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2 **Soil microbes and community coalescence**

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25

26 **Abstract**

27 Community coalescence is a recently introduced term describing the interaction of entire
28 communities and their environments. We here explicitly place the concept of community
29 coalescence in a soil microbial context, exploring intrinsic and extrinsic drivers of such
30 coalescence events. Examples of intrinsic events include the action of earthworms and the
31 dynamics of soil aggregates, while extrinsic events are exemplified by tillage, flooding, litter-
32 fall, outplanting, and the addition of materials containing microbial communities. Aspects of
33 global change may alter the frequency or severity of coalescence events. We highlight
34 functional consequences of community coalescence in soil, and suggest ways to
35 experimentally tackle this phenomenon. Soil ecology as a whole stands to benefit from
36 conceptualizing soil biodiversity in terms of dynamic coalescent microbial assemblages.

37

38 **Keywords:** community coalescence, metacommunity, soil biodiversity, global change,
39 community, disturbance

40

41 **1. Introduction**

42 Community coalescence is a recently coined term (Rillig et al., 2015) describing situations
43 where two or more entire communities (and their environments) interact because pieces of the
44 environment that are large relative to the size of the organisms they contain can be
45 translocated by a variety of forces. While such interactions of whole communities are hard to
46 envisage in the normal context of plant and animal ecology, community coalescence among
47 microbes, especially in the soil, is likely an ever-present feature. Community coalescence is
48 only partially encompassed by existing metacommunity theory (Rillig et al., 2015; Fig. 1; also
49 see there for a pertinent discussion of microbial biogeography), which captures the idea of
50 connectedness, but not of wholesale exchange of environments and communities. To
51 understand the latter in a soil context where community coalescence is likely to be common,
52 thus necessitates a fresh look at features of such exchanges in order to develop suitable theory
53 and experimental approaches. The purpose of this contribution is to more explicitly place the
54 concept of community coalescence in a soil microbial context.

55 Many examples of wholesale exchanges between microbial communities come from the
56 aquatic literature (Livingston et al., 2013; Adams et al., 2014; Souffreau et al., 2014), where

57 flows and confluence of water bodies are the natural force driving such mixing. Here we
58 highlight such coalescence events in soils, and explore how they may help explain the large
59 microbial biodiversity and its spatial and temporal organization. Soils are uniquely suited for
60 thinking about community coalescence, because coalescent phenomena are likely to be
61 commonplace there. Soil microbial soil communities are likely to provide the major systems
62 in which coalescent processes are both functionally important and where they can be
63 empirically investigated. This is in part because soil microbes are at the base of the soil food
64 web, and play key roles for ecosystem processes including interactions regulating plant
65 communities (Bever et al. 2010).

66 In the following, we differentiate between intrinsic (naturally occurring via ecological
67 interactions) and extrinsic (as a result of external influences and disturbance) sources of
68 coalescent events in soil. We separate between these events to illustrate how commonly
69 occurring soil processes can be understood in the light of community coalescence. Both cases
70 have in common the initial development of separate communities, with different abiotic
71 conditions and community composition, which are abruptly mixed by those events.

72

73 **2. Soil-intrinsic coalescence events**

74 Here, we focus on soil-intrinsic coalescence events, and consider external drivers of such
75 events in the next section (see also Fig. 1). First we also need to ask: where (and what) are the
76 microbial communities in soil? Assemblages of organisms can be described at various spatial
77 and temporal scales, and for our purposes we explicitly take a microbial vantage point. Beare
78 et al. (1995), for example, designated various arenas of activities in soil, acknowledging the
79 large physiochemical and community differences that exist in soil, sometimes in very close
80 proximity. Importantly, these fine-scale differences in microbial assemblages potentially
81 provide the source communities engaging in coalescence events. We illustrate this for two
82 examples, earthworms and soil aggregates.

83 *Earthworms.*- The activity of earthworms is a particularly intriguing case of microbial
84 community coalescence, as assemblages from various microhabitats are literally mixed up
85 (Barois et al., 1993), e.g. by breaking up aggregates, then experiencing a passage through the
86 gut, there encountering the earthworm gut microbial assemblage, before being finally released
87 back into the soil (Fig. 1c). The pervasive effects of earthworms on various soil and
88 ecosystem parameters have long been recognized. The perspective we offer here is that the

89 continuous mixing of various soil microbial communities (for example breaking up of soil
90 aggregates), together with mixing of environments, e.g., earthworm gut physicochemical
91 conditions, organic matter pieces, will generate persistent “non-equilibrium” environmental
92 heterogeneity. Similar effects will also occur in other animals inhabiting the soil, such as
93 microarthropods or nematodes, but effects will be much larger with earthworms.

