

# **Ecosystem Processes Related** to Wood Decay

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# Abstract

Wood decay elements include snags, down wood, root wads, tree stumps, litter, duff, broomed or diseased branches, and partially dead trees, all of which contribute to ecological processes and biodiversity of the forest ecosystem. Down wood can serve as reservoirs for moisture and mycorrhizal fungi beneficial to the health and growth of commercial tree species. Decaying wood, leaf litter, small twigs, and roots contribute nutrients and structure to humus and soil organic matter, and host microbes that play beneficial roles in nitrogen cycles and other processes. Snags and down wood provide nurse functions for tree and shrub species, and can aid in restoration of degraded forest environments. Various elements of wood decay provide habitat for many species of wildlife including invertebrates, amphibians, reptiles, birds, and mammals. Fire can influence the amounts and distributions of wood decay elements and enhance or detract desired ecosystem processes, depending on severity, charring, soil temperature, and other factors. Managing wood decay elements for ecosystem processes entails better understanding decay dynamics, the role of coarse wood in soil, the role of wood decay in carbon cycling and sequestration, and other considerations.

Keywords: Wood decay, coarse woody debris, ecosystem processes, forest biodiversity, restoration, habitat.



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## Introduction

This report summarizes research and knowledge of the role of ecosystem processes related to wood decay of forest ecosystems of Washington and Oregon, and serves to complement the website "DecAID, the Decayed Wood Advisor for Managing Snags, Partially Dead Trees, and Down Wood for Biodiversity in Forests of Washington and Oregon."<sup>2</sup> DecAID is a synthesis of data and research results and a planning tool to help inform the management of wood decay elements for biodiversity and species conservation. This current report summarizes research and knowledge of ecosystem processes, including down wood serving as reservoirs for moisture and mycorrhizal fungi; the relationship of nutrients and microbes in decaying wood; the role of snags and down wood as nurse substrates; wildlife and insects associated with wood decay; and the influence of fire on decaying wood; as well as considerations for managing forests for wood decay and their benefits.

## Wood Decay Elements and Their Roles

Wood decay elements—snags, down wood, root wads, tree stumps, litter, duff, broomed or diseased branches, and partially dead trees—provide for more than just wildlife habitat. They also provide resources and substrates for many other organisms that perform vital ecological roles of transformation and cycling of nutrients, decomposition, respiration, and other biologically mediated transformations (Edmonds et al. 1989) (fig. 1). In turn, such roles affect ecosystems far beyond the confines of the wood decay elements per se, and can greatly contribute to overall ecosystem health, soil productivity, and growth of desired tree species (Franklin et al. 2000, Harmon et al. 1986, Tinker and Knight 2000).

## Down Wood as Reservoirs for Moisture and Mycorrhizae

## Moisture reservoirs—

Down wood has a high pore volume and thus can serve as moisture reservoirs and provide persistent microsites that aid in forest recovery after prolonged drought or fire (Amaranthus et al. 1989). For example, in one study in southwest Oregon, down logs provided considerable rooting and mycorrhizal activity, and mean moisture content (157 percent) was 25 times greater than mean soil moisture (6 percent) (Amaranthus et al. 1989).

In forests of western North America, decomposing wood occurs in the organic humus horizon of soils (McFee and Stone 1966) and, indeed, throughout the entire soil horizon (Harvey 1993, Harvey et al. 1976b).

<sup>&</sup>lt;sup>2</sup> https://www.fs.fed.us/r6/nr/wildlife/decaid/.



Figure 1—Example of some wood decay elements: snag, dead branches, down log, and root wad, with the down log functioning as a plant nurse substrate. Lowland old-growth Douglas-fir stand, Eagle Fern Park, Clackamas County, Oregon.

## Mycorrhizal fungi—

Down wood is also a major source of mycorrhizal fungi (Amaranthus et al. 1996). Decaying wood retains moisture and serves as important reservoirs of such fungal activity during dry summer months (Harvey 1993, Harvey et al. 1976a). For example, commonly found in down wood are sporocarps of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) tuberculate ectomycorrhizae, formed by *Rhizopogon vinicolor. R. vinicolor* is more routinely found on seedlings grown in clearcut soils, where it aids the host tree during drought by blocking entrance by pathogens or aphids (Zak 1971). A coarse woody debris-dependent ectomycorrhizal fungus is *Philoderma fallax* (Smith et al. 2000).

To a limited extent, ectomycorrhizae in down wood can break down lignins and convert nutrients including phosphorus, potassium, calcium, magnesium, manganese, and sodium into forms usable by insects, mollusks, and mammals (Maser et al. 1979). Although some ectomycorrhizal fungi have this lignindegrading capacity, it is probably not much compared to decomposer fungi (Smith and Read 1997), which is also found in decomposing down wood, including that of Douglas-fir (Crawford et al. 1990). In general, mycorrhizae provide moisture, phosphate, and nitrogen from the soil to a substantial degree to coniferous plants, and serve as important mediators in soil nutrient cycles (Fogel and Hunt 1983). In this symbiotic relation, conifer trees in turn provide carbohydrates for the mycorrhizae. This relationship is critical for tree productivity, particularly for conifers in relatively infertile soils. Amounts of mycorrhizae are closely correlated with conifer tree growth and tend to be concentrated in the organic horizons of the soil. For example, in one study, during peak growth (June through July), 95 percent of the mycorrhizal mass in a midslope stand of northern Rocky Mountain subalpine fir forests occurred in the organic horizon of the soil. This underscores the important role that decaying wood and the organic soil horizon play on affording fungi and influencing tree production (Harvey 1993).

#### Other fungi and dead wood—

In a boreal forest, Juutilainen et al. (2011) found that occurrence of wood-inhabiting fungi depended on size of the dead wood pieces, but that fungi species inhabiting the smallest dead wood pieces were distinctively different than those inhabiting larger pieces. The authors concluded that surveying only coarse (large size) wood debris will seriously underestimate fungi species richness and abundance. Research by van der Wal et al. (2015) found that decay of oak stumps was provided by ascomycete fungi (molds, mildew, morels, truffles, and others), but that further study is needed on how fungal communities process wood decay and contribute to carbon sequestration of forests.

# Nutrients and Microbes in Decaying Wood Soil structure—

Decaying wood also is a major contributor to humus and soil organic matter that, in turn, help maintain or improve soil structure, productivity, and nutrients (Grier 1978, Rose et al. 2001, Van Cleve and Noonan 1975). The available nitrogen in forest soils is largely found in organic matter and woody material within the soil (Means et al. 1992). Woody material in the soil creates acidic soil conditions, which are favorable for soil microbial activity that helps fix nitrogen.

### Nutrients and microbes-

The amount and distribution of nutrients in woody tissues differ among regions and forest types (Rose et al. 2001). In forests, most of the nutrients used are found in leaf litter, small twigs, and small roots, rather than bound up in larger woody structures (boles, branches, large twigs, and large roots). In a global review, Seibold et al. (2015) noted the benefits of dead wood for biodiversity conservation, and that adjustments to existing experimental studies are needed to study the advanced stages of wood decay. However, after large-scale disturbance such as fires and blowdown, the nutrient pool in woody structures becomes available as an important source to the regenerating forest during secondary succession. Down wood and other wood decay elements likely play key roles in nutrient release (mineralization), particularly as mediated through the biological activities of fungal sporocarps, mycorrhizae and roots, leaching, fragmentation, and insects (Harmon et al. 1986, Hyvonen et al. 2000; see summary in Rose et al. 2001).

That is, when a tree trunk decomposes, free-living nitrogen-fixing bacteria invade and pull available nitrogen into that site from the outside. So the fresh down log does not have very much nitrogen in it, but older decomposing logs serve to pull in nitrogen, making it available then for conifer tree growth.

