A Review of the Role of Fungi in Wood Decay of Forest Ecosystems

Bruce G. Marcot, Ph.D., Research Wildlife Biologist
USDA Forest Service, Pacific Northwest Research Station
Ecological Process and Function Research Program
620 SW Main St., Suite 400
Portland OR 97208 USA
503.347.2277
bmarcot@fs.fed.us

vers.: 17 April 2017

For: Research Note, US Forest Service, Pacific Northwest Research Station

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ABSTRACT

Fungi are key players in the health, diversity, and productivity of forest ecosystems in Pacific Northwest forests, as mycorrhizal associations, pathogens and decomposers, non-timber resources, and food resources for wildlife. A number of invertebrates are associated with wood decay fungi, serve as vectors for fungal pathogens, or are fungivorous (consume fungi) and influence rates of wood decay and nutrient mineralization. In Washington and Oregon, 31 wildlife species among 8 families are fungivores, and at least 14 wildlife species disperse fungi. Down wood can provide nurse substrates for seedlings and beneficial mycorrhizal fungi, refuges from pathogenic soil fungi, sources of nutrients for decay fungi, and substrates supporting overall fungal diversity. Presence, density, distribution, and diversity of fungi are influenced by forest stand management practices, forest age class, and effects of fire. Old forests provide for a suite of rare fungi species. Old legacy trees retained during forest harvest can provide some degree of conservation of beneficial and rare fungi. Fungi can be difficult to detect and monitor; surveying for fungi at various times of the year, for multiple (at least 5) years, and by including hypogeous (below-ground) samples, can improve detection rates. Studies are needed in the Pacific Northwest to quantify the amount of down wood -- number of pieces, sizes, total biomass, percent forest floor cover, and other attributes -- necessary for maintaining or restoring fungal biodiversity and viable levels of individual fungi species, especially rare species.

WHO ARE THE FUNGI?

Formally, the term *fungi* as used here refers to the general taxonomic group of organisms that includes rusts, smuts, mildews, molds, yeasts, and mushrooms, and our focus in this review is largely on the mushrooms associated with wood decay. Fungi most associated with wood decay are the filamentous species of Basidiomycota and Ascomycota (Arnstadt et al. 2016, Swift 1982).

More casually, *fungi* also can include the fungus-like slime molds and water molds. Although not discussed here, these nonetheless can be important ecologically and economically, and are more often considered in forest management under pathogen and disease programs. For example, the water mold *Phytophthora ramorum* is responsible for sudden oak death, a forest disease causing widespread killing of oaks and other trees in the Pacific Northwest (Cobb et al. 2012, Rizzo and Garbelotto 2003).

This review covers the various roles and relationships of fungi in wood decay in forests of the Pacific Northwest, U.S. I also include reference to studies conducted outside the Pacific Northwest when local research on specific topics is unavailable.

ECOLOGICAL FUNCTIONS OF FUNGI

Fungi play a number of ecological roles in forest ecosystems that affect the health, diversity, productivity, and development of their biotic communities. Such roles include mycorrhizal associations with vascular plants, pathogens of commercial tree species, decomposers of coarse organic material, and food resources for wildlife.

Mycorrhizal Associations

Mycorrhizal fungi consist of strings of hyphae that form mutualistic symbiotic relationships with roots of vascular plants, including trees of commercial value, and that aid the plant in nutrient and water update, while the fungi benefit by receiving carbon. Two forms of mycorrhizae are those that grow hyphae from a mantle surrounding the plant roots (ectomycorrhizae) and those with mycelia that embed within the root tissue itself (endomycorrhizae). Allen (1991), O'Dell et al. (1993), and Smith and Read (1997) provided reviews of the structure and function of mycorrhizal fungi.

Fungi as Pathogens

Fungi can also act as pathogens on trees, serving as a cause of tree mortality and altering forest stand structure by opening canopy gaps that, in turn, allow sunlight to penetrate to the forest floor, spurring growth of understory plants and increasing or altering the diversity of plant species (Holah et al. 1993) and other fungi (Christensen 1989). Pathogenic fungi contribute to the accumulation of dead and decaying wood in a forest. Some pathogenic fungi such as heartrot fungi can create habitat conditions for primary and secondary cavity-nesting wildlife species and can alter nutrient cycling (Hennon 1995).

Fungi as Decomposers

Fungi associated with down wood are saprobic, meaning that they derive nutrients from decaying organic material. One such species in the Pacific Northwest is orange jelly (*Dacrymyces chrysospermus*) found on decaying logs of Douglas-fir (*Pseudotsuga* menzeisii; Fig. 1). Other unique fungi associated with down wood and wood decay in the Pacific

Northwest are the birds' nest fungus, *Nidula niveotomentosa* (Fig. 2) and the veined cup, *Disciotis venosa* (Fig. 3).

