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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.

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

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

2. Soil-intrinsic coalescence events

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

2.1. Earthworms

The activity of earthworms is a particularly intriguing case of microbial community coalescence, as assemblages from various microhabitats are literally mixed up (Barois et al., 1993), e.g., by breaking up aggregates, then experiencing a passage through the gut, there encountering the earthworm gut microbial assemblage, before being finally released back into the soil (Fig. 1c). The pervasive effects of earthworms on various soil and ecosystem parameters have long been recognized. The perspective we offer here is that the continuous mixing of various soil microbial communities (for example breaking up of soil aggregates), together with mixing of environments, e.g., earthworm gut physicochemical conditions, organic matter pieces, will generate persistent "non-equilibrium" environmental heterogeneity. Similar effects will also occur in other animals inhabiting the soil, such as microarthropods or nematodes, but effects will be much larger with earthworms.

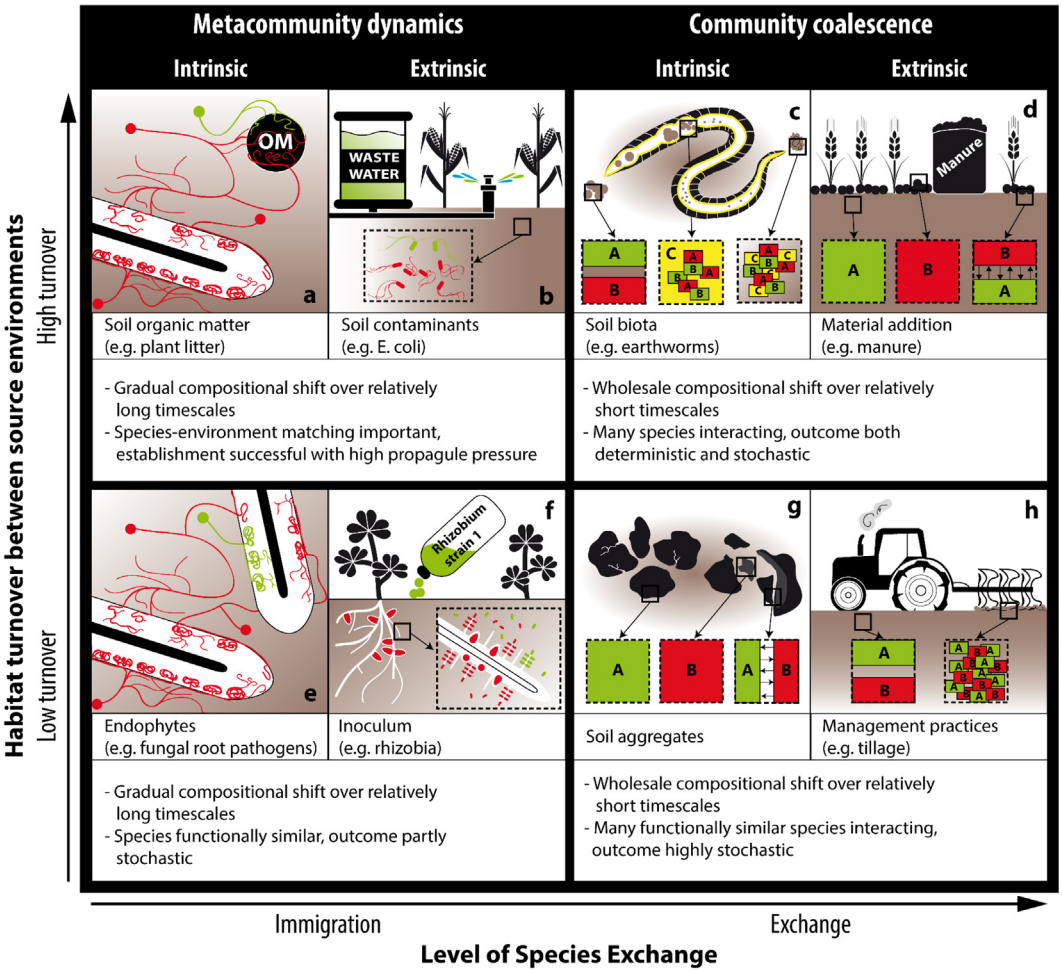

Fig. 1. Conceptual overview depicting metacommunity and coalescence phenomena occurring in soils, divided into intrinsically (a, c, e, g) and extrinsically (b, d, f, h) driven events (see text). The distinction between metacommunity dynamics and community coalescence is depicted as the degree of species (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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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