



Changes through time: integrating microorganisms into the study of succession

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Received 9 March 2010; accepted 1 June 2010

Abstract

Ecologists have documented the process of plant succession for centuries, yet the successional patterns exhibited by microbial communities have received relatively little attention. We examine recent work on microbial succession and show how, despite some key differences, studies of plant succession can serve as a template for understanding microbial succession. We divide the broad range of patterns of microbial primary succession into three categories based on the source of carbon inputs and present conceptual models for each of these categories to explain and predict microbial succession patterns. We show how studies of microbial succession can lead to the development of more comprehensive ecological models of succession and improve our understanding of the processes that regulate microbial diversity in natural and man-made environments.

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Keywords: Microbial colonization; Microbial communities; Microbial diversity; Succession

1. Introduction

Research on succession, defined here as the somewhat orderly and predictable manner by which communities change over time following the colonization of a new environment, has been central to the development of ecological theories for over a century. However, the vast majority of this research has focused on plant communities with succession in microbial communities receiving far less attention. Given that most of the phylogenetic diversity on earth is microbial (Pace, 1997), and given the abundance, ubiquity and biogeochemical importance of microbes, better integration of microbes into conceptual models of ecological succession would benefit multiple disciplines. An ecological perspective on microbial succession may also provide valuable insight into such applied

research topics as plaque formation on teeth, microbial colonization and corrosion of pipes, the production of fermented foods, and composting could all be considered examples of microbial succession (Table 1).

Methodological limitations have made it difficult for ecologists to adequately document microbial succession. Microbial communities are highly diverse, community composition can change rapidly and the vast majority of microbial taxa cannot be identified using standard culture-based methodologies. With recent developments in molecular phylogenetic methods, comprehensive surveys of microbial diversity and patterns of succession can be documented with unprecedented ease. These methodological improvements coincide with a growing recognition that the study of microbial succession presents unique opportunities for ecologists to test, and possibly expand, pre-existing conceptual models of ecological succession. In addition, research on how specific microbial taxa change in abundance during succession may provide

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Table 1
The three general categories of microbial succession, their distinguishing features, and some specific examples.

General succession categories	Distinguishing features	Where this type of microbial succession is likely to be found
Autotrophic	Initial colonizers are predominately autotrophs using light or the oxidation of inorganic compounds to generate energy Little to no organic C initially available	Metal and concrete pipes (Okabe et al., 2007)
	Organic C supply changes relatively slowly over time	Glacial till, volcanic deposits, and other newly-exposed mineral surfaces (Hoppert et al., 2004; Gomez-Alvarez et al., 2007; Nemergut et al., 2007; Schutte et al., 2009) Aquatic biofilms receiving light (Johnson et al., 1997; Besemer et al., 2007)
Endogenous Heterotrophic	Initial colonizers are predominately heterotrophs, respiring or fermenting organic compounds to generate energy	Decomposing wood and litter, compost (Nakasaki et al., 2005; Danon et al., 2008; Novinscak et al., 2009; Rui et al., 2009)
	Succession primarily fueled by organic carbon derived from the substrate itself	Food products including cheese, alcoholic beverages, cured meats, vinegar, cacao fermentation, etc. (Ercolini et al., 2004; Haruta et al., 2006)
	Initial community development can be fast Substrate quality changes over time as succession progresses and substrate is directly modified by microbes	Leaf surface (Osono, 2005; Redford and Fierer, 2009) Skin surface (Fierer et al., 2008a; Costello et al., 2009)
Exogenous Heterotrophic	Initial colonizers are predominately heterotrophic respirers or fermenters Organic carbon supplied by external inputs Initial community development can be fast	Sewage and wastewater bioreactors (Santegoeds et al., 1998; van der Gast et al., 2008) Teeth (Kolenbrander et al., 2006) Aquatic biofilms forming under reduced light conditions (Martiny et al., 2003)
	Organic C quality and quantity not directly controlled by the microbes and can be highly variable over time	Human gut (Palmer et al., 2007; Balamurugan et al., 2008)

This classification scheme is not meant to be all-encompassing. Rather, it is intended to organize the discussion of the successional patterns observed in a wide array of distinct microbial habitats.

important clues (perhaps the only clues) to the natural history and physiology of the majority of taxa that resist laboratory cultivation and isolation.

