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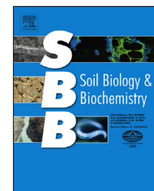

Multi-scale variability analysis reveals the importance of spatial distance in shaping Arctic soil microbial functional communities

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ABSTRACT

Understanding biological diversity and distribution patterns at multiple spatial scales is a central issue in ecology. Here, we investigated the biogeographical patterns of microbial functional genes in 24 heath soils from across the Arctic using GeoChip-based metagenomics and principal coordinates of neighbour matrices (PCNM)-based analysis. Functional gene richness varied considerably among sites, while the proportions of each major functional gene category were evenly distributed. Functional gene composition varied significantly at most medium to large spatial scales, and the PCNM analyses indicated that 14–20% of the variation in total and major functional gene categories could be attributed primarily to relatively large-scale spatial effects that were consistent with broad-scale variation in soil pH and total nitrogen. The combination of variance partitioning and multi-scales analysis indicated that spatial distance effects accounted for 12% of the total variation in functional gene composition, whereas environmental factors accounted for only 3%. This small but significant influence of spatial variation in determining functional gene distributions contrasts sharply with typical microbial phylotype/species-based biogeographical patterns (including these same Arctic soil samples), which are primarily determined by contemporary environmental heterogeneities. Therefore, our results suggest that historical contingencies such as disturbance events, physical heterogeneities, community interactions or dispersal barriers that occurred in the past, have some significant influence on soil functional gene distribution patterns.

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1. Introduction

Understanding the diversity and distribution patterns of populations and communities at multiple spatial scales is a central issue in ecology (Levin, 1992; Borcard and Legendre, 2002; Tuomisto et al., 2003; Zhou et al., 2008). For soil microbes, it is well documented that population and community distributions in natural environments are spatially patterned (Martiny et al., 2006; Ramette and Tiedje, 2007; Hanson et al., 2012). The classic microbiological tenet "Everything is everywhere, but the environment selects" (Baas Becking, 1934) proposes that dispersal is ubiquitous and contemporary environmental factors are the primary mechanism determining distributions of microbial communities. Many recent studies support this hypothesis by demonstrating significant correlations across multiple sites between microbial community structure and environmental variables over large spatial scales (Fierer and Jackson, 2006; Lauber et al., 2009; Chu et al., 2010; Griffiths et al., 2011). Meanwhile, historical contingencies (factors that were important in the past but that are not currently influential such as disturbance events, physical heterogeneities, community interactions, dispersal barriers etc.) have

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also been suggested as important determinants of microbial distributions (Martiny et al., 2006). Several field studies support this latter hypothesis (Cho and Tiedje, 2000; Whitaker et al., 2003), and since the impacts of historical contingencies on microbial communities are likely correlated with spatial distance (Ramette and Tiedje, 2007), it is now believed that microbial species/phylotype distributions are shaped not just by local environmental heterogeneities but also to at least some minor extent by geographic distance (Ge et al., 2008; Griffiths et al., 2011) or dispersal limitation (Martiny et al., 2011).

A wide range of studies have investigated spatial patterning in microbial communities at scales from centimeters to meters (Franklin and Mills, 2003; Philippot et al., 2009), and at the landscape scale (Yergeau et al., 2009; Enwall et al., 2010; Bru et al., 2011; Shi et al., 2015). Spatial autocorrelation has been commonly observed, and can occur at sampling distances up to 739 km (Bru et al., 2011). Techniques to analyze spatial patterns across multiple scales have recently been used in microbial community studies (Martiny et al., 2011; Franklin and Mills, 2003). For example, Ramette and Tiedje (2007) showed that variation in species abundances and community composition within the Burkholderia bacterial group in an agricultural ecosystem was greatest at small scales (between individual plant roots) rather than larger spatial scales (across a field). However, because functional redundancy among microbial phylotypes seems to be very frequent (Lozupone et al., 2012), these taxonomy-based biogeographical studies may be very limited in terms of providing insights as to how spatial heterogeneity in microbial community structure influences biogeochemical processes within and among ecosystems. Nevertheless, some recent studies have demonstrated that for some specific biogeochemical processes, there can be strong spatial linkages between abundances of the functional groups responsible for those processes and activity rates. For example, denitrifier functional gene abundances were highly spatially correlated with a N_2O production in soils at sampling distances up to 5 m at three different Arctic sites (Banerjee and Siciliano, 2012a), and across a pasture at distances from 6 to 16 m (Philippot et al., 2009). Furthermore, the abundances of ammonia-oxidizing genes within archaeal and bacterial communities were spatially correlated with aerobic ammonia oxidation potential rates at distances up to 4 m in the same Arctic soils referred to above (Banerjee and Siciliano, 2012b). However, the question of whether the relationship between phylogenetic structure and functioning in terrestrial soil microbial communities applies across multiple biogeochemical functions and across landscape and larger spatial scales has not yet been investigated.