94 *Soil aggregates.* -Soil aggregates are the building blocks of soil structure, creating pore spaces
95 and providing microbial microhabitats of extreme difference at a very fine spatial scale. For
96 example, aggregate interiors can be anaerobic, differing in a number of physicochemical
97 properties, and as a consequence harbor microbial assemblages quite different from those in
98 the exterior surfaces (Tiedje et al., 1984; Sexstone et al., 1985; Mummey et al., 2006).
99 Disintegration of an aggregate exposes the interior to quite different microbial assemblages
100 (Fig. 1g).

101 The sum of these short-term and local encounter (and re-encounter) events determines the
102 total microbial assemblage at broader scales, including spatial and temporal heterogeneity in
103 the distribution of the assemblage. Even though these processes must be common in soils,
104 and have been documented phenomenologically in the extensive literature on soil disturbance,
105 no study has investigated how community diversity changes during these events, what novel
106 interactions are generated, or how diversity is increased or decreased (i.e. local extinctions;
107 Veresoglou et al. 2015) by such coalescence.

108

109 **3. Human-mediated or externally driven community coalescence events**

110 Many external influences and disturbances would be expected to trigger fine-scaled
111 coalescence events in the soil (Fig. 1). Examples include tillage (Fig. 1h), flooding, litter-fall,
112 outplanting, and the addition of materials containing microbial communities, e.g. compost,
113 stored biochar, or manure (Fig. 1d). While the net effects of all these events have been well
114 studied, the microbial community coalescence aspect remains unquantified and poorly
115 understood; for example, the consequences of material additions to agricultural fields are
116 frequently examined, yet these studies do not disentangle microbial community encounters
117 from the effects of organic matter addition. Flooding is also an interesting case where subsoil
118 communities, which differ in microbes and carbon dynamics (Fierer et al., 2003), would
119 encounter the topsoil community.

120 Global change can change the frequency and severity of these external drivers and thus also of
121 coalescence events. For example, any global change factor affecting primary production (e.g.
122 warming, elevated atmospheric carbon dioxide, artificial light at night) can have ripple-on
123 effects on litter composition, thus creating different sized pulses of microbial inputs entering
124 the soil system. Human-associated pathways also include accidental transport of soil (Hughes
125 et al., 2010; Cowan et al., 2011; MacNeill et al., 2011), yet the extent to which such
126 community coalescence events promote or hinder the dispersal of different types of microbial
127 components is not known.

128

129 **4. Functional consequences**

130 Given that community coalescence may be a common feature in soils, what does this mean
131 for soil microbial community composition, biodiversity and ecosystem function?

132 Microbial communities in close proximity, such as in root-associated habitats or those
133 inhabiting interiors or exteriors of soil aggregates, will have contrasting trait distributions.
134 Depending on the frequency and mixing ratios of community coalescence events, community
135 encounters will result in very different average trait distributions compared to the initial
136 communities before the coalescence events. These new configurations of functional traits will
137 in turn affect plant productivity, decomposition and nutrient cycling. As ecosystem processes
138 encompass quite different habitats within the root-soil system, coalescence will play a major
139 role as a mechanism underlying the relationship between soil microbial diversity and
140 ecosystem functioning (e.g. Bell et al., 2005).

141 The coalescence of very divergent microbial communities from different soil compartments,
142 and even their temporary coexistence, may also offer enhanced opportunities for horizontal
143 gene transfer (Cruz and Davles, 2000), which itself will have important evolutionary and
144 functional consequences, e.g. antibiotic resistance (Rillig et al., 2015). While such co-
145 occurrence could also be caused by regular dispersal events, the sheer scale of exchange
146 during coalescence is likely to be much larger and involve a greater diversity of species.

147

148 **5. The way forward - how to study this phenomenon?**

149 A long term research goal is to identify the contribution of community coalescence to the
150 composition and function of the microbial soil biota. This is now possible because of high-

151 throughput sequencing, but even with the advances in such methods, there are huge
152 challenges, given the fine-scale heterogeneity and complexity of the soil environment, not to
153 mention the huge diversity of microbial taxa. Hence it will be necessary to initially focus on
154 clearly delineated, experimentally tractable compartments, for which soil ecology has already
155 amassed a solid background. The litter-soil interaction is one such system, as is the study of
156 community coalescence in soil aggregate turnover. The former has easily defined and
157 experimentally realizable assemblages, the latter addresses the very essence of soil
158 complexity and structure. Dedicated experiments to disentangle the effects of the movement
159 of the communities from additions of other material during coalescence will be important. For
160 example, in litter-soil interactions, experimentally uncoupling the effects of organic matter
161 addition from the microbial community addition is a challenge. Studies (Koide et al., 2005;
162 Osono, 2005), using culture-based methods, showed that adding sterilized leaves (i.e. without
163 endophytes) to soil led to distinct fungal communities in the leaf litter compared to litter
164 where the endophyte community was not excluded. Similar studies, with a focus on other soil
165 compartments, are feasible and could shed light on the magnitude of effects on both
166 community assembly and functions.

