the effects and importance of many of the events mentioned above (e.g., litter fall), these reports have rarely addressed the microbial community-level interactions. The field of

## Glossary

**$\beta$ -Diversity:** the variation in the identities of species among sites [21].

**Community:** a general and broad term for any recognized assemblage of organisms containing multiple species that interact with one another as a result of their physical proximity.

**Community coalescence:** a joining of previously separate communities (or even ecosystems), forming a new entity that is not easily separable into parts again; this new entity has distinct properties from the parts it unites. The term 'coalescence' is also used in population genetics but in a very different context to indicate that homologous genes in different populations were at some point of necessity identical by descent, that is, their history coalesces, and the genealogy of one gene is sometimes termed its 'coalescent'. This history is usually inferred from DNA sequence data.

**Connectance:** in ecological networks, the fraction of possible interactions that are actually realized.

**Horizontal gene transfer:** transfer of genes among unrelated species; postulated to occur by vectors such as viruses or insects, or by direct uptake of plasmids or environmental DNA.

**Metacommunity:** a collection of local communities linked by dispersal of their component species. The concept is derived from that of the metapopulation, which is a collection of populations of one species linked by dispersal of individuals. Metacommunity dynamics includes ecological 'rescue' of locally 'unfit' species, patch dynamics (appearance and disappearance of habitat patches), extinctions and recolonizations from the regional species pool, and processes such as neutral drift (analogous to genetic drift) and species sorting (analogous to fitness differences).

**Nestedness:** in ecological networks, this measures the tendency for species with few links to exclusively interact with species with many links.

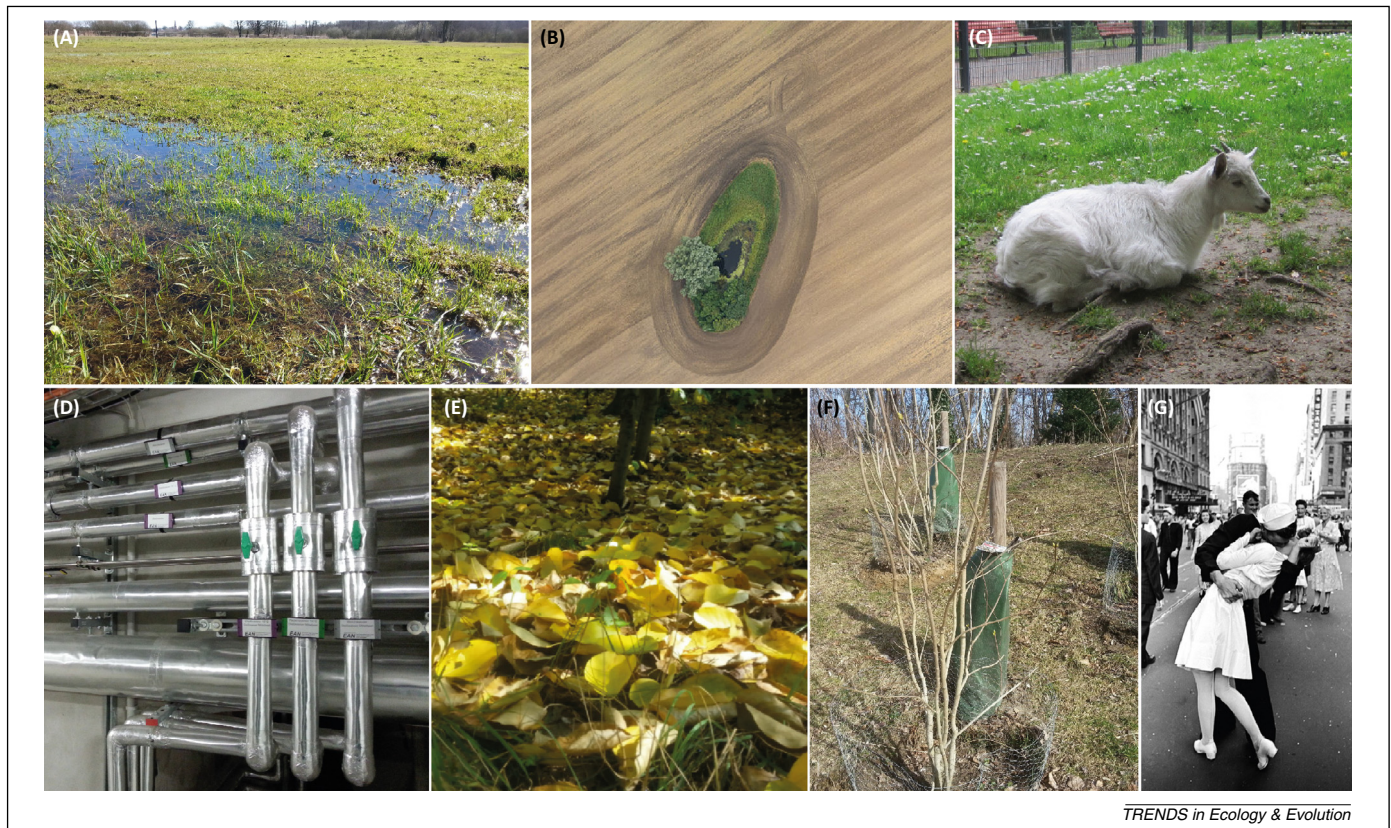
**Network theory:** describes interactions between multiple entities, which in ecology are typically species. Using network theory, communities can be described in terms of direct and indirect interactions among species.

