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# Soil fungal communities respond compositionally to recurring frequent prescribed burning in a managed southeastern US forest ecosystem

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ABSTRACT

Prescribed fire is an important management tool to reduce fuel loads, to remove non-fire adapted species and to sustain fire-adapted taxa in many forested ecosystems of the southeastern USA. Yet, the long-term effects of recurring prescribed fires on soil fungi and their communities in these ecosystems remain unclear. We Illumina MiSeq sequenced and analyzed fungal Internal Transcribed Spacer (ITS2) amplicons from a long-term prescribed burn experiment that has implemented different regimes for nearly a quarter century to evaluate the effects of differing prescribed fire intervals and the season of their implementation on soil-inhabiting fungal communities. Unburned plots were used as a reference to represent the compositional state resulting from fire suppression. Our data show that while the recurring burning or the season of the prescribed burning do not affect richness and diversity of the fungal communities, the frequent (two and three year interval) fires maintain a fire-adapted community that is distinct from those in unburned reference plots. Subsequent indicator taxon analyses identified a total of 37 Operational Taxonomic Units (OTUs) that were more frequent in the frequently implemented burns and 26 OTUs that were more frequent in the fire suppressed treatment. We conclude that frequent prescribed burning maintains fire selected soil fungal communities that may support plant communities that are composed of desired fire adapted or fire tolerant species that dominate the frequently burned areas.


## 1. Introduction

Fire is a commonly implemented management tool used to reduce fuel loads in forested ecosystems of the southeastern USA (Waldrop et al., 1992; Callaham et al., 2012). Fire-regimes need to be continually refined to best fit the management goals (Stephens and Ruth, 2005). In the southeastern USA, silviculture is common and economically important (Talbert et al., 1985; Borders and Bailey, 2001). To properly maintain forest stands for silviculture, fire must be implemented to retain the fire-adapted species and remove competing fire sensitive species (Waldrop et al., 1992; Glitzenstein et al., 1995; Callaham et al., 2012). In many natural southern forest types, fire exclusion can lead to successional changes away from the diverse, fire-adapted ecosystems that developed there following Pleistocene glaciations (Abrahamson and Hartnett, 1990; Kirkman and Mitchell, 2006). Prescribed fire is viewed as a tool for restoration of these ecosystems, and frequent fires can result in overall improvement in terms of plant species richness, and animal food and habitat requirements (Ligon et al., 1986; Kowal et al., 2013; Steen et al., 2013). In determining optimal fire-regimes, a variety of ecosystem properties should be taken into account to ensure ecosystem stability and sustainability in the long-term. In non-fire adapted systems, or systems where fire has been long excluded, frequent fires can significantly reduce soil fungal biomass (Fritze et al., 1993; Pietikäinen and Fritze, 1993; Dooley and Treseder, 2012), reduce the quantity and quality of soil carbon (Neff et al., 2005) as well as change nutrient availability (Wan et al., 2001; Harden et al., 2003; Certini, 2005) indicating that both the biotic and abiotic soil properties are sensitive to fire, at least in the short-term.

Forest fires affect soil microbial communities both in short- and long-term (Holden and Treseder, 2013) and may preferentially select for fire adapted soil-inhabiting microbes. The fire effects and their duration depend on the intensity and frequency of burns (Hebel et al., 2009; Dooley and Treseder, 2012; Holden et al., 2013). Meta-analyses indicate that fires often reduce soil microbial biomass, at least in the short term (Dooley and Treseder, 2012; Holden and Treseder, 2013). Some microbial guilds are more sensitive to fire disturbance than others; Holden et al. (2013) concluded that ectomycorrhizal fungi exemplified such fire sensitive guilds. Others have pointed out specific taxa that are either resistant or adapted to fire disturbance. Examples of such genera include

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*Wilcoxina* (Baar et al., 1999; Fujimura et al., 2005; Kipfer et al., 2010), *Russula*, *Suillus* (Horton et al., 1998), *Coltricia*, *Thelephora* (Visser, 1994), *Rhizopogon*, (Baar et al., 1999; Kipfer et al., 2010), *Tomentella* (Baar et al., 1999), and *Cenococcum* (Kipfer et al., 2010). In conclusion, while the fire effects to fungal biomass are often negative, some fungi respond positively to fire treatments (Fritze et al., 1993; Visser, 1994; Baar et al., 1999; Kipfer et al., 2010) and fruit abundantly soon after fire (Wicklow, 1973, 1975).

Although prescribed burning has become an increasingly important management tool, much of our current understanding of the fire effects on soil properties comes from wildfires. It is still uncertain whether the impacts of wildfires are comparable to those of prescribed burning. Wildfires burn hotter, consume more of the aboveground biomass and organic matter, and result in greater nutrient volatilization (Hatten and Zabowski, 2010) than prescribed fires. This is partly attributable to one of the basic principles of fire management: prescribed fires are usually conducted under conditions that result in lower fire intensity and severity, and generally outside of the high risk conditions that are most conducive to the high intensity wildfires. Choromanska and DeLuca (2001) compared fire severity during a wildfire and prescribed burn in a temperate ponderosa pine forest. They observed that prescribed fire consumed 42% of the fine fuel and resulted in no overstory tree mortality. In contrast, the wildfire consumed all fine fuel and led to complete stand mortality highlighting the dramatic differences between wildfires and management through prescribed burning. Further, although both wildfires and prescribed fires tend to reduce soil fungal biomass (Dooley and Treseder, 2012), prescribed fires resulted in lesser loss of carbon in microbial biomass than wildfires (Choromanska and DeLuca, 2001). Evaluating the long-term effects of recurring prescribed fires on soils and fungal communities therein is important to properly manage forests to avoid compromising the composition and function of the soil fungal communities that are crucial to ecosystem services through nutrient cycling and facilitation of plant productivity (Wardle et al., 2004).

