**Intro.**

* Resistance versus resilience
* Environment versus historical context
* There are fire resistance EM species

**Main findings**

* SR and diversity did not differ although FA sites had higher SR and diversity than FU.
* Community comp differed based on fire history
* Communities were more similar in FU sites than FA, demonstrating that the shift in community composition depends on other factors than disturbance
* Taxonomy differed based on fire history
* No fire adapted species characterized FA, Rhizopogon not abundant and found in both FA and FU sites

**Discussion**

* Species richness found to decrease following fire
* FA community comp. didn’t converge with FU community composition
  + Recolonization 🡪 stochastic process
  + No consistent difference in plant community, no difference in soil chemistry and characteristics
* There are fire resistance EM species
  + We did not find any due to displacement due to competition or environmental change during recovery, not present within community at all, or fire not of sufficient disturbance level.
* Effect of environment (i.e. difference between the two ranges)

Dahlberg, A., J. Schimmel, A.F.S. Taylor, and H. Johannesson. 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. *Biological Conservation* 100: 151-161.

* Looked at survival of EM fungi as mycorrhizas in a clear-cut, a seed tree stand, and an uncut stand of Scots pine in central Sweden, with and without burning at two levels of fire severity.
* Abundance and diversity of EM declined with increasing depth of burn
* Deep burning fires in combo with fire-caused tree mortality can kill much of the existing EM community
* Sites sampled within a year of treatments
* Even when no logging had been done, our hard-burn treatments killed all mycorrhizas while the slight-burn treatments left parts of the existing mycorrhizal flora alive in the soil ([Fig. 2](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub" \l "FIGGR2)).
* Samples taken in the unlogged forest before the burning had more than 85% of their mycorrhizas located in the organic part of the soil, and apparently most of these were killed even in the slight-burn treatment ([Fig. 2b](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub#FIGGR2)). It thus seems probable that EM fungi are more heat-sensitive than plants, for which the lethal temperature (∼55° C, [Granström and Schimmel, 1993](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub" \l "BIB17)), usually does not penetrate deeper into the mor layer than 2–3 cm under the burned surface ([Schimmel and Granström, 1996](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub" \l "BIB49)).
* The majority of the EM fungal taxa encountered, had mycorrhizas also in the upper mineral soil which in most cases seemed to withstand the slight-burn treatments, while in the hard-burn treatments almost no mycorrhizas survived even in the 5–15 cm of sampled mineral soil.
* Of 35 encountered species in the sporocarp survey, 43% were found exclusively in the burned part, 37% exclusively in the unburned part and only 20% of the species encountered were found both in burned and unburned forest. This result also indicates that fire can alter the composition of the EM community. On the other hand, [Jonsson et al. (1999b)](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub" \l "BIB28) found only minor differences in the structure and composition of the EM community between recent (1, 13 and 63 years) and older burns in northern Sweden. The severity of those burns are however not known, and to what degree tree-seedlings colonising severely burned ground will differ in the composition of their mycobionts in comparison with the EM fungal community prior to the fire, remains to be investigated.
* Studies of EM fungal population dynamics suggest that establishment of new fungal individuals from spores are rare events in established forests and mycelial spread is likely to be a more important mechanisms for local colonisation ([Dahlberg, 1997](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub" \l "BIB6), [Jonsson et al., 1999a](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub" \l "BIB29)). Local recruitment limitation might itself explain a high diversity since species have to occur on the same spot before they can compete with each other ([Tillman, 1999](https://www-sciencedirect-com.ezproxy4.library.arizona.edu/science/article/pii/S0006320700002305?via%3Dihub" \l "BIB54)). Chance events of disturbance may thus, combined with the general poor ability to colonise from spores and low abundance of EM fungal taxa in this ecosystem, result in high degree of coexistence of species.

Baar, J., T.R. Horton, A.M. Kretzer, and T.D. Bruns. 2002. Mycorrhizal colonization of *Pinus muricate* from resistant propagules after a stand-replacing wildfire. *New Phytologist* 143: 409-418.