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**Figure 1.** Encounters of entire microbial communities occur in many microbial systems. Examples where such community coalescences are likely occur include (A, B) interaction of aquatic and terrestrial systems, such as during flooding, in riparian zones or near ponds; (C) interaction of communities inside the digestive system (e.g., oral and intestinal communities); (D) mixing of communities inhabiting different water bodies in, for example, human-made industrial systems; (E) various soil inputs, such as animal casts or leaves falling on the soil surface; (F) human-induced movements of material, such as in horticulture or tree outplanting; (G) direct or indirect contact between humans, such as two people kissing (also see Box 1). Photographs from M.C. Rillig (A, C, D, E, F) and Wikimedia Commons (B, Niklas Tschöpe; G, anonymous).

microbial biogeography (Box 2) has long debated the degree of dispersal limitation among microorganisms, and is now also beginning to explore how environment, spatial processes, and biotic context shape local communities. Community coalescence events are part of the dispersal process, but also much more, because such events result in whole communities and their environments interacting. Therefore, it is important to ask how they influence the resulting community, how these consequences can be linked to and illuminated by existing ecological theory, and how such investigations could further inform and expand ecological theory. What is the empirical evidence on community coalescence thus far? How can the problem of entire communities interacting be approached from a theoretical perspective? What are the functional consequences of community coalescence? These are the questions we address here with the goal of stimulating research on this topic; community coalescence is likely to be important not only in the everyday events of microbial ecology but also of increasing importance as the interconnectedness of biological systems increases with global change.

#### Factors influencing the community composition that results from community coalescence

While a number of empirical studies (Box 1) and modeling exercises [2,3] have addressed aspects of what we call community coalescence, there has been no systematic study of such phenomena, and this might in part be due

to a lack of an applicable conceptual framework for classifying these events, estimating their frequency, or predicting their consequences. We believe such separate conceptual development is necessary because the coalescence of communities has features very distinct from those described in other bodies of theory, in particular the processes envisaged in metacommunity theory [4]: (i) metacommunity theory is concerned with dispersal of individuals among local communities and not with their wholesale interchange. Thus in metacommunity theory, dispersal rate depends on the probability that local communities (e.g., on islands) receive immigrants from the metacommunity (e.g., continent), while coalescence is the encounter of entire local communities (e.g., an island community is translocated to another island or to the continent). (ii) Community coalescence also allows for and includes the movement and potential mixing of environments, for example, aquatic environments [5], and not just the movement of communities between environments. (iii) Communities that coalesce do not necessarily belong to a metacommunity in the sense of exchanging species at a low rate and having their structure affected by such an exchange. Coalescence also occurs when there is physical relocation of habitats and accompanying changes of the spatial structuring of the habitat. An example would be the encounter of the leaf microbial communities and the soil biota; these would not normally be considered part of the same metacommunity.



