Soil microbes and community coalescence

1 *Opinion*

2 # Soil microbes and community coalescence

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23 **Running title:** Microbial community coalescence

24 **Word count:** 1724 (without references); **Figures count:** 1

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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, spatial structure, 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

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.

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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-

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

Many organisms have adaptations to exploit regular "meeting" of or re-exposure to different communities and environments. Because of their economic and medical significance, the best examples we have come from parasites, such as gut nematodes and protozoans, many of which rely on the regular contact of soil and gut communities in order to complete their life-cycles. Extending the focus from specific parasites to other "free-living" members of the community around them would be a well worthwhile endeavor. For example identifying which microbes are regularly found in the plant and the soil, or in the gut microbiome and the soil, and asking how they differ in their traits from those that are confined to each compartment alone would be a useful starting point for such research (compare Bai et al. (2015), studying *Arabidopsis* root and leaf microbiome overlap). Parasites with life-cycle components in host and soil compartments are evidence that coalescence events can contribute soil microbial diversity, but we need further studies to quantify this for the whole community. Focusing on these parasitic microbes themselves, and identifying other microbes with correlated distributions and therefore potentially moving with them could provide a useful community module on which to focus for the study of coalescence.

Many innovations in design and approach await study of coalescing soil assemblages. Observational approaches and directed sampling may be very productive in addressing

184 recurrent examples of coalescence such as leaf-litter fall. Equally, it is possible to envisage

185 numerous and imaginative experimental approaches to understanding the impact of

186 coalescence. For example, how would preventing microbial entry through leaf fall change the

187 endophytic microbiome of a tree? How much does the functioning of this endophytic

188 microbiome depend on recurring re-exposure to the leaf-inhabiting community? Importantly,

189 soil ecology as a whole stands to benefit from conceptualizing soil biodiversity in terms of

190 dynamic coalescent microbial assemblages.

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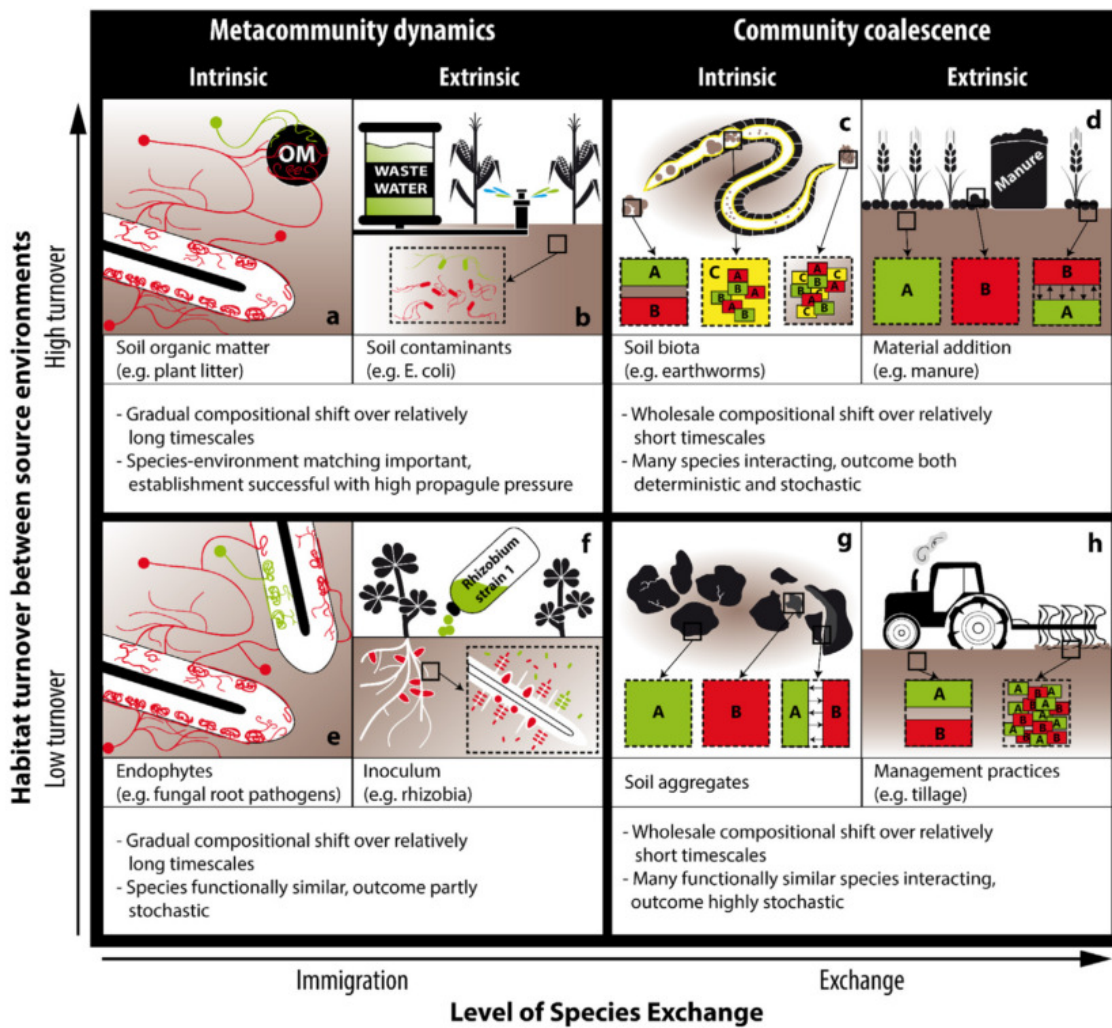239   (1985) **49**:645-651.
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Figure legends

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.