* *Pinus muricate* studied after a stand-replacing wildfire in October 1995.
* Naturally established pine seedlings were harvested 1 year after the fire.
* Dominated by *Rhizopogon*, *Wilcoxina mikolae*, and *Tomentella sublilacina*.
* Used bioassays collected immediately after the fire to determine which mycorrhizal species colonized the burned area from resistant propagules.
  + Dominated by suilloid and ascomycetous fungi (suilloid means *Suillus* and *Rhizopogon*)
  + The same fungi dominated the mycorrhizal flora of seedlings in pre-fire bioassays derived from the same forest site
  + Suggests that resistant propagules were the primary inoculum source for naturally established seedlings.
* Pre-fire stand was dominated by Russulaceae and Thelephoraceae and to a lesser extent by *Amanita* sp.
* 6-months post fire, EM community described by Horton *et al.* 1998
  + Primarily colonized by *Rhizopogon* spp. and *Suillus pungens.*
  + Seedlings established within the formerly forested areas were colonized by *Rhizopogon* and several ascomycetous taxa, but also some pre-fire dominant species such as *Suillus brevipes* and two *Amanita* species.
* Several studies based on sporocarp surveys and morphological descriptions of the mycorrhizal roots report that severe forms of disturbance, such as wildfire, have an impact on the mycorrhizal community by reducing mycorrhizal populations and changing species composition (Parke et al., 1984; Visser, 1995). For example, Visser (1995) noted dominance of Coltricia perennis (L: Fr.) Murr., Thelephora spp. and E-strain fungi in a 6-yr-old Jack pine (Pinus banksiana Lamb.) stand established after a wildfire in Canada, while Inocybe spp., Lactarius spp., Russula spp., Suillus spp. and Tricholoma spp. were abundant in older ("40 yr) stands.
* Horton et al. (1998) suggested that initial colonization of P. muricata by mycorrhizal fungi mainly occurred from resident mycelia and propagules. Excised mycorrhizal root tips can remain viable in the soil for up to 8 months (Ferrier & Alexander, 1985). Viable sclerotia and spores of mycorrhizal fungi were found in coniferous forests up to 2 yr after a wildfire (Miller et al., 1994; Torres & Honrubia, 1997)
* Wildfire in 1995 Oct, Stand replacing fire.
  + - Area sampled was intermediate intensity with trees still standing.
* Five of the seven most abundant colonizers of the field seedlings appear to have survived the fire primarily as resistant propagules. Taxa in this category include R. olivaceotinctus, R. subcaerulescens, Wilcoxina sp. and T. sublilacina, which were found on the bioassay seedlings grown in soil collected immediately after the fire (Fig. 1). These fungi were also found on bioassay seedlings grown in soil collected from the plots in the mature P. muricata forest at the study site prior to the fire, but only T. sublilacina was also observed on the roots of the mature trees within the same cores from which the pre-fire bioassay soil was derived (Taylor & Bruns, 1999). This suggests that viable propagules of these taxa were present in the mineral soil in the mature forest.
* Fire survival of spores and other resistant propagules in the mineral soil was expected, because the high temperatures of forest fires usually extend less than 5 cm into the mineral soil (Whelan, 1995)
* The absence of Lactarius rufus (Scop.: Fr.) Fr., R. brevipes and Amanita species on the 1-yr-old postfire field seedlings was unexpected for two reasons. Firstly, these taxa, together with T. sublilacina, were the dominant species associated with the mature P. muricata prior to the fire (Taylor & Bruns, 1999). Secondly, in an earlier study, Horton et al. (1998) found Russula and Amanita species on 5-month-old seedlings at a burned site 1 km away from the study site. Therefore we know that colonization by Amanitaceae and Russulaceae occurred immediately after the fire.

Egger, K.N. and J.W. Paden. 1986. Biotrophic associations between lodgepole pine seedlings and postfire ascomycetes (Pezizales) in monoxenic culture. *Can J. Bot.* 64: 2719-2725.

* 22 species of postfire ascomycetes belonging to the order pezizales were screened for biotrophic interactions with roots of *Pinus contorta*.
* Pyropyxis rubra (Peck) Egger and Rhizina undulata Fr. were aggressive pathogens that infected the vascular cylinder and killed the seedlings. Tricharina praecox (Karst.) Dennis var. intermedia Egger, Yang & Korf also had some ability to infect the vascular cylinder, but usually did not kill the seedlings. Geopyxis carbonaria (A. & S.) Sacc. and Trichophaea hemisphaerioides (Mont.) Graddon invaded the cortex, forming complex intracellular structures, but did not penetrate the vascular cylinder. They may form mutualistic associations under certain conditions. The only confirmed mutualistic species was Sphaerosporella brunnea (A. & S.) Svrcek & Kubicka, which formed ectendomycorrhizae. Anthracobia maurilabra (Cooke) Boud. and A. tristis (Born., Rouss. & Sacc.) Boud. appear to be primarily root-surface inhabitants with limited capacity to infect cortical tissues through breaks in the epidermis. Gyromitra infula (Schaef.) QuCI. penetrated the epidermis but was unable to overcome host defences against pathogenic infection

Treseder, K.K., M.C. Mack, and A. Cross. 2004. Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. *Ecological applications* 14: 1826-1838.