Our objective is not to summarize previous research on microbial succession; rather, we discuss how conceptual models developed for plant communities might serve as a template for understanding primary succession in microbial communities and specific processes driving succession patterns. We also show how ecologists can use microorganisms to broaden the scope of research on succession and how studies of ecological succession can help microbiologists better understand community dynamics in both natural and artificial environments.

2. Categories of microbial succession

In plant communities, succession is typically divided into two categories, primary and secondary succession, where primary succession occurs on an uncolonized substrate and secondary succession occurs in a previously colonized environment following a severe disturbance. However, in our opinion, these categories are not useful for describing microbial succession as they are essentially distinguished by the presence or absence of soil. Since microbes are not restricted to soil and are far more diverse (both phylogenetically and physiologically) than plant communities, we need a different classification scheme to describe microbial succession. Although there are a myriad of ways microbial succession patterns could effectively be subdivided and no single classification scheme will apply to all situations, we propose three

general operationally-defined categories of microbial succession, all of which would traditionally be considered forms of primary succession (Table 1). We emphasize that we are restricting our discussion to primary succession dynamics, the community changes that occur following the colonization of sterile or nearly sterile environments by microorganisms. We will not focus on temporal changes in microbial communities that occur following disturbances or changes in environmental conditions as these are not considered examples of primary succession unless they lead to the removal of all, or nearly all, microbes in a given environment.

At a basic level, microorganisms can be divided into autotrophs and heterotrophs, with most autotrophs using CO₂ as their carbon (C) source and heterotrophs requiring organic C compounds as their C source. Since these physiologies are fundamentally dissimilar and since the two categories of organisms may co-occur, but are likely to dominate in very distinct types of environments, the initial stages of primary succession could be considered to be divided into categories determined by the source of C for biosynthesis (Table 1). We further divide heterotrophic succession into exogenous and endogenous categories where exogenous succession is fueled by continuous external inputs of organic C, while the majority of organic C supplies in endogenous succession are derived from a single initial input contained within the substrate itself (Table 1). These two categories are also differentiated by the degree to which the developing communities modify and influence the quantity and quality of available C supplies, an effect which is likely to be more pronounced during endogenous succession than during exogenous succession. During

endogenous succession, microbial community structure and the nature of the organic C substrates available in the environment are inextricably linked and will change together as succession progresses. In contrast, the characteristics of the organic C substrate supply are relatively fixed over time during exogenous succession with changes in microbial community dynamics predominately driven by factors other than simply the types and quantities of organic C available to microbes.

3. Patterns in microbial succession

Defining the appropriate timeframe for examining succession can be difficult given that changes in community composition occur over a wide range of time scales and disturbances can alter or interrupt the successional sequence (Delmoral and Bliss, 1993; Chapin et al., 1994; Turner et al., 1998). Like plants, a variety of biotic and abiotic stressors (Table 2) as well as the frequency of secondary disturbance events will affect the speed with which microbial communities develop. Moreover, it is uncertain whether microbial ‘climax’ communities (sensu Clements (1916)) actually exist, rendering any endpoint of succession somewhat arbitrary. Therefore, microbial succession can be assessed over very different time scales in different systems. For example, newly colonized soil environments may undergo successional changes across timeframes of years to decades (Sigler et al., 2002; Nemergut et al., 2007). In contrast, some systems undergo such rapid rates of change and secondary disturbance frequencies that it is more appropriate to examine shifts in the community on the scale of days (see references in Table 1 and Fig. 1).

