

Community Dynamics of Ectomycorrhizal Fungi Following the Vision Fire

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Introduction

Many people that read this chapter may be aware of mammals, birds, and maybe even plant species that are common at Point Reyes, and may have witnessed or have been aware of the ways that these organisms responded to the Vision fire of 1995. Few will be familiar with fungal species at Point Reyes, and even fewer may have noticed their response to the fire. This is unfortunate, because fungi play many critical roles in structuring and maintaining plant (and therefore also animal) communities at Point Reyes. It is understandable, however, because even those of us that study fungi for a living know less about them than plant or animal biologists typically know about their organisms. There are several reasons for our collective ignorance. Fungi can be difficult to identify, so reliable species records are rare. For most of their lives, fungi are microscopic and hidden in soil or plant parts; this makes it difficult to observe their basic life histories and ecology. Finally, relatively few people study fungi, especially when one considers that there are roughly six species of fungi for every plant species on the planet (Hawksworth 1990). The good news is that there is much to learn, and the Vision fire provided an exceptional opportunity to do exactly that.

Getting to the root of Point Reyes plant communities

The goal of this chapter is to heighten awareness of the role of ectomycorrhizal fungi and to

relate what we have learned about this group from the Vision Fire. To start this process it is important for the reader to understand that in nature fine roots of most plants are not simply plants. Instead, they are colonized by fungi in mutualistic interactions known as mycorrhizae. This symbiosis is a way that plants “contract-out” the specialized function of collecting mineral nutrients from soil. They pay their fungal partners with sugar, and in return fungi provide phosphorus, nitrogen, and other mineral nutrients to plants. The vast majority of land plants are normally mycorrhizal, and some plants, such as pines and oaks, require these fungi for normal growth. Similarly, most fungi involved in mycorrhizal symbioses, require plants.

At Point Reyes, and elsewhere, there are three main types of mycorrhizal interactions. Different groups of fungi are involved with each, and plants are generally restricted to one of these three groups (Table 1). For a pine seedling to grow and compete, it must encounter an ectomycorrhizal fungus within the first few months. There are two basic forms of fungi that an uncolonized pine root can encounter: spores and sclerotia, or mycelium. Spores and sclerotia are roughly microscopic equivalent of seeds and tubers, respectively, in plants, and they can be dispersed in various ways to new locations. Mycelium (Fig 1a) is the growing body of a fungus. It is made up of thread-like hyphae. Mycelium can spread locally from a colonized root to a new uncolonized root of a seedling. Note that this latter type of colonization can only work if living roots of a plant, that uses the same general type of mycorrhizal fungi, are in the immediate neighborhood. For example, fungi found on roots of coyote bush and pines are different, and, therefore, pine cannot rely on coyote bush as a reservoir for its fungi. In

Table 1: The three main Mycorrhizal types found at Point Reyes

Mycorrhizal Type	Examples of Plants	Examples of Fungi
Ectomycorrhizae (EM or Ecto)	bishop pine, Douglas-fir, tanbark oak, live oak, manzanita, madrone, alder	Basidiomycetes: mushrooms, boletes, chanterelles, false- truffles, crusts; and Ascomycetes: cup fungi, and true truffles.
Ericoid mycorrhizae	huckleberry, salal	Ascomycetes: particularly <i>Hymenoscyphus ericae</i> , and close relatives.
Arbuscular mycorrhizae (AM, VAM, or endo)	Most plants: coyote bush, California lilac, poison oak, bay laurel, grasses, ferns, herbs	Glomalean fungi: microfungi (e.g. <i>Glomus</i> , <i>Acaulospora</i> , <i>Gigaspora</i>)

contrast, Douglas-fir and pine, or coyote bush and poison oak, share many of the same fungi, and so one plant may inadvertently supply its neighbor with fungi.

There is a genetic difference between spores and mycelium. Spores are produced in fruiting bodies such as mushrooms or truffles, and they are usually the product of a sexual recombination (i.e., they are products of meiosis); therefore each spore is genetically unique. This is different from mycelial growth or sclerotia which are vegetatively (i.e. mitotically) produced and therefore result in the spread of identical fungal genotypes. Understanding this point is important, because later in this chapter we use knowledge of fungal genotypes to infer whether fungi spread primarily by spores or vegetative growth.

