



# Altered edaphic parameters couple to shifts in terrestrial bacterial community structure associated with insect-induced tree mortality



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## ABSTRACT

Unprecedented insect-induced tree mortality has been observed globally and while hydrologic and biogeochemical changes have been recorded, alterations to terrestrial microbial communities, which influence as well as respond to these shifts, are not well understood. The objective of this work was to better understand how bacterial communities are coupled to perturbations in biogeochemically-relevant soil physicochemical parameters resulting from beetle-induced tree death. To this end, soils beneath trees across a beetle-kill spectrum were contrasted in the central Rocky Mountains at both heavily impacted (Chimney, 85% mortality) and moderately impacted (Niwot, 18% mortality) field sites. Soil organic matter (OM), dissolved organic carbon (DOC) and dissolved organic nitrogen were all significantly altered when contrasting soils under healthy versus beetle-attacked trees at Chimney. Bacterial alpha diversity measurements were found to increase with tree death and beta diversity measures showed significant clustering with relation to tree phase. The site was characterized by a significantly higher relative abundance of bacterial clades under healthy trees that were correlated to OM and DOC concentrations. In contrast, compositional changes in soil bacterial communities and edaphic parameters associated with tree phase were not observed at the less impacted Niwot site. Our findings reveal a coupled response between shifts in organic carbon cycling and the bacterial assemblage as a result of large-scale, beetle-induced tree mortality with implications for heterotrophic respiration in near-surface soils and suggests a possible dependence on the level of forest mortality before manifestation.

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## 1. Introduction

Climate change is altering terrestrial ecosystems throughout the world. As a result of increased temperatures and drought, stressed forests are more susceptible to insect attack as evidenced by recent unprecedented tree mortality in North America, Europe, and Asia (Kurz et al., 2008; Williams et al., 2013). In extreme cases such as the Colorado region of the Rocky Mountains, forests are reaching close to 100% tree mortality which has resulted in significant alterations to hydrological and biogeochemical cycles (Morehouse et al., 2008; Mikkelsen et al., 2013a; Bearup et al., 2014a). Decreased forest canopy and transpiration due to widespread tree die off (Mikkelsen et al., 2013c) reduces soil water uptake and potentially increases groundwater recharge (MacDonald and Stednick, 2003; Bearup

et al., 2014a) and soil moisture (Morehouse et al., 2008). Cumulative changes in canopy cover, litter fall, and tree respiration also alter incident radiation possibly increasing soil temperatures (Hais and Kučera, 2008). In concert with these biological responses, these processes have resulted in shifts to the terrestrial biogeochemical cycling of carbon (Kurz et al., 2008; Mikkelsen et al., 2013a, 2013b), nitrogen (Clow et al., 2011; Griffin et al., 2011) and metal/metalloids (Mikkelsen et al., 2014; Bearup et al., 2014b). As recent studies have observed changes to microbial communities after forest disturbance (Hartmann et al., 2012; Štursová et al., 2014) and terrestrial microbial communities have been known to change when soil properties (Hackl et al., 2004; Lauber et al., 2008; King et al., 2010) and tree-specific carbon inputs change (Urbanová et al., 2015), the bark beetle infestation is a relevant scenario in which to investigate the coupled response of terrestrial bacterial communities and the associated edaphic parameters.

Near surface microbial communities mediate essential ecosystem functions such as carbon mineralization and subsurface

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cycling with their soil-surface CO<sub>2</sub> efflux exceeding emissions from fossil fuels by a factor of seven (IPCC, 2007). It has been demonstrated that historical land disturbances (fire, clear-cutting, fertilization, etc.) and the resultant terrestrial alterations are coupled to shifts in the prominent microbial communities within the perturbed ecosystem (Hart et al., 2005; Hannam et al., 2006; Chatterjee et al., 2008; Hartmann et al., 2012; Wertz et al., 2012). However, the bark beetle presents a unique disruption whose correlation to these other disturbances is not fully understood (Adams et al., 2012). After death, the tree remains standing while the roots stop excreting carbon into the soil, which is a primary source of dissolved organic carbon (DOC) for subsurface microbial communities (Grayston et al., 1997). Annual litterfall is also reduced followed by a pulsed drop of needles to the forest floor several years later that provides the heterotrophic microbial community with a different quantity and form of organic carbon (Kaňa et al., 2012). Eventually the degradation of the tree roots and other woody material that has fallen to the ground provides another source of terrestrial carbon to below ground microorganisms. To this end, it is possible that alterations in bioavailable carbon, along with changes in biogeochemical and hydrologic inputs associated with beetle-induced tree mortality have the potential to shift microbial community composition and its associated function as seen in other systems (Hackl et al., 2004; Lauber et al., 2008; Harris, 2009).

Previous research has hypothesized that with the changing soil moisture and temperature regime, coupled to increased substrate availability after needle drop during a bark beetle infestation, microbial decomposition rates will increase (Edburg et al., 2012; Hicke et al., 2012). Surprisingly though, multiple studies have measured above ground carbon fluxes or soil respiration after an insect infestation and in the short term (~years after infestation) have observed either no change or a decrease in soil carbon efflux (Hancock et al., 2008; Morehouse et al., 2008; Nuckolls et al., 2009). Few studies have quantified the number of heterotrophic bacteria after an insect infestation and to our knowledge it has only been reported after a phytophagous insect outbreak in a pine forest (in which the needles are consumed but the tree is not necessarily killed) (Streminska et al., 2006) where they observed an increase in Actinobacteria and fungi due to a larger supply of easily degradable organic matter in litterfall.