Fungi found in decaying wood, litter, and duff serve to recycle nutrients (Fogel and Hunt 1983, Hattenschwiler et al. 2005), particularly nitrogen and carbon, as well as minerals, which can then be used by other organisms. Such decomposition processes also serve to physically and chemically break down soil organic matter and alter soil structure. In coarse down wood, wood fungi help mobilize nitrogen, phosphorus, and potassium during the early decay stages (Harmon et al. 1994). Wood decomposition in German forests of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) is dominated by white-rot fungi (*Phanerochaete chyrsosporium*) which breaks down lignin in wood (Arnstadt et al. 2016).

In cool temperate and subalpine forests of Japan, Osono (2015) found that litter decomposition was more affected by presence of specific fungal families than by the type of litter. Fungi of Basidiomycetes had higher rates of lignin breakdown than did fungi of Xylariaceae.

In western Montana, Harvey et al. (1981) found that soil organic matter ≤ 45 percent by volume of the top 30 cm of soil was associated with increased numbers of ectomycorrhizae, but at > 45 percent the numbers decreased, and the relationship of soil organic matter and ectomycorrhizae was more salient in dry rather than moist sites.

In studying the role of fungi in decomposition of oak stumps, van der Wal et al. (2015) reported finding unique fungal communities in freshly cut trees and in younger stumps, and that old stumps harbored more random assortments of fungal species. They also found that ascomycete fungi likely play a prominent role in wood decay but further testing is needed, and that better understanding fungal roles of wood decay can help improve estimates of carbon sequestration of forests. In southern Sweden, Tyler (1992) likewise found distinct communities of ectomycorrhizal fungi associated with early decay stages of hardwoods.

Fungi as Non-Timber Forest Products

Fungi -- particularly above-ground fruiting mushrooms such as chanterelles, morels, matsutake, boletes, truffles, ganoderma (reishi) and others -- are sought for food, medicinal value, and recreational collection, in an expanding industry (Molina et al. 1993, Schlosser and Blatner 1995, Amaranthus and Pilz 1996, Pilz et al. 1998). Kucuker and Baskent (2017) developed a simulation-based decision-support model to assess the effects of forest management intensity on mushroom occurrence and production. Although developed for northwest Turkey, their system may hold potential for guiding multiple-use forest management in the Pacific Northwest. In a Scots pine forest of central Spain, intensive collection of seasonal sporocarps (above-ground fruiting bodies) of king boletes (*Boletus edulis*) during four productive seasons did not significantly reduce its below-ground mycelium biomass, so that the mushroom was able to sustain its productivity (Parladé et al. 2017). This may have implications for monitoring, discussed further below.

Fungi as Food Resources for Wildlife

Fungi themselves are ingested by a wide variety of invertebrate and vertebrate wildlife (Fogel and Trappe 1978, Maser et al. 1978, Ingham and Molina 1991), as discussed more fully in the next section.

FUNGI AND INVERTEBRATES

Furniss and Carolin (1980) provided a number of examples of insect associations with fungi in forests of the western U.S., as follows. Bark beetles are associated with trees weakened or killed by root-rotting fungi such as Porioa root rot (*Phellinus weirii*), annosus root rot (*Fomes annosus*), and shoestring rot (*Armillaria mellea* and *Phytophthora lateralis*). Some insects, including the smaller European elm bark beetle (*Scolytus multistriatus*), disperse disease-causing fungi, thereby infecting healthy trees. Stain fungi is introduced into weakened trees by bark beetles (especially the western balsam bark beetle, *Dryocoetes confusus*), ambrosia beetles (subfamilies Scolytinae and Platypodinae of Curculionidae), and wood borers (many species and families), the last of which can also mine in sound wood and thereby increase the penetration of wood-rotting fungi in down trees and logs. Ambrosia beetles in particular disperse, introduce, and feed on ambrosia fungi (*Ambrosiella* and *Raffaelea*) and can be highly fungi species-specific. Fir engraver beetles (*Scolytus* spp.) can disperse and introduce brown-stain fungus (*Trichosporium symbioticum*). Some bark beetles (*Gnathotrichus sulcatus*) store and disseminate the symbiotic fungi *Ambrosiella sulcati* and *Raffaelea sulcati*, and the larvae of some horntail insects (*Sirex* and *Urocerus*) feed upon the symbiotic fungi *Amylostereum*. Subterranean termites that comminute (chew) wood fiber are attracted to the wood-decaying fungus *Lenzites trabea*. Among invertebrates associated with yeasts are roundheaded beetles (*Dendroctonus* spp.), bark beetles, and carpenter ants (*Camponotus* spp.). Silver fir beetles (*Pseudohylesinus sericeus*) can be commonly associated with brown-stain fungi and root-rotting fungi including *Armillaria mellea*, *Fomes annosus*, and *Phellinus weirii*.