**Box 1. Evidence of microbial community coalescence**

Below we outline several previous studies that can be used to build a case that community coalescence occurs frequently and has important consequences.

*Encounter and mixing of aquatic communities.* Souffreau *et al.* [35] and Adams *et al.* [36] present an experimental and observational investigation of bacterioplankton community interactions. In these studies, communities encounter each other (e.g., river and lake) and are mixed in a partially new environment. Some of these encounters occur at very rapid rates, namely the flux rates of rivers, and at the level of entire assemblages. Livingston *et al.* [8] studied dynamics of aquatic communities that were experimentally mixed under controlled conditions; this study also explicitly included trophic interactions.

*Interacting microbial communities in roots.* Mummey *et al.* [37] examined segments of roots growing in the immediate vicinity of roots of another plant species. The root-colonizing fungal communities were more similar to that of a heterospecific neighboring plant than the typical community of the species to which the root belonged. This was interpreted as propagules of one fungal community 'overwhelming' those of another. Hausmann and Hawkes [38] found similar effects in controlled pot experiments. Given that plant roots in communities typically intermingle, this coalescence of root-borne or rhizosphere microbial communities could be commonplace.

*Microbial communities in the human body.* Qin *et al.* [39], using a metagenomic study of patients with liver cirrhosis, found evidence for invasion of microbes from the mouth into the gut. A possible reason was a change in bile production in patients with disease, which permitted invasion by bacteria from the oral microbiome. It thus seems that entire microbial communities, occurring 'in series' in the digestive system, interact in complex ways and whose coalescence is under metabolic or environmental control.

*Transfer of oral microbial communities by kissing.* Kort *et al.* [40] studied the exchange of bacteria after intimate kisses, including both observational and experimental data. They found substantial community exchange, leading to similarities among partners in oral microbiomes. Using tracer bacteria, the authors calculated an average transfer rate of 80 million bacteria per few-second kiss.

Community coalescence can occur in several ways (Figure 2), and these interaction modes could be captured by different types of theory. Coalescence events might differ in the degree to which different environments are involved in the coalescence, including the creation of 'mixed' environments or entry into one environment, the relative size of the interacting communities (mixing ratios), the nature of the contact interface, and aspects of the temporal nature of the coalescence events. Certain situations could then be grouped according to these interaction modes to derive predictions for general rules; for example, in the kissing situation the donated community would be experiencing the largely unaltered environment of the recipient, the added community would be relatively small compared with the recipient community, the contact interface would be a surface, and the interaction would be pulsed with relatively short duration.

Some of these situations can be linked to existing bodies of ecological theory. For example, if one community is moved to the environmental setting of another, environmental filtering [6] would likely benefit the subset of species that already inhabited the recipient environment. In cases where one community is added to another, priority effects [7] will be important, likely leading to invasion-resistance of the recipient community. The number of

individuals partaking in the community transfer will also be important for the outcome; when the transferred communities include only a small subset of the component species, metacommunity theory [4] might become more applicable.

It is likely that coalescing microbial communities will also contain predators and parasites [8], such that the ecology of trophic interactions could be brought to bear on the problem. For example, given that many predators are generalists, consuming a wide range of prey, the lack of specific adaptations to predators could result in altered top-down control of the coalesced community than in either of the two original communities. Conversely, during the coalescence, specialist pathogens and consumers might suffer disproportionately, as the density of their hosts would decline.