Residual (dead, decaying) tree roots can also add to soil organic matter and can play positive roles in soil ecology. Removing soil organic matter by removing or reducing natural levels of wood decay elements, including old tree roots, stumps, and down wood, results in lowering soil cation exchange capacity, reducing soil moisture retention, and increasing soil compaction (Amaranthus and Steinfeld 1997; Li and Crawford, in press; Page-Dumroese et al. 1998).

#### Nitrogen cycles—

Nitrogen can get into forest soils through two microbial processes: (1) symbiotic processes of nitrogen-fixation by bacteria, which live in nodules on roots of plants such as alfalfa (*Medicago sativa* L.) and red alder (*Alnus rubra* Bong.) that use energy supplied by the host plants; and (2) nonsymbiotic processes of nitrogen fixation, through free-living, nitrogen-fixing bacteria that use energy from the organic matter in the soil. Forest management essentially depends on this latter process, although the former process occurs uncommonly in forest soils as well. The free-living, nitrogen-fixing soil bacteria occur within decayed logs on the top of the soil. Such logs are thought of as a nitrogen sponge or nitrogen pump (Harvey 1993).

Free-living, nitrogen-fixing soil bacteria are more common in wood within the soil in dry sites than in wet sites. Again, this highlights the important role of down and decaying wood. The bacteria concentrate in the organic soil horizon, where nitrogen is stored and fixed. That is, nitrogen storage and fixation both occur in soil woody material. Plants with nitrogen-fixing root symbionts in forests of Oregon and Washington include *Alnus, Ceanothus, Shepardia, Astragalus, Lupinus,* and *Trifolium*.

Standing snags, too, play roles in providing forests with nutrients. A decomposing snag, like down wood, serves as a nitrogen sponge. Once fallen, it begins its life as soil wood and provides the ecological services thereof.

## Snags and Down Wood as Nurse Logs

## Nurse snags and logs-

Large broken-top snags (fig. 2), high-cut stumps (fig. 3), and large down wood (coarse woody debris) often serve as nurse sites for many tree and shrub species (O'Hanlon-Manners and Kotanen 2004) (fig. 4) and can play key roles in restoration of degraded environments (Padilla and Pugnaire 2006). In the Pacific Northwest, plants often found growing on down wood include tree species such as *Picea sitchensis* (Bong.) Carrière, *Tsuga heterophylla* (Raf.) Sarg., *A. rubra, Pseudotsuga menzeisii, Thuja plicata* Donn ex D. Don (Harmon and Franklin 1989, Harmon et al. 1986), *Picea engelmannii* Parry ex Engelm., and *Abies lasiocarpa* (Hook.) Nutt. (Brang et al. 2003), as well as many fern, shrub, and herb species. Western hemlocks may retain a stilt-root appearance well after their nurse substrate has long decayed (fig. 5).



Figure 2—A mature western hemlock growing from a nurse stump. Mixed-conifer forest, Tryon Creek State Park, western Oregon.



Figure 3—A western hemlock growing from a western red-cedar high-cut stump. The stump was cut in the early 1900s by use of a "misery whip" two-man saw, and still shows a springboard notch used to hold a plank on which the sawyers stood. Mixed-conifer forest, Tryon Creek State Park, western Oregon.



Figure 4—A heavily decayed down log serving as a plant nurse substrate for ferns and moss. Mixed-conifer forest, Tryon Creek State Park, western Oregon.



Figure 5—A live western hemlock with high stilt roots remaining after its nurse stump substrate has long since rotted away. Mixed-conifer forest, Tryon Creek State Park, western Oregon. Nurse logs can provide highly space-efficient growing substrates for trees; for example, Graham and Cromack (1982) reported that 94 to 98 percent of the tree seedlings growing on coarse woody debris in a *P. sitchensis–T. heterophylla* forest occurred on only 6 to 11 percent of the forest floor. Decomposing nurse logs provide a superior seedbed for some plants because the logs concentrate nutrients, store water, accelerate soil development and organic matter input, reduce erosion, and lower competition from mosses and herbs (Rose et al. 2001). Coarse wood can also help stabilize slopes and stave off surface erosion.

## Seedling establishment—

Down wood, including nurse logs, can facilitate seedling establishment in other ways, as well. Gray and Spies (1997) found that the shade from woody debris facilitated seedling establishment in canopy gaps within forest stands. Additionally, they found that western hemlock seedling establishment under forest canopies was greater on retained decayed wood than on forest floor or mineral soil. Acker et al. (2017) also found that tree regeneration following fire in mountain hemlock (*T. mertensiana* (Bong.) Carrière) forest was more likely to be found in proximity to downed logs on the north, shaded side.

# Wildlife and Insects Associated With Wood Decay and Down Wood

Information on wildlife species associated with snag size and density, and down wood size and percentage of cover, is available within the DecAID databases (see footnote 2).

## Birds—

Many studies are available on use of snags, partially dead trees, hollow trees, trees with decaying limbs, and down wood, by primary and secondary cavity-nesting species of birds (e.g., Charter et al. 2016, Lorenz et al. 2015, many others) (figs. 6 through 9). Other references are reviewed elsewhere here.



Figure 6—Sign of pileated woodpecker (*Dryocopus pileatus*) foraging on a down Douglas-fir log. Pileated woodpecker feeding cavities are notable for their large oval shape. Douglas-fir forest, Gifford Pinchot National Forest, Cascade Mountains, southern Washington.



Figure 7—Sign of pileated woodpecker extensive foraging on a standing snag. Mixed-conifer forest, Tryon Creek State Park, western Oregon.



Figure 8—Sign of sapsucker (*Sphyrapicus varius*) foraging on a down log. Mixed-conifer forest, Tryon Creek State Park, western Oregon.



Figure 9—Natural cavity caused by limb breakage in a mature Douglas-fir, used as a nest site by northern spotted owls (*Strix occidentalis caurina*). Old-growth mixed-conifer forest, Deschutes National Forest, Oregon.

## Mammals—

Many instances of wildlife and insect use of decayed wood and down wood can be found in the literature (Fischer and McClelland 1983). As examples, Bull and Blumton (1999) reported that fuels reduction following timber harvest in lodgepole pine (*Pinus ponderosa* Lawson & C. Lawson) forests resulted in a decline in numbers of red squirrels, snowshoe hares (*Lepus americanus*), and red-backed voles (*Myodes* spp.), but an increase in chipmunks. Tallmon and Mills (1994) reported use of logs by California red-backed voles in a forest patch. Tinnin and Forbes (1999) reported red squirrel nests in witches' brooms in Douglas-fir trees. Bull et al. (2000) reported on black bear (*Ursus americanus*) dens in hollow trees and logs in northeastern Oregon. Hollow logs can provide denning and escape cover for fishers (*Pekania pennanti*), martens, and other species (figs. 10 and 11). Sloughing bark on live trees and snags can provide roost or nest sites for bats, brown creepers (*Certhia americana*), and other organisms (fig. 12).



Figure 10—Naturally hollowed old-growth log, cross-sectioned along a trail; likely used by squirrels and other mammals for a resting site. Wind River Experimental Forest, Cascade Mountains, southern Washington.



Figure 11—Naturally hollowed old-growth Douglas-fir log, also serving as a nurse substrate for moss, sword ferns (*Polystichum munitum*), and other plants. Mixed-conifer forest, Tryon Creek State Park, western Oregon.



Figure 12—Old-growth ponderosa pine snag with sloughing bark. The space under the bark is often used as roost or nest sites for bats, brown creepers, and other species. Old-growth mixed-conifer forest, Malheur National Forest, Oregon.

Many forest-dwelling mammals associated with wood decay elements (Aubry et al. 2003, Bowman et al. 2000, Butts and McComb 2000) eat mycorrhizal fungi and disperse the spores through their feces (Maser and Maser 1988, Maser et al. 1978). The feces often contain  $N_2$ -fixing microbes (Li et al. 1986a, 1986b), which in turn play vital roles for tree establishment and the maintenance of ecosystem productivity (Li and Crawford, in press).