In general, wood-boring insects are known to transport many fungal genera (Schowalter 2000). Ulyshen (2016) reported that invertebrates that are particularly influential in promoting wood decomposition include wood-boring beetles (Coleoptera) and termites (Termitoidae) especially fungus-farming macrotermitines. In a broad study of 13 temperate tree species, Kahl et al. (2017) found that wood decay rates were mediated by enzyme activity and diversity of beetle species. Wood decays more rapidly when it incurs decay fungi introduced by wood-boring beetles, wasps, and termites, than when it is initially inoculated with mold fungi by bark and ambrosia beetles (Schowalter 2000). This is because mold fungi can catabolize carbohydrates and thereby inhibit later colonization of decay fungi.

Species interactions that affect changes in fungal and insect communities during wood decay are, in general, poorly understood, and long-term studies are needed. In a boreal forest in central Sweden, Weslien et al. (2011) found that a bark beetle (*Hylurgops palliatus*) and a wood-borer (M*onochamus sutor*) colonized stumps during the first year following cutting; their saproxylic (decaying or dead wood-dependent) functions were mediated by the wood-decaying fungus *Fomitopsis pinicola*, which eventually provided habitat in the stumps 10 years later for a rare, wood-living beetle *Peltis grossa*. Thus, the researchers suggested this as an example of managing for rare or threatened insect species by understanding the links between saproxylic taxa such as the beetles and the fungi.

Some members of the darkling beetle family Tenebrionidae are associated with fungi (White 1983; Fig. 4). For example, the forked fungus beetle *Bolitotherus cornutus* is nocturnal and during the day they inhabit hard shelf fungi or crevices where the fungi are attached. The darkling beetles *Diaperis* spp. and *Playtdema* spp. occur under bark and in fungi. The aptly-named handsome fungus beetles of family Endomychidae, such as the Idaho handsome fungus beetle *Mycetina idahoensis*, occur under bark in rotting wood and in fungi on which they feed (Haggard and Haggard 2006).

Fungivorous insects are typically associated with late-successional forests (Schowalter 2000) and can influence the diversity of fungi in decaying wood in both managed and natural forests (Muller et al. 2002). Fungivorous springtails apparently serve to transfer secondary metabolites (catalpol, an iridoid glucoside) from host plants to arbuscular endomycorrhizal fungi (Duhamel et al. 2013). This functions in the fungi to prevent it from being grazed. In this triad of relationships, the springtails benefit from the fungal food source, the fungi benefits from avoiding grazing, and the host plant benefits from using the symbiotic fungi to absorb soil nutrients.

In other symbiotic relationships, Macrotermitinae termites deposit all their feces in their tended gardens of the fungus T*ermitomyces* spp. (Basidiomycetes). Individual termite species of this group tend to be associated with, and feed only on, specific species of these fungi (Edwards 2000).

Nutrients in woodland soils can be greatly affected by some invertebrate associations with fungi, as reported by Crowther et al. (2011a). Invertebrate grazers in soil can determine the composition of fungal decomposer communities. For example, isopods were found to feed selectively on the cord-forming fungus *Resinicium bicolor*, thus preventing the competitive exclusion of two fungi species in soil and wood. Similar mediating functions were also observed with soil nematodes. Thus, conditions affecting soil invertebrates can also affect their influence on fungal communities and associated nutrient cycles. Also, invertebrate fungivory can influence decay rates of wood and nutrient mineralization and decomposition (Crowther et al. 2011b).

Some mycorrhizal fungi produce nonnitrogeneous chemical defenses including pyrethroids that are toxins absorbed through insect exoskeletons (Schowalter 2000).

FUNGI AND WILDLIFE

In Washington and Oregon, some 31 wildlife species among 8 families are known to be fungivores (Table 1).