Examining selected studies of microbial succession, we find that biomass accumulation is (not surprisingly) often highest in the earlier stages of succession, tapering off as succession progresses and resources become more limiting (Fig. 1). In contrast, the apparent changes in community-level diversity, the accumulation of new taxa over time, are far more variable and there is no single pattern shared by all of the microbial communities (Fig. 1). This variability in observed diversity patterns could partly be related to differences between the studies in the methods used to assess diversity, the

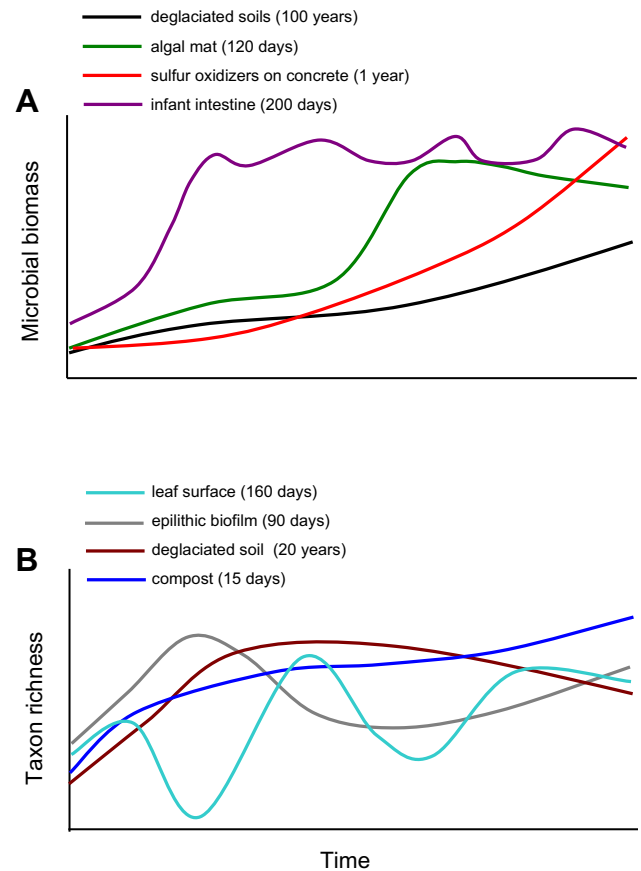


Fig. 1. Contrasting successional patterns in some selected microbial environments, examining the amount of microbial biomass in a given habitat and changes in taxon richness over time. For each example, the length of time that succession was monitored is indicated in the figure legends. Both axes are unitless and graphs are qualitative representations of the data presented in each study; information on the time frames over which each study was conducted (and the relevant x-axis scales for each study) are provided in the legend. References for Fig. 1A = glacial soil (Sigler et al., 2002), algal mat (Johnson et al., 1997), sulfur oxidizers on concrete (Okabe et al., 2007), intestine (Palmer et al., 2007). References for Fig. 1B = epilithic biofilm (Jackson et al., 2001), deglaciating soil (Nemergut et al., 2007), compost (Peters et al., 2000), phyllosphere (Redford and Fierer, 2009).

frequency of environmental disturbances that effectively ‘interrupt’ succession, and the distinct types of succession examined. However, much of this variability could simply be a product of differences in the time scales over which succession was observed. Although diversity and biomass are only two indices, they do illustrate that, as with plant communities, there is no single pattern followed by all microbial communities that adequately describes the observed changes in diversity during succession.

4. Mechanisms underlying microbial succession

Despite some key differences between plant and microbial succession, both are likely shaped by the same core set of processes (Table 3). Therefore, pre-existing conceptual models of plant succession can be applied to microbial succession in the three aforementioned categories (Fig. 2). Below we focus

Table 2

Some of the more important sources of environmental (non-resource) stress that can shape microbial diversity during succession (examples of microbial habitats where these individual factors may be particularly relevant are listed).

