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Reference:

Rillig Matthias C., Antonovics Janis, Caruso Tancredi, Lehmann Anika, Powell Jeff R., Veresoglou Stavros D., Verbruggen Erik.- Interchange of entire communities : microbial community coalescence
Trends in ecology & evolution - ISSN 0169-5347 - 30:8(2015), p. 470-476
Full text (Publishers DOI): <http://dx.doi.org/doi:10.1016/J.TREE.2015.06.004>
To cite this reference: <http://hdl.handle.net/10067/1272220151162165141>

Opinion

Interchange of entire communities: microbial community coalescence

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Keywords: communities; mixing; community coalescence; metacommunity; environment;
networks; biodiversity; global change

Abstract

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 quite frequently, at time scales relevant to understanding community structure? Here we develop the idea that events reminiscent of the

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 (see 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 macro-organisms (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 microbial biogeography (see Box 2) has long debated the degree of dispersal limitation among micro-organisms, 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, and how these consequences can be linked to and illuminated by existing 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 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 inter-connectedness of biological systems increases with global change.

Factors influencing community composition resulting from community coalescence

While a number of empirical studies (see Box 1) and modelling 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 quite 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.

Community coalescence can occur in a number of ways (see 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 in order 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 to 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 modelled 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 non-interacting (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]. Quite 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 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 last 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 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 (see 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 β -diversity can be particularly promising [21-23], because changes in β -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 metacommunity 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* fashion. 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 quite 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, i.e. 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 (Fig. 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 prior to 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 quite 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 quite 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 are 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 (see Fig. 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 which 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 consequence 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 (see 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

Microbial communities have an exceptional applied significance in many different fields from medicine and biotechnology to environmental remediation and horticulture. 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 (see Box 1). Community coalescence could also be eminently applicable to industrial processes, such as waste water treatment. Can community coalescence be used to 'engineer' microbial consortia [33] better suited to tasks than single communities? In agriculture, 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.

Conclusion

Our paper argues for the dedicated study of microbial community coalescence, which we anticipate will address a set of new research questions (see 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 environmental protection. 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 macro-organisms, especially given the context of ever increasing connectedness of global ecosystems.

267

268 **Glossary**

269 **β -diversity:** the variation in the identities of species among sites [21].

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

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

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

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

283 **Metacommunity:** a collection of local communities linked by dispersal of their component
284 species. The concept is derived from that of the metapopulation, which is a collection of
285 populations of one species linked by dispersal of individuals. Metacommunity dynamics includes
286 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.

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 which 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 liver cirrhosis patients, 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.

328

329 **Box 2. Microbial biogeography**

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

343

344

345 **Box 3. Outstanding research questions**

346 Have repeated and continuous coalescence events contributed to the high microbial diversity in
347 some habitats, like the soil?

348 Do ‘hybrid’ communities exhibit a broader functional range and higher productivity compared to
349 communities entering a coalescence event?

350 Will members of communities with a history of coalescence have a higher persistence upon
351 interaction with a ‘naïve’ community?

352 Can better mechanistic understanding of community coalescence help predict community-level
353 migration and/ or mixing as a result of global change?

354 Can we predict properties of coalescent communities using approaches derived from the study
355 of interacting networks?

356 Have microbes evolved specific adaptations to survive or profit from repeated coalescence
357 events? What form do these adaptations take? Are alternative life-forms and complex life-cycles
358 involved? When would antagonistic vs. mutualistic interactions be favored?

359 Is it possible to identify groups of microbes, or microbial traits, that are characteristic of
360 coalescent events and can these be used as indicators of the coalescent history of a community?

361

Figure legends

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 e.g. 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 MC Rillig (A, C, D, E, F) and Wikimedia Commons (B: Niklas Tschöpe, G: anonymous).

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 vs. adding one community to another), the mixing ratios (equal vs. unequal community proportions), the interaction interface (communities coalesce via surface touching vs. wholesale mixing) or the temporal dynamics of community coalescence events (intermittent pulses vs. regular exchange). General factors can be linked to existing bodies of ecological theory (see text).