167 Many organisms have adaptations to exploit regular "meeting" of or re-exposure to different
168 communities and environments. Because of their economic and medical significance, the best
169 examples we have come from parasites, such as gut nematodes and protozoans, many of
170 which rely on the regular contact of soil and gut communities in order to complete their life-
171 cycles. Extending the focus from specific parasites to other "free-living" members of the
172 community around them would be a well worthwhile endeavor. For example identifying
173 which microbes are regularly found in the plant and the soil, or in the gut microbiome and the
174 soil, and asking how they differ in their traits from those that are confined to each
175 compartment alone would be a useful starting point for such research. Although we know of
176 no detailed comparative study of soil and gut microbiota, co-infection by soil/water
177 transmitted gut parasites is well established (Brooker and Clements 2009; Knowles et al.
178 2013). In plants, based on metagenomic analysis of plant compartments and soil,
179 Zarraonaindia et al. (2015) have suggested that "the soil serves as a primary reservoir for
180 potential plant-associated bacteria", and Bai et al. (2015) have shown substantial taxonomic
181 and functional overlap of root and leaf microbiota in *Arabidopsis*. Parasites with life-cycle
182 components in host and soil compartments are evidence that coalescence events can
183 contribute soil microbial diversity, but we need further studies to quantify this for the whole
184 community. Focusing on parasitic microbes themselves, and identifying other microbes with

185 correlated distributions and therefore potentially moving with them could provide a useful
186 community module on which to focus for the study of coalescence.

187 Many innovations in design and approach await study of coalescing soil assemblages.
188 Observational approaches and directed sampling may be very productive in addressing
189 recurrent examples of coalescence such as leaf-litter fall. Equally, it is possible to envisage
190 numerous and imaginative experimental approaches to understanding the impact of
191 coalescence. For example, how would preventing microbial entry through leaf fall change the
192 endophytic microbiome of a tree? How much does the functioning of this endophytic
193 microbiome depend on recurring re-exposure to the leaf-inhabiting community? Importantly,
194 soil ecology as a whole stands to benefit from conceptualizing soil biodiversity in terms of
195 dynamic coalescent microbial assemblages.

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198 **References**

- 199 Adams HE, Crump BC, Kling GW. Metacommunity dynamics of bacteria in an arctic lake:
200 the impact of species sorting and mass effects on bacterial production and
201 biogeography. *Frontiers in Microbiology* (2014) **5**:82. doi: 10.3389/fmicb.2014.00082.
- 202 Bai Y, Müller DB, Srinivas G, Garrido-Oter R, Potthoff E, Rott M, Dombrowski N,
203 Münch PC, Spaepen S, Remus-Emsermann M, Hüttel B, McHardy AC, Vorholt JA,
204 Schulze-Lefert P. Functional overlap of the Arabidopsis leaf and root microbiota.
205 *Nature* (2015) **528**:364–369.
- 206 Barois I, Villemin G, Lavelle P, Toutain F. Transformation of the soil structure through
207 *Pontoscolex corethrurus* (Oligochaeta) intestinal tract. *Geoderma* (1993) **56**:57-66.
- 208 Beare MH, Coleman DC, Crossley DA, Hendrix PF, Odum EP. A hierarchical approach to
209 evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant and*
210 *Soil* (1995) **170**:5-22.
- 211 Bell T, Newman JA, Silverman BW, Turner SL, Lilley AK. The contribution of species
212 richness and composition to bacterial services. *Nature* (2005) **436**:1157–1160.
- 213 Bever JD, Dickie IA, Facelli E, Facelli JM, Klironomos JN, Moora M, Rillig MC, Stock WD,
214 Tibbett M, Zobel M. Rooting theories of plant ecology in microbial interactions.
215 *Trends in Ecology & Evolution* (2010) **25**:468-478.
- 216 Brooker S, Clements ACA. Spatial heterogeneity of parasite co-infection: Determinants and
217 geostatistical prediction at regional scales. *International Journal of Parasitology*
218 (2009) **39**: 591-597.
- 219 Cowan DA, Chown SL, Convey P, Tuffin M, Elughes K, Pointing S, Vincent WF. Non-
220 indigenous microorganisms in the Antarctic: assessing the risks. *Trends in*
221 *Microbiology* (2011) **19**:540-548.
- 222 de la Cruz F, Davies J. Horizontal gene transfer and the origin of species: lessons from
223 bacteria. *Trends in Microbiology* (2000) **8**:128-133.
- 224 Fierer N, Allen AS, Schimel JP, Holden PA. Controls on microbial CO₂ production: a
225 comparison of surface and subsurface soil horizons. *Global Change Biology* (2003)
226 **9**:1322-1332.
- 227 Hughes KA, Convey P, Maslen NR, Smith RIL. Accidental transfer of non-native soil
228 organisms into Antarctica on construction vehicles. *Biological Invasions* (2010)
229 **12**:875-891.
- 230 Koide K, Osono T, Takeda H. Colonization and lignin decomposition of *Camellia japonica*
231 leaf litter by endophytic fungi. *Mycoscience* (2005) **46**:280-286.