* Read’s hypothesis: litter layer/O horizon development correlates to AM (scarce litter) and EM (abundant litter) belowground communities.
* Looked at upland forests in Alaska 3, 15, 45, and 80 years postfire
* Soil organic matter accumulated 2.8 fold over time
* Fire did not noticeably reduce the abundance of AM fungi.
* EM colonization required ip to 15 years to return to pre-fire levels.
  + Dominant mycorrhizal groups shifted from Am to EM as succession progressed.
* Microbes that mineralize organic compounds (EM and bacteria) recovered more slowly than those that cannot.
* Our results indicate that microbial succession may influence soil carbon and nitrogen dynamics in the first several years following fire, by augmenting carbon storage in glomalin while inhibiting mineralization of organic compounds.
* [**Read (1991)**](https://esajournals-onlinelibrary-wiley-com.ezproxy4.library.arizona.edu/doi/full/10.1890/03-5133#i1051-0761-14-6-1826-read1) has hypothesized that the amount of soil organic matter present in an ecosystem may control the dominance of major mycorrhizal groups. Specifically, he has suggested that arbuscular mycorrhizal (AM) fungi should dominate where nutrients are primarily in mineral form, because since this group only acquires inorganic compounds. In contrast, ectomycorrhizal (ECM) fungi should be most abundant in forests with a well‐developed litter layer, because they produce enzymes that mineralize organic material such as proteins, cellulose, and phosphorus compounds (**[Abuzinadah and Read 1989](https://esajournals-onlinelibrary-wiley-com.ezproxy4.library.arizona.edu/doi/full/10.1890/03-5133" \l "i1051-0761-14-6-1826-abuzinadah1)**, [**Read 1991**](https://esajournals-onlinelibrary-wiley-com.ezproxy4.library.arizona.edu/doi/full/10.1890/03-5133#i1051-0761-14-6-1826-read1)). In extreme cases, ericoid mycorrhizal fungi should be favored on mor soils. This group can degrade even extremely recalcitrant compounds such as lignin (**[Haselwandter et al. 1990](https://esajournals-onlinelibrary-wiley-com.ezproxy4.library.arizona.edu/doi/full/10.1890/03-5133" \l "i1051-0761-14-6-1826-haselwandter1)**), chitin (**[Leake and Read 1990](https://esajournals-onlinelibrary-wiley-com.ezproxy4.library.arizona.edu/doi/full/10.1890/03-5133" \l "i1051-0761-14-6-1826-leake2)**), and tannins (**[Leake 1987](https://esajournals-onlinelibrary-wiley-com.ezproxy4.library.arizona.edu/doi/full/10.1890/03-5133" \l "i1051-0761-14-6-1826-leake1)**). This hypothesis can be applied to long‐term changes in soil chemistry observed during secondary succession in boreal forests. Specifically, burned areas should be dominated by AM fungi in early stages and ECM fungi in later stages. Ericoid fungi may take over at the final stages if soils are moist enough to form bog‐like conditions that inhibit decomposition.

Cairney, J.W.G. and B.A. Bastias. 2007. Influence of fire on forest soil fungal communities. *Canadian Journal of Forest Research* 37: 207-215.

Visser, S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist* 129: 389-401.

* Jack pine stand followed post fire, 6, 41, 65, 122 year old stands
* Early stand age
  + *Coltricia perennis*
  + *Thelephora* spp.
* Multi-stage fungi
  + *Suillus brevipes*
  + *Inocyble* spp.
  + *Cenococcum geophilum*
  + *Mycelium radices atrovirens*
* Late stage
  + *Cortinarius* spp.
  + *Lactarius* spp.
  + *Russula* Spp.
  + *Tricholoma* spp.
  + *Hygrophorus* spp.
  + *Hydnellum peckii*
  + *Suillus tomentosus*
  + *Piloderma byssinum*
  + *Sarcodon seabrosus*
* Increase in species richness between the 6 and 41-year old stands
* Wasn’t a complete turnover of species from early to late rather the multistage species were joined by late stage species.
* EM composition and structure stabilized 41 years after wildfire.

Stendell, E.R., T.R. Horton, and T.D. Bruns. 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. *Mycological Research* 103: 1353-1359.

* Investigated one year after a prescribed ground fire. Before and after fire
* Destruction of the litter /organic layer resulted in an 8 fold reduction in total EM biomass. Biomass in mineral layer not affected.
* In unburned plots, members of the Russulaceae and Thelephoraceae most abundant and frequent and species of most other taxa were rare.