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Point by point response to reviewer comments Rillig et al., TREE-D-15-00083

Editor comments

I continue to like the overall idea of the manuscript and that is the general feeling of both reviewers. However, there are also some serious concerns and these will need to be fully addressed. In particular, Reviewer 2 has identified some ideas and literature that appear to have been missed. If appropriate, we could change the format to a Review. To some extent, Opinions and Reviews merge into one another and Reviews should also include novel material such as a new perspective or a new synthesis. It would also need to be clear, both in your manuscript and your responses to the reviewers, how your manuscript develops and differs from what is already available, especially the results of the workshop described by Reviewer 2.

Response: Thanks for these comments. We deal with the specific issues below. We have decided to stay with an *Opinion*, rather than *Review* paper format, since it was possible to accommodate the required changes in terms of references and text limits.

Reviewer 2 also has some concerns about the use of the term "coalescence". This will need to be clarified at the very least. Reviewer 1 found use of the concept thought-provoking so I would argue for keeping it as long as you can satisfy the concerns of Reviewer 2.

Response: We think it is important to use a term that is not yet used in community ecology. Of all terms we considered, coalescence was the most appropriate, even though we were aware of the use of coalescence in an evolutionary context, which really does mean something entirely different in a radically different context. To some extent, issues like this cannot be fully avoided, but from the context it should be quite clear. The real advantage of coining a term like *community coalescence* is that it can serve as a tag with the help of which papers on this topic are more readily identified. Currently there is no such term. We have changed the manuscript to use 'community coalescence' instead of 'coalescence', when we first define it (and in the Glossary) to avoid this possible confusion. See more detailed comments below.

Reviewer 2 feels the microbial ecology aspects are insufficiently developed and so, of course, this will have to be fully dealt with in your revision. If you found yourself needing to include an additional author for this, we could accommodate that.

Response: We agree. Please see comments below. We have added a box on this topic in the revision and now give the reader the necessary background.

* Please follow our Instructions to Authors for the correct style for the reference list.

* A solidus (/) can be ambiguous, therefore, please change ALL solidi to 'and', 'or', 'and/or' or '-' where appropriate.

* Please note that the figures should 'stand alone' and thus figure legends need to be explanatory rather than just descriptive.

* Please use the accepted nomenclature for all gene and protein symbols, italicizing gene names where appropriate.

* Please include GenBank accession numbers for all genes. Please use bold and underlined text and with uppercase letters (e.g. **A12345**), stating that they are GenBank accession numbers.

* For clarity we use 'might' or 'can' rather than 'may' because 'may' implies doubt or permission, please change any use of 'may' to 'might' or 'can' as appropriate.

* Please note that it is your responsibility to obtain permission to reproduce copyrighted material (i.e. figures, tables or excerpts that have been published online or in print) from the publishers of the original material. This is also relevant to figures that have been altered in any way. You should retain the original permission form on its return from the copyright holder. Please note that it is courteous to inform the author of the original material of your intent to use their published work.

Response: We have checked the manuscript; in particular we have replaced the occurrences of 'may' in the manuscript.

Reviewer #1:

Overall, I think this paper could make a valuable contribution to the literature, acting as a foundation for new research on microbial community coalescence and its functional consequences. Having read the paper, I didn't feel that it identified a clear framework for future research on community coalescence; rather it gave a very broad overview of types of coalescence events, ways of exploring them with theory, and some varied thoughts on possible functional consequences of events. This is useful, but I did feel a bit disappointed that more wasn't offered in terms of a clear conceptual framework for taking the field forward; rather, the paper seems to jump from one issue to another in some parts, and didn't really develop a clear message. This was perhaps most evident in the section on 'functionality', which touches on many points, but doesn't develop any to a significant degree. Also, the applied section reads like a bit of a bolt on, and perhaps could just be integrated more into the introduction and functional sections, simply highlighting the relevance of the coalescence in the current and future world. This would then leave more space to develop the final conclusion section, which could identify more the key concepts of the paper and research challenges to be addressed, which are currently in box 3.

Having said this, I do think that the paper makes an important contribution, and it has succeeded in leaving me thinking about coalescence as a concept, which I hadn't really considered in this way before. So, in sum, I think the paper has much potential, but I offer some suggestions that might help focus its messages.

