

Spotlight

Embracing Community Ecology in Plant Microbiome Research

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Community assembly is mediated by selection, dispersal, drift, and speciation. Environmental selection is mostly used to date to explain patterns in plant microbiome assembly, whereas the influence of the other processes remains largely elusive. Recent studies highlight that adopting community ecology concepts provides a mechanistic framework for plant microbiome research.

Community Ecology as a Framework for Plant Microbiome Research

The discipline of community ecology offers a mechanistic framework to unravel how eco-evolutionary processes operate at the fine scales from individuals to populations, modulating the distribution of species in space and time. In a recent conceptual synthesis, Vellend [1] advocates that any given community is modulated by the interplay of four high-level processes, namely selection, dispersal, drift, and speciation. Selection is defined as the result of biotic and abiotic effects, in combination with interactions ensuing fitness differences across individuals or species. This process has traditionally been adopted to explain patterns in plant microbiome assembly, for instance those associated with differences in microbiome composition owing to soil type, plant genotype, exudate profiles, and/or agricultural practices [2]. To date, however, the importance of the other processes in plant microbiome assembly has been largely ignored.

Dispersal is defined as the movement of species from one location to another, and accounts for the introduction of species within a local community. The consequences of dispersal are dependent on the diversity, abundance, and composition of the donor and recipient communities. The theme of dispersal has often been explored in studies of invasion ecology and in investigations of ecological resilience and resistance of microbial communities in the face of disturbances. In addition, dispersal timing and frequency are crucial but often overlooked factors that structure plant microbiomes (see below). The effect of drift – in other words random changes in population sizes via stochastic birth and death events – on the community is pronounced for low-abundant species because they are more prone to occasionally become extinct. Nemergut *et al.* [3] further conceptualized that, in a community context, drift is expected to be important when selection is weak and when the overall population size and diversity status is low. These conditions are commonly observed in the initial establishment of microbial communities in host-associated environments. Speciation (or ‘diversification’ *sensu* Nemergut [3]) is the evolutionary process by which, through growth rates, mutation, recombination, and horizontal gene transfer, microbes diversify and adapt to changing environmental conditions. Of crucial importance is that diversification leads to the generation of novel microbial genotypes and, at a large scale, contributes to variations in community composition. This process has greater importance for spatially separated systems by shifting the strength and/or mechanism by which selection operates.

The appreciation of community ecology as a framework unfolds a sweeping perspective on plant microbiome research. It allows a pragmatic change from focusing on questions such as ‘who is there’ and

‘what they are doing’ towards a more fundamental understanding of the building blocks that underpin any given community assembly and spatiotemporal dynamics. That is, studies across distinct soil types, plant genotypes, and scales are likely to result in idiosyncratic outcomes of factors that determine the structure of plant microbiomes. However, community ecology enables for a conceptual and mechanistic unification by (i) quantifying the degree to which these four high-level processes operate across distinct systems, and (ii) identifying the mechanisms (biotic and/or abiotic) that regulate their relative influences across time and space [4].

How Can Community Ecology Help in Engineering Plant Microbiomes?

The ongoing revolution in plant microbiome research has unequivocally shown that microbes impact on plant growth, nutrition, and tolerance to (a)biotic stresses. To date, however, these microbiome-associated phenotypes (MAPs) [5] have been primarily qualitative and taxonomy-driven rather than quantitative and trait-based. Hence, translating fundamental knowledge into effective strategies to manipulate and engineer plant microbiomes remains a major challenge. This is evidenced by the numerous failed attempts to effectively manipulate and engineer single microbial strains as biofertilizers and/or biocontrols that consistently perform at large temporal scales and across different geographic locations. Within this context, Oyserman *et al.* [5] recently introduced the concept of the ‘modular microbiome’ – microbial consortia that are engineered in concert with the plant genotype to confer different but mutually compatible MAPs to a single host or host population.

