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1 Opinion

2 **Interchange of entire communities: microbial community coalescence**

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15

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

18

19 **Abstract**

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

30

31 **Great American Interchange *en miniature*?**

32 Alfred Russell Wallace [1] was perhaps one of the first to consider what would happen when
33 previously separated communities meet – in his case at a very large spatial and temporal scale,
34 in what has become known as the *Great American Interchange*: the linking of North and South
35 America by the appearance of the Isthmus of Panama. The result of such wholesale migration,
36 mixing and joining of communities was likely a multifold of establishments, species exchanges
37 and extinctions, massive effects at any rate. What if community encounter events like these were
38 not exceptional singularities, but were to occur quite frequently, at time scales relevant to
39 understanding community structure? Here we develop the idea that events reminiscent of the

40 *Interchange* could be common in microbial systems, and with potentially even greater degrees
41 of mixing. We think this is the case because in nature, pieces of the environment much larger and
42 more persistent than an individual microbe, and indeed containing entire local microbial
43 communities, are routinely moved (see Figure 1 and Box 1). Forces that move pieces of the
44 environment containing entire microbial assemblages include gravity (falling leaves), animals
45 (e.g. burrows and casts), growth of macro-organisms (plant roots encountering each other in the
46 soil), wind (dust movement), flow in liquids (natural or industrial water bodies mixing, movement
47 inside the human body) or human activities (horticultural outplanting, ploughing or movement
48 of wood). We propose the term *community coalescence* (see Glossary) to describe such
49 community interchange events (Box 1).

50 While the literature is replete with studies on the effects and importance of many of the events
51 mentioned above (e.g. litter fall), these reports have rarely addressed the microbial community-
52 level interactions. The field of microbial biogeography (see Box 2) has long debated the degree
53 of dispersal limitation among micro-organisms, and is now also beginning to explore how
54 environment, spatial processes, and biotic context shape local communities. Community
55 coalescence events are part of the dispersal process, but also much more, because such events
56 result in whole communities and their environments interacting. Therefore, it is important to ask
57 how they influence the resulting community, and how these consequences can be linked to and
58 illuminated by existing ecological theory. What is the empirical evidence on community
59 coalescence thus far? How can the problem of entire communities interacting be approached
60 from a theoretical perspective? What are functional consequences of community coalescence?
61 These are the questions we address here with the goal of stimulating research on this topic;

62 community coalescence is likely to be important not only in the everyday events of microbial
63 ecology, but also of increasing importance as the inter-connectedness of biological systems
64 increases with global change.

65

66 **Factors influencing community composition resulting from community coalescence**

67 While a number of empirical studies (see Box 1) and modelling exercises [2, 3] have addressed
68 aspects of what we call community coalescence, there has been no systematic study of such
69 phenomena, and this might in part be due to a lack of an applicable conceptual framework for
70 classifying these events, estimating their frequency, or predicting their consequences. We
71 believe such separate conceptual development is necessary because the coalescence of
72 communities has features quite distinct from those described in other bodies of theory, in
73 particular the processes envisaged in metacommunity theory [4]: (i) Metacommunity theory is
74 concerned with dispersal of individuals among local communities, and not with their wholesale
75 interchange. Thus in metacommunity theory, dispersal rate depends on the probability that local
76 communities (e.g. on islands) receive immigrants from the metacommunity (e.g. continent) while
77 coalescence is the encounter of entire local communities (e.g. an island community is
78 translocated to another island or to the continent). (ii) Community coalescence also allows for
79 and includes the movement and potential mixing of environments, for example aquatic
80 environments [5], and not just the movement of communities between environments. (iii)
81 Communities that coalesce do not necessarily belong to a metacommunity in the sense of
82 exchanging species at a low rate, and having their structure affected by such an exchange.

83 Coalescence also occurs when there is physical relocation of habitats and accompanying changes
84 of the spatial structuring of the habitat. An example would be the encounter of the leaf microbial
85 communities and the soil biota; these would not normally be considered part of the same
86 metacommunity.

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

98 Some of these situations can be linked to existing bodies of ecological theory. For example, if one
99 community is moved to the environmental setting of another, environmental filtering [6] would
100 likely benefit the subset of species that already inhabited the recipient environment. In cases
101 where one community is added to another, priority effects [7] will be important, likely leading to
102 invasion-resistance of the recipient community. The number of individuals partaking in the
103 community transfer will also be important for the outcome; when the transferred communities

104 include only a small subset of the component species, metacommunity theory [4] might become
105 more applicable.

