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Stand-replacing wildfires alter the community structure of wood-inhabiting fungi in southwestern ponderosa pine forests of the USA

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ABSTRACT

Increases in stand-replacing wildfires in the western USA have widespread implications for ecosystem carbon (C) cycling, in part because the decomposition of trees killed by fire can be a long-term source of CO_2 to the atmosphere. Knowledge of the composition and function of decay fungi communities may be important to understanding how wildfire alters C cycles. We assessed the effects of stand-replacing wildfires on the community structure of wood-inhabiting fungi along a 32-yr wildfire chronosequence. Fire was associated with low species richness for up to 4 yr and altered species composition relative to unburned forest for the length of the chronosequence. A laboratory incubation demonstrated that species varied in their capacity to decompose wood; *Hypocrea lixii*, an indicator of the most recent burn, caused the lowest decomposition rate. Our results show that stand-replacing wildfires have long-term effects on fungal communities, which may have consequences for wood decomposition and C cycling.

Introduction

Tree mortality in the western USA has increased in recent years due to a combination of drought, insect outbreaks, and wildfire (Westerling *et al.* 2006; Van Mantgem *et al.* 2009; Allen *et al.* 2010), changes that have profound implications for carbon (C) storage and cycling. In particular, large, high-severity wildfires often kill trees but do not consume all the tree biomass, and the C flux from decomposition of these dead trees can exceed net primary production for years to decades (Kashian *et al.* 2006). The length of time that recently burned forests function as net sources of atmospheric CO_2 is uncertain; high-severity burns in mixed conifer and ponderosa pine forests of the Inland Northwest remain net atmospheric sources for 4–5 yr (Meigs *et al.* 2009), whereas similar burns in southwestern ponderosa pine forests are likely to remain a

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net source for decades (Dore *et al.* 2008; Hurteau & Brooks 2011). A stronger mechanistic knowledge of the controls on wood decomposition would enhance our understanding of ecosystem C dynamics following high-severity wildfires.

Wildfire alters many of the factors that limit the decomposition of wood, including colonization by saprotrophic organisms, substratum quality and quantity, and abiotic environmental characteristics (Harmon *et al.* 1986). Wildfire reduces fungal inoculum sources due to heat-induced mortality (Raison 1979; Choromanska & DeLuca 2002; Korb *et al.* 2004). The maximum ground temperatures reached in forest fires range from 200 °C to 300 °C (Neary *et al.* 1999), while fungal mortality occurs at temperatures $<$100 °C (Dunn *et al.* 1985). The distance and arrangement of the fungal inoculum source are key factors controlling fungal recolonization following wildfire; further, reductions of soil-based fungal inoculum by fire make dispersal ability, either *via* airborne spores, animal transport, or migration of mycelium in the soil, critical to fungal establishment in wood (Kirby *et al.* 1990). Fungi that overcome dispersal limitations in a recently burned area are likely to encounter abundant wood substratum, but it will probably be at least partially charred. Charring decreases decomposition rates (Cornwell *et al.* 2009), but may provide greater habitat opportunities for microbes because of increased surface area (Pietikäinen *et al.* 2000). Post-fire changes in abiotic variables, such as microclimate and nutrient availability, may also alter the responses of wood-inhabiting fungi. Wildfires generally cause an increase in land surface temperatures, and they alter chemical characteristics of soil, notably by increasing the pH and nutrient availability (Hart *et al.* 2005); the interactions of all these variables may affect the establishment of fungi.

Although the environmental changes resulting from fire are likely to affect the diversity and community composition of decay fungi, few studies have examined the short- and long-term effects of fire on fungi (Cairney & Basitas 2007). Prescribed burning favors certain species of fungi, causing moderate to strong alterations in community composition (Olsson & Jonsson 2010; Berglund *et al.* 2011). Species richness declines in the first year following prescribed burning (Olsson & Jonsson 2010), but also recovers within 1–5 yr (Berglund *et al.* 2011). Even fewer studies have focused on the effects of wildfire on wood-inhabiting fungi. In a study in a boreal forest, wildfire disturbance had a short-term effect on species richness, but little effect on community composition (Lumley *et al.* 2001). However, similar studies on wildfire or prescribed burning have not been conducted in more arid environments where fire frequency and intensity have increased in recent years.

An understanding of how the composition of fungal communities changes over time is of particular relevance to climate change science because species composition may affect wood decomposition rates, and thus have consequences for C cycling. Although fungal community structure is thought to be more important in the later stages of decay, when the majority of the C remaining is in the form of lignin (McGuire & Treseder 2010), species assemblage history may be important in determining these later-stage communities (Fukami *et al.* 2010). Several laboratory experiments have confirmed that complex species interactions, including a legacy of exudates in the wood, promote the growth of certain secondary fungal colonizers while inhibiting others (Niemelä *et al.* 1995; Holmer *et al.* 1997; Heilmann-Clausen & Boddy 2005). As a result, the initial colonizers of a wood substratum can be instrumental in determining subsequent species succession, and this can have associated impacts on rates of wood decomposition (Fukami *et al.* 2010; Lindner *et al.* 2011).

Southwestern ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests are an excellent model ecosystem to examine wildfire effects on wood decomposition and C cycling for numerous reasons. First, ponderosa pine forests are widespread in the southwestern USA, comprising almost half of the commercial forest land in Arizona, Utah, New Mexico and Colorado (Schubert 1974). Also, the Southwest is predicted to suffer large-scale tree mortality due to its high sensitivity to drought, predicted increases in ambient temperatures, and related increases in wildfire frequency and bark beetle outbreaks (Williams *et al.* 2010). The land-use history in these forests also has strongly influenced the risk of wildfire and associated tree mortality. Historic forests underwent frequent, low-intensity surface fires, but the introduction of land management practices (cattle grazing, timber harvest, and active fire suppression) by Euro-American settlers led to a shift to infrequent, stand-replacing wildfires (Covington & Moore 1994b). Research on southwestern ponderosa pine ecosystems is relevant to other forests in the western USA because these land management practices are widely applied across the region, and climate models predict widespread drought conditions and warmer temperatures (Easterling *et al.* 2000; Hoerling & Kumar 2003). Finally, the relatively common incidence of stand-replacing wildfires in the last ~40 yr (Stephens 2005; Littell *et al.* 2009) has provided the opportunity to construct a chronosequence of burned sites for examining the post-fire legacy of decaying wood.

In this study, we compared the diversity and species composition of wood-inhabiting fungi associated with wildfires of varying ages to that of adjacent unburned stands of ponderosa pine in northern Arizona. Relatively little is known about the fungi responsible for wood decay in these forests beyond sporocarp surveys (Gilbertson 1974), but evidence suggests that sporocarps may not be representative of the entire fungal community in wood (Allmér *et al.* 2006; Lindner *et al.* 2011). Therefore, we used a combination of mycelial isolation and molecular techniques to identify wood-inhabiting fungi community structure. We also measured the decomposition potential of a subset of the species in the laboratory. We hypothesized that wildfire would initially affect the fungal community structure by decreasing fungal species richness and diversity (due to heat-induced mortality and dispersal limitations) and altering species composition (as a result of changes in environmental conditions); however, these effects would diminish with time since fire as the environmental impacts of fire lessen and substratum quality becomes a stronger driver of community structure than dispersal abilities. We also hypothesized that the species of fungi we isolated would vary in their ability to decompose the same substratum. Specifically, we hypothesized that the early colonizers characteristic of recent fires would be less able to decompose wood than species characteristic of unburned forests, because of a trade-off between rapid colonization