Response: Many thanks for these supportive and constructive comments. We address them below in detail.

Highlights

I didn't find the highlights to be very useful. It would be more helpful to say what coalescence is as the first highlight and then something on how it is approached and what its consequences might be. The last point on scale isn't clear.

Response: We agree. Highlights have been revised following the reviewer's suggestions; they now read:

- *Community coalescence* is the interchange of entire microbial communities
- Lack of terminology and concepts have hampered research
- *Community coalescence* can be addressed with tools including network theory
- *Community coalescence* likely has important functional and applied consequences
- Empirical research should address factors governing *community coalescence*

Introduction

This section identifies what the concept is, with a few examples, but it might also be useful to highlight that coalescence could have significant functional consequences, which is considered in the paper, and will global change accelerate coalescence, meaning that it is likely more relevant in a changing world? I suspect this will be the case, especially in relation to things like invasion, land use and climate change (e.g. range expansions etc). This could perhaps be developed more, to at least identify the relevance of coalescence events in a changing world. Also, while coalescence might not have been considered from a microbial community context, the literature is replete with studies of the functional significance of the identified events, which indirectly involve microbes (e.g. falling litter, burrows and casts, dust movement and nutrient enrichment, water flow). Maybe this should be acknowledged.

Response: We think this is a good point. We added to the Background section the point about global change, in the final sentence “(...), *but also of increasing importance as the inter-connectedness of biological systems increases with global change.*”

We also added ‘global change’ as a keyword to facilitate finding this paper also in this context.

We also liked the second point, because it strengthens the case we aim to make, and have added the following:

“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. (...)”

Factors influencing community coalescence

This section reads well and I just have two comments. The first concerned the point about bringing two communities together so that they are close. I was a bit unclear how this fitted into the concept, especially regarding ecotones, which I realise are functionally important, but they are very different to the events identified in the introduction, which involve true mixing and generally occur very quickly. This might need some further explanation, especially regarding the coalescence of communities, which is hardly mentioned. Also, what is perhaps more relevant here is range expansion of plants, animals and microbes. Second, I felt that more mention should also be made of the changing environment, especially in terms of resource supply, which will be substantially altered during these coalescence events, both as a result of the resource input itself, but also the change in

community. I just felt that this point needed more emphasis as changes in community composition will also result from changes in resource supply and limitations in the new environment.

Response:

1) Ecotones

We agree that this discussion on ecotones is confusing, since this is not coalescence, as the reviewer correctly points out. We have therefore decided to delete this section.

2) changing environment during events (resources)

We agree; this is a very important point we had not really discussed. We have not made these changes in this particular section, but we have dedicated an entire new paragraph in the “functional consequences” section to the consideration of environmental mixing (while referring to Fig. 2 – see our responses below).

Networks

This section reads well, aside the last paragraph on page 6 (line 129-134) which I didn't feel offered much, as doesn't actually say how these measures will be useful and seem like pretty obvious metrics. Personally, I would drop this paragraph and elaborate more on new approaches (page 7).

Response:

1) We agree. We have deleted the sentence “*For example....diversity measures.*” We have kept the last sentence as an introductory statement to link with the last paragraph in this section.

2) We did elaborate more on the network approaches, and have added two new paragraphs with detail on these.

Consequences for functionality

As mentioned above, this is the weakest and least coherent section, in that it glances over various approaches and ideas, but gives little insight into actual consequences for function. For example, it is mentioned that trait based approaches offer potential, but how this informs on functional consequences of community coalescence isn't expanded on. There are many examples in the literature of how such approaches are used to understand how community change influences functions, including studies on plants, animals, and microbes, which could be referred to here to illustrate how this approach could help here. Also, it is unclear how the functional hybrid hypotheses will inform function in this context, at least from the text. Overall, I just felt that this section needed to be re-thought, in that it doesn't explicitly relate to function. Perhaps examples would help to illustrate more clearly, illustrating how the different factors identified in Figure 2 (e.g. mixing ratios, interfaces, and temporal dynamics), influence community coalescence and its consequence for ecosystem functions, drawing on what is already known about consequences of species gain and

loss. It just seems a bit like there is a myriad of different types of coalescence events, but the paper offers little in terms of understanding how different types of events have functional consequences and the characteristics of these.