Vonhof and Barclay (1997) found western long-eared bats using tree stumps. Rabe et al. (1998) found bats using ponderosa pine snags as breeding roosts in northern Arizona. Kroll et al. (2012) called for future research on the effectiveness of current regulations on snag management in intensively managed landscapes for conservation of cavity-dependent birds and bats in the Pacific Northwest.

#### Amphibians-

Aubry et al. (1988) reported on use of down wood by plethodontid salamanders in Douglas-fir forests in Washington. In the western Cascade Ranges of northern Oregon, Alkaslassy (2005) found that occurrence of plethodontid salamanders was positively influenced by greater rainfall, canopy closure, and volume of coniferous coarse woody debris, and were absent in locations lacking coniferous logs in advanced decay stages.

#### Invertebrates and insects—

A number of papers report use of standing and down wood-decay elements by invertebrates (e.g., Koenigs et al. 2002), including use of residual snags in clearcuts (Kaila et al. 1997) and hollow trees (Ranius 2000), and the interplay between woodboring beetles and wood-decay fungi (Weslien et al. 2011). Many other examples can be found in the DecAID Advisor. Ulyshen (2016) reviewed the mechanisms and influence of invertebrates on wood decomposition, noting that the primary mechanisms are enzymatic digestion, tunneling and wood fragmentation, biotic interactions, and nitrogen fixation.

Several studies have provided some insights on the use of tree hollows by invertebrates and insects, although such studies are few in the Pacific Northwest. In Sweden, Taylor and Ranius (2014) found that tree hollows provide for a unique assemblage of oribatid mite species. Müller et al. (2014) found that hollow European beech trees provide key habitat for saproxylic beetles, and other studies likewise reported on the value of tree hollows for beetles (Ranius and Hedin 2001, Sverdrup-Thygeson et al. 2010).

Many studies report on saproxylic beetles, including bark beetles and other native and exotic forest insect pests, not covered in this brief review (although for some recent work in the Pacific Northwest and beyond, see Aukema et al. 2010; Brin et al. 2011; Carlsson et al. 2016; Donato et al. 2013; Edworthy et al. 2011; Floren et al. 2014; Gossner et al. 2013; Janssen et al. 2011; Klutsch et al. 2014; Ranius 2000, 2001; Ranius et al. 2011; and others).

#### Ecosystem engineers—

A number of species—including fungi, rooted plants, microbes, invertebrates, birds, and mammals—serve as "ecosystem engineers" when they fell live trees to create down wood (fig. 13), create cavities in snags or down wood (fig. 14), break down coarse woody debris (fig. 15), chew wood fiber, and engage in chemical and nutrient transformation of decaying wood (Hart et al. 2005, Petrosillo and Zurlini 2016, Thompson et al. 2016). Pileated woodpeckers, in particular, can create so many feeding and exploratory cavities in snags so as to contribute greatly to the snag's disintegration and ultimate decomposition, including creation of shredded wood piles at the base of the tree bole; in turn, such bark piles can serve as habitat for a variety of snakes, lizards, and amphibians (fig. 16). Cavity-creation in standing and down trees also can serve as a point of introduction of fungi, insects, and other organisms participating in wood decay (fig. 17).



Figure 13—Cottonwood felled by American beaver (*Castor canadensis*) activity. Beaver can act as "ecosystem engineers" and contribute to wood decay elements. Middle Fork John Day River, Oregon.



Figure 14—Northern flicker (*Colaptes auratus*) in a nest cavity created in a snag. White Salmon, Cascade Mountains, southern Washington.



Figure 15—A Douglas-fir log torn apart by a black bear in search of grub forage. Like beavers (fig. 13), black bears also can serve as "ecosystem engineers" by hastening decomposition and decay of down wood. Douglas-fir/Oregon white oak forest, Medford District, Bureau of Land Management, southern Oregon.

Bruce



Figure 16—An old Douglas-fir heavily used by pileated woodpeckers for foraging, creating a pile of bark and wood chips at the base, which can be habitat for a variety of amphibians, reptiles, and small mammals. Such bark-chip microhabitats are little studied in the Pacific Northwest. Mixed-conifer forest, Tryon Creek State Park, western Oregon.



Figure 17—Woodpecker cavities in a Douglas-fir snag. Such cavities can create entry points for wood-decaying fungi and invertebrates, and can serve as roost and nest sites for other wildlife. Douglas-fir/ Oregon white oak (*Quercus garryana*) forest, Medford District, Bureau of Land Management, southern Oregon.

## Fire and Decaying Wood

## Effect of fire on wood decay ecology-

Fire can affect the amount and distribution of wood decay elements (Everett et al. 1999) and their associated ecological roles and microbial constituents (Hansen et al. 1991, Harvey 1994, Harvey et al. 1976a) with various influences on soil productivity and subsequent growth of conifer trees (Acker et al. 2017, Zabowski et al. 2000). Intense, hot fires can do a lot of damage to the soil ecosystem by excessively removing decaying wood from the forest floor (fig. 18). In forests of the inland Western United States, Harvey (1993) found that severe and extreme burns resulted in loss of major amounts of mineralizable nitrogen and organic matter that provided nutrient-cycling roles, whereas slight burns had little effect.



Figure 18—Result of concentrated, hot burning of a slash pile following clearcutting in a mixed-conifer forest. This activity here on private timber land—may reduce fuels, but it also reduces soil productivity, tree regeneration, and down wood habitat for wildlife. White Salmon, Cascade Mountains, southern Washington.

Hart et al. (2005) listed the many services and functional roles of soil microorganisms, including their influence on nutrient development and transfer, improving soil structure, and providing plant roots with mutualisms that improve health. They reported that fire alters soil communities in the short term through mortality of microorganisms and in the long term by altering plant community composition, and that research needs to focus more on the influence of long-term plant community responses on mutually dependent soil microflora. In the central eastern Cascade Range of Washington, Hatten et al. (2005) found little difference in soil attributes (pH, carbon, nitrogen, carbon:nitrogen ratio, cation exchange capacity, base saturation (percent), hydrophobicity and extractable phosphorus) between unburned forests of ponderosa pine and Douglas-fir, compared with sites burned by low-severity fires, and that attendant soil processes were not adversely affected by such fire regimes there.

Other studies of the influence of fire on coarse woody debris, biodiversity, and plant communities have been conducted in New Mexico (Holden et al. 2006), the intermountain West (Jenkins et al. 2008), the Sierra Nevada of California (Johnson et al. 2005, Knapp et al. 2005), the Rocky Mountains (Naficy et al. 2010, Romme et al. 2011), Arizona (Passovoy and Fule 2006), Australia (Bassett et al. 2015, Haslem et al. 2011, Lindenmayer et al. 2012, McLean et al. 2015), New Zealand (McIntosh et al. 2005), and elsewhere.

### Effect of fire on amounts and distribution of dead wood-

Wildfire can greatly increase the net amount of down wood in a stand (fig. 19), whereas timber harvesting may increase or decrease down wood, depending on postharvest and site preparation activities, and if unmerchantable woody material is left on site, piled and burned, or otherwise removed, and depending on time since last fire, the type and intensity of fire, and other factors (Kimmey and Furniss 1943, Lowell et al. 1992, Morris 1970). In the eastern Cascades of Washington, Lyons-Tinsley and Peterson (2012) found that young stands of dry mixed-conifer forests were resilient to wildfire if surface fuel loading was low when the stand was established. Peterson et al. (2015) reported that logging following wildfire in mixed-conifer forests of eastern Washington and Oregon can greatly reduce surface fuel levels up to four decades after the fire incident, but the amount remaining depends on volumes and sizes of wood removed, logging methods, fuel treatments, and other management activities.



Figure 19—Down wood resulting from an extensive stand-replacing wildfire in a dry Douglas-fir forest. Such down wood can provide some habitat for small mammals and other wildlife and contribute organic matter and nutrients to the soil. Tower and Summit Burn, Malheur National Forest, Oregon.