We propose here that future directions in plant microbiome research would benefit

by incorporating community ecology theory. In particular, community ecology can provide a foundation upon which prospective experimental designs can be developed and ecological theories can be tested. For instance, understanding how community assembly processes interplay in structuring plant microbiomes over the course of plant development is crucial (Figure 1). A quantitative framework for the relative importance and quantitative influences of community assembly processes and the mechanistic underpinning has been previously reported [1,6] and successfully applied across divergent systems (e.g., [6,7]). This effort can enhance our predictability

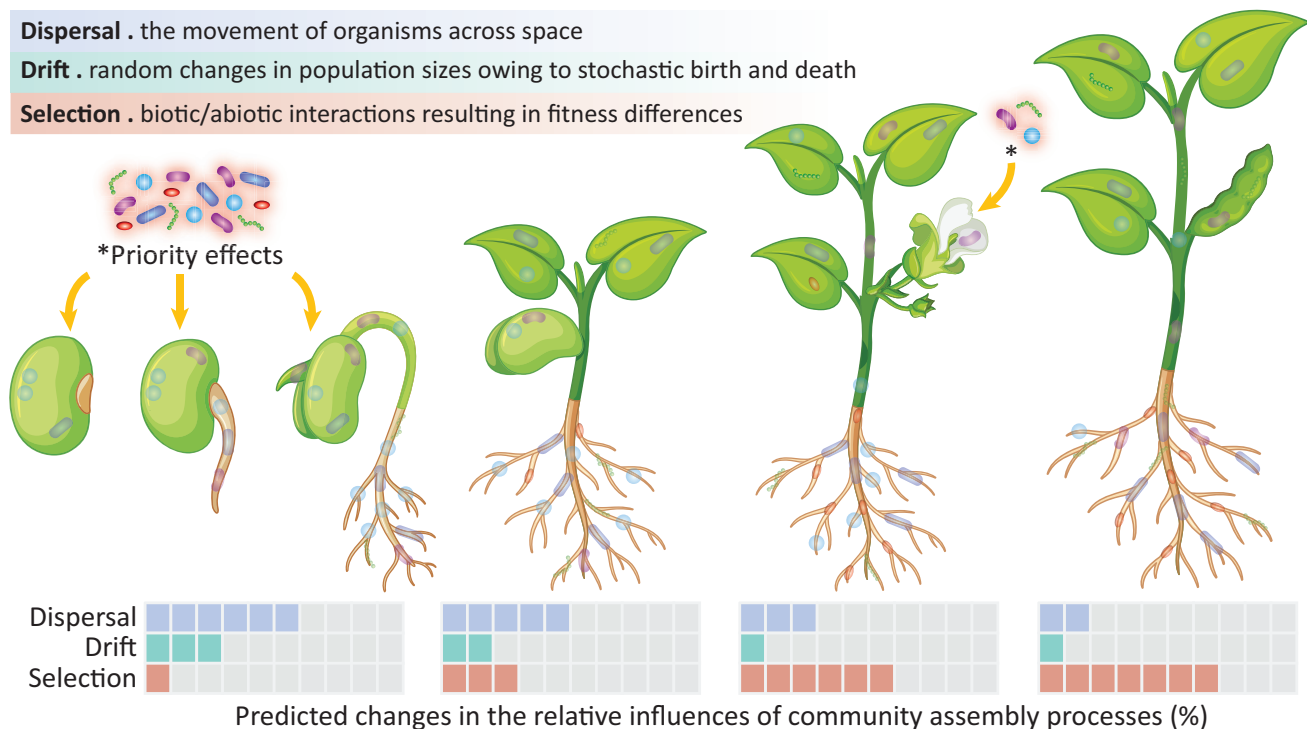
of the factors that determine the successful establishment of introduced microbial strains or modular microbiomes in the context of the recipient ('indigenous') plant-associated microbiome. In a recent study, Niu *et al.* [8] reported the development of a greatly simplified 'modular' bacterial community in a gnotobiotic maize model system. By narrowing down the complexity of the root-associated microbiome, these authors reported an effective consortium (or 'module') consisting of only seven strains (*Enterobacter cloacae*, *Stenotrophomonas maltophilia*, *Ochrobactrum pituitosum*, *Herbaspirillum frisingense*, *Pseudomonas putida*, *Curtobacterium pusillum*, and

Chryseobacterium indologenes). They elegantly showed that the removal of one strain (*E. cloacae*) led to collapse of the root-associated community and the concomitant loss of protection of the host plant against the fungal pathogen *Fusarium verticillioides*. Their findings constitute a classic example of how the order in which microbes disperse towards and/or colonize plant-roots, in other words priority effects, impact on microbiome assembly (through coexistence dynamics) and on microbiome functionality. The studies by Vannette and Fukami [9] and Toju *et al.* [10] provide additional enlightening examples of the role of dispersal and priority effects on the