Response: We see the reviewer's point. We have done the following to improve the logical coherence of this section:

- We have added an introductory sentence in which we now clearly state what we will discuss. *"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)."* The section is then structured according to these three consolidated topics.
- We have taken up the excellent suggestion to work more with Fig. 2 (factors influencing coalescence events), to which we now refer several times, also giving examples where appropriate
- We have deleted the discussion of community hybrids (functional relevance not clear)
- We have deleted the short section on rare biosphere (since it had no functional connotations)
- We added a new section on the environment (point (i))
- We explain why we include the two evolutionary considerations

While we also liked the reviewer's suggestion to expand more on the trait-based approaches, we feel this would not be possible within the word limit. But we have added additional citations.

Reviewer #2: Comments on Rillig et al. for TREE

It is always interesting, and sometimes refreshing, when researchers from one field apply concepts and theories developed in their realm to a rather different field. In this case the concepts are from historical biogeography, evolution, and a bit of macroecology, and those ideas are applied to microbial ecology, more specifically, the composition of microbial assemblages.

At the outset, one issue is that the composition of microbial assemblages, especially in soils, remains very much a matter of ongoing investigation, with the complexity of these assemblages still posing challenges to the rapidly developing modern techniques such as metagenomics sequencing. We still don't know much about what is where, or in other words, microbial biogeography, if it exists (I think that it probably does), remains poorly known. That said, there are historical antecedents to the core of this paper that the authors would do well to incorporate. The historical null hypothesis, otherwise known as the Baas-Becking (1934, *Geobiologie of inleidende tot de milieukunde*, The Hague) hypothesis among microbiologists, is roughly summarized as "Everything is everywhere, but the environment selects". This idea has also been embraced by some biologists working on larger unicellular organisms (Finlay and Fenchel, 2004, *Protist*) to suggest that these organisms also enjoy cosmopolitan distributions by virtue of their cosmological population sizes and powers of dispersal. There are others who don't believe it (Foissner, 2004, *Protist*). The controversy, and its causes, has been nicely summarized by Martiny et al. (*Nature Reviews Microbiology*, 2006), who also make a case for the likely existence of some sort of microbial biogeography. The Martiny et al. paper grew

out of a NCEAS working group that deliberately brought together traditionally trained microbiologists, macroecologists working on "large" organisms, and some people spanning both worlds to foster the kind of interdisciplinary cross-fertilization that Rillig et al seem keen to address. The point of reviewing this ancient to recent history of the study of microbial geographic distributions, which are central to this manuscript, is that the authors seem to be unaware of this literature. The point is that microbes are widely viewed with having ways to get around that trump the wholesale kinds of multispecies dispersal events that the authors envision. Not such a good start.

Response: Thanks for this comment. We were in fact fully aware of these papers; we think it is a very good idea to bring elements of this biogeography discussion into the paper since, as the reviewer states, this is fundamentally relevant to our discussion.

In order to address this point we have added a new box on Microbial biogeography, in which we highlight some of the pertinent literature, including the papers the reviewer mentioned.

We have (to keep within the limits of the Opinion paper) integrated the text in the box on metacommunities to the pertinent section in the paper's main text (i.e., we still have the same number of display items).

I'm also a bit uncomfortable with the analogy of multispecies microbial dispersal events and the "Great American Interchange". The latter almost certainly did not result from the wholesale movement of communities among continents, but rather was a consequence of the dispersal and migration of individual taxa over time, once the land bridge was established. Did the biota gradually mix and sort? Sure, but not in the way envisioned for microbes.

