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Soil microbes and community coalescence

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Abstract

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

Keywords: community coalescence, metacommunity, soil biodiversity, global change, community, disturbance

1. Introduction

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

Many examples of wholesale exchanges between microbial communities come from the 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

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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Figure legends

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