Understanding spatial distributions of soil functional genes at large scales is a high priority in terms of predicting terrestrial ecosystem responses to global land use and climate changes (He et al., 2010a; Zhou et al., 2012; Chan et al., 2013; Feng et al., 2014). In a previous study, we documented the pattern and influences of environmental heterogeneity and geographic distance on bacterial community structure in heath tundra soils that were sampled from across a large part of the Arctic (Chu et al., 2010). Our overall goal in this current study was to investigate the patterns and controls on functional gene distributions in those same soils to directly compare taxonomically-based and trait-based biogeographical patterns and the relative influences of environmental and spatial factors. Characterizing the 'pure' influence of spatial scale on the biogeography of microbial communities is complex because other categories of potential explanatory variables such as those associated with environmental heterogeneity can also vary across space. Most previous studies of this issue have investigated the influences of local environment and spatial distance separately, without accounting for potential covariation (Fierer and Jackson, 2006; Lauber et al., 2009; Chu et al., 2010; Feng et al., 2014). The Principal Coordinates of Neighbor Matrices (PCNM) analytical approach was specifically developed to model community structures across a wide range of scales and to characterize the relative influences of the explanatory factors both separately, and in combination, at multiple different spatial scales (Borcard and Legendre, 2002).

To characterize soil microbial functional genes in these soils, we utilized the GeoChip 4.0 array which contains probes for ~152,000 biogeochemically important functional genes (Hazen et al., 2010; He et al., 2010b; Yang et al., 2013; Tu et al., 2014). Using the GEOCHIP and PCNM analytical approaches on the same triplicate samples from the 24 heath tundra sites across the Arctic that we had used in our study of microbial community phylogenetic composition (Chu et al., 2010), we specifically address the following three questions:

I) Are distributions of microbial functional genes in Arctic soils more spatially structured at large or small scales?
II) Can the spatial structure of soil microbial functional genes be categorized into discrete spatial scales that are associated with heterogeneities in environmental variables?
III) What is the relative importance of spatial distance as compared to local environment in determining the distribution patterns of microbial functional genes in heath soils across the Arctic?

2. Methods and materials

2.1. Soil sampling

Surface soil organic samples were collected from 24 heath tundra sites (at least 190 km apart from each other) across the Canadian, Alaskan and European Arctic in the summer of 2007 and 2008 as described by Chu et al. (2010). At each site, soil samples were collected close to the top of exposed ridges at three similar locations (20–100 m apart) from below dry heath vegetation in which at least one of the following plant species was common: *Empetrum* spp., *Cassiope* spp. or *Dryas* spp. The soil type immediately underlying this vegetation was typically an Orthic Dystric Static Cryosol (Paré, 2011. Canadian Soil Classification System - http://sis.agr.gc.ca/cansis/taxa/cssc3/CY/SC/index.html). Samples of the top surface dark brown/black organic soil were cut out with a serrated knife (that was wiped off with a clean tissue before sampling from subsequent locations) from a ~12 cm × 12 cm area to 2–5 cm depth and placed in a separate plastic bag. All the samples were immediately shipped to Kingston, Canada where they were stored at −20 °C until processing. Details of the soil sampling and of each site's geographical, ecological, and biogeochemical characteristics (including methods for the latter) have been described previously (Chu et al., 2010). Unfortunately, climatic data were not available for many of the sites because they did not have local weather stations.

2.2. GeoChip analysis

DNA was extracted from 5 g fresh weight of soil from each sampling location (n = 72 in total) using a freeze-grinding mechanical lysis method as described previously (Zhou et al., 1996). We used GeoChip 4.0 to analyze DNA samples as described previously (Lu et al., 2012; Yang et al., 2013; Tu et al., 2014). Briefly, DNA was labeled with the fluorescent dye Cy-5 using a random priming method and then purified with the QIA quick purification kit (Qiagen, Valencia, CA, USA) according to the manufacturer's

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