



Phylogenetic diversity analyses reveal disparity between fungal and bacterial communities during microbial primary succession



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ABSTRACT

Early community assembly of fungi and bacteria differ in many ways, including their contrasting successional trajectories. We examined if fungal and bacterial primary successional dynamics are phylogenetically constrained. Microbial communities were queried across a recently deglaciated forefront using three measures of phylogenetic diversity. We analyzed these data at the Kingdom (fungi) and Domain (bacteria) levels plus at less-inclusive taxonomic hierarchies (Phylum and Class) as well as selected, well-defined functional groups (N-fixing and photosynthetic bacteria). Fungi and bacteria differed in their phylogenetic distributions across successional age. Phylogenetic diversity estimates did not change over successional age for fungi, whereas bacteria were strongly structured phylogenetically over successional age. Further, our results suggest that analyses at Kingdom or Domain levels may prove inadequate to understand successional dynamics. Investigations should include both broad (Kingdom or Domain) and less inclusive groups (perhaps metabolically distinct taxa) to better dissect community dynamics.

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1. Introduction

Primary successional dynamics of microbial communities are crucial for understanding community assembly rules, nutrient transformations and pedogenesis that may facilitate colonization and/or growth of vascular plants (Fierer et al., 2010). These early colonizing microorganisms drive patterns in ecosystem processes (Schmidt et al., 2008), transform/utilize ancient or recalcitrant carbon (Bardgett et al., 2007), and potentially facilitate the development of higher-trophic level food webs (Walker and de Moral, 2003; Jumpponen et al., 2015). During primary succession microbial communities establish onto virgin landscapes where little or no organic legacies exist, [e.g. volcanic substrata (Gemma and Koske, 1990), sand dunes (Brown, 1958), deglaciation (Schmidt et al., 2008), new island formation following to volcanic action (Martinson et al., 2015)]. Of these, studies on glacier forefronts

can be particularly useful for examination of ecosystem development as many glaciers have well-documented recession rates and consist of short-term seres allowing for detailed examination through space for time substitution chronosequences (Walker et al., 2010). Molecular studies on microbial primary succession at glacier forefronts have been conducted via rRNA community fingerprinting (Sigler and Zeyer, 2002), cloning and sequencing (Jumpponen, 2003), PLFAs (Ohtonen et al., 1999; Tscherko et al., 2005), and T-RFLPs (Zumsteg et al., 2012). Studies on early microbial primary succession using next generation sequencing (NGS) have largely focused on shifting taxon abundances to understand community dynamics during succession (Schütte et al., 2010; Balaalid et al., 2012; Knelman et al., 2012) and often target only a fraction of the microbial constituents: e.g. root-associated fungi (Balaalid et al., 2012), or plant colonizing bacteria (Knelman et al., 2012). While targeting specific microbial community constituents allows for detailed interrogation of a particular successional aspect, focusing solely on one group (bacteria, fungi, or archaea) can limit our understanding of the microbial community as a whole.

Much about how fungal and bacterial communities assemble remains unresolved. Particularly, the similarity of successional dynamics of fungi and bacteria has been understudied. The first deep-sequencing (NGS) queries into joint fungal and bacterial primary

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successional dynamics are beginning to emerge (Brown and Jumpponen, 2014; Cutler et al., 2014). One intriguing result from these pioneering studies is that fungal and bacterial communities differ in their successional trajectories. Such findings are in contrast with earlier studies (Zumsteg et al., 2012) that demonstrate trajectory similarities possibly as a result of the limited depth of inquiry that T-RFLPs allow compared to NGS. Both Brown and Jumpponen (2014) and Cutler et al. (2014) found that bacteria and fungi have contrasting community wide and taxonomic successional trajectories but in different ways. Brown and Jumpponen focused on early successional dynamics (0–80 years) across a glacier forefront and found a tight link between plant establishment and bacterial communities, although both fungal and bacterial communities were mainly influenced by successional age. In contrast, Cutler and coauthors queried a more extensive successional timeframe (165–852 years) and found that fungi were closely linked to plant establishment but bacteria less so. The reason for this discrepancy is uncertain but may be a result of differing successional ages, substrate associated nutrient limitations (glacier forefront vs. volcanic deposition), or geographic location.

Colonization of newly developed substrates presents challenges as opportunities to colonize are hindered by strong environmental/biotic filtering (Jumpponen et al., 2015). For a glacier forefront, abiotic filters include strong UV irradiation, drastic diurnal temperature fluctuations, long-lasting snow cover, and extreme nutrient limitations (Jumpponen et al., 2012). Establishment is likely related to evolutionary histories that constrain the traits mandatory for successful establishment and dispersal (Dini-Andreote et al., 2015). That is, microbes that are suited for a given environment likely share similar niches through shared evolutionary histories that account for the success in establishment (Philippot et al., 2010). Such a phylogenetic signal that influences establishment may be even more evident for fungi (Maherali and Klironomos, 2007). It is in this light that cross-domain investigation into phylogenetic and evolutionary constraints of microbial succession can shed light into community assembly rules and successional dynamics.