The pre-fire ectomycorrhizal community

We have studied mycorrhizal fungi associated with Bishop pine in the Limantour road area of Point Reyes since 1991. We have done this in two ways. First, we have collected mushrooms, truffles, and other fruiting bodies of fungi of interest. Second, we have examined roots of Bishop pine trees or seedlings and used molecular-based identification methods to catalogue fungi present and to quantify their frequencies and abundance (Table 2).

This work has revealed several interesting features of mycorrhizal community associated with Bishop pine. One of the most unexpected findings of our early work was that some species that exhibit the most abundant fruiting were rare or low abundance species on roots, and conversely, some species that were dominant colonizers of roots, appeared to be rare fruiters. For example, one of the most abundant fruiters was *Suillus pungens* (Fig 1d), but in mature forests, we only found it colonizing roots when we looked directly below its mushrooms, and even then it was not the most common or abundant species. One of the most dominant species on roots of bishop pine was *Tomentella subulilacina*. It took us about four years to identify this species, which we initially knew only from DNA sequences obtained directly from pine roots. We had missed its fruiting bodies because they consist of tiny brown crusts that form on woody litter on the forest floor (Fig 1b). Once we learned this, we were able to find it fruiting fairly often, but biomass (i.e., the collective weight) of its fruiting is still substantially lower than *Suillus pungens*. Other species that dominated the root community in mature Bishop pine forests

included *Russula* and *Lactarius* species (Fig 1c). These can be common fruiters at Point Reyes, but were never as abundant as *Suillus*. Several *Amanita* species, especially *A. francheti*, *A. muscaria*, and *A. gemmata* were common, and sometimes abundant prefire fruiters, and were often co-dominant species on roots (Gardes and Bruns 1996; Horton and Bruns 1998; Taylor and Bruns 1999).

The abundant fruiting of *Suillus pungens* allowed us to examine how it spread in pre-fire forests. We did this by collecting and mapping its mushrooms in a 50 X 30 meter plot and by using molecular genetic methods to determine the genotypes present. As explained above, this information could tell us whether this fungus spreads primarily by spore, or by vegetative growth. What we found was that a single genotype, termed a "genet", covered over 360 sq. meters of this area (Bonello et al. 1998). This was an area large enough to include about 30 mature pine trees. That meant that this species was very good at spreading vegetatively and moving from root to root across a pine forest. Parallel strategies among plants such as bracken fern and blackberries, are well known by botanists. Using the age of the forest we could estimate a minimum growth rate of a half a meter/year for the species. We thought this was likely to be a conservative estimate, because position of mushrooms delimited only the minimum area that was occupied by this genet (Bonello et al. 1998). However, there were two ways that we could have overestimated the spread rate. First, if our molecular methods were not sensitive enough to differentiate closely related genotypes, then we would mistakenly conclude that the different individuals were a single genet. This turned out to be an unlikely error because we were able to show that our methods could separate single-spore isolates from a single mushroom. This is approximately the equivalent of separating full-sibs (i.e., brother and sisters in the animal world). Another way we might have overestimated growth rate is if the genet we observed was older than the forest. This would only be possible if *Suillus pungens* could survive periodic fires that establish new bishop pine forests. At the time, we had no way to test this idea.

One final prefire study gave us a crucial piece of information: it showed us that in addition to the species that were common on roots, and that fruited frequently, there were species that had dormant spores and sclerotia stockpiled in the soil (Taylor and Bruns 1999). In other chapters of this volume, reference is made