Foster et al. (1998) reported that ecological results and subsequent patterns of forest development after various kinds of major, infrequent disturbance events fire, hurricanes, tornadoes, volcanic eruptions, and floods—differed greatly depending on the disturbance, the abiotic environment (especially topography), and the composition and structure of the vegetation at the time of the disturbance. Franklin et al. (2000) similarly found great differences in kinds and amounts of legacy wood (large, remnant trees, snags, and down wood) resulting from even-age silvicultural disturbances (especially clearcutting) and natural disturbances, such as windthrow (figs. 20 and 21), wildfire, and volcanic eruptions.



Figure 20—Canopy gap likely created by a sudden microburst wind event. Sky Lakes Wilderness, Upper Klamath Lake, southern Oregon.



Figure 21—"Jackstraw" down logs and branches created by the microburst event shown in figure 20. Sky Lakes Wilderness, Upper Klamath Lake, southern Oregon.

Acker et al. (2013) reported that snags persisted standing, in a mountain hemlock forest in the Cascade Range of Oregon following wildfire, at a rate of >75 percent after 5 years and >50 percent after 10 years, with larger diameter snags persisting longer. Snag persistence rate was higher than expected because of the cold climate and shorter growing season for decay organisms than in lower elevation forests. The authors further hypothesized that patches of high-severity fire can effectively block the spread of crown fires for decades.

Dunn and Bailey (2016) studied the effect of the absence of fire and fires of varying severity on tree mortality and forest stand structure in Douglas-fir forests of the western Cascades of Oregon. They found that larger diameter at breast height (d.b.h.) trees, except for western hemlock, had lower probability of mortality from fire, and that larger d.b.h. snags had lower falling rates postfire and with lower severity fire. They concluded that mixed-severity fire creates structural diversity in Douglas-fir forests of the Pacific Northwest and should be provided through fire management programs to maintain the fire regime into the future.

## Burning in timber harvests—

In one study in lodgepole pine forests of Wyoming, Tinker and Knight (2000) found that with repeated timber harvests, dead wood remaining as slash and stumps may decline and that forest floor and surface soil characteristics may be beyond the historical range of variability of naturally developing stands. In another study, burning of logging residue ("slash") after clearcutting aided second-year survival and height growth of seedlings planted in a high-elevation subalpine fir and lodgepole pine forest in north-central Washington (Lopushinsky et al. 1992). However, longer term effects of removing wood decay elements from subsequent growing forests were not included in this study, and productivity (seedling growth and survival, as distinguished from initial seedling establishment) may later decline (Minore 1986).

## Fire and fungi—

Dead wood, and to a lesser extent humus, are habitat for mycorrhizae that provide for early forest regeneration in moist, moderate, and dry conditions alike, but especially so in dry conditions. When dead wood and soil organic matter are reduced or removed, such as by site preparation and slash burning, plantations might still become established, but subsequent tree growth, health, and survival may be poor (Harvey 1993).

### Safety considerations—

Human safety can be a major concern with wildfire or prescribed fires, and such concerns may override the need to retain wood decay elements in fire-prone forests near human habitations (Winter et al. 2002). Balancing forest restoration with safety concerns is complex (Fule et al. 2001) and beyond the scope of this discussion.

## Effect of charring—

Case-hardening or external charring of down logs from surface fires does not significantly reduce the microbial and mycorrhizal functions of the wood, and, in fact, is habitat for a number of fungi species that specifically tolerate such charred surfaces. However, charring and hardening might adversely affect the value of down wood and the soil organic horizon as habitat for some invertebrates and wildlife (Simon et al. 2002, Wikars and Schimmel 2001).

## Soil temperature effects—

Standing live trees and snags have little direct effect on soil temperature during forest fires. Rather, it is the down wood, especially the large coarse wood on the forest floor, that affects soil temperature during burns (Harvey 1993).

## Fire and wildlife—

Effects of fire on wildlife populations and habitats have been studied in various aspects. As an example, in Idaho, Saab et al. (2007, 2011) found diverse responses to postfire salvage logging and time since wildfire among seven cavity-nesting bird species, depending on the birds' foraging behaviors and habitat selections. However, nesting survival differed little among the species in part because the salvage logging prescription included retention of more than half of the snags >23 centimeters (9.1 inches) d.b.h. Wiebe (2014) studied the response of northern flickers (*Colaptes auratus*) to low- to moderate-severity fires and found delayed egg laying and smaller clutches in newly excavated cavities on burned sites, and that nests were depredated during the first 3 years after fires, thus reducing productivity even when total density of nesting birds was maintained.

In some circumstances, fire can create tree hollows (fig. 22) and provide snags (fig. 23) that can be used by a wide variety of wildlife (fig. 24). In ponderosa pine forests of south-central Oregon, Wightman et al. (2010) suggested retention of larger decayed snags to provide nesting habitat for white-headed woodpecker (*Picoides albolarvatus*) in recently burned forests. Slash piles from prescribed burns or thinnings can serve as habitat for a wide variety of wildlife species (fig. 25).



Figure 22—Fire scar in an old-growth live ponderosa pine, creating a partially hollow interior that can be used by denning mammals, roosting bats, and other species. Old-growth mixed-conifer forest, Malheur National Forest, Oregon.

Figure 23—An extensive stand of charred snags created by a stand-replacing wildfire. This area contained a remarkably high concentration of Lewis' woodpeckers (*Melanerpes lewis*), American kestrels (*Falco sparverius*), and other species, attracted to the sudden availability of many snags as foraging and nesting substrates. Tower and Summit Burn, Malheur National Forest, Oregon.





Figure 24—American kestrel using a charred and partially hollowed snag, created by a stand-replacing fire, as a perch, nest, and foraging site. Tower and Summit Burn, Malheur National Forest, Oregon.



Figure 25—Large slash piles created from a forest thinning operation designed to reduce tree density and fire hazard. Retaining some slash piles can provide hiding habitat for mustelids, lizard, snakes, and other species. Wenatchee National Forest, Washington.

## Managing Forests for Wood Decay Benefits: How and How Much?

Managing forest for resilience and sustainability is a key objective under current public forest planning in the Pacific Northwest.

## Dynamics of wood decay—

Little research has quantified the role of wood decay in providing for forest biodiversity, sustainability, productivity, and resilience in forests of Washington and Oregon. A few studies have been conducted in other regions and biomes (e.g., Clark et al. 2002 in tropical forests). Thus, we have not yet been able to develop quantitative guidelines for the type, amount, and distribution of wood decay elements needed to maintain specific levels of productivity, tree growth, and other ecosystem processes. However, it is clear that such processes associated with wood decay elements are nonetheless a natural and vital part of native forests and ecosystem processes, as reviewed here, and deserve further study for better understanding how environmental factors, including fire, insects, weather, and wind, drive the dynamics of wood decay (e.g., Garbarino et al. 2015).

## Coarse wood in soils—

Decaying wood is a natural part of forest ecosystems. If depleted, it may take a long time to get wood back into a forest soil. Woody material that is completely buried in some soils of the inland West have been carbon dated to about 500 years old, and some might be 1,000+ years old, especially in stable soils on flat slopes (Harvey 1993). So coarse down wood that enters the soil generally tends to stay there. As well, forest soils tend to develop in place, unlike agricultural soils. All this means that restoring natural levels of coarse wood incorporated into soil horizons may be an immensely long-term process. Also, in some instances, down wood can serve to help stabilize slopes and reduce soil erosion (fig. 26).

Within soil horizons, some tree species' wood is more persistent than others, especially pines, larches, and Douglas-fir, which decompose largely to a "brown rotted wood" condition. These species have very high persistence times within soils, as they have high lignin content that resists decomposition. This means that their beneficial function as reservoirs for moisture, mycorrhizae, microbes, and nutrients can last for decades and centuries.



Figure 26—An example of how down logs laid along contour lines can provide some stability to the slope by intercepting material and stabilizing soil. Old-growth mixed-conifer forest, Malheur National Forest, Oregon.