In this study we hypothesized that shifts in both edaphic parameters and the terrestrial bacterial community could be correlated to beetle infestation; in essence, that the terrestrial ecosystem under a beetle-impacted tree would be distinct from one under a healthy tree. As recent investigation has shown increases in soil respiration and terrestrial CO<sub>2</sub> release with additional soil carbon inputs in a warming climate (Giardina et al., 2014), it is imperative that we fully understand the response of soil microbial communities in analogous scenarios such as climate-induced forest disturbances where terrestrial carbon inputs can be altered. A recent study in the Bohemian Forest mountain range in Central Europe observed significant changes in fungal biomass after spruce beetle infestation but saw smaller changes in bacterial biomass (Štursová et al., 2014). While that study performed a detailed analysis of fungal communities, it did not focus on structural changes in bacterial ecology. Research in North America found that despite increases in soil nitrogen pools after beetle-induced tree death of limber pines (*Pinus flexilis*), the bacterial community remained unaffected (Ferrenberg et al., 2014). Our study complements these recent investigations by comparing soil physicochemical parameters and bacterial community structure (using next-generation sequencing of the 16S rRNA gene) under lodgepole pines (*Pinus contorta*) across multiple time points in two North American bark beetle infested sites. Importantly, the two sites encompass varying levels of forest mortality with one site more severely impacted by beetle-induced tree death than the other (85% mortality compared

to 18% mortality) with field sampling spanning the snow-free period of 2013. We ensured adequate sampling depth by temporally sampling composite soils under a carefully selected matrix involving the same green phase (healthy, transpiring trees), red phase (beetle-killed, no longer transpiring but retain needles) and grey phase (beetle-killed, dropped needles) trees at both sites.

## 2. Material and methods

### 2.1. Field sites and sample collection

Two montane, beetle-impacted sites were chosen for sample collection due to similar climates, geology and prior comparison studies (Biederman et al., 2014), but varying levels of bark beetle infestation. Though residing in different states, both sites are in the Central Rocky Mountains around 3000 m in elevation with mean annual air temperatures of 1–3 °C and precipitation around 800 mm/yr. Both sites contained Inceptisol soils with weakly developed soil horizons. Additional soil characteristics for Niwot can be found in Xiong et al. (2011) and for Chimney in Mikkelsen et al. (2014) or Knight et al. (1985). To determine the local level of tree mortality (including all mature tree species), sampling areas within the sites consisted of three 65' × 20' rectangles. The first site, Niwot Ridge Long-Term Ecological Research Site (Niwot) in Colorado (40°1'58"N, 105°32'47"W) has been moderately impacted by bark beetles with a local site mortality of 18.2 ± 4.5% and a local tree density of 34 ± 12 trees per sampling rectangle. This led to many of the sampled dead trees being completely surrounded by alive and transpiring trees. The second, heavily infested site is located at Chimney Park (Chimney), Wyoming (41°40'82"N, 106°7'93"W) and had experienced over 75% tree mortality by 2011 (Biederman et al., 2014) with a local level of mortality within the sampling plots of 84.6 ± 6.3% and a local tree density of 44 ± 3 trees per sampling rectangle.

Samples were taken in the summer of 2013 from under lodgepole pine (*P. contorta*) trees at both sites; this was two years after the analogous 2011 Ferrenberg et al. (2014) sampling event of *P. flexilis* in a nearby section of Niwot. As trees begin to die from bark beetle attack, they undergo a temporal succession in which various hydrological and biogeochemical changes occur. This succession has been divided up into phases, which will be referenced throughout the study. The 'green' phase is considered to be when the tree is still alive, healthy and transpiring. The 'red' phase marks mortality, occurring within a year after a successful attack; at this point, the tree has ceased transpiration but still retains the majority of its needles (now red in color). The 'grey' phase occurs approximately 3–5 years after infestation at which point the tree has dropped its needles. Soil was sampled downslope within 1 m of the trunk and from the top 5 cm of the mineral soil layer with litter and visible organic material excluded (Ferrenberg et al., 2013, 2014). Soil samples were taken using a sterilized stainless steel spoon and 50 ml conical tubes to sample horizontally from three soil core pits per tree (Li et al., 2012). To ensure a representative soil sample from under each tree, three boreholes were dug under each tree and ten samples collected per borehole, creating a homogenized 30 grab-sample composite per tree. Unlike Ferrenberg et al. (2014) where they sampled 50 random trees once during March of 2011, our soil samples for biogeochemical and microbial analyses were taken at both sites from under the same 3 green phase, 3 red phase and 3 grey phase trees at each sampling event with 1 green tree, 1 red tree and 1 grey tree per sampling rectangle as described above. This enabled us to explore seasonal variation in addition to beetle-impact with three distinct sampling events taking place at Niwot (June, July and August) and with two events at Chimney (June and August). Overall, each sampling event at each site contained n = 9 composite samples (3 green, 3 red and 3 grey) for a season total of

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