Table 1. Fungivorous wildlife species of Washington and Oregon (source: O'Neill et al. 2001, Jacobs and Luoma 2008). * = also disperses fungi

Family	Common name	Scientific name
Cervidae	Black-tailed Deer	*Odocoileus hemionus columbianus*
Cervidae	Mule Deer	*Odocoileus hemionus hemionus*
Cervidae	Rocky Mountain Elk*	*Cervus elaphus nelsoni*
Cervidae	Roosevelt Elk*	*Cervus elaphus roosevelti*
Dipodidae	Pacific Jumping Mouse	*Zapus trinotatus*
Geomyidae	Camas Pocket Gopher	*Thomomys bulbivorus*
Geomyidae	Northern Pocket Gopher	*Thomomys talpoides*
Geomyidae	Townsend's Pocket Gopher	*Thomomys townsendii*
Muridae	Bushy-tailed Woodrat	*Neotoma cinerea*
Muridae	Canyon Mouse	*Peromyscus crinitus*
Muridae	Columbian Mouse*	*Peromyscus keeni*
Muridae	Creeping Vole	*Microtus oregoni*
Muridae	Deer Mouse*	*Peromyscus maniculatus*
Muridae	Pinon Mouse	*Peromyscus truei*
Muridae	Southern Red-backed Vole*	*Myodes gapperi*
Muridae	Western Red-backed Vole*	*Myodes californicus*
Muridae	White-footed Vole*	*Arborimus albipes*
Ochotonidae	American Pika	*Ochotona princeps*
Sciuridae	Douglas' Squirrel*	*Tamiasciurus douglasii*
Sciuridae	Golden-mantled Ground Squirrel	*Spermophilus lateralis*
Sciuridae	Least Chipmunk*	*Tamias minimus*
Sciuridae	Northern Flying Squirrel*	*Glaucomys sabrinus*
Sciuridae	Red Squirrel*	*Tamiasciurus hudsonicus*
Sciuridae	Townsend's Chipmunk	*Tamias townsendii*
Sciuridae	Siskiyou Chipmunk*	*Tamias siskiyou*
Sciuridae	Western Gray Squirrel*	*Sciurus griseus*

Sciuridae	Yellow-pine Chipmunk	*Tamias amoenus*
Soricidae	Pacific Shrew	*Sorex pacificus*
Soricidae	Trowbridge's Shrew	*Sorex trowbridgii*
Soricidae	Vagrant Shrew	*Sorex vagrans*
Suidae	Feral Pig	*Sus scrofa*

Taxonomy based on: American Society of Mammalogists, http://www.science.smith.edu/departments/Biology/VHAYSSEN/msi/default.html

Some fungi are dispersed on the beaks of foraging and cavity-excavating woodpeckers (Jusino et al. 2016), thereby serving to inoculate live and dead trees. Fungi such as truffles and their ectomycorrhizal sporocarps are key food resources for northern flying squirrels (*Glaucomys sabrinus*) (Lehmkuhl et al. 2004); in turn, flying squirrels are a key prey species of northern spotted owls (*Strix occidentalis caurina*) in parts of the owl's range.

Some fungi are highly detrimental to some species of wildlife, such as the deadly amphibian disease of chytridiomycosis caused by the fungus *Batrachochytrium dendrobatidis*, and white-nose syndrome, which is debilitating and deadly to bats, caused by the fungus *Pseudogymnoascus destructans*. However, there is no evidence that these fungal pathogens are related to wood decay.

Fungi-dispersing wildlife in this region (Table 1) number at least 14 species including American pika (*Ochotona princeps*). Species of deer and elk can disperse fungi through their pellets (Fig. 5a,b). Small mammals, such as white-footed voles (Manning et al. 2003), are among the species that are documented as dispersers of mycorrhizal fungi (Maser et al. 1978, Luoma et al.2003).

In general, fungi species with hypogeous sporocarps (that release spores below ground), such as truffles, depend on animals for dispersal. Jacobs and Luoma (2008) studied four forest rodents (Townsend's chipmunk, Siskiyou chipmunk, western red-backed vole, and southern red-backed vole) that serve as dispersers of truffles including *Rhizopogon* and as prey for northern spotted owls. They found that isolated green-tree retention in harvest blocks reduced consumption of truffles by the voles, and that the impact could be offset by including green-tree aggregates within a dispersed retention matrix.

Maser and Maser (1988) reported that all squirrels of five genera and eight species in Oregon conifer forests are mycophagous (eat fungi), particularly consuming belowground fruiting bodies of at least 26 genera of mycorrhizal fungi. Northern flying squirrels proved to be a nearly obligate fungivore. In general, they found that squirrels may be vital links involving below-ground mycorrhizal fungi, nitrogen-fixing bacteria, yeast, and conifer trees.

Marcot (2002) demonstrated how a "functional web" can be depicted for wildlife associated with various wood decay elements (snags, down wood, litter, duff, mistletoe brooms, dead parts of live trees, hollow living trees, natural tree cavities, bark crevices, and live remnant or legacy trees), including wildlife species responsible for dispersing fungi, in Washington and Oregon.

