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Shifts in soil fungi and extracellular enzyme activity with simulated climate change in a tropical montane cloud forest

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ABSTRACT

Tropical montane cloud forests are vulnerable to climate change. The cloud layer is lifting, causing warmer and drier conditions. With climate change, tropical ecosystems have the potential to accentuate global CO_2 emissions because of their significant influence over global C cycling. Unfortunately, we do not know how this will affect belowground communities, like soil fungi, and the vital ecosystem processes they control. We performed a soil translocation experiment along an elevation gradient in Monteverde, Costa Rica to assess how fungal communities, soil decomposition, and extracellular enzyme activity (EEA) of C-degrading enzymes may shift with climate change. Soils were translocated to four lower elevation sites. These sites spanned 4 °C increases in temperature and a 20% decline in soil moisture. We used microbial cages to isolate the fungal community and monitor how soil fungi would respond to warmer, drier conditions. Fungal abundance and diversity increased with warmer and drier conditions. Fungal communities also shifted. Specifically, we found changes in the richness of fungal phyla. Richness of lichen-forming fungi, pathogens, wood saprotrophs, and yeasts increased. In addition, we found that EEA was higher under warmer and drier conditions. Our results suggest that high elevation soils may shift towards an increased capacity to decompose C under future climate conditions. Moreover, with climate change, animals or plants in tropical montane cloud forests may be exposed to a greater richness of fungal pathogens. Overall, our study reveals that the lifting cloud layer may affect the fungal community within these forests, which in turn may affect both the structure and function of these forests.

1. Introduction

Clouds distinguish tropical montane cloud forests from lowland forests. Unfortunately, this cloud layer is lifting because of increased sea surface temperatures, causing warmer temperatures and increased dry days (Karmalkar et al., 2011; Lawton et al., 2001; Still et al., 1999). These changes have implications for global C cycling owing to the disproportionate influence that tropical forests have over C cycling. For instance, tropical forests contain one third of the world's C (Jobbágy and Jackson, 2000). They also exchange more carbon dioxide (CO_2) with the atmosphere than any other ecosystem (Pan et al., 2011). In addition, there is more soil C in montane forests than lowland forests (Grieve et al., 1990; Raich et al., 2006). The fate of that C will depend on decomposition by soil fungi. In tropical montane cloud forests, studies have shown dramatic effects of climate change aboveground: plants and animals are migrating upslope to maintain their optimal climates (Colwell et al., 2008; Feeley and Silman, 2010; Thomas et al., 2004), and biodiversity is declining due to fungal pathogens (Pounds et al., 1999, 2006). But, we have little information regarding how climate change may alter belowground communities—including fungi—and their influence on ecosystem C.

Cloud immersion is vital because it affects the structure and function of these forests (see Dalling et al., 2016; Fahey et al., 2016). These effects extend beneath the soil. The dense cloud layer yields cooler temperatures, more rainfall, less light (reducing photosynthesis), and higher humidity (reducing evapotranspiration) compared to adjacent lowland forests (Schawe et al., 2010). These conditions lead to slower rates of decomposition and nutrient cycling (Bruijnzeel et al., 1993; Grubb, 1977). Decomposition rates are especially low at high elevations where temperatures become even cooler (Vitousek et al., 1994). This pattern is accentuated as soils become waterlogged and anaerobic (Schuur, 2001; Silver et al., 1999). Slower rates of decomposition at high elevations lead to a buildup of soil organic matter (Raich et al., 2006) and soil C pools (Dieleman et al., 2013; Girardin et al., 2010; Schuur et al., 2001).

Fungi are the primary decomposers in soil (de Boer et al., 2006) and are also important pathogens in tropical ecosystems (Gilbert, 2005). The lifting cloud layer could affect soil fungi, because they are sensitive

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to changes in temperature and precipitation (Allison and Treseder, 2008; Hawkes et al., 2011; McGuire et al., 2011). For example, warmer conditions could support faster decomposition of the organic-rich soil at high elevations, providing fungi with greater C and N availability. This increase in resources could promote diversification, and allow fungi to become more abundant. Moreover, richness of free-living filamentous fungi (many of which are decomposer fungi) and yeasts (simple C decomposers) tends to be greater at lower elevations (with warmer and drier soils) in tropical montane cloud forests (Looby et al., 2016). These relationships suggest that richness of these decomposer groups may increase under climate change.

Shifts in the fungal community could affect decomposition through changes in extracellular enzyme activity (EEA). Fungi produce extracellular enzymes that break down and target specific forms of C. Extracellular enzyme activity may also be altered with climate change, because enzymes at high elevations have greater temperature sensitivity (Nottingham et al., 2016). The effects on soil C could be dramatic because decomposition can increase exponentially with temperature (Benner et al., 2010). Overall, warmer temperatures in tropical montane cloud forests may allow certain fungi to proliferate, stimulating decomposition and CO_2 release from the soil.

Fungal pathogens can also influence community dynamics by infecting certain animals, plants, and other fungi. In tropical montane cloud forests, there have already been severe declines in aboveground biodiversity due to the proliferation of fungal pathogens (Pounds et al., 1999, 2006). Moreover, disease in terrestrial organisms is expected to increase with climate change (Harvell et al., 2002). With continued climate change, fungal pathogens could proliferate and aboveground species could be exposed to new pathogens.

