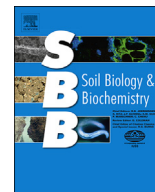




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Interactions between soil phototrophs and vascular plants in Himalayan cold deserts

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ABSTRACT

The high-elevation cold deserts in Tibet and Himalaya are rich in soil cyanobacterial communities, which facilitate an initial establishment of vascular plants. During the following succession, the increasing cover of vascular plants modifies light intensity and nutrient availability for soil cyanobacterial community and other soil phototrophs. Despite the importance of soil phototrophic community for ecosystem functioning, surprisingly little is known about the actual interactions between vascular plants and soil phototrophs and about their variation along environmental gradients in high-elevation cold deserts. In this study, we disentangle the direct impact of vascular plants on soil phototrophic community, mainly on cyanobacteria, from indirect ones mediated through modification of soil chemistry and temperature stress along an unprecedented elevational gradient (5200–6000 m a.s.l.) using a combination of conditional inference trees, co-correspondence analysis and variation partitioning. We found that vascular plants and cyanobacteria substantially differ in their response to increasing elevation. While species richness, diversity and abundance of vascular plants decreased with elevation, the species richness, diversity and abundance of cyanobacteria growing below vascular plants did not change with elevation and the richness, abundance and diversity of cyanobacteria from bare soil increased with elevation. Cyanobacteria were generally more abundant and diverse in bare soil than in vegetated soil. This difference was caused mainly by the substantially higher abundance of cyanobacteria from orders Chroococales and Nostocales in bare soils. The diversity of cyanobacteria from vegetated-soil was unrelated to vascular plant cover, but the diversity of cyanobacteria from bare soil strongly declines with increasing plant cover. In vegetated soils, the composition of soil cyanobacterial communities was affected mainly by the species composition of vascular plants. In bare soil, the composition of soil cyanobacterial communities was driven mainly by the soil chemistry and elevation. Cyanobacterial assemblages were also indirectly affected by vascular plants through changes in soil texture and fertility, with finer and more nutrient rich soils hosting less diverse cyanobacterial communities. Our results shed light on the interactions between soil cyanobacteria and vascular plants in the high-elevation cold deserts and disentangle the role of different ecological filters in structuring soil phototrophic communities in the rapidly-warming Himalayas.

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1. Introduction

Understanding ecological linkages between above- and below-ground biota is crucial for understanding biodiversity patterns and ecosystem functioning (Haichar et al., 2014; Wardle et al.,

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2004). Most information about plant-soil microbe interactions comes from productive environments, where plants play a dominant role (e.g. Kaye and Hart, 1997; Berg and Small, 2009). Less is known about these interactions in arid environments, where plants are typically sparse (e.g. Lozano et al., 2014). Arid habitats cover over one third of the Earth's surface (Laity, 2009), including the cold and arid high-elevation zones of Tibet and Himalaya. One consequence of the extreme desert environment is that the diversity of macroorganisms is often limited, and microorganisms may have a more influential role in governing key surface and subsurface bioprocesses (Makhalanyane et al., 2015).

The response of plant species to a changing environment can be moderated by abiotic factors (e.g. nutrient availability and pH) as well as biotic interactions with soil organisms (Angel et al., 2016). The interactions between vascular plants and soil phototrophs (cyanobacteria and microalgae) play an important role in cold deserts (Rehakova et al., 2011). In particular, cyanobacteria as primary producers and fixers of atmospheric nitrogen may drive the development of plant communities (Belnap and Eldridge, 2003; Janatkova et al., 2013; Makhalanyane et al., 2013). They also produce exopolysaccharides, which enhance water uptake and retention (Johansen and Shubert, 2001), increase soil stabilization (Kubeckova et al., 2003) and consequently may facilitate the persistence of other organisms such as vascular plants or microfungi in the desert environment (e.g. Belnap and Eldridge, 2003).

Soil microbial communities are abundant in different types of soil in the cold deserts of Tibet and Himalaya (Rehakova et al., 2011, 2015; Janatkova et al., 2013) where they prepare deglaciated substrates for the establishment of vascular plants (Aschenbach et al., 2013; Angel et al., 2016). However, the increasing cover of vascular plants during primary succession gradually reduces the bare surface area and modifies the light and nutrient availability for soil phototrophs. Little is still known about the patterns and processes of these interactions. It is important to disentangle the impact of vascular plants on phototrophic soil microorganisms, which involve (i) direct effects through resources and space occupation, and (ii) indirect influence mediated through the modification of soil abiotic conditions. Many studies have clearly demonstrated the importance of both kinds of processes in shaping the community patterns of plants and soil microorganisms (Angel et al., 2010; Bachar et al., 2012; Finkel et al., 2011, 2012). However, most comparative studies either lack a convincing number of discrete sampling sites (Mitchell et al., 2012), or do not perform a direct comparison between organisms in the same landscape context with the same set of plots. These methodological differences have limited our ability to draw firm conclusions regarding the relative importance of biotic and abiotic effects in different groups of organisms with different dispersal traits and/or different responses to environmental variables.