Table 2. Ectomycorrhizal fungi observed with bishop pine in Limantour Rd area

	Pre-fire Fruiting	Pre-fire EM	Pre-fire Bioassay	Post-fire EM	Post-fire Fruiting
Amanitaceae					
<i>Amanita pachycolea</i>	I			I-1	
<i>A. francheti</i>	A	F			I-5
<i>A. gemmata</i>	F	F			F-2
<i>A. muscaria</i>	F	F			I-2
<i>A. magnaverrucata</i> ¹	I				
Boletales					
<i>Chalciporus piperatoides</i>	I				
<i>Chroogomphus vinicolor</i>	F				A-2
<i>Suillus brevipes</i>	I				
<i>S. pungens</i>	A	I		I-1	A-2
<i>S. tomentosus</i>	I				
<i>Boletus edulis</i>	F				
<i>B. subtomentosus</i>	I				
<i>B. chrysenteron</i>	F				I-2
<i>Boletoid</i> spp.		F			
<i>Rhizopogon salabrosus</i> ²	F	F	D	A-2	F-4
<i>R. occidentalis</i> ³	I		A	A-2	A-5
<i>R. smithii</i>			F		A-5
<i>R. olivaceotinctus</i>			F	A-2	?
<i>R. rubescens</i>			F		?
<i>R. vulgaris</i>			?		A-5
unidentified suilloid (probably <i>Rhizopogon</i>)				A-2	
Cortinariaceae					
<i>Dermocybe</i> spp.	F				
<i>Cortinarius</i> spp.	F				
<i>Hebeloma</i> cf. <i>crustuliniforme</i>	I				F-2
<i>Inocybe</i> spp.	F				F-5
<i>Inocybe subocracea</i>	F				?
Thelephoraceae					
<i>Tomentella subulilacina</i>	F?	D			
<i>Tomentella</i> spp.		F			
<i>Thelephora</i> cf. <i>terrestris</i>	I				F-5
Russulaceae					
<i>Lactarius rufus</i>	F	A			F-5
<i>L. fragilis</i> var. <i>rubidus</i>	I				
<i>Russula brevipes</i>	F	A		R-1	
<i>R. amoenolens</i>	I	D			A-6
<i>R. rosacea</i>	F				
<i>R. cf. xerompelina</i>	F	A			
<i>R. sp.</i>					R-5
Cantharellaceae					
<i>Cantharellus cibarius</i> s.l.	I				
<i>Clavulina</i> sp. ⁴	F?	F		F-1	
Corticiaceae					
<i>Amphinema byssoides</i>	?				F-5
Hymenochaetaceae					
<i>Coltricia perennis</i>					F-2
Tricholomataceae					
<i>Laccaria amethysteo-occidentalis</i>	F	I			
<i>L. proxima</i>	I				I-3
Ascomycota					
<i>Tuber californicum</i>	?			F	?
<i>Tuber</i> spp.	?			A	I?-5
<i>Wilcoxina mikolae</i>	?			A	?
<i>Wilcoxina</i> sp.	?			A	?
<i>Cenococcum geophilum</i>	NA	F	F	F	NA
<i>Phialophora</i> sp.	NA		F	A-1	

I infrequent, F frequent; A abundant; D dominant (usually abundant at every site); for post-fire species the season when it was first observed is given. ? may have been missed for various technical reasons. ¹ the Limantour road area is the type location for the species; ² referred to as *R. subcaerulescens* in cited publications; ³ referred to as *R. ochraceorubens* in cited publications; ⁴ referred to as *Cantharoid 1* in publications from Point Reyes cited.

to a soil “seedbank” for plants. What we are talking about here is the fungal equivalent: a soil **sporebank**. We assayed the sporebank by removing soil, air-drying it, and then planting bishop pine seedlings into it. After about a year the roots of the seedling were examined to see which fungi had colonized them. We call this approach a “**bioassay**”, because we are using pine seedlings to assay soil for compatible mycorrhizal fungi contained in it. It turned out that the species we found in our bioassays were almost entirely different from those that were present on roots of mature trees that had been present in the very same soil samples. The only species that was dominant on roots of mature trees and also common in bioassays was *Tomentella subulilacina*, but the species that dominated bioassays were from two different groups of fungi: *Rhizopogon* species, and Ascomycetes, such as *Wilcoxina* and *Tuber*. In fact, spores of the *Rhizopogon* species were so abundant that even when the soil was diluted 100-fold with sterile soil, most seedlings were colonized by a *Rhizopogon* species (Taylor and Bruns 1999). We have now found that *Rhizopogon* sporebanks are widespread features throughout California pine forests (Kjøller and Bruns 2003).

