Opinion

Interchange of entire communities: microbial community coalescence

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

Great American Interchange *en miniature*?

Alfred Russell Wallace [1] was perhaps one of the first to consider what would happen when previously separated communities meet – in his case at a very large spatial and temporal scale, in what has become known as the Great American Interchange: the linking of North and South America by the appearance of the Isthmus of Panama. The result of such wholesale migration, mixing and joining of communities was likely a multifold of establishments, species exchanges and extinctions; massive effects at any rate. What if community encounter events like these were not exceptional singularities, but were to occur very frequently, at timescales relevant to understanding community structure? Here, we develop the idea that events reminiscent of the Great American Interchange could be common in microbial systems, and with potentially even greater degrees of mixing. We think this is the case because in nature, pieces of the environment much larger and more persistent than an individual microbe, and indeed containing entire local microbial communities, are routinely moved (Figure 1 and Box 1). Forces that move pieces of the environment containing entire microbial assemblages include gravity (falling leaves), animals (e.g., burrows and casts), growth of macroorganisms (plant roots encountering each other in the soil), wind (dust movement), flow in liquids (natural or industrial water bodies mixing, movement inside the human body), or human activities (horticultural outplanting, ploughing, or movement of wood). We propose the term community coalescence (see Glossary) to describe such community interchange events (Box 1).

While the literature is replete with studies on the effects and importance of many of the events mentioned above (e.g., litter fall), these reports have rarely addressed the microbial community–level interactions. The field of

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Glossary

β-Diversity: the variation in the identities of species among sites [21].
Community: a general and broad term for any recognized assemblage of organisms containing multiple species that interact with one another as a result of their physical proximity.
Community coalescence: a joining of previously separate communities (or even ecosystems), forming a new entity that is not easily separable into parts again; this new entity has distinct properties from the parts it unites. The term 'coalescence' is also used in population genetics but in a very different context to indicate that homologous genes in different populations were at some point of necessity identical by descent, that is, their history coalesces, and the genealogy of one gene is sometimes termed its 'coalescent'. This history is usually inferred from DNA sequence data.
Connectance: in ecological networks, the fraction of possible interactions that are actually realized.
Horizontal gene transfer: transfer of genes among unrelated species; postulated to occur by vectors such as viruses or insects, or by direct uptake of plasmids or environmental DNA.
Metacommunity: a collection of local communities linked by dispersal of their component species. The concept is derived from that of the metapopulation, which is a collection of populations of one species linked by dispersal of individuals. Metacommunity dynamics includes ecological 'rescue' of locally 'unfit' species, patch dynamics (appearance and disappearance of habitat patches), extinctions and recolonizations from the regional species pool, and processes such as neutral drift (analogous to genetic drift) and species sorting (analogous to fitness differences).
Nestedness: in ecological networks, this measures the tendency for species with few links to exclusively interact with species with many links.
Network theory: describes interactions between multiple entities, which in ecology are typically species. Using network theory, communities can be described in terms of direct and indirect interactions among species.