**Network theory and other approaches to model and analyze coalescent communities**

With these modes of interaction in mind, coalescence might be usefully modeled by using network approaches. Interaction matrices describe the dynamics of every species as a function of the other species, and in binary form the interaction matrix depicts the topology of interactions, for example, in a food web. In the context of community coalescence, we could describe the topology of two (or more) initially noninteracting (e.g., physically separated) admixed communities and investigate the network topology resulting from coalescence. The advantage of employing network theory to coalescence is that there is already a body of theory pertaining to this situation in other areas of science [9,10]. Independently, Kramer *et al.* [11] have used the term coalescence in the context of semi-independent neuronal networks that under some circumstances start to interact. Synchronization of networks [9] is also potentially relevant to coalescence: when communities start to coalesce, there can be a transient period during which they maintain their individual temporal patterns but eventually become synchronized, with potentially destabilizing effects at the system level [12]. The study of temporal fluctuations following a coalescence event can therefore yield key insights important for understanding the assembly and stabilization of the resultant community. A fascinating aspect of the study of temporal fluctuations in networks is that communities coming in contact with one another maintain some internal temporal coherence (i.e., network modules [13]), at least for some period of time. This coherence suggests that these communities interact as internally integrated units rather than just as a collection of many species that suddenly interact with another collection of species, resulting in a coalescent process where species replacement occurs within these newly interacting integrated units rather than a more stochastic rearrangement of interactions within the entire new network. This type of network dynamic is an emergent property of the whole network, which arises from the fact that components of local communities can in some cases act as whole units with strong interactions within these units and weak interactions between [14]. We suggest that studying temporal synchronization [9,10] in coalescing microbial populations is an exciting multidisciplinary