## Managing for wood decay in soil—

Harvey (1993) has initially recommended, in forests of the inland West, the provision of about 30 percent of organic volume content in soils to maintain peak mycorrhizae amounts in the organic soil horizon. This translates to about 22 to 34 metric tons/hectare (10 to 15 short tons/acre) of surface down wood, which should be relatively large woody residue, scattered across areas with minimal soil disturbance. This recommendation was generally supported by research (e.g., Graham 1981, Graham and Cromack 1982, Harvey et al. 1989) that also found a variation among forest types throughout the Southwestern and Western United States, with western hemlock/*Clintonia* forests with much higher levels, and grand fir/*Acer* forests with much lower levels. In some forests, providing more than 22 to 34 metric tons/hectare (10 to 15 short tons/acre) of coarse down wood may impart a fire hazard. In forests of the inland West, one standard is that about 135 metric tons/hectare (60 short tons/ acre) is a fire hazard (Harvey 1993). So this still gives a broad scope for managing variable amounts of soil organic matter and the coarse woody debris that creates it in inland West forests.

Harvey (1993) also recommended providing coarse, large down wood as sources of soil wood for future nitrogen and nutrient sources, and leaf litter, small twigs, and roots as more immediate sources of nitrogen. But it is only as large chunks does decaying wood provide its most beneficial, long-term ("time-released") ecological services. Large decaying wood provides an acidic, high-phenolic, lignin matrix that best serves conifers and certain soil microbes (but not herbaceous plants and other microbes). Coarse wood in the soil is a unique and critical element for forest productivity.

Chipping of fuel wood and distributing the chips on site does not seem to be an ecologically viable way of reducing excess fuels. In one experiment in a high-elevation forest in Wyoming, Harvey (1993) found that rainfall leached large amounts of toxic, water-soluble phenolics from the chips, and as a result, all tree seedlings died on the site. This leaching also caused soil structure to become blocked after a winter freeze.

Instead, Harvey (1993) recommended potentially using chips to create "artificial logs" (e.g., the artificial "Aqua Log" produced by Big Creek Stream Care Products<sup>3</sup>) to cover <25 percent of the area, creating piles large enough to provide deposits of large coarse wood similar to natural levels. Whether such an approach is economical has not been studied.

## Wood decay and carbon sequestration—

In recent years, much attention has been placed on managing forests for biomass and carbon sequestration, with woody debris being noted to play a role in carbon retention (Bantle et al. 2014, Cousins et al. 2015, Fraver et al. 2013, Schmid et al. 2016). Magnússon et al. (2016) studied the complex interplay of decomposer organisms and wood decay in carbon transfer and sequestration in forest soils. Moroni et al. (2015) highlighted the little-studied but vital role of buried wood as sources and storage of carbon in forest ecosystems, and Hagemann et al. (2010) suggested that bryophytes can play important roles in burying dead wood, reducing its decomposition rate and increasing its carbon storage function.

<sup>&</sup>lt;sup>3</sup> The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

## For Further Reading

This review is by no means an exhaustive survey of research and literature on the topics covered here. In particular, excluded are most references conducted outside the Western United States and in other countries and continents. Here are a few additional resources of potential pertinence to the geographic area and the forest and vegetation types covered by the DecAID Advisor:

See Harmon et al. (1986), Rose et al. (2001), and Maser and Trappe (1984) for more information on ecosystem processes related to wood decay.

Franklin et al. (2000) and Foster et al. (1998) discussed the ecological roles of wood legacies left in forest stands after timber harvesting.

Harvey (1994) and Harvey et al. (1994); also see Hollenstein et al. (2001) and Brown et al. (2003) for discussion on managing forests for wood decay elements.

We have not discussed the role of wood decay in riparian and aquatic systems, although these roles are also vital to maintaining productivity and diversity of those systems (e.g., Keim et al. 2000, Sedell and Maser 1994) and to influencing carbon pools (Chen et al. 2005, Sutfin et al. 2016) and wildlife use (Stephens and Alexander 2011).

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# **Literature Cited**

- Acker, S.A.; Kertis, J.; Bruner, H.; O'Connell, K.; Sexton, J. 2013. Dynamics of coarse woody debris following wildfire in a mountain hemlock (*Tsuga mertensiana*) forest. Forest Ecology and Management. 302: 231–239.
- Acker, S.A.; Kertis, J.A.; Pabst, R.J. 2017. Tree regeneration, understory development, and biomass dynamics following wildfire in a mountain hemlock (*Tsuga mertensiana*) forest. Forest Ecology and Management. 384: 72–82.
- **Alkaslassy, E. 2005.** Abundance of plethodontid salamanders in relation to coarse woody debris in a low elevation mixed forest of the west Cascades. Northwest Science. 79(2–3): 156–163.

- Amaranthus, M.P.; Page-Dumroese, D.; Harvey, A.; Cazares, E.; Bednar, L.F.
  1996. Soil compaction and organic matter affect conifer seedling nonmycorrhizal and ectomycorrhizal root tip abundance and diversity. Res. Pap. PNW-RP-494.
  Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 12 p.
- Amaranthus, M.P.; Parrish, D.S.; Perry, D.A. 1989. Decaying logs as moisture reservoirs after drought and wildfire. In: Alexander, E., ed. Proceedings of the watershed 1989 symposium on stewardship of soil, air, and water resources.
  R10-MB-77. Juneau, AK: U.S. Department of Agriculture, Forest Service, Alaska Region: 191–194.
- Amaranthus, M.P.; Steinfeld, D.E. 1997. Soil compaction after yarding of small-diameter Douglas-fir with a small tractor in southwest Oregon. Res. Pap. PNW-RP-504. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 7 p.
- Aubry, K.B.; Biswell, B.L.; Hayes, J.P.; Marcot, B.G. 2003. The ecological role of tree-dwelling mammals in western coniferous forests. In: Zabel, C.; Anthony, R., eds. Mammal community dynamics: management and conservation in the coniferous forests of western North America. Cambridge, MA: Cambridge University Press: 405–443. Chapter 12.
- Aubry, K.B.; Jones, L.L.C.; Hall, P.A. 1988. Use of woody debris by plethodontid salamanders in Douglas-fir forests in Washington. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 32–37.
- Aukema, B.H.; Zhu, J.; Møller, J.; Rasmussen, J.G.; Raffa, K.F. 2010. Predisposition to bark beetle attack by root herbivores and associated pathogens: roles in forest decline, gap formation, and persistence of endemic bark beetle populations. Forest Ecology and Management. 259(3): 374–382.
- Bantle, A.; Borken, W.; Ellerbrock, R.H.; Schulze, E.D.; Weisser, W.W.; Matzner, E. 2014. Quantity and quality of dissolved organic carbon released from coarse woody debris of different tree species in the early phase of decomposition. Forest Ecology and Management. 329: 287–294.

Bassett, M.; Chia, E.K.; Leonard, S.W.J.; Nimmo, D.G.; Holland, G.J.; Ritchie, E.G.; Clarke, M.F.; Bennett, A.F. 2015. The effects of topographic variation and the fire regime on coarse woody debris: insights from a large wildfire. Forest Ecology and Management. 340: 126–134.