Environmental stress	Example of microbial habitat where the stress may be particularly important
Water availability (Ψ) and rapid changes in Ψ	Leaf surface
Shear stress	Water pipes
UV radiation	Exposed rocks
Antibiotics/antimicrobials	Human gut
Temperature (including freezing/thawing)	Surface soils
Salinity	Estuarine sediments
Redox status (particularly O_2)	Sewage bioreactors
Metal toxicity	Wastewater treatment systems
pH	Fermenting foods

Table 3
Key processes that shape successional dynamics in both plant and microbial communities, with some examples where these processes may be particularly evident.

Process	Examples where the process may apply to microbial succession
Dispersal limitation (Foster and Tilman, 2003)	Inoculation of food products, development of communities in water pipes and other semi-isolated habitats
Resource reduction via uptake (competition) (Tilman, 1985)	Microbial uptake of nutrients, substrate catabolism, light interception
Facilitation between community members that reduce environmental stress (Callaway and Walker, 1997)	Biofilm production in mixed microbial communities, metal detoxification,
Facilitation via increasing availability of limiting resources (Chapin et al., 1994)	N ₂ -fixation, phosphatase production, syntrophic interactions
Increasing environmental stress (Westman and Whittaker, 1975)	Acidification by fermenting bacteria, production of antibiotics, generation of heat by microbial activity during composting
Changes in low-intensity disturbances (Lugo and Scatena, 1996)	Viral lysis, bacterial grazing

The cited references refer to more detailed descriptions and examples of these processes as they may occur in plant succession.

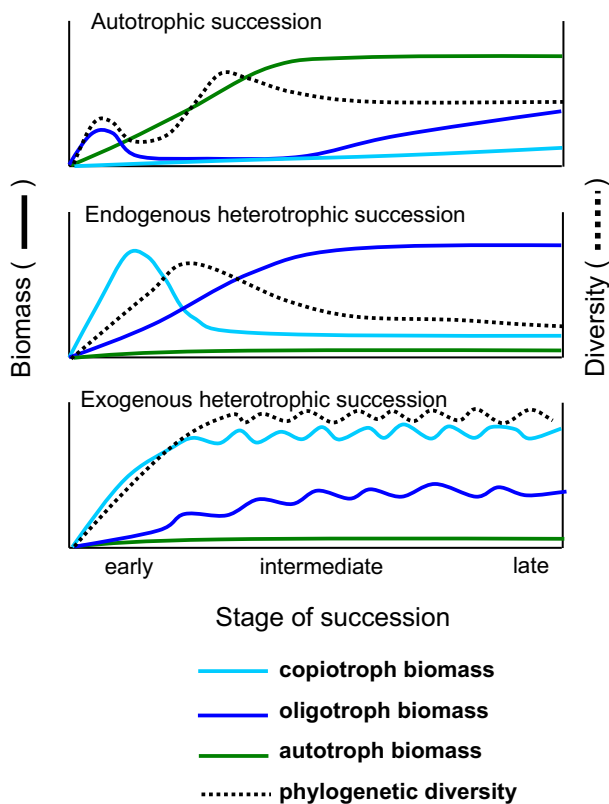


Fig. 2. Conceptual models of how microbial communities change during succession for the three categories shown in Table 1. Shown are the predicted changes over the course of succession in heterotrophic microbial biomass (either copiotrophs or oligotrophs), autotrophic microbial biomass, and the phylogenetic diversity of the communities. Note that these are idealized patterns, the observed patterns may be distinct (compare this figure to Fig. 1) due to a number of confounding factors described in the text.

on three key aspects of these conceptual models: the role of dispersal in colonization, shifts in resource limitations, and changes in phylogenetic diversity as succession progresses.