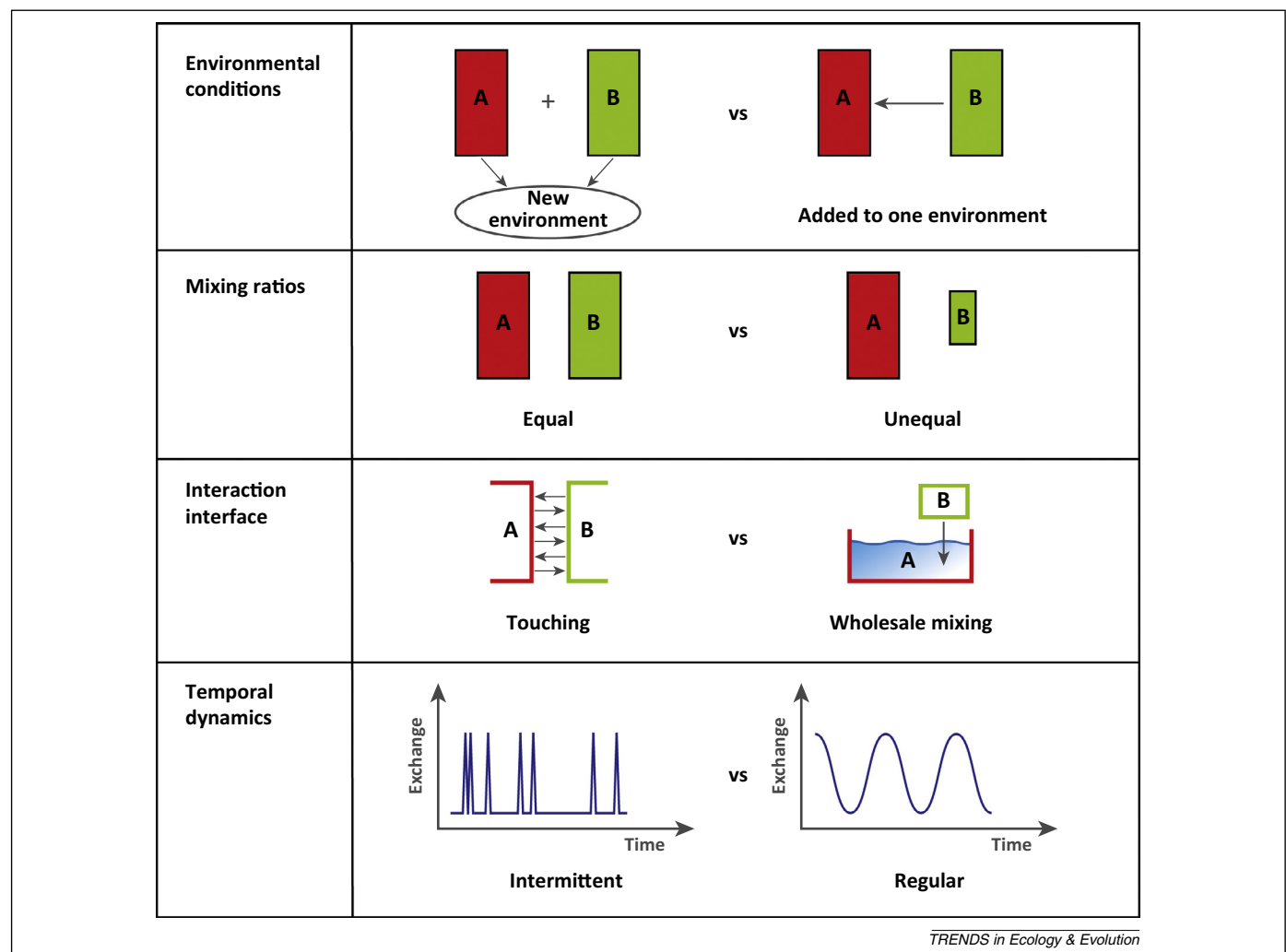
### Box 2. Microbial biogeography

In the past decade, there has been a resurgence of interest in microbial biogeography and researchers have started to explicitly test and conceptualize whether ‘biogeographical rules’ also apply to microorganisms [41–44]. In this field, the major issue has been establishing the relative roles of dispersal limitation and environmental filtering as two fundamental factors that can shape microbial community turnover [45]. It has been argued that the potentially large dispersal distance of microbes precludes the ‘existence of microbial biogeography’ [46]. There is substantial variation among microbial taxa in dispersal capacity (e.g., [47,48]) and this debate, not surprisingly, has largely settled in favor of at least ‘some’ dispersal limitation shaping biogeography of microbes [49]. This has focused attention on the fact that interactions among microbes are likely potent causes of community variation and deserving of more attention (see, e.g., [43,50]). The idea of community coalescence adds a further dimension to these discussions because it considers how whole communities and their environments interact with each other and how this impacts on the dynamics of its members.

perspective with which to document and understand such processes.

More classical network metrics such as (whole-network) modularity, connectance, and nestedness [15,16] could also

be used to describe networks in response to coalescence. Interestingly, in network science modules are also called ‘communities’ [13] and can be qualitatively defined as relatively dense subsets of vertices (i.e., species in our case) that are more tightly connected internally than with the rest of the network. The quantitative definition of modules is not a trivial task (e.g., [13,17]) but by equating two interacting modules with two coalescing communities, ecologists can exploit network tools to investigate coalescence in terms of changes in network community structure. Furthermore, this type of interaction is not explicitly considered in current ecological models describing community assembly from a metacommunity perspective, possibly because in the past few decades community ecologists have often adopted the implicit idea of communities as taxonomic assemblages or functional guilds at a given spatial and temporal scale. In other words, community boundaries are generally defined based on the unit that was sampled (whether an area or volume at a given time) as opposed to the interactions occurring among members of the sample or the sampled units themselves. Therefore, the identification of modules during the coalescent process and how



**Figure 2.** Illustration of some factors that are likely to influence the outcome of community coalescence. These factors include environmental conditions (entry of communities into new environment versus adding one community to another), the mixing ratios (equal versus unequal community proportions), the interaction interface (communities coalesce via surface touching versus wholesale mixing), or the temporal dynamics of community coalescence events (intermittent pulses versus regular exchange). General factors can be linked to existing bodies of ecological theory (see main text).

these modules interact has the potential to enhance ecological understanding at a profound level.