Post-fire Ectomycorrhizal Communities

Within about three months after the fire Bishop pine seedlings were starting to establish. The first fungi to colonize their roots were “dark-septate” fungi, probably related to *Phialophora* sp. (Horton et al. 1998). The role of these fungi is unclear. They are not strictly ectomycorrhizal in their morphology, as they often penetrate root cells, and prior work has given conflicting evidence for their mutualistic or parasitic interactions. Our earlier bioassay work had shown that *Phialophora*-like fungi were present in the sporebank (Taylor and Bruns 1999). Arbuscular mycorrhizal fungi were also among the first colonists of young pine roots, but as mentioned above, these are not normally thought to be important symbionts with pine (Table 1), so again their role in the post-fire community is unclear (Horton et al. 1998). Ectomycorrhizal associations were found in some one-month-old seedlings, and their frequency increased with time, such that about 85% of five-month-old seedlings contained at least some ectomycorrhizal roots. Among surviving 1-year and 2-year old seedlings, all were ectomycorrhizal (Baar et al. 1999; Grogan et al. 2000).

Composition of post-fire ectomycorrhizal communities had a strong resemblance to the com-

position of the pre-fire sporebank community, and this resemblance appears to be caused by survival of the soil sporebank (Baar et al. 1999). Immediately following the fire we collected soil samples from sites that we had studied prior to the fire, and when we bioassayed these samples we found the same fungi were still present. Thus the sporebank survived the fire. For *Rhizopogon* and *Tuber* species, which were very abundant at some sites, it is likely that the sporebank alone may account for their post-fire success. New dispersal is unlikely to explain the observed pattern for several reasons. Both genera fruit underground as truffles, and spores contained in these fruiting bodies either stay put in the soil (Miller et al. 1994), or are eaten by mammals, such as mice, squirrels, and deer, and dispersed to new locations via their scat (Maser et al. 1978). For these reasons, post-fire dispersal from unburned areas would be unlikely to provide the high frequency of truffle inoculum necessary to account for the abundance of these fungi observed on post-fire seedlings. Fruiting within the burn area is also an unlikely source, as it was uncommon and essentially restricted to areas around the few surviving Douglas-firs in the first year following the fire. Most *Rhizopogon* species, and perhaps *Tuber* species as well, have narrow host ranges, and would not associate with both Douglas-fir and pine (Massicotte et al. 1994; Molina and Trappe 1994).

Some fungi that colonized post-fire seedlings, and have wind-borne spores, probably did disperse into the burned area in the first few wet seasons following the fire. *Hebeloma cf. crustuliniforme* is the best example of this strategy. It was not common prior to the fire, and was not found in the bioassays, but it was common in year one and year two samples after the fire (Baar et al. 1999). *Hebeloma* species are known from other studies to be early colonizers of disturbed sites (Gryta et al. 1997; Gryta et al. 2000). *Wilcoxina* species may be an example of a mixed strategy. They were over-represented in post-fire seedlings relative to their apparently low abundance in the sporebank. This suggests that additional dispersal or perhaps fire-activation of the sporebank was important for these fungi. Prior studies show that they are common in post-fire settings, and are capable of wind dispersal (Egger et al. 1991).

The fungi that were dominant members of the pre-fire community were not eliminated by the fire, only reduced in their dominance. In fact, they were found at the very earliest sampling of post-fire seedling and at all subsequent sampling times (Horton et al. 1998; Baar et al. 1999;

Grogan et al. 2000). One of the pre-fire dominants, *Tomentella sublilacina*, was represented in the sporebank community, as determined from our bioassays, and its frequency in the sporebank was very similar to its frequency on the post-fire seedlings (Baar et al. 1999). In addition, we have since shown that its spores are an effective inoculum for pine seedlings under laboratory conditions (Lilleskov and Bruns 2003). Thus, for this species spore survival could account for its post-fire occurrence.