- Bowman, J.C.; Sleep, D.; Forbes, G.J.; Edwards, M. 2000. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management. 129(1–3): 119–124.
- Brang, P.; Moran, J.; Puttonen, P.; Vyse, A. 2003. Regeneration of *Picea* engelmannii and Abies lasiocarpa in high-elevation forests of south-central British Columbia depends on nurse logs. Forestry Chronicle. 79(2): 247–252.
- Brin, A.; Bouget, C.; Brustel, H.; Jactel, H. 2011. Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. Journal of Insect Conservation. 15(5): 653–669.
- Brown, J.K.; Reinhardt, E.D.; Kramer, K.A. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. Gen. Tech. Rep. RMRS-GTR-105. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 16 p.
- **Bull, E.L.; Akenson, J.J.; Henjum, M.G. 2000.** Characteristics of black bear dens in trees and logs in northeastern Oregon. Northwestern Naturalist. 81: 148–153.
- Bull, E.L.; Blumton, A.K. 1999. Effect of fuels reduction on American marten and their prey. Res. Note PNW-RN-539. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 9 p.
- **Butts, S.R.; McComb, W.C. 2000.** Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. Journal of Wildlife Management. 64(1): 95–104.
- **Carlsson, S.; Bergman, K.-O.; Jansson, N.; Ranius, T.; Milberg, P. 2016.** Boxing for biodiversity: evaluation of an artificially created decaying wood habitat. Biodiversity and Conservation. 25(2): 393–405.
- Charter, M.; Izhaki, I.; Mocha, Y.B.; Kark, S. 2016. Nest-site competition between invasive and native cavity nesting birds and its implication for conservation. Journal of Environmental Management. 181: 129–134.
- Chen, X.; Wei, X.; Scherer, R. 2005. Influence of wildfire and harvest on biomass, carbon pool, and decomposition of large woody debris in forested streams of southern interior British Columbia. Forest Ecology and Management. 208(103): 101–114.

- Clark, D.B.; Clark, D.A.; Brown, S.; Oberbauer, S.F.; Veldkamp, E. 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. Forest Ecology and Management. 164(1–3): 237–248.
- **Cousins, S.J.M.; Battles, J.J.; Sanders, J.E.; York, R.A. 2015.** Decay patterns and carbon density of standing dead trees in California mixed conifer forests. Forest Ecology and Management. 353: 136–147.
- Crawford, R.H.; Carpenter, S.E.; Harmon, M.E. 1990. Communities of filamentous fungi and yeast in decomposing logs of *Pseudotsuga menziesii*. Mycologia. 82(6): 759–765.
- **Donato, D.C.; Harvey, B.J.; Romme, W.H.; Simard, M.; Turner, M.G. 2013.** Bark beetle effects on fuel profiles across a range of stand structures in Douglasfir forests of Greater Yellowstone. Ecological Applications. 23(1): 3–20.
- Dunn, C.J.; Bailey, J.D. 2016. Tree mortality and structural change following mixed-severity fire in *Pseudotsuga* forests of Oregon's western Cascades, USA. Forest Ecology and Management. 365: 107–118.
- Edmonds, R.L.; Binkley, D.; Feller, M.C.; Sollins, P.; Abee, A.; Myrold, D.D.
  1989. Nutrient cycling: effects on productivity of Northwest forests. In: Perry, D.A.; Meurisse, R.; Thomas, B.; Miller, R.; Boyle, J.; Means, J.; Perry, C.R.; Powers, R.F., eds. Maintaining the long-term productivity of Pacific Northwest forest ecosystems. Portland, OR: Timber Press: 17–35.
- Edworthy, A.B.; Drever, M.C.; Martin, K. 2011. Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. Forest Ecology and Management. 261(2): 203–210.
- Everett, R.; Lehmkuhl, J.; Schellhaas, R.; Ohlson, P.; Keenum, D.; Riesterer,
  H.; Spurbeck, D. 1999. Snag dynamics in a chronosequence of 26 wildfires on
  the east slope of the Cascade Range in Washington state, USA. International
  Journal of Wildland Fire. 9(4): 223–234.
- Fischer, W.C.; McClelland, B.R. 1983. A cavity-nesting bird bibliography including related titles on forest snags, fire, insects, disease, and decay.
  Gen. Tech. Rep. INT-140. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 79 p.
- Floren, A.; Müller, T.; Dittrich, M.; Weiss, M.; Linsenmair, K.E. 2014. The influence of tree species, stratum and forest management on beetle assemblages responding to deadwood enrichment. Forest Ecology and Management. 323: 57–64.

- Fogel, R.; Hunt, G. 1983. Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. Canadian Journal of Forest Research. 13: 219–232.
- Foster, D.R.; Knight, D.H.; Franklin, J.F. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems. 1: 497–510.
- Franklin, J.F.; Lindenmayer, D.; MacMahon, J.A.; McKee, A.; Magnuson, J.; Perry, D.A.; Waide, R.; Foster, D. 2000. Threads of continuity. Conservation Biology in Practice. 1(1): 9–16.
- Fraver, S.; Milo, A.M.; Bradford, J.B.; D'Amato, A.W.; Kenefic, L.; Palik, B.J.; Woodall, C.W.; Brissette, J. 2013. Woody debris volume depletion through decay: implications for biomass and carbon accounting. Ecosystems. 16(7): 1262–1272.
- Fulé, P.Z.; Waltz, A.E.M.; Covington, W.W.; Heinlein, T.A. 2001. Measuring forest restoration effectiveness in reducing hazardous fuels. Journal of Forestry. 99(11): 24–29.
- Garbarino, M.; Marzano, R.; Shaw, J.D.; Long, J.N. 2015. Environmental drivers of deadwood dynamics in woodlands and forests. Ecosphere. 6(3): 1–24. doi:10.1890/ES14-00342.1
- **Gossner, M.M.; Floren, A.; Weisser, W.W.; Linsenmair, K.E. 2013.** Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. Forest Ecology and Management. 302: 404–413.
- **Graham, R.L.L. 1981.** Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Corvallis, OR: Oregon State University. 152 p. Ph.D. dissertation.
- Graham, R.L.; Cromack, K., Jr. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Canadian Journal of Forest Research. 12: 511–521.
- Gray, A.N.; Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology. 78: 2458–2473.
- Grier, C.C. 1978. A *Tsuga heterophylla–Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Canadian Journal of Forest Research. 8: 198–206.

- Hagemann, U.; Moroni, M.T.; Gleißner, J.; Makeschin, F. 2010. Accumulation and preservation of dead wood upon burial by bryophytes. Ecosystems. 13(4): 600–611.
- Hansen, A.J.; Spies, T.A.; Swanson, F.J.; Ohmann, J.L. 1991. Conserving biodiversity in managed forests. BioScience. 41(6): 382–392.
- Harmon, M.E.; Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology. 70: 48–59.
- Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, F.J.P.; Gregory, S.V.;
  Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.;
  Lienkaemper, G.W.; Cromack, K., Jr.; Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research. 15: 133–302.
- Hart, S.C.; Deluca, T.H.; Newman, G.S.; MacKenzie, M.D.; Boyle, S.I. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. Forest Ecology and Management. 220(1–3): 166–184.
- Harvey, A. 1993. Soil structure and function. Taped lecture as part of seminar series "Soil: The Foundation of the Ecosystem." Blue Mountains Research Institute, Oregon. Produced by U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR 97204.
- Harvey, A.E. 1994. Integrated roles for insects, diseases and decomposers in fire dominated forests of the inland Western United States: past, present and future forest health. In: Sampson, R.N.; Adams, D.L.; Enzer, M.J., eds. Assessing forest ecosystem health in the inland West. New York: Haworth Press: 211–220.
- Harvey, A.E.; Jurgensen, M.F.; Larsen, M.J. 1976a. Intensive fiber utilization and prescribed fire: effects on the microbial ecology of forests. Gen. Tech. Rep. INT-28. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 46 p.
- Harvey, A.E.; Larson, M.J.; Jurgensen, M.F. 1976b. Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. Forest Science. 22: 393–398.
- Harvey, A.E.; Geist, J.M.; McDonald, G.I.; Jurgensen, M.F.; Cochran, P.H.; Zabowski, D.; Meurisse, R.T. 1994. Biotic and abiotic processes in eastside ecosystems: the effects of management on soil properties, processes, and productivity. Gen. Tech. Rep. PNW-GTR-323. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 70 p.