WOOD DECAY AND FUNGI

The dynamics of wood decay are linked closely to the presence and ecological functions of fungi. Decay of down wood proceeds through a series of stages marked by degree of wood breakdown, changes in the diversity of associated biota, progressions of nutrient transformations, and other processes. Spies and Cline (1988) and Maser et al. (1979) provided a 5-category classification system of wood decay, progressing from recently downed wood with intact bark, branches, and twigs (decay class I) to advanced states of wood breakdown into soft textures of duff (decay class V).

Throughout this mini-successional sequence of wood decay, fungi, along with mesoarthropods and other species, play key physical and biochemical roles in wood decomposition and nutrient cycling. In particular, in young and old Douglas-fir stands, the ectomycorrhizal fungus *Piloderma fallax* increases in occurrence in relation to percent cover of down wood of the advanced decay class V. The presence of truffle and false truffle fungi has also been shown to be associated with proximity to (within 1 meter of) down wood (Amaranthus et al. 1994).

Down wood, throughout its decay sequence, also serves to retain moisture, which promotes growth of ectomycorrhizae (Harvey et al. 1976, 1978; Amaranthus et al. 1989; Harmon and Sexton 1995), and which thereby serves as refugia for seedlings and mycorrhizal fungi. Such "reservoir" functions of down wood can be particularly salient in xeric forests and during dry seasons, providing for establishment of beneficial mycorrhizal fungi as a forest stand regrows (O'Hanlon-Manners and Kotanen 2004) and serving as "nurse logs" for seedlings of vascular plants (Kropp 1982, Harmon and Franklin 1989) such as western hemlock (*Tsuga heterophylla*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (Brang et al.2003). Nurse logs also can act as refuges from pathogenic soil fungi (O'Hanlon-Manners and Kotanen 2004).

Decaying down wood provides nutrients for decay fungi and pathogens. Studies in North America and Scandinavia both reveal that high diversity of wood-decay fungal species is associated with the presence of large down wood (Kruys, et al. 1999, Crites and Dale 1998, Ohlson et al. 1997, Høiland and Bendiksen 1996, Bader et al. 1995, Wästerlund and Ingelög

1981). Høiland and Bendiksen (1996) found that rare wood-inhabiting fungal species occurred primarily on long (mean 11 meters) and well-decayed (average decay class III) down wood. Kruys and Jonsson (1999) found that fungal species diversity is associated with total surface area of down wood.

FUNGI IN FOREST MANAGEMENT

Functioning forest ecosystems in the Pacific Northwest depend on the diversity and viability of fungal species. The presence, density, distribution, and diversity of fungi are influenced by forest stand management practices and by forest age class (Trofymow et al. 2003, Heithecker and Halpern 2006, Pilz and Perry 1984, O'Dell et al. 1992, Clarkson and Mills 1994, Cázares et al. 1998, Stendell et al. 1999, Colgan et al. 1999). And, in turn, plant community structures including wood decay elements are influenced by fungi in complex feedback systems (van der Heijden et al. 1998).

In a study in France, Paillet et al. (2017) reported that snags, more than just large live trees, provide the bulk of tree microhabitats including cavities, fungi conks, and bark features, and that strict forest reserves contain a greater abundance of such microhabitats than do managed forests.

Influence of Forest Management Activities

Thinning and clearcutting alter the fungal community and can reduce the production of sporocarps and ectomycorrhizae. Rydin et al. (1997) found that habitat loss and some forest management practices in Europe have led to declines in the diversity of fungi and in the presence of rare fungal species. Bert et al. (1994) reported that many fungal species in Swedish forests are threatened by the loss of old trees and declines in coarse woody debris. Arnstadt et al. (2016) noted that higher intensities of forest management in Germany negatively impact the volume of dead wood and richness of fungal species sporocarps. Parladé et al. (2017) found that clearcutting and partial cutting of Scots pine forests in central Spain equally and sharply reduced the mycelium biomass of king boletes (*Boletus edulis*).

In European Norway spruce stands, Lõhmus (2011) studied the influence of clearcutting, planting, and thinning on polypore (bracket) fungi. Results indicated that distinct polypore communities were present in clearcuts but their species richness declined over time and increased again 20 years post-cutting and following tree planting. Most polypore species were found in mature, unmanaged, naturally-regenerated stands; thinning reduced species richness 15%; and distinct polypore communities were present in young stands on nutrient-rich soils.