For all other pre-fire dominants and co-dominants, such as species in the Russulaceae and Amanitaceae, the manner in which they survived is less clear. The fact that they were present within the first few months, suggests that new dispersal alone may not account for their presence. The two most obvious ways for survival are 1) as spores and 2) as mycelium or colonized root tips. Superficially the spore option seems unlikely, because we have never recovered any species in the Russulaceae or the Amanitaceae in our bioassays, and studies elsewhere suggest that spores are not very effective inoculum under laboratory conditions (Deacon and Fleming 1992). The “under laboratory conditions” caveat may be important however, because field conditions are different, and difficult to replicate. Recent work on genet sizes in the Russulaceae and Amanitaceae at Point Reyes and in neighboring areas shows that spore establishment must be an ongoing process in undisturbed forests (Redecker et al. 2001); therefore it could also be important in post-fire environments. Survival of mycelium on dying root tips is possible, as it has been observed in other types of disturbance such as logging (Hagerman et al. 1999), and circumstantial evidence suggests that it is common in ground fires where overstory trees are not killed (Jonsson et al. 1999; Stendell et al. 1999). We have made two observations that suggest that mycelial survival might have occurred in the Vision fire. First, we observed what appeared to be dead *Russula*-colonized root tips of mature trees within the same soil core as new *Russula* root tips on a seedling. Second, we observed that new *Russula* tips tended to be deeper in the soil, where mycelial survival might be expected to be highest. However, neither observation is particularly convincing, as spore inoculum might also follow the same patterns. The best evidence would be to demonstrate that the same genotype of a particular fungus was found both before and after the fire. Unfortunately, it was not possible to test for genet survival with any of the dominant species, as we did not have prefire genetic data

from the same locations where we observed post-fire species occurrence.

Suillus pungens, which was an abundant fruiter but a rare mycorrhizal type in prefire forests, is the only species in which we have been able to test directly for post-fire survival. This was possible because we had extensive pre-fire genetic data for it from one location where it recolonized after the fire. Our results showed that all of the post-fire *Suillus pungens* genotypes were new; thus, spore colonization appears to be the most important process for this species (Bruns et al. 2003). This answer was disappointing to us in one sense, because we had hoped to find a solid example of mycelial survival. It was good news in a different way; it showed that our previous assumption that clonal spread starts with establishment of a new forest was a good one, and therefore, estimates of minimum growth rate for *Suillus pungens* remain conservative.

Spatial patterning of fungal species in the post-fire environment provided additional clues as to how they might have survived. Grogan et al. (2000) showed that the pattern of species occurrence appeared to be random with respect to either space between seedlings or occurrence on different parts of the root system of individual seedlings. In other words, inoculum for individual species behaved like point-sources. This patterning does not resolve the spore versus mycelium question, but it does suggest that if mycelium was involved it was very limited in spatial coverage. Thus, widespread mycelial survival appears unlikely, but rare transfer from individual dying root tips to newly established seedling cannot be eliminated.

The fact that *Rhizopogon* species were found on all pine seedlings sampled within the former coastal scrub community, shows that these were dispersed spores that probably have laid dormant for many years (Horton et al. 1998). These conclusions are based on the fact that fruiting of *Rhizopogon*, like many other ectomycorrhizal fungi in the area, would only occur in conjunction with pine or Douglas-fir, and neither tree existed in the scrub community prior to the fire. Thus, spores of *Rhizopogon* must have been dispersed there at some point in the past. Recall that these are animal dispersed spores, which therefore might be expected to have a rather spotty spatial distribution. To achieve the observed uniform distribution, would roughly require a *Rhizopogon*-containing rodent or deer dropping every 100 square centimeters. This becomes feasible if the spatial

distribution results from dispersal over many years followed by a long dormancy.

Most *Rhizopogon* species appear to be early successional species. In fact, the only pine-associated *Rhizopogon* that we found as root colonist in the pre-fire forest was *R. salebrosus*. Other species were occasionally found fruiting, but primarily in disturbed settings, such as parking lots, or former quarry sites. In addition there is evidence that these *Rhizopogon* species may be relatively weak competitors. Our soil bioassays showed that they are the most frequent colonists when air-dried soil is extensively diluted with sterile soil, yet their colonization frequency drops in undiluted soil as the frequency of competitors increase. Similarly, they are less abundant in fire sites that were previously parts of large forested tracts, such as those studied by Horton et al. (1998) and Grogan et al. (Grogan et al. 2000), and they are most abundant on seedlings that established in the former scrub community and in small patches of former forest such as the site studied by Baar et al. (1999).

Fruiting in post-fire forests

Most of our efforts have been focused on root colonization rather than fruiting. As a result, our records on mushroom and truffle production are only qualitative, and are prone to under-recording of infrequent species (Table 2). Our data for truffles, such as *Rhizopogon* and *Tuber* species, and small cup fungi, such as *Wilcoxina* spp., are particularly sparse, since truffles fruit below-ground and require directed effort to find, and tiny cup fungi are easily overlooked. Nevertheless, some patterns are obvious, and transcend these sampling deficiencies.