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

113

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

115 With these modes of interaction in mind, coalescence might be usefully modelled by using
116 network approaches. Interaction matrices describe the dynamics of every species as a function
117 of the other species, and in binary form the interaction matrix depicts the topology of
118 interactions, for example in a food web. In the context of community coalescence, we could
119 describe the topology of two (or more) initially non-interacting (e.g. physically separated)
120 admixed communities, and investigate the network topology resulting from coalescence. The
121 advantage of employing network theory to coalescence is that there is already a body of theory
122 pertaining to this situation in other areas of science [9, 10]. Quite independently Kramer *et al.*
123 [11] have used the term coalescence in the context of semi-independent neuronal networks that
124 under some circumstances start to interact. Synchronization of networks [9] is also potentially

125 relevant to coalescence: when communities start to coalesce, there can be a transient period
126 during which they maintain their individual temporal patterns but eventually become
127 synchronized, with potentially destabilizing effects at the system level [12]. The study of temporal
128 fluctuations following a coalescence event can therefore yield key insights important for
129 understanding the assembly and stabilization of the resultant community. A fascinating aspect of
130 the study of temporal fluctuations in networks is that communities coming in contact with one
131 another maintain some internal temporal coherence (i.e. network modules [13]), at least for
132 some period of time. This coherence suggests that these communities interact as internally
133 integrated units rather than just as a collection of many species that suddenly interact with
134 another collection of species, resulting in a coalescent process where species replacement occurs
135 within these newly interacting integrated units rather than a more stochastic rearrangement of
136 interactions within the entire new network. This type of network dynamic is an emergent
137 property of the whole network, which arises from the fact that components of local communities
138 can in some cases act as whole units with strong interactions within these units and weak
139 interactions between [14]. We suggest that studying temporal synchronization [9, 10] in
140 coalescing microbial populations is an exciting multidisciplinary perspective with which to
141 document and understand such processes.

142 More classical network metrics such as (whole-network) modularity, connectance and
143 nestedness [15, 16] could also be used to describe networks in response to coalescence.
144 Interestingly, in network science modules are also called ‘communities’ [13] and can be
145 qualitatively defined as relatively dense subsets of vertices (i.e. species in our case) that are more
146 tightly connected internally than with the rest of the network. The quantitative definition of

147 modules is not a trivial task (e.g. [13, 17]) but by equating two interacting modules with two
148 coalescing communities, ecologists can exploit network tools to investigate coalescence in terms
149 of changes in network community structure. Furthermore, this type of interaction is not explicitly
150 considered in current ecological models describing community assembly from a metacommunity
151 perspective, possibly because in the last few decades community ecologists have often adopted
152 the implicit idea of communities as taxonomic assemblages or functional guilds at a given spatial
153 and temporal scale. In other words, community boundaries are generally defined based on the
154 unit that was sampled (whether an area or volume at a given time) as opposed to the interactions
155 occurring among members of the sample or the sampled units themselves. Therefore, the
156 identification of modules during the coalescent process and how these modules interact has the
157 potential to enhance ecological understanding at a profound level.

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

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

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

180

181 **Potential consequences of coalescence for community-level functionality**

182 So far we have considered which factors might influence what communities resulting from
183 coalescence events might look like in terms of composition or network structure. However, it is
184 quite likely that community coalescence can also have strong functional consequences. We see
185 three main topics that should be the focus of future research: (i) degree of environmental mixing;

186 (ii) dependence of functional consequences on traits of microbial species; and (iii) evolutionary
187 implications of coalescence (horizontal gene transfer and adaptations).

188 First, environmental mixing is explicitly included in the concept of community coalescence, and
189 therefore drastic changes in the environment during coalescence, i.e. changes in resources,
190 abiotic factors and biotic interactants, will also have to be considered. Some types of community
191 coalescence will lead to more drastic environmental changes with pervasive functional
192 consequences, such as the addition of communities to a new environment, with near-equal
193 mixing ratios (Fig. 2). Examples here would be predominantly from aquatic systems. Conversely,
194 environmental shifts will be least important for community coalescence events involving
195 relatively small additions of one community to another, with merely surfaces touching, and the
196 larger community remaining in its 'home' environment (like a quick kiss). Likely, any drastic
197 resource changes (e.g. nutrients and carbon) and altered abiotic conditions (e.g. pH and
198 temperature) will lead to species losses, for example by exceeding tolerances or via competitive
199 exclusion, with concurrent losses of functional traits from the resulting community.