Fungi in Old Forests

Under the Northwest Forest Plan (NWFP) in western Washington and Oregon and northwestern California, the Survey and Manage Program listed 234 rare fungi species found in late-successional and old-growth forests (Molina 2008), many species of which are associated with various aspects of wood decay. Molina (2008) noted that some two-thirds of these species also occurred outside late-successional forest reserves under the NWFP, suggesting that conservation of fungal biodiversity may benefit from additional guidelines outside the reserves.

More recently, the Interagency Special Status and Sensitive Species Program of the Pacific Northwest Region of U.S. Forest Service and Bureau of Land Management has taken over the role and duties of the Survey and Manage Program, including providing an annotated bibliography of rare species of fungi of California, Oregon, and Washington[1].

Managing for Fungal Species and Communities

Except for sensitive or listed species, no general guidelines are in place to provide for conservation or restoration of fungal communities, including those associated with wood decay elements. It is known, though, that retention of legacy trees -- usually mature or old-growth trees retained during forest harvest operations -- can provide some degree of conservation of beneficial fungi such as mycorrhizae (Smith, et al 2000). Retaining green trees has been attributed by Luoma (2001) to the retention the rare truffle *Arcangeliella camphorata* which is otherwise lost in clearcuts such as demonstrated in southwest Oregon (Clarkson and Mills 1994, Amaranthus et al. 1994). In Washington, Cline et al. (2005) reported that Douglas-fir seedlings nearer (< 6 m) to residual mature Douglas-fir trees in recently harvested green-tree retention units had higher species richness and diversity of ectomycorrhizal fungi than did seedlings far from residual trees. They thus suggested that residual mature, legacy trees can maintain or accelerate recovery of ectomycorrhizal fungi following harvest. As well, retained stumps can provide environments for conks and other fungi (Fig. 6).

In some cases, active management can help retain or restore desired fungi by deliberately introducing fungi in live trees. This can help foster wood decay and create snags and dead parts of live trees for wildlife habitat, such as demonstrated by Bednarz et al. (2013) and Filip et al. (2011) in forests of Oregon and Washington.

[1] http://www.fs.fed.us/r6/sfpnw/issssp/documents3/cpt-fu-effects-guidelines-att3-annotated-bibliography-2013-10.docx

To maintain fungal biodiversity, the habitat and resource associations of multiple species need to be considered. This can be achieved, in part, by providing a range of sizes and decay classes of down wood, although such associations of individual species and their responses to various amounts, patterns, sizes, decay classes, and timing of down wood are poorly known and need much study. In general, though, providing down wood as well as living host plants of the correct ages and species can help maintain fungal diversity.

In Sweden, Edman and Jonsson (2001) and Edman et al. (2007) reported that the spatial distribution of down logs and wood-decaying fungi are influenced by wind and gap-phase dynamics in forests of old-growth Norway spruce. They also found that rare fungi species have specific substrate associations and that temporal variations in the patterns of canopy gaps and down wood abundance can affect fungi biodiversity. White et al. (2012) studied the effect of a massive ice storm in forests of southern Quebec, Canada, which caused forest canopy gap openings that became colonized by wood-rotting fungi, saproxylic insects, salamanders, and other organisms. Such canopy gap dynamics apparently served to maintain the diversity of opening-dependent taxa including some fungi.

However, in a study of ectomycorrhizal fungi based on epigeous sporocarps in a cedar-hemlock forest of northwest British Columbia, Canada, Durall et al. (1999) found that fungal species richness decreased exponentially as a function of increasing size of forest gap cutblocks, particularly in gaps > 900 m^2. Maximum fungal species richness was found ≤ 7 m from the forest edge. They suggested sampling both sporocarps and root tips for accurately determining the ectomycorrhizal fungal community.

In a study of northern hardwood forests, Brazee et al. (2014) found various fungi species associated with a variety of conditions, including stumps, down wood of small (< 20 cm diameter) through large (> 40 cm diameter) sizes, well-decayed substrates, minor host tree species, and canopy gaps. In Norway spruce forests of Sweden, Edman et al. (2004) found that fungi was more common in sites rich in down wood, and that fungi species richness was greater associated with large logs than with small logs. Crawford et al. (1990) found that filamentous fungi and yeast communities in Douglas-fir logs varied between decay classes III and IV, and that they discovered a total of 18 genera and 36 species of fungi among logs of both decay classes.

Studies are needed in the Pacific Northwest to quantify the amount of down wood -- number of pieces, sizes, total biomass, percent forest floor cover, and other attributes -- necessary for maintaining or restoring fungal biodiversity and viable levels of individual fungi species, especially rare species. Although no such specific guidelines exist in the Pacific Northwest, it can be assumed that drier or more xeric forest types may require greater amounts of down wood that do wetter or more mesic forest types. Also, fungi tend to occur in patchy distributions because of the patchy occurrence of their substrates. Providing down wood of various sizes, species, and decay classes in patchy distributions throughout stands in managed forest landscapes may help restore and maintain desired fungal communities.