Soil microbial communities may recover within a growing season or two after a fire disturbance, especially if undisturbed stands or undisturbed mineral soils serve as an inoculum source (Grogan et al., 2000; Barker et al., 2013). Yet, the recovery times of many ecosystem attributes tend to be long. Eddy covariance studies and vegetation surveys suggest that re-establishment of primary productivity may require more than a decade after fires in boreal forests (Mack et al., 2008; Amiro et al., 2010; Goulden et al., 2011). Following wildfires, fungal hyphal lengths in the organic horizon required more than two decades to return to pre-fire levels (Holden et al., 2013) and soil fungal succession can continue several decades after a wildfire disturbance (Visser, 1994). However, Fritze et al. (1993) estimated a 12-year recovery time to a pre-fire state after a prescribed fire event. Finally, post-fire effects on soil carbon and organic matter may similarly persist a decade after a fire in boreal systems (Johnson and Curtis, 2001; Treseder et al., 2004). These studies, as well as recent meta-analyses (Dooley and Treseder, 2012; Holden and Treseder, 2013), strongly suggest that post-fire community shifts back to an unburned state may require more than a decade. However, the community and abiotic soil property recovery after low-intensity prescribed fires remain largely unknown.

In this study, we took advantage of a long-term experiment that has implemented different burning regimes for nearly a quarter century, thus allowing a unique means to address questions about long-term effects of recurring fires on soils and communities therein. The objectives of the implemented fire regime management were to retain the native fire adapted plant community. Unburned plots were used as a reference to represent the undesirable compositional state resulting from no fire management or continuing fire suppression. Since the experiments have controlled both fire frequencies and the season of the fire treatments, we aimed to address (1) if recurring prescribed fires have a long-term effect on soil fungal communities; (2) if these responses depend on fire interval (2-yr, 3-yr, 6-yr); and (3) if these responses depend on timing (summer vs. winter) of the burn. Our data provide further evidence that fire regimes that apply prescribed burning at frequent intervals maintain fire adapted soil fungal communities that are distinct from those inhabiting areas under fire exclusion management. As the vegetation in the frequently burned plots is largely composed of desired species, it may be inferred that the soil fungal communities residing in these plots are adapted to the recurring fires and thus better support such plant communities under frequent prescribed burning regimes.

## 2. Materials and methods

### *2.1. Study site*

The long-term prescribed burn experiment is located in the Hitchiti Experimental Forest (HEF) in Jones County, Georgia, U.S.A., part of the Oconee District of the Chattahoochee-Oconee National Forest. HEF is in the Ocmulgee branch of the Altamaha River Basin approximately 18 km east of Gray, Georgia. Overstory is composed primarily of ectomycorrhizal loblolly pine (*Pinus taeda* L.) stands that are typical and widely distributed throughout the Southern Piedmont region of the southeastern United States. Southern pine stands are important both economically and ecologically: they are managed for timber harvest as well as to provide wildlife habitat. Before conversion to forest, large proportions of HEF, including the sites for the current experiment, were used for cotton production. After the severely eroded and degraded lands were converted to forest, the stands remained a mix of pines and hardwoods and had not been burned for at least 50 years before a fire regime was established in 1989. Upon conversion to forest from cotton plantation, the area was planted with *P. taeda*, which has remained the dominant tree species at the site. The implemented fire treatments have resulted in compositional shifts in the stands and generally favor the more fire-adapted pines at the cost of the understory hardwoods.

### *2.2. Soils*

Common to the Georgia Piedmont, the study site contains highly eroded Alifsols and Utilsols. According to the United States Department of Agriculture Soil Conservation Service mapping (http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs142p2_051233.pdf), the soils represent Wilkes and Davidson Series. Wilkes Series are shallow, well-drained soils with moderately slow to slow permeability. Davidson Series consists of very deep, well-drained, and moderately permeable soils. These soils formed on uplands in the Piedmont, and are classified as loamy, mixed, active, thermic, shallow Typic Hapludalfs and are found on gently sloping to moderately steep uplands in the Piedmont.

### *2.3. Experimental design*

A long-term fire management experiment at HEF was been implemented from 1989 until 2008. The experiment contains 24 plots, each ~0.8 ha in size and assigned to burn treatments randomly. Plots are spread across an area of approximately 70 ha in the southwestern corner of HEF, and most are isolated on the landscape although some share a border with a neighboring plot. All plots were burned upon establishment, excluding unburned control plots, with low intensity backfires during the winter of 1988/