200 The second aspect to consider is the trait space occupied by the communities prior to and after
201 coalescence (this is in part dependent on the discussion of environments above). Trait-based
202 approaches are increasingly being applied to microbial systems [26-28]. If the input communities
203 occupy quite dissimilar trait space from each other, and if these are partially maintained after
204 coalescence, then one could expect the resulting community to occupy an even wider trait space
205 than either of the original communities, likely also representing altered functionality [28],
206 including potentially greater productivity. The converse could be expected if input communities

207 are quite similar in trait space: then members might merely substitute for each other in the
208 resulting community, not causing wholesale functional changes, with similar productivity.

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

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

219 A second evolutionary question is whether frequent coalescence events in microbial
220 communities have brought about adaptations in member species, which in turn have functional
221 consequence at the community level. For example, many parasites have evolved life-cycle stages
222 in the gut of the host as well as in the soil, and the transfer of parasite stages between these
223 habitats occurs as a part of the coalescence of soil and gut communities (see Box 1). Another
224 example is the exchange of endophyte microbial communities cycling between leaves and the
225 soil. Do adaptations to coalescing communities occur in these and other microbial groups?
226 Predictions from evolutionary ecology on traits related to within- and between species
227 interactions are strongly contingent on levels of mixing (e.g. [30]): traits related to cooperative

228 or mutually beneficial behavior are favored by spatial structure, and conversely 'selfish' non-
229 cooperative behaviors are favored in well-mixed systems. This is because this structuring
230 determines which individuals and/ or species are likely to iteratively interact over a prolonged
231 period of time, allowing cooperation to evolve. Given the propensity of positive interaction in
232 structured populations and communities, cycles of isolation followed by re-encounters in the
233 form of coalescence events might have a profound influence on the evolution of traits of the
234 constituent species and individuals.

235

236 **Applied relevance**

237 Microbial communities have an exceptional applied significance in many different fields from
238 medicine and biotechnology to environmental remediation and horticulture. It is likely that an
239 explicit consideration and conceptual treatment of coalescence involving microbial communities
240 inhabiting the human body, some of which are in intense exchange with the environment
241 (including other humans), could lead to a better understanding of their function in public health
242 [29, 31] and open new directions in biomedical research (e.g. gut microbiome interactions [32]);
243 in fact, some of the most intriguing empirical examples of coalescence so far stem from this area
244 of public health (see Box 1). Community coalescence could also be eminently applicable to
245 industrial processes, such as waste water treatment. Can community coalescence be used to
246 'engineer' microbial consortia [33] better suited to tasks than single communities? In agriculture,
247 the coalescence concept could help frame situations where substrates (e.g. biochar, manures,
248 compost and even crop seeds carrying endophyte communities) are added to resident soil

249 microbial communities. In the context of global change and ever increasing connectedness of
250 global ecosystems, this concept can be very useful in capturing properties and dynamics of novel
251 communities and ecosystems [34]. But some of the most exciting potential applications are likely
252 to be completely unforeseeable until systematic study of these processes has commenced.

253

254 **Conclusion**

255 Our paper argues for the dedicated study of microbial community coalescence, which we
256 anticipate will address a set of new research questions (see Box 3). This will require a joint effort
257 from multiple disciplines and the empirical study of microbial communities that meet, of their
258 functional properties, as well as the development of models to simulate their dynamics and
259 evolution. Through this effort the concept of community coalescence can help better understand
260 the complexity of microbial assemblages and open avenues for the targeted manipulation of such
261 assemblages for human use in industry, medicine or environmental protection. While the
262 examples we have used are microbial in nature, we think that general insights derived from
263 microbial ecology might also be useful for understanding equivalent processes at larger
264 timescales in macro-organisms, especially given the context of ever increasing connectedness of
265 global ecosystems.

266

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

287 habitat patches), extinctions and recolonizations from the regional species pool, and processes
288 such as neutral drift (analogous to genetic drift) and species sorting (analogous to fitness
289 differences).

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

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

295

Box 1. Evidence of microbial community coalescence

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

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

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

314 *Microbial communities in the human body.* - Qin *et al.* [39], using a metagenomic study of liver
315 cirrhosis patients, found evidence for invasion of microbes from the mouth into the gut. A

316 possible reason was a change in bile production in patients with disease, which permitted
317 invasion by bacteria from the oral microbiome. It thus seems that entire microbial communities,
318 occurring 'in series' in the digestive system, interact in complex ways and whose coalescence is
319 under metabolic or environmental control.

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

325

326

327

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

362 **Figure legends**

363

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

373

374

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

382

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