- Haslem, A.; Kelly, L.T.; Nimmo, D.G.; Watson, S.J.; Kenny, S.A.; Taylor, R.S.;
  Avitabile, S.C.; Callister, K.E.; Spence-Bailey, L.M.; Clarke, M.F.; Bennett,
  A.F. 2011. Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. Journal of Applied Ecology. 48(1): 247–256.
- Hatten, J.; Zabowski, D.; Scherer, G.; Dolan, E. 2005. A comparison of soil properties after contemporary wildfire and fire suppression. Forest Ecology and Management. 220(1–3): 227–241.
- Holden, Z.A.; Morgan, P.; Rollins, M.G.; Wright, R.G. 2006. Ponderosa pine snag densities following multiple fires in the Gila Wilderness, New Mexico. Forest Ecology and Management. 221(1–3): 140–146.
- **Hollenstein, K.; Graham, R.L.; Shepperd, W.D. 2001.** Biomass flow in western forests: simulating the effects of fuel reduction and presettlement restoration treatments. Journal of Forestry. 99(10): 12–19.
- Hyvonen, R.; Olsson, B.A.; Lundkvist, H.; Staaf, H. 2000. Decomposition and nutrient release from *Picea abies* (L.) Karst. and *Pinus sylvestris* L. logging residues. Forest Ecology and Management. 126(2): 97–112.
- Janssen, P.; Hébert, C.; Fortin, D. 2011. Biodiversity conservation in old-growth boreal forest: black spruce and balsam fir snags harbour distinct assemblages of saproxylic beetles. Biodiversity and Conservation. 20(13): 2917–2932.
- Jenkins, M.J.; Hebertson, E.; Page, W.; Jorgensen, C.A. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecology and Management. 254: 16–34.
- Johnson, D.W.; Murphy, J.F.; Susfalk, R.B.; Caldwell, T.G.; Miller, W.W.; Walker, R.F.; Powers, R.F. 2005. The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. Forest Ecology and Management. 220(1–3): 155–165.
- Juutilainen, K.; Halme, P.; Kotiranta, H.; Mönkkönen, M. 2011. Size matters in studies of dead wood and wood-inhabiting fungi. Fungal Ecology. 4(5): 342–349.
- Kaila, L.; Martikainen, P.; Punttila, P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation. 6: 1–18.
- Keim, R.F.; Skaugset, A.E.; Bateman, D.S. 2000. Dynamics of coarse woody debris placed in three Oregon streams. Forest Science. 46(1): 13–22.

- **Kimmey, J.W.; Furniss, R.L. 1943.** Deterioration of fire-killed Douglas-fir. Tech. Bull. 85. Washington, DC: U.S. Department of Agriculture, Forest Service. 61 p.
- Klutsch, J.G.; Beam, R.D.; Jacobi, W.R.; Negrón, J.F. 2014. Bark beetles and dwarf mistletoe interact to alter downed woody material, canopy structure, and stand characteristics in northern Colorado ponderosa pine. Forest Ecology and Management. 315: 63–71.
- Knapp, E.E.; Keeley, J.E.; Ballenger, E.A.; Brennan, T.J. 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. Forest Ecology and Management. 208(103): 383–397.
- Koenigs, E.; Shea, P.J.; Borys, R.; Haverty, M.I. 2002. An investigation of the insect fauna associated with coarse woody debris of *Pinus ponderosa* and *Abies concolor* in northeastern California. In: Laudenslayer, W.F., Jr.; Shea, P.J.; Valentine, B.E.; Weatherspoon, C.P.; Lisle, T.E., eds. Proceedings of the symposium on the ecology and management of dead wood in western forests. Gen. Tech. Rep. PSW-GTR-181. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 97–110.
- Kroll, A.J.; Lacki, M.J.; Arnett, E.B. 2012. Research needs to support management and conservation of cavity-dependent birds and bats on forested landscapes in the Pacific Northwest. Western Journal of Applied Forestry. 27(3): 128–136.
- Li, C.Y.; Crawford, R.H. [In press]. The biological significance of coarse woody debris in forest ecosystems. In: Yang, J.C., ed. Sino-American forestry technology cooperation symposium on sustainable management of temperate and subtropical plantation ecosystems. Taipei, Taiwan: Council of Agriculture.
- Li, C.Y.; Maser, C.; Fay, H. 1986a. Initial survey of acetylene reduction and selected microorganisms in the feces of 19 species of mammals. Great Basin Naturalist. 46: 646–650.
- Li, C.Y.; Maser, C.; Maser, Z.; Caldwell, B.A. 1986b. Role of three rodents in forest nitrogen fixation in western Oregon: another aspect of mammalmychorrizal fungus-tree mutualism. Great Basin Naturalist. 46: 411–414.
- Lindenmayer, D.B.; Blanchard, W.; McBurney, L.; Blair, D.; Banks, S.; Likens, G.E.; Franklin, J.F.; Laurance, W.F.; Stein, J.A.R.; Gibbons, P. 2012. Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. PLoS ONE. 7(10): e41864. doi:10.1371/journal.pone.0041864.

- Lopushinsky, W.; Zabowski, D.; Anderson. T.D. 1992. Early survival and height growth of Douglas-fir and lodgepole pine seedlings and variations in site factors following treatment of logging residues. Res. Pap. PNW-RP-451. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 22 p.
- Lorenz, T.J.; Vierling, K.T.; Johnson, T.R.; Fischer, P.C. 2015. The role of wood hardness in limiting nest site selection in avian cavity excavators. Ecological Applications. 25(4): 1016–1033.
- Lowell, E.; Willits, S.; Krahmer, R. 1992. Deterioration of fire-killed and firedamaged timber in the Western United States. Gen. Tech. Rep. PNW-GTR-292. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 12 p.
- Lyons-Tinsley, C.; Peterson, D.L. 2012. Surface fuel treatments in young, regenerating stands affect wildfire severity in a mixed conifer forest, eastside Cascade Range, Washington, USA. Forest Ecology and Management. 270: 117–125.
- Magnússon, R.Í.; Tietema, A.; Cornelissen, J.H.C.; Hefting, M.M.; Kalbitz, K. 2016. Tamm review: sequestration of carbon from coarse woody debris in forest soils. Forest Ecology and Management. 377: 1–15.
- Maser, C.; Anderson, R.G.; Cormack, K., Jr.; Williams, J.T.; Martin, R.E.
  1979. Dead and down woody material. In: Thomas, J.W., ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 78–95.
- Maser, C.; Maser, Z. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Naturalist. 48: 358–369.
- Maser, C.; Trappe, J.M. 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 56 p.
- Maser, C.; Trappe, J.M.; Nussbaum, R.A. 1978. Fungal-small mammal relationships with emphasis on Oregon coniferous forests. Ecology. 59: 799–809.
- McFee, W.W.; Stone, E.L. 1966. The persistence of decaying wood in the humus layer of northern forests. Soil Science Society of America Proceedings. 30: 512–516.

- McIntosh, P.D.; Laffan, M.D.; Hewitt, A.E. 2005. The role of fire and nutrient loss in the genesis of the forest soils of Tasmania and southern New Zealand. Forest Ecology and Management. 220(1–3): 185–215.
- McLean, C.M.; Bradstock, R.; Price, O.; Kavanagh, R.P. 2015. Tree hollows and forest stand structure in Australian warm temperate *Eucalyptus* forests are adversely affected by logging more than wildfire. Forest Ecology and Management. 341: 37–44.
- Means, J.E.; MacMillan, P.C.; Cromack, K., Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, U.S.A. Canadian Journal of Forest Research. 22: 1536–1546.
- Minore, D. 1986. Effects of site preparation on seedling growth: a preliminary comparison of broadcast burning and pile burning. Res. Note PNW- RN-452. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 12 p.
- Moroni, M.T.; Morris, D.M.; Shaw, C.; Stokland, J.N.; Harmon, M.E.;
  Fenton, N.J.; Merganičová, K.; Merganič, J.; Okabe, K.; Hagemann, U.
  2015. Buried wood: a common yet poorly documented form of deadwood.
  Ecosystems.18(4): 605–628.
- Morris, W.G. 1970. Effects of slash burning in overmature stands of the Douglasfir region. Forest Science. 16: 258–270.
- Müller, J.; Jarzabek-Müller, A.; Bussler, H.; Gossner, M.M. 2014. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. Animal Conservation. 17(2): 154–162.
- Naficy, C.; Sala, A.; Keeling, E.G.; Graham, J.; DeLuca, T.H. 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecological Applications. 20(7): 1851–1864.
- **O'Hanlon-Manners, D.L.; Kotanen, P.M. 2004**. Logs as refuges from fungal pathogens for seeds of eastern hemlock (*Tsuga canadensis*). Ecology. 85(1): 284–289.
- Padilla, F.M.; Pugnaire, F.I. 2006. The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment. 4(4): 196–202.