232 Knowles SCL, Fenton A, Petchey OL, Jones TR, Barber R, Pedersen AB. Stability of within-
233 host parasite communities in a wild mammal system. *Proceedings of the Royal Society*
234 *Series B* (2013) **280**:201305598.

235 Livingston G, Jiang Y, Fox JW, Leibold MA. The dynamics of community assembly under
236 sudden mixing in experimental microcosms. *Ecology* (2013) **94**:2898-2906.

237 McNeill M, Phillips C, Young S, Shah F, Aalders L, Bell N, Gerard E, Littlejohn R.
238 Transportation of nonindigenous species via soil on international aircraft passengers'
239 footwear. *Biological Invasions* (2011) **13**:2799-2815.

240 Mummey DL, Rillig MC, Six J. Endogeic earthworms differentially influence bacterial
241 communities associated with different soil aggregate size fractions. *Soil Biology &*
242 *Biochemistry* (2006) **38**:1608-1614.

243 Osono T. Colonization and succession of fungi during decomposition of *Swida controversa*
244 leaf litter. *Mycologia* (2005) **97**:589-597.

245 Rillig MC, Antonovics J, Caruso T, Lehmann A, Powell JR, Veresoglou SD, Verbruggen E.
246 Interchange of entire communities: microbial community coalescence. *Trends in*
247 *Ecology & Evolution* (2015) **30**:470-476.

248 Sexstone AJ, Revsbech NP, Parkin TB, Tiedje JM. Direct measurement of oxygen profiles
249 and denitrification rates in soil aggregates. *Soil Science Society of America Journal*
250 (1985) **49**:645-651.

251 Souffreau C, Pecceu B, Denis C, Rummens K, De Meester L. An experimental analysis of
252 species sorting and mass effects in freshwater bacterioplankton. *Freshwater Biology*
253 (2014) **59**:2081-2095.

254 Tiedje JM, Sexstone AJ, Parkin TB, Revsbech NP, Shelton DR. Anaerobic processes in soil.
255 *Plant and Soil* (1984) **76**:197-212.

256 Veresoglou SD, Halley J, Rillig MC. Extinction risk of soil biota. *Nature Communications*
257 (2015) **6**: 8862.

258 Zarraonaindia I, Owens SM, Weisenhorn P, West K, Hampton-Marcell J, Lax S, Bokulich
259 NA, Mills DA, Martin G, Taghavi S, van der Lelie D, Gilbert JA. The soil microbiome
260 influences grapevine-associated microbiota. *mBio* (2015) **6**(2):e02527-14.
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263 **Figure legends**

264 Fig. 1. Conceptual overview depicting metacommunity and coalescence phenomena occurring
265 in soils, divided into intrinsically (a, c, e, g) and extrinsically (b, d, f, h) driven events (see
266 text). The distinction between metacommunity dynamics and community coalescence is
267 depicted as the degree of species (and environmental) exchange along the x-axis, in reality a
268 continuum ranging from individual species dispersing to the wholesale interchange
269 characteristic of community coalescence. The y-axis shows the degree of difference between
270 the source environments for either metacommunity or community coalescence events. Picture
271 inserts illustrate examples and text describes the nature and outcome of exchanges among
272 communities. In the metacommunity examples, red colored organisms represent established
273 and green colored the newly arriving species. For the coalescence examples, the red, green
274 and yellow colored shapes display different communities.