



Long-term changes in soil microbial communities during primary succession



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ABSTRACT

Soil microbial communities (SMCs) play a critical role in the cycling of carbon and nutrients in terrestrial ecosystems, as well as regulating plant productivity and diversity. However, very little is known about long-term (decades–centuries) structural changes in these communities. The development of aboveground–belowground linkages during century-scale succession is also poorly understood. Our study addressed this knowledge gap by investigating SMC and plant communities undergoing primary succession on an 850-year chronosequence of lava flows in Iceland. We hypothesised that communities of microfungi and bacteria would respond to progressive changes in vegetation and that SMC diversity would increase with terrain age. Soil samples were collected from three lava flows at different stages of primary succession (165, 621 and 852 years after lava flow emplacement). Plant community composition was surveyed as the samples were collected. The composition of the SMCs present in the soil was determined using amplicon pyrosequencing. The physical and chemical properties of the soil were also analysed. The results of the study indicated changes in plant and fungal communities with increasing terrain age. Distinct plant and fungal assemblages were identified on the three sites and both communities became richer and more diverse with increasing terrain age. There was also evidence to suggest the development of mycorrhizal associations on older sites. In contrast, the composition and structure of the bacterial communities did not change systematically with terrain age. Similarly, there were few changes in soil properties: SOM concentrations and pH, both of which have been demonstrated to be important to SMCs, were constant across the chronosequence. These results suggest that plant community composition is significant for fungal communities, but less relevant for bacterial communities. This finding has implications for studies of primary succession and the biogeochemical impact of vegetation change in high-latitude ecosystems.

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1. Introduction

The changes that occur in plant and animal communities during primary succession (ecosystem development on terrain with no biological legacy) have been studied for decades (Walker and del Moral, 2003). However, very little is known about long-term (decades–centuries) primary succession in soil microbial communities (SMCs). SMCs play a critical role in the cycling of carbon and nutrients in terrestrial ecosystems as well as regulating plant productivity and diversity (van der Heijden et al., 2008). Understanding long-term changes in such communities is therefore essential to

efforts to model and manage ecological change, including the restoration of degraded ecosystems (Kirk et al., 2004). Some attention has been given to changes in SMCs (particularly bacteria) over comparatively short periods of time (e.g. Jumpponen, 2003; Nemergut et al., 2007; Schütte et al., 2009; Sigler et al., 2002); the succession of mycorrhizal fungi over relatively short timescales has also received attention (Last et al., 1987). However, technological barriers (specifically, problems in describing the high diversity of microbial communities) have meant that, until recently, the focus has been on aggregate SMC function rather than taxonomy. Furthermore, the studies that have been published are largely based on glacial forelands (Schaaf et al., 2011). This study aims to address this gap by investigating SMC dynamics across an 850-year chronosequence of lava flows in Iceland.

A lack of comparability between previous studies means that it is difficult to form a clear picture of SMC succession. Most

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researchers agree that SMC biomass increases during primary succession (Bardgett et al., 2005). There is also some evidence of progressive change in the structure of SMCs during succession. For example, Nemergut et al. (2007) observed increases in SMC diversity with increasing terrain age and Schütte et al. (2009) and Nicol et al. (2005) reported similar patterns for bacterial and archaeal communities, respectively. The functional diversity of SMCs may also increase as primary succession unfolds (e.g. Tscherko et al., 2003). However, these patterns are not universal. For example, Sigler et al. (2002) reported a decrease in bacterial diversity with increasing terrain age. Furthermore, Sigler et al. (2002) and Jumpponen (2003, studying fungal communities), could find no evidence of SMC succession; both studies stressed the importance of site-specificity and stochastic effects in SMC assembly. The central research question posed by this study is therefore: do SMCs (specifically soil bacteria and fungi) undergo predictable changes, analogous to those observed in plant communities, during long-term (multi-century) primary succession? Based on existing studies, we hypothesised that:

H1: changes in SMC composition would parallel changes in above-ground vegetation; hence, there would be progressive change in SMCs with terrain age, with distinct bacterial and fungal communities on sites at different stages of primary succession.

H2: the taxonomic diversity of fungal and bacterial communities would increase with terrain age, as ecosystem development progressed and new niches (e.g. different types of organic substrate) became available.