4.1. Role of dispersal in succession

Just as seed dispersal has a large influence on the succession patterns observed in plant communities, the types and quantities of microbes that can successfully colonize a given substrate will have a large influence on successional trajectories. This is a well-studied phenomenon in food products (Beresford et al., 2001), and in other microbial habitats including leaf litter (Strickland et al., 2009) and waste compost (Vargas-Garcia et al., 2007). The oft-quoted statement “everything is everywhere: but the environment selects” (Baas-Becking, 1934; deWit and Bouvier, 2006) has been used to imply that the high dispersal rates and large population sizes of microorganisms render geography inconsequential to microbial distribution (Martiny et al., 2006). However, given that all microorganisms are not likely to have equivalent dispersal capabilities over timescales relevant to succession (Telford et al., 2006; Jenkins et al., 2007), this paradigm may be less applicable to understanding succession, particularly in environments where succession can occur rapidly. Further, most types of microbes appear to have low abundances in a given environment. These organisms, which represent the so-called ‘rare biosphere’ (Sogin et al., 2006), may not necessarily differ in their dispersal abilities from more abundant microbes, but because of their rarity, they would inherently have a lower probability of successfully dispersing to new substrates.

We would expect relationships between how widely microbes are distributed in the environment and their relative appearance during the succession process. As is often observed in plant communities (McIntyre et al., 1995), initial colonization is most likely to be performed by cosmopolitan taxa (Fig. 2) because they are, by definition, more widely dispersed and thus more likely to provide the initial inocula. As succession progresses, endemic taxa should become more dominant in communities as dispersal constraints become less relevant to community assembly and resource limitations become relatively more important, selecting for more oligotrophic taxa (Fierer et al., 2007; Shrestha et al., 2007).

In addition to differences in dispersal potential, there are also stochastic processes that may influence the types (or order) of microbial colonization in a given environment (Hubbell, 2001) and initial colonizer communities are unlikely to be identical, even across environments that may be very similar. Even slight differences in the initial colonizer communities could alter successional trajectories, particularly in environments where inter-specific competition is likely to be important (Fukami and Morin, 2003). The effects of stochastic variation may become less important as communities develop over time, but in communities that are changing quickly or those in which primacy is important, this source of variability may make successional trajectories far less predictable. Such stochastic processes are likely to be

particularly relevant to understanding succession in environments where the atmosphere is the dominant source of inocula given that airborne microbial communities appear to be highly variable across time and space (Brodie et al., 2007; Fierer et al., 2008b).

4.2. Changes in resource limitation during succession

Plant succession patterns are often considered to be regulated by changes in limiting resources through time (Connell and Slatyer, 1977; Grime, 1979; Tilman, 1985). For example, Tilman (1985) hypothesized that changes in the ratio of resources (primarily light and nitrogen) available to plants could regulate succession. Although this oversimplifies succession, there appears to be some consensus on the importance of resource capture capacity and tolerance to low resource conditions in driving community structure (Grace, 1991). Resource availability is also likely to be a fundamental driver of microbial succession, but the limiting resources and environmental factors regulating succession will be more complex given the far greater physiological diversity contained within microbial communities and the breadth of environments in which succession can occur. In autotrophic succession, nutrients and light (or the availability of inorganic electron donors) are likely to be the primary resources limiting biomass accumulation. However, in the earliest stages of autotrophic succession, heterotrophs may also be in relatively high abundance, utilizing trace levels of available carbon (Okabe et al., 2007; Roeselers et al., 2007). During endogenous heterotrophic succession, labile substrates will be consumed first, supporting copiotrophic microbial taxa that are later replaced by more oligotrophic taxa that metabolize the remaining, more recalcitrant, organic C pools in the later stages of succession (Rui et al., 2009). In exogenous heterotrophic succession, resource supply is likely to change less over the course of succession, but variability over shorter time scales in the quantity or quality of organic carbon supplies may lead to rapid shifts in the relative abundances of copiotrophs and oligotrophs (Fig. 2), a phenomenon that may be particularly relevant in wastewater treatment systems (Forney et al., 2001).