In this framework, expectations derived from simulations of coalesced communities [18–20] could serve as null models for comparison of predicted with observed outcomes. Current work on ecological networks (e.g., classical food webs) typically uses effects of single invasions or species removals to derive estimates of how stable those networks are [16], but different results might be expected when entire networks meet. Using model microbial communities with a known network architecture would be one approach to test how the outcome of coalescence varies with interaction frequency, size of communities, and environmental context (Figure 2 and Box 1).

Other tools might be helpful in characterizing the patterns emerging from coalescence as well. The study of null models and  $\beta$ -diversity can be particularly promising [21–23], because changes in  $\beta$ -diversity reflect the effects of immigration dynamics and biotic interactions.

However, the analysis of coalescent events presents new challenges that require the validation of existing approaches and the development of new ones. For example, community dissimilarity patterns across the landscape can provide insight into the extent that exchange between local communities occurs and can be conceptualized in a meta-community framework [24]. But a coalescence framework is needed to determine the degree to which admixing influences the structure and functioning of the communities. There might be *a priori* expectations based on the original admixing communities where these can be identified and sampled; alternatively, network analysis could allow accounting for their composition in an *a posteriori* manner. Importantly, however, we anticipate that coalescent events would result in complex outcomes and that careful consideration will need to be given to whether existing common metrics or null models can be used off-the-shelf or not [25].

### Potential consequences of coalescence for community-level functionality

So far, we have considered which factors might influence what communities resulting from coalescence events might look like in terms of composition or network structure. However, it is fairly likely that community coalescence can also have strong functional consequences. We see three main topics that should be the focus of future research: (i) degree of environmental mixing; (ii) dependence of functional consequences on traits of microbial species; and (iii) evolutionary implications of coalescence (horizontal gene transfer and adaptations).

First, environmental mixing is explicitly included in the concept of community coalescence and therefore drastic changes in the environment during coalescence, that is, changes in resources, abiotic factors, and biotic interactants, will also have to be considered. Some types of community coalescence will lead to more drastic environmental changes with pervasive functional consequences, such as the addition of communities to a new environment, with near-equal mixing ratios (Figure 2). Examples here would be predominantly from aquatic systems. Conversely, environmental shifts will be least important for community

coalescence events involving relatively small additions of one community to another, with merely surfaces touching, and the larger community remaining in its ‘home’ environment (like a quick kiss). Likely, any drastic resource changes (e.g., nutrients and carbon) and altered abiotic conditions (e.g., pH and temperature) will lead to species losses, for example, by exceeding tolerances or via competitive exclusion, with concurrent losses of functional traits from the resulting community.

The second aspect to consider is the trait space occupied by the communities before and after coalescence (this is in part dependent on the discussion of environments above). Trait-based approaches are increasingly being applied to microbial systems [26–28]. If the input communities occupy very dissimilar trait space from each other, and if these are partially maintained after coalescence, then one could expect the resulting community to occupy an even wider trait space than either of the original communities, likely also representing altered functionality [28], including potentially greater productivity. The converse could be expected if input communities are very similar in trait space: then members might merely substitute for each other in the resulting community, not causing wholesale functional changes, with similar productivity.

The third point to consider is evolutionary implications of coalescence. Here, we see two main avenues for systematic study: horizontal gene transfer made possible by transient coexistence and adaptations to coalescence events.

Community coalescence could permit organisms from highly diverging habitats (e.g., river water and soil) and with dissimilar traits to at least transiently coexist, especially with recurring events (Figure 2). This co-occurrence can permit horizontal gene transfer between very dissimilar organisms, an issue of considerable importance in trying to quantify, for example, the rates of transfer of antibiotic resistance (e.g., [29]). As such, these transient communities can be ‘incubators’ for rapidly-evolving species that exhibit different trait combinations, potentially resulting in altered ecosystem functionality.