- Page-Dumroese, D.S.; Harvey, A.E.; Jurgensen, M.F.; Amaranthus, M.P. 1998. Impacts of soil compaction and tree stump removal on soil properties and outplanted seedlings in northern Idaho, USA. Canadian Journal of Soil Science. 78: 29–34.
- **Passovoy, M.D.; Fulé, P.Z. 2006.** Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. Forest Ecology and Management. 223(1–3): 237–246.
- Peterson, D.W.; Dodson, E.K.; Harrod, R.J. 2015. Post-fire logging reduces surface woody fuels up to four decades following wildfire. Forest Ecology and Management. 338: 84–91.
- **Petrosillo, I.; Zurlini, G. 2016.** The important role of ecological engineers in providing ecosystem services at landscape level. Animal Conservation. 19(6): 500-501.
- Rabe, M.J.; Morrell, T.E.; Green, H.; deVos, J.C., Jr.; Miller, C.R. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. Journal of Wildlife Management. 62(2): 612–621.
- **Ranius, T. 2000.** Minimum viable metapopulation size of a beetle, *Osmoderma eremita*, living in tree hollows. Animal Conservation. 3: 37–43.
- **Ranius, T. 2001.** Constancy and asynchrony of *Osmoderma eremita* populations in tree hollows. Oecologia. 126(2): 208–215.
- Ranius, T.; Hedin, J. 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia. 126(3): 363–370.
- Ranius, T.; Martikainen, P.; Kouki, J. 2011. Colonisation of ephemeral forest habitats by specialised species: beetles and bugs associated with recently dead aspen wood. Biodiversity and Conservation. 20(13): 2903–2915.
- Romme, W.H.; Boyce, M.S.; Gresswell, R.; Merrill, E.H.; Minshall, G.W.;
  Whitlock, C.; Turner, M.G. 2011. Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. Ecosystems. 14(7): 1196–1215.
- Rose, C.L.; Marcot, B.G.; Mellen, T.K.; Ohmann, J.L.; Waddell, K.L.; Lindley, D.L.; Schreiber, B. 2001. Decaying wood in Pacific Northwest forests: concepts and tools for habitat management. In: Johnson, D.H.; O'Neil, T.A., eds. Wildlife-habitat relationships in Oregon and Washington. Corvallis, OR: Oregon State University Press: 580–623.

- Saab, V.A.; Russell, R.E.; Dudley, J.G. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor. 109(1): 97–108.
- Saab, V.A.; Russell, R.E.; Rotella, J.; Dudley, J.G. 2011. Modeling nest survival of cavity-nesting birds in relation to postfire salvage logging. Journal of Wildlife Management. 75(4): 794–804.
- Schmid, A.V.; Vogel, C.S.; Liebman, E.; Curtis, P.S.; Gough, C.M. 2016. Coarse woody debris and the carbon balance of a moderately disturbed forest. Forest Ecology and Management. 361: 38–45.
- Sedell, J.; Maser, C. 1994. From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans. Delray Beach, FL: St. Lucia Press. 200 p.
- Seibold, S.; Bässler, C.; Brandl, R.; Gossner, M.M.; Thorn, S.; Ulyshen, M.D.;
  Müller, J. 2015. Experimental studies of dead-wood biodiversity—a review identifying global gaps in knowledge. Biological Conservation. 191: 139–149.
- Simon, N.P.; Stratton, C.B.; Forbes, G.J.; Schwab, F.E. 2002. Similarity of small mammal abundance in post-fire and clearcut forests. Forest Ecology and Management. 164(1–3): 163–172.
- Smith, J.E.; Molina, R.; Huso, M.M.P.; Larsen, M.J. 2000. Occurence of *Piloderma fallax* in young, rotation age, and old-growth stands of Douglasfir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, USA. Canadian Journal of Botany. 78: 995–1001.
- Smith, S.E.; Read, D.J. 1997. Mycorrhizal symbioses. 2<sup>nd</sup> ed. New York: Academic Press. 605 p.
- Stephens, J.L.; Alexander, J.D. 2011. Effects of fuel reduction on bird density and reproductive success in riparian areas of mixed-conifer forest in southwest Oregon. Forest Ecology and Management. 261(1): 43–49.
- Sutfin, N.A.; Wohl, E.E.; Dwire, K.A. 2016. Banking carbon: a review of organic carbon storage and physical factors influencing retention in floodplains and riparian ecosystems. Earth Surface Processes and Landforms. 41: 38–60.
- Sverdrup-Thygeson, A.; Skarpaas, O.; Ødegaard, F. 2010. Hollow oaks and beetle conservation: the significance of the surroundings. Biodiversity and Conservation. 19(3): 837–852.
- **Tallmon, D.; Mills, L.S. 1994.** Use of logs within home ranges of California redbacked voles on a remnant of forest. Journal of Mammology. 75(1): 97–101.

- **Taylor, A.R.; Ranius, T. 2014.** Tree hollows harbour a specialised oribatid mite fauna. Journal of Insect Conservation. 18(1): 39–55.
- Thompson, S.; Vehkaoja, M.; Nummi, P. 2016. Beaver-created deadwood dynamics in the boreal forest. Forest Ecology and Management. 360: 1-8.
- **Tinker, D.B.; Knight, D.H. 2000.** Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems. 3: 472–483.
- Tinnin, R.O.; Forbes, R.B. 1999. Red squirrel nests in witches' brooms in Douglas-fir trees. Northwestern Naturalist. 80: 17–21.
- **Ulyshen, M.D. 2016.** Wood decomposition as influenced by invertebrates. Biological Reviews. 91: 70–85.
- Van Cleve, K.; Noonan, L.L. 1975. Litter fall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. Canadian Journal of Forest Research. 5: 626–639.
- van der Wal, A.; Ottosson, E.; de Boer, W. 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. Ecology. 96(1): 124–133.
- Vonhof, M.J.; Barclay, R.M.R. 1997. Use of tree stumps as roosts by the western long-eared bat. Journal of Wildlife Management. 61(3): 674–684.
- Weslien, J.; Djupström, L.B.; Schroeder, M.; Widenfalk, O. 2011. Long-term priority effects among insects and fungi colonizing decaying wood. Journal of Animal Ecology. 80(6): 1155–1162.
- **Wiebe, K.L. 2014.** Responses of cavity-nesting birds to fire: testing a general model with data from the Northern Flicker. Ecology. 95(9): 2537–2547.
- Wightman, C.S.; Saab, V.A.; Forristal, C.; Mellen-McLean, K.; Markus,
  A. 2010. White-headed woodpecker nesting ecology after wildfire. Journal of Wildlife Management. 74(5): 1098–1106.
- Wikars, L.O.; Schimmel, J. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. Forest Ecology and Management. 141(3): 189–200.
- Winter, G.J.; Vogt, C.; Fried, J.S. 2002. Fuel treatments at the wildland-urban interface: common concerns in diverse regions. Journal of Forestry. 100(1): 15–22.

- Zabowski, D.; Java, B.; Scherer, G.; Everett, R.L.; Ottmar, R. 2000. Timber harvesting residue treatment: Part 1. Responses of conifer seedlings, soils and microclimate. Forest Ecology and Management. 126(1): 25–34.
- Zak, B. 1971. Characterization and classification of mycorrhizae of Douglas-fir.
  II. *Pseudotsuga menziesii + Rhizopogon vinicolor*. Canadian Journal of Botany.
  49: 1079–1084.

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