Surveys of wood-inhabiting fungi in spruce-hardwood forests of central Finland (Juutilainen et al. 2011) found a distinct fungal community in the smallest pieces of down wood; by excluding pieces < 1cm diameter, fungi species richness, including rare species, was underestimated by 10% and occurrences by 46%. Surveying fungi only in larger down wood (coarse woody debris) seriously underestimated richness and abundance of dead wood-associated fungi.

It takes time for mycorrhizae to colonize down wood and coarse woody debris, because most mycorrhizal fungi in wood are associated with roots. A good example is *Boletus* (*Aureoboletus*) *mirabilis*, which always fruits from decay class 4 or 5 wood, but that is because it is mycorrhizal with the roots of hemlock in the wood. This time delay needed for colonization and association with roots highlights the role and value of retaining some late seral forests and old legacy trees as refugia and as source material for beneficial fungi (Clarkson and Mills 1994). Otherwise, sources may be relegated to disturbance-resistant fungi spores remaining in soil or in whatever unburned down wood may remain after disturbance (Baar et al. 1999). Still, reappearance of some fungi may appeared delayed following disturbance, such as chanterelles (*Cantharellus*) appearing in western hemlock stands after 20 years following disturbance along the Washington coast (Pilz et al. 1998). But once established in appropriate habitat conditions, mycelial colonies of fungi can persist for many years (Smith et al. 1992, De la Bastide et al. 1994, Dahlberg and Stenlid 1995).

Lehmkuhl et al. (2007) discussed a decision-aiding model FuelSolve that can be used to guide management of fuels in forests under multiple objectives such as providing habitat for northern spotted owls and their prey, along with live and dead vegetation, mycorrhizal fungi, and arboreal lichens, as elements of the owl's habitat.

Further ideas on managing Pacific Northwest forests for fungi can be found in Molina et al. (2001).

Monitoring Fungi

Fungi are often difficult to detect, especially for determining the presence of rare, sparsely-distributed, and seldom-fruiting species. Most species can be detected only when they produce reproductive structures such as cups, truffles, conks, and mushrooms (Figs. 7 a,b). Different species may produce such detectible structures at different times and seasons (Hunt and Trappe 1987, Luoma 1991), depending on species-specific relationships to nutrient availability and environmental conditions of temperature, light, pH, and moisture. O'Dell et al. (1996) recommended surveying for fungi at various times of the year, particularly in spring and autumn, for at least five years, to provide any assurance of detection.

Lassauce et al. (2011) tested the idea that dead wood volume could be monitored as an index to species richness of saproxylic beetles and fungi in various forest types. However, they found that correlations were only moderately significant and concluded that dead wood volume is likely an imprecise indicator of saproxylic beetle and fungi biodiversity. Further, the efficacy of using dead wood volume to indicate saproxylic beetle diversity differed between boreal and temperate forests, with slightly greater predictability in the former. They suggested that additional landscape-level variables, such as the type and decay class of dead wood, be included in monitoring dead wood and associated organisms. Parladé et al. (2017) suggested that surveys of soil mycelium masses (Fig. 8) can usefully indicate the response of some fungi to management activities, and could be useful adjuncts to monitoring sporocarp fruiting bodies of interest to gatherers.

Another challenge to monitoring fungi related to wood decay is to identify the appropriate spatial and temporal scales. In a review of studies on saproxylic species (fungi, beetles, and lichens) and associated dead wood distribution in Europe, Sverdrup-Thygeson et al. (2014) identified key information gaps. They found a large variation among taxa of such species in response to spatial and temporal variations in dead wood patterns. They suggested that timelag effects, in particular, need more study at landscape scales and for listed saproxylic species before firm management guidelines can be developed for them.

INFLUENCE OF FIRE

The main influence of fire on wood decay-associated fungi relates to how much sound or decaying wood is created or destroyed. Prescribed fires and wildfires alike can kill part or all of standing trees which, if not engulfed and fully charred, could provide fungi substrates standing or down. Fire also can eliminate fungi substrates, particularly with piling and burning of forest slash following timber harvests.

In forests of the eastern Cascades of Oregon, Smith et al. (2017) studied soil fungal and bacterial communities and biogeochemical processes following severe and less severe burns. They found that soil fungi and bacteria steadily recolonized following the burns, but with a different community composition between the two fire severities. The greatest difference in fungal and bacterial community composition was evident early after the burns and became more similar over time.

