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Effect of heat on interspecific competition in saprotrophic wood fungi

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ABSTRACT

Some boreal wood fungi that are associated with forest fire or open dry habitats have an increased resistance to heat in comparison to species associated with a less specific distribution or species found in mesic forests. We hypothesize that extreme temperature-stress experienced during fires will favor species adapted to heat and, ultimately, the composition of species inhabiting logs in such habitats will change. Competitiveness after temperature stress was examined in three fire-associated species – *Dichomitus squalens*, *Gloeophyllum sepiarium* and *Phlebiopsis gigantea* – and three non fire-associated species – *Ischnoderma benzoinum*, *Phellinus pini* and *Fomitopsis pinicola*. There was a difference between the fire-associated species and the non fire-associated species with respect to competitive strength after heat stress. All fire-associated species had an advantage after heat treatment, colonizing a larger volume of wood than any non-fire-associated competitor. Our findings suggest that increased heat tolerance of mycelia can exert a competitive balance shift after forest fire. It shows that a system governed by forest fire will be dominance controlled under certain conditions. Furthermore, from a management perspective, during a prescribed burning, certain species already present in the ecosystem will be favored if the fire is not allowed to totally consume the substrates.

Introduction

The main effect of disturbance on an ecosystem is to push the succession of species in a particular direction, ultimately affecting the community structure. The effect will depend on the nature and intensity of disturbance as well as the architecture of the community (Townsend et al., 2008). It has been shown that a fluctuating disturbance factor, such as temperature, increases species diversity in communities of wood decomposing fungi, possibly due to the presence of species with different temperature optima within the community (Toljander et al., 2006). Such communities appear to react to disturbance in accordance with the intermediate disturbance hypothesis, which states that an intermediate level of disturbance is most beneficial in respect to species diversity (Connell, 1978). In ecosystems governed by fire, it has been shown that a low frequency of disturbance is the most favorable for species richness (Schwilk et al., 1997); this may be related to a time lag which seems to be required before some species fruit after the disturbance (Junninen et al., 2008). However, there are species of wood-inhabiting fungi that only appear after a forest fire and are lost from the system if there

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is no burning (Junninen et al., 2008; Gärdenfors, 2010; Olsson, 2008). Thus, to evaluate the effect of forest fire as a disturbance it is necessary to consider species richness on a landscape scale rather than isolated ecosystems. The mechanisms or processes that are responsible for certain fungal species only appearing after fire remain unknown. Penttilä (2004) hypothesized that it was the result of space becoming available for colonization after forest fire. In this scenario, the system would be founder controlled (Yodzis, 1986) and adaptation to fires would be associated with the mechanism of spore dispersal and/or the capacity of spores to colonize a charred surface. Another hypothesis introduced by Carlsson et al. (2012) is that the majority of fire-associated species survive burning and that the event shifts the interspecific competitive balance within the community. In this scenario, the system is dominance controlled and the adaptation would be associated with the ability to cope with extreme temperature stress during the fire as well as the ability of mycelia to tolerate modification of the substratum caused by burning. We examine the latter, i.e. the effect of a disturbance to cause a shift in the interspecific competitive balance.

Forest fire is a major disturbance factor in boreal forests (Harrison, 1958; Zackrisson, 1977; Linder et al., 1997; Östlund et al., 1997; Ryan, 2002). Non-anthropogenic fires are mainly caused by lightning and generally affect large areas (Wein and McLean, 1983; Pyne et al., 1996). Early human influence in forests caused an increase in ignitions, but the fires were much smaller. The birth of modern forestry and more efficient means of fire suppression made forest fires scarce in Fennoscandia (Zackrisson, 1977; Niklasson and Granström, 2000). Over the course of time, many boreal forest species, including wood-inhabiting fungi, have adapted to repeated exposure to fire. Species favored by, or adapted to, fire are declining and are considered to be threatened or near threatened (Larsson, 1997; Berg et al., 2002; Gärdenfors, 2010; Rassi et al., 2010). For fungal species confined to pine, the loss of fire from the ecosystem poses a serious threat. Fire regimes in spruce forests, in contrast, are somewhat different as these forests burn with a lower frequency but the fire severity is much greater with a greater consumption of substrata (Penttilä, 2004), suggesting that there is likely to be lower selection pressure for heat tolerance on spruce-inhabiting species. It has been shown that rare wood-inhabiting fungi associated with spruce suffer to a greater extent than with pine if there is a stand replacing disturbance (Penttilä et al., 2006).