Phylogenetic diversity (integration of phylogenetic distances into community ecology to infer community and functional dynamics; see Webb, 2000) frameworks have been widely applied to understand many communities (see Table 1 in Vamosi et al., 2009), including trees (Webb, 2000) and mammals (Cardillo, 2011). Despite the common use of phylogenetically conserved gene regions for bacterial and fungal amplicon libraries, studies of bacterial (Horner-Devine and Bohannan, 2006) and fungal (Anderson et al.,

2004; Merckx et al., 2012; Rämä et al., 2014) phylogenetic diversity are rare and largely focus on specific groups of microbes at lower taxonomic levels. Rarer still are studies targeting microbial phylogenetic diversity across environmental gradients but some have focused on altitudinal effects (Bryant et al., 2008). Some bacterial phyla may shift phylogenetically with altitude (Wang et al., 2012), whereas no such shifts were apparent for Sebacinoid fungi (Garnica et al., 2012). To our knowledge, concurrent phylogenetic diversity analyses of fungi and bacteria are currently lacking. Here, we integrate evolutionary history of microbial communities assembling in a primary successional environment – a component crucial to an improved understanding of successional dynamics (O'Dwyer et al., 2012).

Bacterial communities may converge compositionally along glacier forefronts during early primary succession as evidenced by declining standard deviations of ordination loading scores with distance from the receding glacier's terminus (Brown and Jumpponen, 2014). Similarly, fungal communities may converge phylogenetically (Jumpponen et al., 2012): older communities are more phylogenetically related as compared to more recently established communities. Evidence for bacterial and fungal convergence across early successional age is circumstantial at best (based on Jumpponen et al., 2012; Brown and Jumpponen, 2014) and the underlying reasons for these observations remain poorly understood. In this contribution, we explicitly test if the observed compositional convergence is phylogenetically constrained. Additionally, we employ a taxonomically hierarchical approach in our analyses and posit that the use of multiple taxonomic hierarchical ranks is required for a more complete understanding of microbial community assembly.

2. Materials and methods

2.1. Sampling location

The forefield of Lyman Glacier is located within the Wenatchee National Forest in Glacier Peaks Wilderness Area in Washington State, USA (48°10'14"N, 120°53'44"W; ~1900 m a.s.l.). The glacier has receded more than 1 km over the past ~120 years (Jumpponen et al., 1998). Plant (Jumpponen et al., 2012) successional dynamics as well as bacterial and fungal community succession in response to plant establishment (Brown and Jumpponen, 2014) have been previously characterized at this site. Soils at the forefront mainly consist of Entisols and are rocky and with limited nitrogen (less than 0.1% total soil N) and carbon (ca 3% total soil carbon by dry weight) under established vegetation near the terminal moraine (Jumpponen et al., 1998) with even more limited availabilities in unvegetated soils. There is no apparent increase in total N or C with forefront development in either vegetated or unvegetated soils. However, the forefront contains many surface depressions that may act as safe sites aiding plant establishment and viability (Jumpponen et al., 1999).

2.2. Sampling and sequence generation

We used soil samples and extracted DNA from previous research efforts (Brown and Jumpponen, 2014) in the current analyses. Briefly, topsoil was sampled along the deglaciated chronosequence (150 m, 300 m, 450 m, 600 m, and 750 m from the glacier terminus representing circa 90 years of successional time) for a total of 68 experimental units (across the five distances) and non-vegetated soil as well as rhizospheric soils from four plants with differing mycorrhizal habits were sampled. In our previous analyses (Brown and Jumpponen, 2014) successional age was much more influential in structuring microbial communities than vegetation (Brown and

Table 1

Proportion of samples that are significantly phylogenetically clustered compared in 1000 iterations against randomly generated trees (null model – independent swap). NTI – Nearest Taxon Index and NRI – Net Relatedness Index tested using a 2×2 contingency table with Fisher's Exact Test. Non-significant P-values are presented parenthetically.

	NTI (significant experimental units)	NRI (significant experimental units)	Fisher's Exact Test P-value
All fungi	67.3%	44.2%	0.0015
Ascomycota	51.0%	57.1%	NS (0.685)
Basidiomycota	100%	100%	NS (1.00)
All Bacteria	57.1%	6.3%	<0.0001
Acidobacteria	66.7%	33.3%	0.0005
Actinobacteria	51.6%	12.9%	<0.0001
α -Proteobacteria	62.3%	0.0%	<0.0001
β -Proteobacteria	100%	40.0%	NS (0.167)
γ -Proteobacteria	100%	80.0%	NS (1.00)
Diazotrophs	60.0%	20.0%	NS (0.524)
Photosynthetic	40.0%	60.0%	NS (1.00)

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