As with plants, successional trajectories can be altered by microbes responding to, or directly changing, the availability of nutrients required for biomass production (e.g. N, P, and micronutrients). There are well-established stoichiometric constraints on microbial biomass production (Redfield, 1958; Cleveland and Liptzin, 2007) and nutrient limitation is invariably a major factor influencing succession dynamics (Cherif and Loreau, 2007). For example, several studies support the importance of nitrogen limitation in early autotrophic microbial community succession (Kastovska et al., 2005; Gomez-Alvarez et al., 2007; Schmidt et al., 2008). However, differences in substrate and specific environmental conditions make it very difficult to predict which resources will be limiting at different stages in succession, particularly for heterotrophic communities. For example, nutrient limitation during succession on decomposing litter or in fermenting

foods will be highly variable and dependent on the nature of the substrate itself. This unpredictability is compounded by the distinct nutrient requirements of different microbial taxa. For example, changing from a bacterial to a fungal-dominated community over the course of succession can lead to fundamental differences in nutrient limitation, even if nutrient levels are held constant, as these taxa often have distinct stoichiometries (Cherif and Loreau, 2007). Likewise, the presence of specific taxa which can alleviate nutrient limitation directly (e.g. free-living N₂-fixing bacteria or fungi capable of solubilizing mineral-bound phosphorus) can lead to pronounced changes in nutrient availability over the course of microbial succession.

4.3. Changes in phylogenetic diversity

Although the observed diversity patterns are variable (Fig. 1), we can make some general predictions regarding how phylogenetic diversity (the number of distinct lineages represented by taxa within a given community) might change along the three successional sequences if resource limitations are the dominant factors regulating successional dynamics. In all three types of succession, we would expect phylogenetic diversity to increase during the initial stages of succession as communities become established (Jackson et al., 2001; Jackson, 2003). In the case of autotrophic succession, we would expect diversity to asymptote over time as niche space becomes filled and few new niches emerge as resource availability stabilizes (Jackson, 2003) (Fig. 2). During endogenous heterotrophic succession, we might expect (following the intermediate-resource hypothesis, (Tilman and Pacala, 1993; Rosenzweig, 1995)) that peak diversity would occur midway through succession when there is a coalescence of an intermediate supply of all limiting resources and a maximum diversity in the organic carbon pools available for catabolism. Phylogenetic diversity (but not necessarily community composition) should stabilize over the course of exogenous heterotrophic succession if resource supplies are maintained at reasonably constant levels over time (Fig. 2).

Of course, all of these predicted changes in diversity are predicated on the assumption that resource availability is the dominant factor regulating succession. We know that this is not the case; environmental (non-resource) stresses, such as those listed in Table 2, and trophic interactions (Chauhan et al., 2009) can also have important influences on microbial successional dynamics, making the apparent changes in diversity more difficult to predict (see Fig. 1). We would expect the levels, rates and direction of changes in these factors to have particularly important influences on successional trajectories in earlier stages of succession. As communities develop over time, they may become less sensitive to some of these environmental stresses by their ability to modify the microbial habitat (e.g. biofilm production) or by increases in the abundances of taxa that are either resilient or resistant to the stresses (Besemer et al., 2007; Schimel et al., 2007). However, because environmental stresses that are persistent or are of sufficient magnitude can alter community dynamics

regardless of the successional stage, studies of microbial succession must consider both resource supplies and environmental conditions (at scales relevant to microbes) in order to understand functional and phylogenetic changes in community composition.

5. Comparing microbial and plant succession

Although similar processes are likely to drive microbial and plant succession (see above and Table 3), there are key differences that make direct comparisons difficult. For example, although plants can effectively persist in dormant states as seeds, dormancy is likely to be a more common occurrence in microbial communities with dormancy having a strong effect on microbial community dynamics (Jones and Lennon, 2010). Likewise, physiological diversity is nearly always going to be far higher for microbial communities than plant communities given that nearly all plants are photoautotrophs but photoautotrophism is just one of many metabolic strategies utilized by microorganisms. This is also true for individual taxa; a single bacterial taxon (a term which can be defined at various levels of phylogenetic resolution) can exhibit high levels of metabolic versatility, using a wide range of electron donors and acceptors (e.g. *Shewanella oneidensis*, Heidelberg et al., 2002) or switching from autotrophic to heterotrophic metabolic pathways. This versatility is unique to microbial succession given that most plants cannot cease to photosynthesize and adopt alternate physiological strategies to generate energy as environmental conditions change. This high level of physiological versatility may allow one bacterial taxon to persist or even dominate in various stages of succession, even if environmental conditions and resource availabilities change dramatically over time. Another key difference is that microbial communities are often far more phylogenetically diverse than plant communities and this diversity may generate more complex networks of species interactions and less repeatable successional patterns given the breadth of taxa capable of inoculating a given habitat (Fukami and Morin, 2003).