Wood-inhabiting fungi constantly compete for space in their habitat, as dead wood on the forest floor supports a variety of fungal species and other wood-inhabiting organisms (Holmer and Stenlid, 1993; Renvall 1995; Boddy, 2000; Stokland et al., 2012). Studies utilizing new molecular techniques confirm that more fungal species are present in a substratum than simply those that can be observed fruiting (Ovaskainen et al., 2010; Kubartova et al., 2012). After colonization, fungal mycelia expand throughout the substratum until their growth is inhibited by either substrate availability (Jennings & Lysec, 1999) or antagonistic interactions with other species/individuals. Once the community is closed, its composition may change as a result of antagonism and/or large changes in factors such as temperature, water content and wood chemistry (Boddy et al., 2008).

Several boreal species of wood-inhabiting fungi are known to show a remarkable resistance to heat. When cultivated in their natural substratum, these species can survive temperatures that are greatly elevated compared to their growth optima (Humphrey and Siggers, 1933; Miric and Willeitner, 1984; Schmidt, 2006; Boddy et al., 2008; Carlsson et al., 2012). Fungal species that are commonly found in open dry forests or on fire fields have a higher relative tolerance to elevated temperatures than species preferring moist forest habitats (Carlsson et al., 2012). However, the variations in temperature inside a log during a forest fire are unknown and some of the species favored by forest fire dynamics could also survive the disturbance. We hypothesize that fungi with high heat tolerance may out-compete less tolerant species after a forest fire, i.e. when a fungal community is subjected to elevated temperatures there will be a shift in the competitive balance, allowing mycelia from certain species to expand at the expense of others.

The aim of the present study is to test whether exposure to heat stress, similar to forest fire conditions, confers a competitive advantage on fire-associated fungi compared to other species. We exposed our study species to high, but non-lethal, temperatures in order to mimic the conditions of a forest fire. Laboratory tests with pairings of different species inoculated onto wood provide an indication of their relative competitiveness to examine the effect of prior heat exposure. The results should contribute to understanding the effect of heat on fungal communities already present in an ecosystem before a forest fire.

Materials and methods

Study species

We chose six species with known heat tolerance (see below) (Carlsson et al., 2012). Three species with a strong relationship either to forest fire or open dry habitats and three species not associated with such habitats were included. We selected species that could tolerate moderate to extreme temperatures. All tolerate a temperature increase of $\sim 1.4\,^{\circ}\mathrm{C}\,\mathrm{min}^{-1}$ up to a maximum of 55.8 °C (±2.69) and the fire-associated species can tolerate an increase of $\sim 3.3\,^{\circ}\mathrm{C}\,\mathrm{min}^{-1}$ up to 101.8 °C (±8.56) (Carlsson et al., 2012).

The fire-associated species studied were *Dichomitus squalens*, *Phlebiopsis gigantea* and *Gloeophyllum sepiarium* (Table 1), all of which have a circumboreal distribution (Ryvarden and Gilbertson, 1993). All primarily grow in open, dry habitats, such as burned forests and clear cuts. *P. gigantea* and *G. sepiarium* are very common, while *D. squalens* is very rare in boreal Europe (Niemelä, 2005), where it is saprotrophic mainly on Scots pine (*Pinus sylvestris*) wood. In North America *D. squalens* is common on Ponderosa pine (*P. ponderosa*), both as a parasite and a saprotroph. Ponderosa pine forests burn with a high frequency (Westerling et al., 2003) and, *D. squalens* also exhibits a strong relationship to forest fire in Eastern Finland (Junninen et al., 2008). *G. sepiarium* and *P. gigantea* are abundant in a wide range of dry habitats and both show extreme tolerance to heat: *G. sepiarium* has been found to survive 95 °C for 4 hr in its natural habitat (Schmidt, 2006). Both show an