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Impact of slope exposure on chemical and microbiological properties of Norway spruce deadwood and underlying soil during early stages of decomposition in the Italian Alps



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ABSTRACT

Mountain forest ecosystems are particularly sensitive to changing environmental conditions that affect the rate of deadwood decay and, thus, also soil carbon turnover and forest productivity. Little is known about how slope exposure and climate influence microbial abundance and activity in general, and wood-inhabiting bacteria during deadwood decomposition in particular. Therefore, a field experiment using open mesocosms was carried out along an altitudinal gradient (from 1200 to 2000 m above sea level) in the Italian Alps to evaluate the impact of exposure (north (N)- vs. south (S)-facing sites) on microbial biomass (double stranded DNA, dsDNA); microbial abundance (real-time PCR-based: fungi; dinitrogen reductase, nifH; ammonia-monooxygenase, amoA); and several hydrolytic enzyme activities involved in the main nutrient cycles during decomposition of Picea abies wood blocks $(2 \times 5 \times 5 \text{ cm})$ over a 2-year period. In addition, soil physico-chemical and (micro)biological properties were determined at each site. The cooler, moister and more acidic conditions at north-facing slopes led to an increase in the wood and soil fungal abundance. Furthermore, soil nitrogen-related bacterial functional genes (*nifH* and *amoA*) gave a contrasting response to exposure in terms of abundance: nifH (N > S, altitude and decay time-dependent); ammonia-oxidising bacteria (AOB; S > N, altitude and decay time-dependent); ammonia-oxidising archaea (AOA; N > S, only at 2000 m a.s.l.). The AOB and AOA abundance, however, was below the detection limit in the wood blocks. Soil microbial biomass was in general higher at the north-facing slopes, whereas in the wood exposure affected to a lesser extent the microbial biomass. Overall, the exposureeffect on the microbial biomass and abundance as well as for most of the enzymatic activities was altitude- and decay time-dependent.

1. Introduction

Deadwood — the residue of living trees such as stumps, standing and fallen dead trees, fallen branches and coarse woody debris (CWD) (Zhou et al., 2007) — is one of the most important carbon stocks in forest ecosystems (Pan et al., 2011). Deadwood decay rate is determinant for the soil carbon turnover and forest productivity (Zhou et al., 2007). As woody material decays, its structure and chemical composition gradually change over time, which can result in a turnover of the wood-inhabiting microbiota as species are replaced by those better adapted to the substrate according to their biochemical requirements (Rajala et al., 2012). All of these changes can ultimately

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Fig. 1. Overview of the study area (Trentino Alto Adige, Italia) (Egli et al., 2006; Fravolini et al., 2016).

have consequences on the chemical and biological properties of the forest floor, especially the organic soil surface due to the incorporation of decaying woody material over the course of decomposition (Strukelj et al., 2013; Fravolini et al., 2016).

Fungi are considered the primary wood decomposers based on the ability to breakdown complex substrates such as lignin and cellulose, which can comprise 60-75% of wood dry mass (Meier et al., 2010). In particular, white-rot fungi efficiently degrade lignin via oxidative metalloenzymes such as laccases and manganese peroxidases (Valentín et al., 2014; Kielak et al., 2016). During the decay process, the fungal activity may increase the acidic conditions in wood that may result in an adverse environment for the bacterial colonization (Kielak et al., 2016). However, there are indications of both antagonist and beneficial fungal-bacterial interactions occurring in wood as reviewed by Johnston et al. (2016). In line with this, Hoppe et al. (2014) found positive correlations between fungal sporocarps and the richness of *nifH* (dinitrogen reductase) genes in deadwood logs from Fagus sylvatica and Picea abies. This is in accordance with the pioneering studies from Merrill and Cowling (1966) and Larsen et al. (1978) who suggested that associations with nitrogen-fixing bacteria might enable fungi to overcome their nitrogen deficiencies for vegetative and generative growth. Indeed, nitrogen is a very limited nutrient in early stages of wood decay and can be accumulated over time (Baldrian et al., 2016; Gómez-Brandón et al., 2017; Hu et al., 2017). The role of nitrogen-fixing bacteria is to bind the atmospheric dinitrogen (N2) into a biologically accessible form (NH₃), and the *nifH* gene is considered the most useful marker to study the distribution and diversity of diazotrophic microorganisms in forest ecosystems (Levy-Booth and Winder, 2010; Levy-Booth et al., 2014).

The biological oxidation from ammonia (NH₃) to nitrite (NO₂⁻) is also of great relevance in forest soils (Levy-Booth et al., 2014), as it is the rate-limiting step of the nitrification process. This reaction is carried out by both ammonia-oxidising bacteria (AOB) and archaea (AOA), which can be quantified by the ammonia-monooxygenase (*amoA*) gene (Rotthauwe et al., 1997; Francis et al., 2005; Leininger et al., 2006). Previous studies have suggested that AOB and AOA respond differently to the environmental conditions, with one or the other being more competitive under a given set of conditions, as they belong to separate phylogenetic domains with different cell biochemical and metabolic process (Erguder et al., 2009). Acidity (pH) and the availability of nitrogen forms in wood are the major drivers affecting the abundance of both AOB and AOA communities (Harmon et al., 1986; Cornelissen et al., 2012; Levy-Booth et al., 2014; Ribbons et al., 2016).

Topographic features such as slope aspect largely influence the local climate and the amount of solar irradiation intercept by the slope orientation affecting the soil biogeochemical processes (Ascher et al., 2012; Egli et al., 2016; Bardelli et al., 2017) and deadwood decay dynamics (Petrillo et al., 2015, 2016; Fravolini et al., 2016) in mountain ecosystems. These latter studies highlighted the changes in deadwood chemistry decay dynamics in response to the thermal conditions represented by different exposure along a climosequence approach. However, scarce attention has been paid so far on the influence of slope exposure on the deadwood inhabiting microbiota in terms of microbial abundance and activity and how these microbiological features change over time (during the decay process). Moreover, due to the often-time slow decomposition, deadwood can directly affect the nutrient and microbiota turnover in forest soils through the so-called "proximity effects" (Gonzalez-Polo et al., 2013) To date, few studies have addressed the changes in both deadwood and the forest floor over time from a microbiological viewpoint (van der Wal et al., 2007; Risch et al., 2013). Therefore, a field mesocosm experiment was carried out along an altitudinal gradient in the Italian Alps in order to evaluate the impact of exposure (north- vs. south-facing sites) on the abundance of fungi and nitrogen-related bacterial functional genes (nifH and amoA) assessed by real-time PCR, during decomposition of Picea abies wood blocks (2 \times 5 \times 5 cm) and the underlying soil (0–5 cm; in direct contact with the wood blocks). Furthermore, several potential enzymatic activities involved in the main nutrient cycles in both P. abies wood blocks and the underlying soil were also determined as a function of exposure and over a 2-year observation period.

In the same *in-field* mesocosm study, Fravolini et al. (2016) found that a higher soil moisture and clay content (related to a higher weathering of the soils) along with a lower pH seemed to accelerate wood decay at the north-facing slopes. We therefore hypothesised that: (1) the microbial biomass and activity will be higher at the north- than at the south-facing slopes during *P. abies* deadwood decomposition, and such effects on microbial communities will be altitude- and time-dependent; (2) the abundance of fungal and nitrogen-related bacterial functional genes will be higher at the end of the monitoring study due to the higher release of nutrients with the progressing wood decay.

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