Fruiting usually occurs in the rainy season, October through April. The first such season following the fire (i.e., winter 1995-96) we observed no fruiting of any ectomycorrhizal species except near the few surviving Douglas-fir trees. This is probably an accurate observation, as pines, shrubs, and herbs were not very dense and so above-ground fruiting, when it occurred, was obvious. The following year, winter 1996-7) we observed the first few mushrooms of ectomycorrhizal fungi in areas that contained only pine seedlings. Fruiting was not abundant in this year, but *Hebeloma cf. crustuliniforme*, and *Coltricia perennis* were among the most common fruiters. Neither was common prior to the fire, and both are known to be early successional ectomycorrhizal fungi. Other species that fruited in the second season,

such as *Suillus pungens*, *Chroogomphus vinicolor*, *Boletus chrysenteron*, *Amanita muscaria*, and *A. gemmata*, were species that had been common fruiters in the pre-fire forest.

Notably absent until the 2000-2001 wet season were any species in the Russulaceae, despite the presence of some species on seedling roots in the first few months after the fire (Horton et al. 1998). In some ways this lack of correspondence between fruiting and mycorrhizae fits the pre-fire pattern, where species in the Russulaceae were often dominant on the roots, but were minor components in the above-ground fruiting record (Gardes and Bruns 1996). In the post-fire community, they lost their dominant position below-ground and were essentially absent in the fruiting record. However, by the winter of 2002-3, *Russula amoenolens* became a dominant fruiter; this was the first time in either pre or post fire settings where we observed abundant fruiting of this species.

By year four 1998-99, *Suillus pungens* and *Chroogomphus vinicolor* began to become truly abundant fruiters. In fact, it was hard to walk through the young pine forests without noticing these two species. In winter 2000-2001 season we found that fruiting of several *Rhizopogon* species was very abundant during late February and early March. We also found ample evidence of rodent and deer feeding on these truffles. This is a necessary step for dispersal of *Rhizopogon*, and it underlines one of the ways that these fungi connect plant and animal communities at Point Reyes.

Suillus, *Chroogomphus*, and *Rhizopogon* are members of the Suilloid lineage within the Boletales (Bruns et al. 1998), and so their similar post-fire behavior may be a result of evolutionarily shared characters. In particular spores of all three genera may be long-lived residents of the sporebank. As discussed above, this is likely the case with *Rhizopogon*; the situation in the other two genera is less clear. *Suillus* occasionally shows up in bioassays (unpubl. results), but not nearly as commonly as *Rhizopogon*. Thus, if post-fire abundance of *Suillus* is due to its sporebank, there must be additional factors that function to activate its spores in the natural setting. It has become clear in recent years that members of the Gomphidiaceae, such as *Chroogomphus*, may primarily be parasitic on *Suillus* and *Rhizopogon* species, and their hyphae are often found within mycorrhizae of *Suillus* and *Rhizopogon* (Agerer 1990; Olsson et al. 2000). This behavior could explain why *Chroogomphus vinicolor* is a common fruiter and yet we have never found its mycorrhizae. It

Six important ectomycorrhizal fungi associated with bishop pine.

A: A bishop pine seedling grown in the laboratory and colonized by *Rhizopogon salebrosus* is shown. Arrows point toward the white mycelium of the fungus.