Translocation experiments along elevation gradients have become increasingly important in understanding the fate of C under climate change (Malhi et al., 2010; Sundqvist et al., 2013). Translocation studies have shown that soil respiration (Chen, 2012; Zimmermann et al., 2009) and litter decomposition (Salinas et al., 2011; Scowcroft et al., 2000) may increase with changing climate conditions. But, more detailed information is needed on how soil fungal communities and EEA may be altered.

In a previous study, we characterized soil properties and fungal community composition along an elevation gradient on the Pacific slope of the Cordillera de Tilarán in Monteverde, Costa Rica (Looby et al., 2016). Here, we performed a soil translocation experiment along this elevation gradient to determine how fungal communities would change with warmer and drier conditions. High elevations in Monteverde are predicted to be the most vulnerable to climate change (Karmalkar et al., 2008). Thus, we focused on effects of climate change on soils from the highest elevation site. We translocated these high-elevation soils to four lower elevation sites associated with 1, 2, 3, and 4 °C increases in temperature, and a 4–20% decline in soil moisture. Moving soils from high to low elevations simulates the decline in cloud cover associated with the lifting cloud layer; and thus, soils experienced warmer temperatures and drier conditions.

We hypothesized that fungal abundance and diversity would increase in soils moved to lower elevation sites. Furthermore, we hypothesized that fungal community composition would shift in soils moved to lower elevations, because fungal phyla and functional groups may vary in their responses to climate. Finally, we hypothesized that EEA would increase in soils moved to lower elevations sites due to warmer temperatures and drier conditions. To test these hypotheses, we measured fungal abundance, diversity, and community composition, and EEA of C degrading enzymes.

2. Materials and methods

2.1. Study sites

In August 2013, an elevation transect was established along the Pacific slope of the Cordillera de Tilarán within the Monteverde Cloud Forest Reserve (10°18′N, 84°47′W) in Monteverde, Costa Rica (Looby et al., 2016). The transect ranges from 1305 to 1850 m.a.s.l. (meters above sea level), with sites established at approximately every 50 m increase in elevation. In this study, we used field sites located every 100 m increase in elevation, including 1430, 1549, 1656, 1743, and 1850 m.a.s.l. Field sites are all located within primary, undisturbed forest and cover three Holdridge life zones: premontane, lower montane, and montane forests (Holdridge, 1967). All soil along the transect is classified as inceptisols (Centro Científico Tropical, personal communication).

2.2. Soil translocation design and collection

We used a soil translocation experiment to test how increased temperatures and decreased precipitation would affect fungi and extracellular enzyme activity. More specifically, soils were moved to lower elevations so that fungal communities would experience warmer temperatures and drier conditions. We measured soil temperature at two locations at each site from November 25, 2014 to April 18, 2015 using iButton temperature loggers (QA supplies, Norfolk, VA) to verify the temperature range across our translocation sites. We also measured soil temperature at four random locations at each elevation at the time of sample collection. Based on our observations, a change of approximately 100 m in elevation corresponds to a one-degree (°C) temperature change in soil.

To manipulate the fungal community, soil was enclosed in microbial cages. Each cage was 10 cm × 10 cm and made of nylon mesh with a pore size of 0.45 μm (Maine Manufacturing, ME, USA). This pore size prevents new fungi from entering, while allowing exchange of water, nutrients, organic compounds, and some bacteria with the local environment. Microbial cages have been effective in isolating microbial communities in prior studies (Allison et al., 2013; Holden et al., 2015; Reed and Martiny, 2013). By transplanting fungi via these microbial cages, we were able to monitor how the fungal community would change with warmer and drier conditions.

Soil from 1850 m.a.s.l. was translocated to low-elevation sites to simulate warmer temperatures and drier conditions (Table 1). Soil was also placed into microbial cages and kept at 1850 m.a.s.l. as a reference site, and thus represented 0 °C warming and 0% drying. Temperature is presented as increase in soil temperature compared to the reference site. Soil moisture content (%) declined with decreasing elevation. This was determined after collection by taking subsamples of soil from each cage and measuring gravimetric moisture content. Gravimetric moisture content was determined by drying subsamples of soil at 65 °C and then re-weighing them. Soil moisture is presented as decline in soil moisture (%) compared to the reference site.

Twenty soil cores (2 cm diameter by 10 cm deep; mostly O horizon) were collected along an established 20 m straight line at 1850 m.a.s.l. in November 2014. Soils were transported to the lab and homogenized

Table 1
Site characteristics of soil translocation experiment simulating climate change. Soil was placed in microbial cages and were translocated from 1850 m.a.s.l. to four lower elevation sites that warmer and drier. Five replicates were placed at each elevation. Soil was kept at 1850 m.a.s.l. and used as a reference. Thus, these soils represented 0 °C warming and 0% drying.

Elevation (m.a.s.l.)	Latitude (N)	Longitude (W)	Temperature change from 1850 m.a.s.l. (°C)	Moisture change from 1850 m.a.s.l. (%)
1850	10°19′02.02″	84°47′40.03″	0	0
1743	10°18′57.64″	84°47′47.83″	1	−4.17
1656	10°18′48.69″	84°47′57.74″	2	−10.8
1549	10°18′18.40″	84°47′46.36″	3	−20.0
1430	10°17′28.81″	84°47′30.97″	4	−19.9