Another key difference is that evolutionary processes are likely to play a far more important role in microbial succession than plant succession given the short generation times of many actively-growing microbial populations and the potential for high rates of horizontal gene transfer (Ochman et al., 2000). Although evolution is undoubtedly important in regulating ecological dynamics in plant communities (e.g. Davis and Shaw, 2001), such phenomena cannot generally be observed on time scales relevant to the average grant funding period. Since microbial communities can be surveyed using molecular methods that capture phylogenetic information on community members, the incorporation of evolution into the study of microbial succession should be relatively straightforward and the conceptual models generated from this work can then be applied to other communities in which evolution proceeds at a more stately pace.

The rapid rate of succession observed in many microbial communities also permits the testing of ecological principles

that are far more difficult to test with plant communities. For example, because observing succession in plant communities at one location can take many decades, plant ecologists frequently substitute space for time by examining chronosequences. There is a long history of using chronosequences to study succession and such chronosequences (e.g. sand dune succession, 'old field' succession, glacial till succession) are featured prominently in many ecology textbooks. However, there are a number of important limitations associated with using chronosequences to study succession dynamics (Johnson and Miyanishi, 2008), limitations that would not influence studies of microbial succession where succession can be observed in real time. Likewise, the small size of microbial microcosms lend themselves to well-replicated, laboratory-based manipulative experiments that could be used to test specific models of succession (e.g. Besemer et al., 2007) just as such microcosms have been used to examine other fundamental ecological phenomena (e.g. Jiang and Morin, 2004).

6. Future perspectives

Studying microbial succession is difficult because microbial communities are often diverse, the ecological roles of microbes are typically poorly known, non-destructive sampling can be problematic and the environmental conditions of microbial habitats can be difficult to characterize because important environmental gradients may occur across a few microns. However, new tools are now available that allow microbial communities and habitats to be surveyed across time at unprecedented levels of detail. For example, barcoded pyrosequencing (Hamady et al., 2008) allows phylogenetic data to be collected in hundreds of samples at a depth of coverage of thousands of sequences per sample. Additionally, Nano-SIMS (Herrmann et al., 2007) permits the quantification of environmental characteristics at scales that are actually relevant to microorganisms. Of course, harnessing the power of these new tools requires that they be used in well-designed studies that test specific conceptual questions.

Because plant ecologists have wrestled with the topic of succession for decades, microbiologists do not have to 're-invent the wheel' and can utilize some of the same concepts and approaches that been used to study plant succession. For example, plant ecologists recognize the value of extended time series for understanding successional dynamics, particularly when those time series encompass relatively rare events (e.g. Lugo and Scatena, 1996). However, since most studies in microbial ecology focus on dynamics that occur over relatively short time scales, such long-time series data are often lacking or undervalued. In addition, we know that plant community succession cannot be understood by exclusively examining plants given that non-plant taxa (e.g. grazers and herbivorous insects) can have important effects on plant community development (Hobbs, 1996; Carson and Root, 2000). A similar phenomenon is also likely to occur in microbial communities. Microbial ecologists often focus on a single taxonomic group (e.g. bacteria or specific groups of bacteria) even in environments where a broad suite of

microorganisms, including bacteria, archaea, viruses and a diverse suite of microbial eukaryotes are likely to interact. Studies that span a range of trophic, physiological, and phylogenetic levels are likely to yield a more comprehensive understanding of microbial succession dynamics.

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