A second evolutionary question is whether frequent coalescence events in microbial communities have brought about adaptations in member species, which in turn have functional consequences at the community level. For example, many parasites have evolved life-cycle stages in the gut of the host as well as in the soil, and the transfer of parasite stages between these habitats occurs as a part of the coalescence of soil and gut communities (Box 1). Another example is the exchange of endophyte microbial communities cycling between leaves and the soil. Do adaptations to coalescing communities occur in these and other microbial groups? Predictions from evolutionary ecology on traits related to within- and between-species interactions are strongly contingent on levels of mixing (e.g., [30]): traits related to cooperative or mutually beneficial behavior are favored by spatial structure, and conversely ‘selfish’ non-cooperative behaviors are favored in well-mixed systems. This is because this structuring determines which individuals and/or species are likely to iteratively interact over a prolonged period of time, allowing cooperation to evolve. Given the propensity of positive interaction in structured populations and communities, cycles of isolation followed



by re-encounters in the form of coalescence events might have a profound influence on the evolution of traits of the constituent species and individuals.

### Applied relevance and concluding remarks

Microbial communities have an exceptional applied significance in many different fields from medicine and biotechnology to sustainable agriculture. It is likely that an explicit consideration and conceptual treatment of coalescence involving microbial communities inhabiting the human body, some of which are in intense exchange with the environment (including other humans), could lead to a better understanding of their function in public health [29,31] and open new directions in biomedical research (e.g., gut microbiome interactions [32]); in fact, some of the most intriguing empirical examples of coalescence so far stem from this area of public health (Box 1). In environmental applications, progress could be possible by considering if community coalescence can be used to 'engineer' microbial consortia [33] better suited to tasks than single communities. In sustainable agriculture, ecological restoration or remediation the coalescence concept could help frame situations where substrates (e.g., biochar, manures, compost, and even crop seeds carrying endophyte communities) are added to resident soil microbial communities. In the context of global change and ever-increasing connectedness of global ecosystems, this concept can be very useful in capturing properties and dynamics of novel communities and ecosystems [34]. But some of the most exciting potential applications are likely to be completely unforeseeable until systematic study of these processes has commenced.

In this opinion article, we argue for the dedicated study of microbial community coalescence, which we anticipate will address a set of new research questions (Box 3). This will require a joint effort from multiple disciplines and the empirical study of microbial communities that meet, of their functional properties, as well as the development of models to simulate their dynamics and evolution. Through this effort the concept of community coalescence can help

better understand the complexity of microbial assemblages and open avenues for the targeted manipulation of such assemblages for human use in industry, medicine, or sustainable agriculture. While the examples we have used are microbial in nature, we think that general insights derived from microbial ecology might also be useful for understanding equivalent processes at larger timescales in macroorganisms, especially in the context of global change.

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### Box 3. Outstanding research questions

- Have repeated and continuous coalescence events contributed to the high microbial diversity in some habitats, such as the soil?
- Do 'hybrid' communities exhibit a broader functional range and higher productivity compared with communities entering a coalescence event?
- Will members of communities with a history of coalescence have a higher persistence upon interaction with a 'naïve' community?
- Can better mechanistic understanding of community coalescence help predict community-level migration and/or mixing as a result of global change?
- Can we predict properties of coalescent communities using approaches derived from the study of interacting networks?
- Have microbes evolved specific adaptations to survive or profit from repeated coalescence events? What form do these adaptations take? Are alternative life forms and complex life cycles involved? When would antagonistic versus mutualistic interactions be favored?
- Is it possible to identify groups of microbes, or microbial traits, that are characteristic of coalescent events and can these be used as indicators of the coalescent history of a community?

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