2. Materials and methods

Soil samples were collected from three lava flows at different stages of primary succession. Plant community composition was surveyed as the samples were collected. The composition of the SMCs present in the soil was determined by amplicon pyrosequencing. The physical and chemical properties of the soil, both of which are important to SMCs, were also analysed.

2.1. Study sites

It is clearly difficult to observe long-term ecosystem development directly, necessitating the use of space-for-time substitution (chronosequences) to infer multi-century ecological change (Walker et al., 2010). The use of chronosequences is well-established in ecology and soil science (Matthews, 1992; Stevens

and Walker, 1970; Walker et al., 2010; Wardle et al., 2004). This study utilised a well-dated chronosequence of lava flows on Mt Hekla, Iceland (64° 00' N, 19° 40' W) to investigate long-term (multi-century) changes in SMC composition. The chronosequence has been described in detail in Bjarnason (1991) and Cutler et al. (2008). The Hekla sites are particularly well-suited to chronosequence studies as a) the age of the lava flows is well constrained (to a sub-annual level in some cases); b) the lava flows are close to each other and at the same altitude, ensuring that the sites have similar environmental conditions and accessibility to propagules and c) the lava flows have similar slopes, substrate chemistry and surface physiognomy (Bjarnason, 1991). The region has a cool, maritime climate with mean January and July air temperatures of $-1.7\text{ }^{\circ}\text{C}$ and $11.0\text{ }^{\circ}\text{C}$, respectively, and a mean annual rainfall of around 1200 mm. The lava flows varied in age (165–852 years) but were otherwise similar in all respects. Younger lava flows do exist (e.g. those emplaced in the 1980 and 1947 CE eruptions of Mt Hekla), but these flows do not have soil cover and were therefore omitted from this study. The lava has been dated by contemporary accounts and tephrochronology (Thorarinsson, 1967), giving excellent age constraint. All of the flows have an altitude around 300 m above sea level and are composed of blocky, a' a lava with a similar geochemistry. The survey sites used are characterised by fine, free-draining andosols (Arnalds, 2004). The lava flows undergo slow vegetation succession (Bjarnason, 1991). The vegetation on the younger surfaces is dominated by a thick mat of the moss *Racomitrium lanuginosum* with scattered patches of the pioneer lichen *Stereocaulon vesuvianum*. Vascular plants establish on surfaces ~ 100 years old and increase in abundance with terrain age. The oldest surfaces are characterised by hardy shrubs, notably willow (e.g. *Salix phylicifolia*), birch (*Betula pubescens*) and ericaceous shrubs such as *Vaccinium* spp. Plant taxonomic richness and diversity increase monotonically across the chronosequence (Cutler, 2010).

2.2. Sampling

Soil samples were collected from lava flows emplaced in 1845, 1389 and 1158 CE (i.e. surfaces that were 165, 621 and 852 years old in August 2010) (Fig. 1). Two transect lines were established on flat sites on each flow. Each transect line comprised three $2\text{ m} \times 2\text{ m}$ quadrats 10 m apart. Soil samples were collected from two opposing corners of the quadrats, resulting in a total of six samples per transect and 36 samples in total. Sampling was carried out on a scale relevant to the spatial scale of the vegetation (cm to m) and the sampling strategy aimed for a balance between spatial resolution and coverage, within the available resources. A soil core

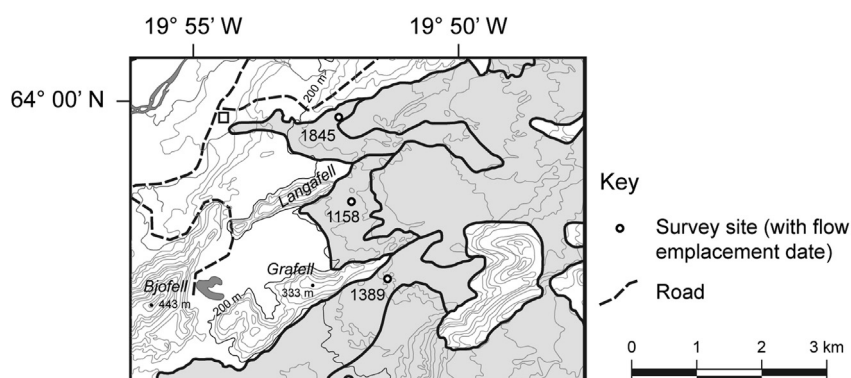


Fig. 1. Location plan. The lava flows are shaded. Contours are at 25 m intervals.

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