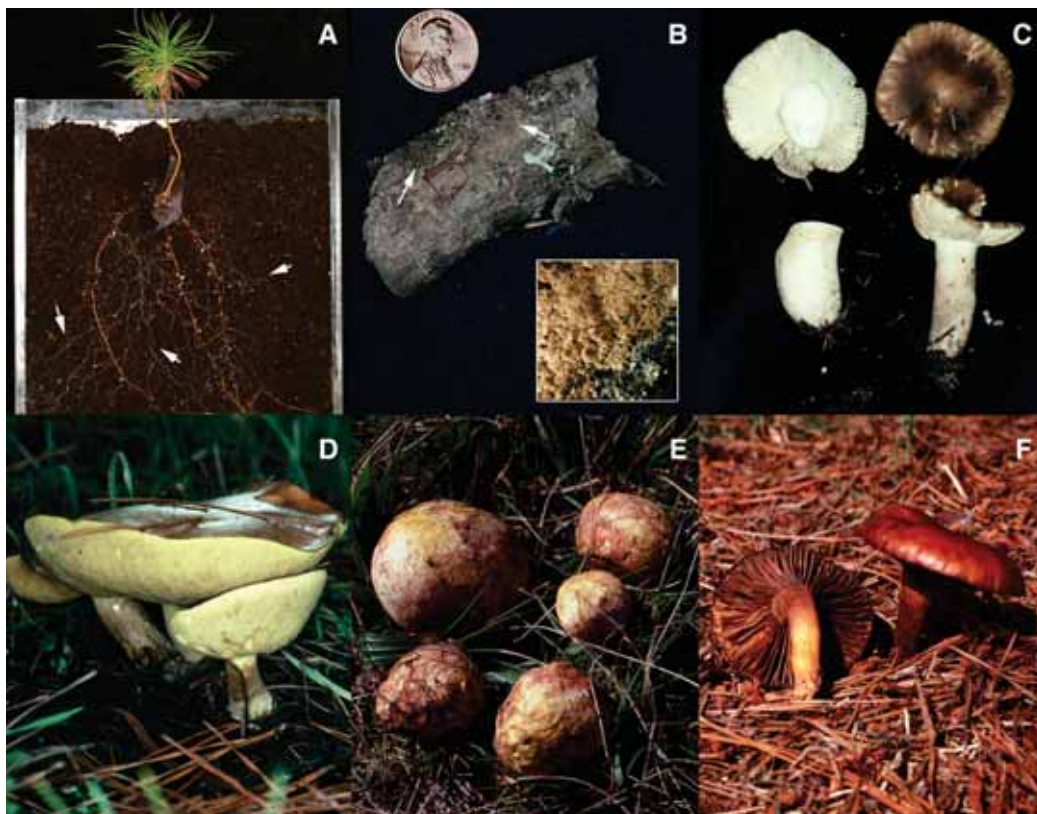
B: *Tomentella subulilacina* was one of the most abundant colonizers of bishop pine roots before the fire. Its fruiting bodies are small crusts, which are often formed on pieces of bark or wood on the forest floor. The arrows show such crusts on a small piece of bark collected from the pre-fire forest. The insert shows a 40X magnification of a *Tomentella subulilacina* fruiting body. This small crust would be densely packed with spores.

C: *Russula amoenolens* was another dominant fungus in the pre-fire forest, but its mushrooms, which are about the size of a fist, were rare.

D: In contrast, mushrooms of *Suillus pungens* were abundant in the prefire forest, but it colonized relatively few roots. *Suillus pungens* is an even more abundant fruiter in the post-fire forest. Its mushrooms are large and often weigh over 100 grams.

E: *Rhizopogon occidentalis* and other *Rhizopogon* spp. were abundant colonizers of the post-fire seedlings. Their fruiting bodies, which are shown here, are false-truffles. They are about marble to golf-ball sized and fruit below ground. Rodents and deer dig them up and disperse the spores in their scat.

F: *Chroogomphus vinicolor* is the most abundant post-fire mushroom in the five-year old post-fire forest. It appears to be a parasite of *Suillus* and *Rhizopogon* species.



would also mean that their spores would easily be missed in a laboratory bioassay.

Conclusions

The fungal ectomycorrhizal community associated with bishop pine changed quantitatively with the fire. It went from a community dominated by *Tomentella subulilacina*, *Russula*, and *Lactarius* species to one dominated by *Rhizopogon*, *Wilcoxina*, and *Tuber* species. Colonization of these post-fire dominants, especially *Rhizopogon* and *Tuber*, was the result of an extensive soil sporebank that survived the fire and provided inoculum for bishop pine seedlings. This sporebank was probably established in the years immediately after earlier fires when abundant fruiting and dispersal of these taxa were likely to have occurred. We expect most of *Rhizopogon*, *Tuber*, and *Wilcoxina* species will be eventually replaced by the taxa that previously dominated the mature forest. How quickly this will occur, and whether other species will dominate at intermediate times, remains unknown. These questions and others remain, and Point Reyes continues to be a great place to look for the answers.

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