Dispersal . the movement of organisms across space

Drift . random changes in population sizes owing to stochastic birth and death

Selection . biotic/abiotic interactions resulting in fitness differences



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Figure 1. Conceptual Figure Depicting the Relative Influences of Community Assembly Processes That Mediate the Establishment and Dynamics of Plant-Associated Microbiomes. The seed and emerging root system are more prone to priority effects because they are initially exposed to primary colonization. Priority effects are also hypothesized to be important during microbiome assembly of emerging flowers and leaves. The external surfaces of aboveground sections of the plant (leaves, shoots) are more prone to microbial dispersal (e.g., via air, insects) and drift, given their exposure to abiotic (UV radiation, temperature) and biotic (plant pathogen, insects) stressors. Drift is also expected to be intensified in communities with low densities and richness that are regularly exposed to dispersal [12]. Belowground, the rhizobiome is hypothesized to be influenced by a complex interplay of selection, dispersal, and drift, with a gradual change in selection as the plant ages. The mechanisms mediating the balance among these community assembly processes across distinct plant sections vary according to plant genotype/phenology (exudation profile), soil type (physicochemical properties including pH, organic matter content, and moisture), biotic/abiotic stressors, and agricultural management practices. The process of speciation (or 'diversification') is only expected to be pronounced among sets of communities that do not exchange individuals through dispersal [1,3,6]. The relative influence of this particular process is not depicted in the conceptual figure.

functional properties of plant microbiomes that colonize floral nectar. They found not only that priority effects generate variability in species colonization and community divergences [9], but also that such divergence can persist for an extended period within and across floral generations [10]. Based on the available literature it is difficult to grasp to what extent priority effects influence rhizobium assembly in natural settings, and the degree to which this effect may persist across plant generations. Such investigations will provide insight into how manipulation of plant microbiomes should take into account how orderly species arrive in the system, and how their interactions modify the local environment and lead to coexistence through community assembly. In synthesis, by recognizing that microbiomes are modular entities dynamically influenced by well-defined eco-evolutionary processes, fundamentals of community ecology provide a promising path towards engineering plant microbiome systems.

Perspectives

Transforming our broader fundamental understanding of microbe–plant interactions into practical management strategies requires the integration of community ecology theory into plant microbiome research. We see new avenues for experimental designs in plant microbiome research that can profit from this quantitative framework. For instance, to what extent do plant seeds and seedlings treated with synthetic microbial communities develop distinct and stable microbiome assemblages? (e.g., [11]). What is the relative influence of priority effects in determining the success of seed endophytes through plant generations and across distinct plant genotypes? How do distinct microbiomes and the expression of plant-beneficial traits change over the course of plant development? Further, to what extent do abiotic (e.g., heat, drought) and biotic (e.g.,

pathogen, insect) stressors affect the relative importance of the four high-level processes (selection, dispersal, drift, and speciation) in plant microbiome assembly and functioning?

Our perspective is that community ecology offers the tools and concepts to develop a more holistic and mechanistic synthesis in plant microbiome research. It is likely that more studies will progressively appear in the literature that contextualize the interplay of community processes in plant microbiome assembly. In this sense, this article anticipates a call for action highlighting recent studies that provide a valuable guideline to assist these future research directions. In doing so, we foresee that adopting an ecological perspective and systems approach in plant microbiome research enables a path forward towards enhancing the effectiveness and practical implementation of modular microbiomes for the sustainable production of food, feed, and fiber.

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Spotlight

NPR1 in JazzSet with Pathogen Effectors

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NON-EXPRESSOR OF PATHOGENESIS-RELATED GENES 1 (NPR1) is a master regulator of salicylic acid (SA)-mediated systemic acquired resistance (SAR), a broad-spectrum disease resistance mechanism in plants. NPR1 controls approximately 90% of SA-dependent transcriptome in Arabidopsis. Here, we discuss how pathogen effectors manipulate NPR1 functions in different cellular compartments to establish disease.

Up first: Regulation of NPR1 in diverse cellular states

Plants detect molecular components of the invading pathogens including microbial-associated molecular patterns (MAMPs) and pathogen effectors, rewire the flow of biological information, and