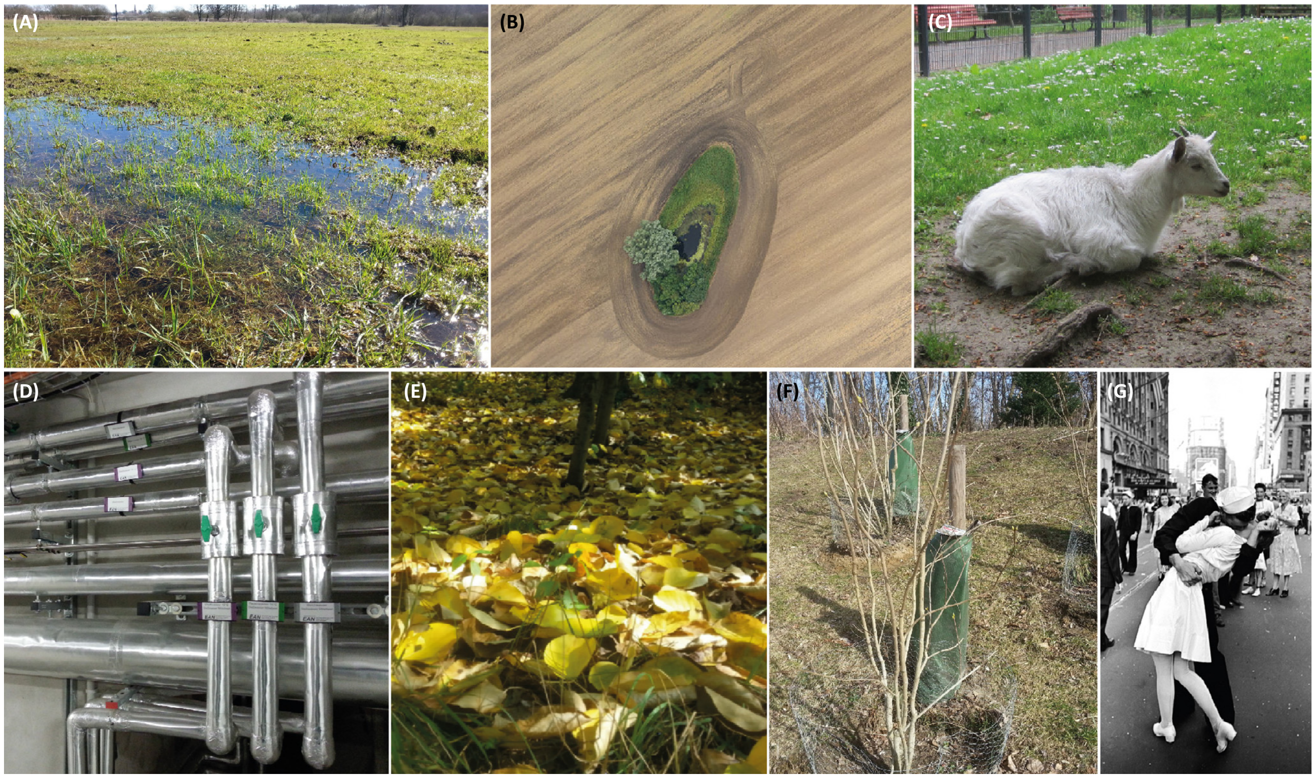

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Figure 1. Encounters of entire microbial communities occur in many microbial systems. Examples where such community coalescences are likely occur include **(A, B)** interaction of aquatic and terrestrial systems, such as during flooding, in riparian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

microbial biogeography (Box 2) has long debated the degree of dispersal limitation among microorganisms, and is now also beginning to explore how environment, spatial processes, and biotic context shape local communities. Community coalescence events are part of the dispersal process, but also much more, because such events result in whole communities and their environments interacting. Therefore, it is important to ask how they influence the resulting community, how these consequences can be linked to and illuminated by existing ecological theory, and how such investigations could further inform and expand ecological theory. What is the empirical evidence on community coalescence thus far? How can the problem of entire communities interacting be approached from a theoretical perspective? What are the functional consequences of community coalescence? These are the questions we address here with the goal of stimulating research on this topic; community coalescence is likely to be important not only in the everyday events of microbial ecology but also of increasing importance as the interconnectedness of biological systems increases with global change.

Factors influencing the community composition that results from community coalescence

While a number of empirical studies (Box 1) and modeling exercises [2,3] have addressed aspects of what we call community coalescence, there has been no systematic study of such phenomena, and this might in part be due to a lack of an applicable conceptual framework for classifying these events, estimating their frequency, or predicting their consequences. We believe such separate conceptual development is necessary because the coalescence of communities has features very distinct from those described in other bodies of theory, in particular the processes envisaged in metacommunity theory [4]: (i) metacommunity theory is concerned with dispersal of individuals among local communities and not with their wholesale interchange. Thus in metacommunity theory, dispersal rate depends on the probability that local communities (e.g., on islands) receive immigrants from the metacommunity (e.g., continent), while coalescence is the encounter of entire local communities (e.g., an island community is translocated to another island or to the continent). (ii) Community coalescence also allows for and includes the movement and potential mixing of environments, for example, aquatic environments [5], and not just the movement of communities between environments. (iii) Communities that coalesce do not necessarily belong to a metacommunity in the sense of exchanging species at a low rate and having their structure affected by such an exchange. Coalescence also occurs when there is physical relocation of habitats and accompanying changes of the spatial structuring of the habitat. An example would be the encounter of the leaf microbial communities and the soil biota; these would not normally be considered part of the same metacommunity.