In Swedish forests of Scots pine, Jonsson et al. (1999) compared chronosequences of ectomycorrhizae in stands burned by low-intensity wildfire and unburned late-successional stands. They found most of the common species in all sites, suggesting that ectomycorrhizae exhibit a continuity following low-intensity burning. Importantly, the below-ground species composition was not reflected in that of the above-ground sporocarps.

FUNGI AS A CONSERVATION CHALLENGE

Maintaining and restoring desired wood decay-associated fungi can be quite a challenge for management (O'Dell et al. 1996) given the problems of intermittent detectability, variable dispersal, patchy distributions, and lack of scientific information on species' life histories and habitat requirements. Further challenges include identifying species, the need for taxonomic studies, and incomplete understanding of their ecological functional roles in forest ecosystems. Studies conducted over the past decade have shed light on some fungi species in some geographic areas and forest types of the Pacific Northwest (e.g., see above for the footnote on the annotated bibliography).

In a global review of conservation strategies for managing dead wood for biodiversity, Seibold et al. (2015) found many information gaps and, at best, only scattered management guidelines. Their meta-analysis revealed that most studies have focused on early stages of wood decay and that some taxa, including fungi, are under-represented. The studies do confirm the overall benefits of dead wood for biodiversity, but there is a need for research on advanced decay stages and on the influence on non-saproxylic organisms.

Still, fungi are key players in native and productive forests, and offer important roles in nutrient cycling, food sources, tree production, and maintenance of soil health.

ACKNOWLEDGMENTS

This review is based in part on, and is updated from, a previous essay by Tina Dreisbach (2002), posted as part of the DecAID Decayed Wood Advisor version 2.20 (Mellen et al. 2002), and also borrows in part from Marcot et al. (in prep.[2017]). The original report by Driesbach reviewed by Jane E. Smith, Randy Molina, Thomas O'Dell, Efrén Cázares, and the DecAID Science Team. I acknowledge and thank their work. My thanks to Dan Luoma, Steven Acker, and Kim Mellen-McLean for helpful reviews of the current manuscript.

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Figure 1. Orange jelly mushroom, *Dacrymyces chrysospermus* (prev. *D. palmatus*), found on a down log of Douglas-fir in the Cascade Mountains of southwestern Washington. Photo by Bruce G. Marcot.

Figure 2. Bird's nest fungus, *Nidula niveotomentosa*, on a moist Douglas-fir log in the central coast range of Oregon. This unique fungal structure consists of a nest cup called a peridium, that holds "egg" structures called peridioles which contain spore bodies called gleba. In bird's nest fungi, the peridioles are held in place in the cups with a gelatinous glue-like material until they disperse from splashing raindrops. Species of *Nidula* can reproduce both sexually and asexually, and they produce a ketone chemical with the flavor of raspberry. Photos by Bruce G. Marcot.

Figure 3. Veined cup fungus, poss. *Disciotis venosa*, in forest litter and down wood fragments, in a Douglas-fir forest of the southern Washington Cascade Mountains. This is one of several brown-colored cup fungi. Although related to the sought-after morel mushrooms, veined cups are likely toxic if eaten raw. They are partially mycorrhizal and thus can play a role in maintaining tree productivity and forest health. Photo by Bruce G. Marcot.

Figure 4. A darkling fungus beetle (Tenebrionidae) collected in mid-elevation conifer forests of the Cispus area south of Mount St. Helens, Washington Cascade Mountains. Photo by Bruce G. Marcot.

Figure 5 a,b. Fungi dispersed via pellet droppings from Rocky Mountain elk. Tower and Summit Burn, Malheur National Forest, eastern Oregon. Photo by Bruce G. Marcot.

Figure 6. Cut stumps, along with coarse and fine down wood and other wood decay elements, can provide substrates for wood-decaying fungi such as these conks of *Fomatopsis pinicola*. Gifford Pinchot National Forest, Washington. Photo by Bruce G. Marcot.

Figure 7 a,b. Fruiting bodies (sporocarps) of fungi may appear intermittently, seasonally, or rarely, depending on the species, its rarity, and environmental conditions, making monitoring a challenge. 7a: Sporocarps of *Galerina marginata*, a most deadly species, on a down Douglas-fir log. 7b: Sporocarps from *Mycea* mycelia beneath the log; their mycelia commonly grow from fine woody debris and litter. Photos by Bruce G. Marcot.

7a

7b

Figure 8. Fungi mycelium mass beneath a log. Studies suggest that monitoring just the fruiting bodies (sporocarps, Fig. 7) may underestimate fungal community diversity, and that surveying soil mycelium masses can better indicate response of fungi to forest management activities. Photo by Bruce G. Marcot.