Response: We completely agree. However, we rather like the analogy as a captivating lead-in to the paper. But as all analogies it only goes so far; nevertheless this is somewhat similar to the 'touching surfaces' mode of coalescence (compare Fig. 2), but still the reviewer is correct. We did alter the text to do more justice to the limitations of this analogy, and to highlight that the degree of interchange is more pronounced:

"(...) events reminiscent of the Interchange with a potentially even greater degree of mixing"

"Community coalescence", as the term is used here, has the potential to be confusing. Coalescence is one of those terms used by evolutionary biologists which has more than a bit of jargon to it. I hear it used frequently, but because I am not one of the elect, I'm never quite sure what it means. I think it mostly refers to the notion that various statistical analyses and models can be used to trace back the point in time when different members of a complex lineage originally diverged. This makes its application/appropriation to communities a bit obscure, perhaps because it reverses the temporal perspective. In evolution, coalescence is retrospective, here it is the opposite. I think that the authors are really talking about community assembly, which has a fairly well -accepted meaning that includes an array of interactions and stochastic processes (e.g. Weiher and Keddy, 1999). Maybe they are talking about something more like community accretion, a largely stochastic process where neutral processes account for the accumulation of non-interacting species. Then there is biotic homogenization, which describes the breakdown of biogeographic barriers and the subsequent

changes in community composition that occur, which can both increase or decrease diversity, depending on the situation.

Response: We think it is quite important to coin a distinct term, along for the ability to ‘tag’ publications and thus identify and assemble a pertinent body of literature; this is an important task of this paper. We agonized quite a bit over the term to be used, and converged on two final candidates: ‘coalescence’ and ‘confluence’. We decided on coalescence, even though we were aware of the different meaning of ‘coalescence’ in the field of evolution, since confluence seemed too narrowly aquatic. We would argue that the potential for confusion is relatively minor, since the context is radically different, and we advocate use of ‘*community coalescence*’. We do not think that the other terms the reviewer proposes capture what we are after here.

We have changed ‘coalescence’ to ‘community coalescence’ when we first defined the term, and also in the title, glossary and at other key positions in the text (like headers, keywords and highlights) to avoid any possible confusion with the other use in evolution. To make the latter even more clear, we have added the meaning of this term from population genetics in the definitions in the glossary.

As for accounting for the diversity of microbes in communities, there are some interesting models and experiments that suggest that intransitive interactions mediated by networks of growth inhibitors/antibiotics and resistance genes for same can promote high diversity in spatially heterogeneous environments, like soils (Czaran et al. PNAS 2002, and Kerr et al. Nature 2002). The models and experiments also predict that high diversity won't be maintained in spatially homogenous environments, which argues that the processes envisioned by the Willig et al. probably depend on very infrequent to rare dispersal, if they have anything to do with diversity.

Response: We fully agree that there are many other mechanisms mediating coexistence of microbes, including the ones mentioned by the reviewer. We think these points are not mutually exclusive, however: for example, coalescence events could lead to the formation of intransitive interaction networks via addition of new interactants. We believe in the text it is clear that community coalescence is but one factor potentially accounting for the diversity of microbes in communities. The point to which this comment may be directly referring (biodiversity of microbes, including rare biosphere) has been deleted from manuscript as a consequence of restructuring the section on function (see reviewer 1).

Highlights for Rillig *et al.* **Coalescence of entire communities: microbial community interchange**

- *Community coalescence* is the interchange of entire microbial communities
- Lack of terminology and concepts have hampered research
- *Community coalescence* can be addressed with tools including network theory
- *Community coalescence* likely has important functional and applied consequences
- Empirical research should address factors governing *community coalescence*

Figure 1

Figure 1.



Figure 2

Figure 2.

Environmental conditions	<div><div><div><div>A</div><div>B</div></div><div>+</div><div><div>new environment</div></div></div><div>vs.</div><div><div><div>A</div><div>B</div></div><div>←</div><div>added to one environment</div></div></div>
Mixing ratios	<div><div><div>A</div><div>B</div></div><div>equal</div><div>vs.</div><div><div><div>A</div><div>B</div></div><div>unequal</div></div></div>
Interaction interface	<div><div><div><div>A</div><div>B</div></div><div>touching</div><div>vs.</div><div><div><div>B</div><div>A</div></div><div>wholesale mixing</div></div></div></div>
Temporal dynamics	<div><div><div><div>exchange</div><div>time</div></div><div>intermittent</div><div>vs.</div><div><div><div>exchange</div><div>time</div></div><div>regular</div></div></div></div>

[Click here to download Original Figure File: Fig 1 REVISED coalescence photos.jpg](#)

[Click here to download Original Figure File: Fig 2 Coalescence-modes \(original file\).jpg](#)