Jonsson, L., A. Dahlberg, M.C. Nilsson, O. Zackrisson, and O. Kårén. 2003. Ectomycorrhizal fungal communities in late-succession Swedish boreal forests, and their composition following wildfire. *Molecular Ecology* 8: 205-215.

* Comparison with adjacent unburned late-successional stands.
* Strong effects of spatial variation which were stronger than the effects of fire on Em fungal species composition.
* Most of the common species tended to be found in all sites, suggesting that EM fungal communities show a high degree of continuity following low-intensity wildfires.
* Species richness was not affected by fire, whereas the evenness of species distribution of mycorrhizas was lower in the burned stands

Glassman, S.I., C.R. Levine, A.M. DiRocco, J.J. Battles, and T.D. Bruns. 2016. Ectomycorrhizal fungal spore bank recovery and sever forest fire: some like it hot. *The ISME Journal* 10: 1228-1239.

* Before and after fire. Used pine seedling bioassays and HTS before and after

Kipfer, T., B. Moser, S. Egli, T. Wohlgemuth, and J. Ghazoul. 2011. Ectomycorrhiza succession patterns in *Pinus sylvestris* forests after stand-replacing fire in the Central Alps. *Oecologia* 167: 219-228.

* Are EM communities transformed by fire and, if so, for how long?
* Investigated the resistance and resilience of EM fungal communities on a chronosequence of 12 *Pinus sylvestris* stands in Switzerland and Italy affected by fire between 1990 and 2006.
* Soil samples from burned and unburnt forests were analyzed for EM using a bioassay.

Results:

* EM species were lower in samples from recently burnt sites than unburnt forests and increased with time since fire reaching levels of adjacent forests after 15-18 years.
* Community composition changed after fire but did not converge to that of unburnt sites over the 18 year period
* *Rhizopogon roseolus* and *Cenococcum geophilum* were abundant in both sites and adjacent forest.
* The response of organisms to high-severity fire disturbance can be described in terms of **resistance**, i.e. the extent to which a community is displaced by disturbance, and **resilience**, i.e. the rate of recovery of a community following disturbance (Pimm 1984; Attiwill 1994).
  + resistance is measured as similarity in species composition before and after disturbance
  + resilience is defined as the time needed for the species composition on a site to return to its original state after a disturbance (Halpern 1988; Moretti et al. 2006; Bruelheide and Luginbu¨hl 2009).
  + The impact of fire disturbance on plants has been investigated both in terms of resistance and resilience of species richness or abundance of certain functional groups (Keeley et al. 1981; Delarze et al. 1992; Esposito et al. 1999; Kazanis and Arianoutsou 2004).
  + As a general pattern, succession of post-fire plant communities has been found to be a function of survival of propagules (e.g. seed bank) and dispersal of new propagules onto that site (Whelan 1995). For tree species, an additional aspect emerges: the availability of EcM fungi.
* Field studies found that species number decreases following fire (Dahlberg et al. 2001; Smith et al. 2004; Smith et al. 2005) and EcM community structure changes (Jonsson et al. 1999; Stendell et al. 1999; Grogan et al. 2000; Buscardo et al. 2010).
* Experiments with soil heating have further demonstrated that EcM species react differ- ently to fire effects (Izzo et al. 2006; Peay et al. 2009; Kipfer et al. 2010).
* Regarding EcM community resilience (sensu Attiwill 1994), there are two chronosequence stud- ies that have evaluated EcM communities over long periods (C100 years; Visser 1995; Twieg et al. 2007), but the first decades after fire disturbance were only poorly resolved. In both studies, however, it is concluded that changes in EcM community composition are most dramatic in ﻿these first decades after a fire event.
* The following questions were addressed:
  + (1) To what extent are EcM species number reduced and community composition changed after fire disturbance?
  + (2) At what rates do species number increase after the fire?
  + (3) Do EcM fungal communities converge to pre-fire composition?
  + (4) Are burnt sites primarily colonized by species that survived the fire, by abundant species from the adjacent forest, or both?
* ﻿=The fact that, in our study, the similarity between burnt and non-burnt EcM communities varied considerably between sites (Fig. 2) and showed no temporal trend (Fig. 3) may have several reasons:
  + first, the forest stand age may affect the EcM community composition in non-burnt sites, with community composition of younger stands more similar to disturbed sites than older stands due to species succession over time. This is supported by our finding that the sites with the highest similarity between forest and burn are all less than 70 years old (Fig. 3).
  + Second, re-colonization is, to some extent, a stochastic process with early arriving species benefitting from low competition. Consequently, succession pathways may vary according to the availability of fungal propagules in the first months or years after fire

Peay, K., M. Garbelotto, and T. Bruns. 2009. Spore heat resistance plays an important role in disturbance-mediated assemblage shift of ectomycorrhizal fungi colonizing *Pinus muricate* seedlings. *Journal of Ecology* 97: 537-547.