Despite the importance of soil microbial communities in cold ecosystems (Rehakova et al., 2011; Capkova et al., 2016), their structure and functions have been rarely studied in remote mountain regions such as the Himalayas (Janatkova et al., 2013). This high altitude region is being strongly impacted by climate change and this could cause significant decline in biodiversity across a wide variety of alpine habitats (Xu et al., 2009). These changes in biodiversity can alter ecosystem processes and the resilience and resistance of ecosystems to environmental change (Korner, 2003). Without baseline data on plant-microbe interactions, however, we cannot track the effects of climate change, and without an understanding of the drivers of community assembly, we cannot predict how climate change may affect this high-altitude ecosystem. The majority of microbial-plant interaction studies have focused on the bacterial domain (e.g. symbiotic N₂-fixing bacteria and rhizobacteria) (Hayat et al., 2010) and

mycorrhiza (e.g. Brundrett, 2009).

The main goal of this study was to investigate the variation in soil phototrophic communities (mainly cyanobacteria) and co-occurring vascular plants in the location with the highest-growing vascular plants in the world. Specifically, we explored: (i) differences in the cyanobacterial species richness and composition between vegetated and bare ground soil, (ii) the associations between cyanobacteria and vascular plant species composition, cover and environmental variables along an elevational gradient from 5200 to 6000 m a.s.l., and (iii) disentangled the direct effects of vascular plants (competition for space and resources) on soil phototrophs from indirect effects (modification of soil abiotic conditions such as nitrogen and phosphorus availability).

2. Materials and methods

2.1. Location

The fieldwork was conducted in summer 2009 in two mountain areas of Ladakh, Jammu and Kashmir State, India: in the Eastern Karakoram Range in the Nubra Valley (34°45'N, 77°35'E) and in the southwestern extension of the Tibetan Plateau on the western slope of Chamser Kangri Peak above Tso Moriri Lake (32°59'N, 78°24'E) in alpine and subnival zones (for details see Dvorsky et al., 2013; Dolezal et al., 2016).

2.2. Sampling plots

To explore biotic interactions between vascular plants and soil phototrophs, we established 105 permanent plots, each 1 m² in size, between 5210 and 6029 m a.s.l. The plots were 5–10 m of elevation apart. In each plot species composition, richness and abundance of vascular plants and soil phototrophs were recorded. Within each plot, soil phototrophs and soil chemistry were analyzed in bare soil and also in vegetated soil if total plant cover was more than 20%. Plots were established within the alpine and subnival zone on a gentle west-facing slope. Lower alpine zone (approx. 5200–5400 m a.s.l.) was dominated by *Carex sagaensis*, *Oxytropis pauciflora*, and *Leontopodium leontopodium*, while the upper alpine zone (approx. 5400–5600 m a.s.l.) was dominated by *Thylacospermum caespitosum*, *Potentilla pamirica*, *Poa attenuata*, and *Astragalus confertus*. Subnival zone (approx. 5600–6000 m a.s.l.) hosted sparse vegetation with common *Ladakiella klimesii*, *Waldheimia tridactylites*, *Saussurea gnaphalodes*, *S. inversa*, and *Stellaria decumbens*.

Within each plot, two types of soil composite samples (each 150 g) were collected for chemical analyses and for assessing composition and diversity of phototrophic communities. First, a mixed sample consisting of five randomly distributed subsamples of soil, each 10 cm² in area and 1–5 cm deep, was collected from bare soil surface, at least 10 cm away from patches of vascular plants, with a sterile spatula. Second, a mixed sample consisting of five randomly distributed subsamples of soil was collected from the rhizosphere of plants, each 10 cm² in area and 1–5 cm deep. The soil samples from the rhizosphere were collected up to the elevation of 5900 m, where plant cover was still up to 20%. This allowed sampling of soil from beneath the vascular plants. The soil was air-dried on aluminum plates for 10 h and then placed in sterile 100 ml polypropylene bags (Nasco Whirl-Pak®). After the transport to the laboratory, the physico-chemical analyses were performed immediately. The samples for analyses of phototrophs were stored at –20 °C for a maximum of 4 months prior to analysis. In the laboratory, biovolume, the number of phototrophs cells and the taxonomical composition were determined using light and epifluorescence microscopy (Olympus BX 60). The biovolume was

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