* Goal: to determine the specific mechanisms through which the disturbance affects EM communities
* Method: 1) experimentally simulated the effects of fire by growing seedlings in field soil exposed to factorial combinations of soil heating and ash addition. 2) followup experiment: to see whether selective mortality of EM spores might contribute to these patterns.
* Both soil heating and ash addition cased changes to soil chemical environment and altered the fungal assemblages found on seedling roots.
  + Larger effects on community arose from soil heating 🡪 overall simplification and increasing dominance of a few taxa with ruderal life-history strategies.
* Follow-up: heat exposure had strong negative effects on all species tested. However, spore heat tolerance was highest for the species that showed the greatest increase in abundance on seedlings grown in heated soils.
* Fire alters below-ground communities through changes in soil chemistry and mortality of resident organisms due to soil heating and selective mortality. Disturbances favor competitively inferior species and may help maintain diversity of EM assemblages at the landscape scale.

Buscardo, E., S. Rodríguez-Echeverría, M.P. Martín, P. De Angelis, J.S. Periera, and H. Freitas. 2010. Impact of wildfire return interval on the ectomycorrhizal resistant propagules communities of a Mediterranean open forest. *Fungal Biology* 114: 628-636.

* Goal: study effects of high and low wildfire frequencies on the resistant propagules communities (RPCs) of Mediterranean open pine forest.
* A short fire return interval (i.e. high wildfire frequencies) reduced the speces richness of the EM community found on *Q. suber*, promoted species like *Rhizopogon roseolus*, and reduced the abundance of other species (e.g. *R. luteolus*).
* The abundance of *Inocybe jacobi* was positively affected by long fire return interval, but decreased significantly with recurrent fires. These results indicate that changes in fire frequency can alter the structure, composition, and diversity of EM communities, which could compromise the resilience of the ecosystem in highly disturbed areas.

A. Cowan, J. Smith, S.A. Fitzgerald. 2016. Recovering lost ground: effects of soil burn intensity on nutrients and ectomycorrhiza communities of ponderosa pine seedlings. *Forest Ecology and Management* 378: 160-172.

* Fuel accumulation and climate shifts are predicted to increase the frequency of high-severity fires in pon- derosa pine (Pinus ponderosa) forests of central Oregon. The combustion of fuels containing large downed wood can result in intense soil heating, alteration of soil properties, and mortality of microbes. Previous studies show ectomycorrhizal fungi (EMF) improve ponderosa seedling establishment after fire but did not compare EMF communities at different levels of soil burn intensity in a field setting. For this study, soil burn intensity effects on nutrients and EMF communities were compared at Pringle Falls Experimental Forest, La Pine, Oregon. Twelve replicate sites were used, each with three treatments: high intensity soil burn from large downed wood combustion (HB), low intensity soil burn (LB), and unburned control (UB). Temperatures lethal to fungi were detected at 0-cm, 5-cm, and 10-cm depths in HB soils and 0-cm depth in LB soils. Ponderosa pine seedlings planted post-burn were harvested after four months for EMF root tip analysis. We found: (a) greater differences in soil properties and nutrients in HB soils com- pared to LB and UB soils; (b) no differences in EMF richness and diversity among treatments; (c) weak differences in community composition based on relative abundance between UB and either burn treat- ments; and (d) EMF composition in HB and LB treatments correlated with soil carbon and organic matter contents. These results support the hypothesis that the combustion of large downed wood can alter the soil environment directly beneath it. However, an EMF community similar to LB soils recolonized HB soils within one growing season. Community results from both burn treatments suggest an increase in patchy spatial distribution of EMF. We hypothesize that quick initiation of EMF recolonization is possible depending on the size of high intensity burn patches, proximity of low and unburned soil, and survival of nearby hosts. The importance of incorporating mixed fire effects in fuel management practices will help to provide EMF refugia for ponderosa pine forest regeneration.

Post-fire fungi

Geopyxis carbonaria

EM deep in soil may escape the detrimental penetration of heat and thus link the EM fungal community between fire affected forest generations (Mikola *et al.*, 1964).

The effect of slash burning on the commencement of mycorrhizal association.