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The Role of Deadwood in the Carbon Cycle: Implications for Models, Forest Management, and Future Climates

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Abstract

Deadwood represents a significant carbon pool and unique biodiversity reservoir in forests and savannas but has been largely overlooked until recently. Storage and release of carbon from deadwood is controlled by interacting decomposition drivers including biotic consumers (animals and microbes) and abiotic factors (water, fire, sunlight, and freeze–thaw). Although previous research has focused mainly on forests, we synthesize deadwood studies across diverse ecosystems with woody vegetation. As changing climates and land-use practices alter the landscape, we expect accelerating but variable rates of inputs and outputs from deadwood pools. Currently, Earth system models implicitly represent only microbial consumers as drivers of wood decomposition; we show that many other factors influence deadwood pools. Forest management practices increasingly recognize deadwood as an important contributor to forest dynamics, biodiversity, and carbon budgets. Together, emerging knowledge from modeling and management suggests a growing need for additional research on deadwood contributions to carbon storage and greenhouse gas emissions.

1. INTRODUCTION: DEADWOOD AND THE CARBON CYCLE

Plants constitute ~80% of all living biomass (Bar-On et al. 2018) and assimilate one fifth of atmospheric carbon each year (Keenan & Williams 2018). Plants developed adaptive strategies to partition this carbon into leaf, branch, stem, root, and reproductive tissues. Plant carbon is returned to the atmosphere and released into the soil through decomposition, including biotically via microbes and animals and abiotically via fire, solar radiation, leaching, and freeze–thaw cycles (**Figure 1**). Different plant growth forms have subsequently emerged, with long-lived plants, including trees, shrubs, and lianas, developing stems made of woody tissue to achieve positive competitive outcomes and longevity. Woody plants are found across ecosystems around the globe (Crowther et al. 2015), although woody species increase in relative abundance toward the tropics (Zanne et al. 2014). While the distribution and decomposition patterns of leaf litter are relatively well understood (Cornwell et al. 2008, García-Palacios et al. 2013, Krishna & Mohan 2017), those of woody tissues are more uncertain. As a large carbon pool (Pan et al. 2011) that harbors forest biodiversity (Stokland et al. 2012), deadwood represents an integral part of the carbon cycle. Throughout this review, we synthesize current knowledge on deadwood contributions to the carbon cycle, with a view to better understanding and predicting future changes in these contributions as abiotic and biotic drivers of outputs (i.e., decomposition rates of deadwood) respond to global change processes.

We begin by summarizing the basics of the global importance of deadwood pools, including their distributions, and give a brief introduction to processes driving their inputs and rates and forms of outputs (see the sidebar titled Terms). Then, we focus in depth on how inputs and outputs from deadwood pools are driven by different abiotic and biotic decomposition drivers acting across spatial and temporal scales, how these inputs and outputs are likely to respond to future changes in climate and land use, and how to model the contributions of deadwood to the carbon cycle and better predict changes therein. Finally, we discuss what lessons can be learned from the current state of knowledge on deadwood and the carbon cycle to inform land management and offer potential future research directions.

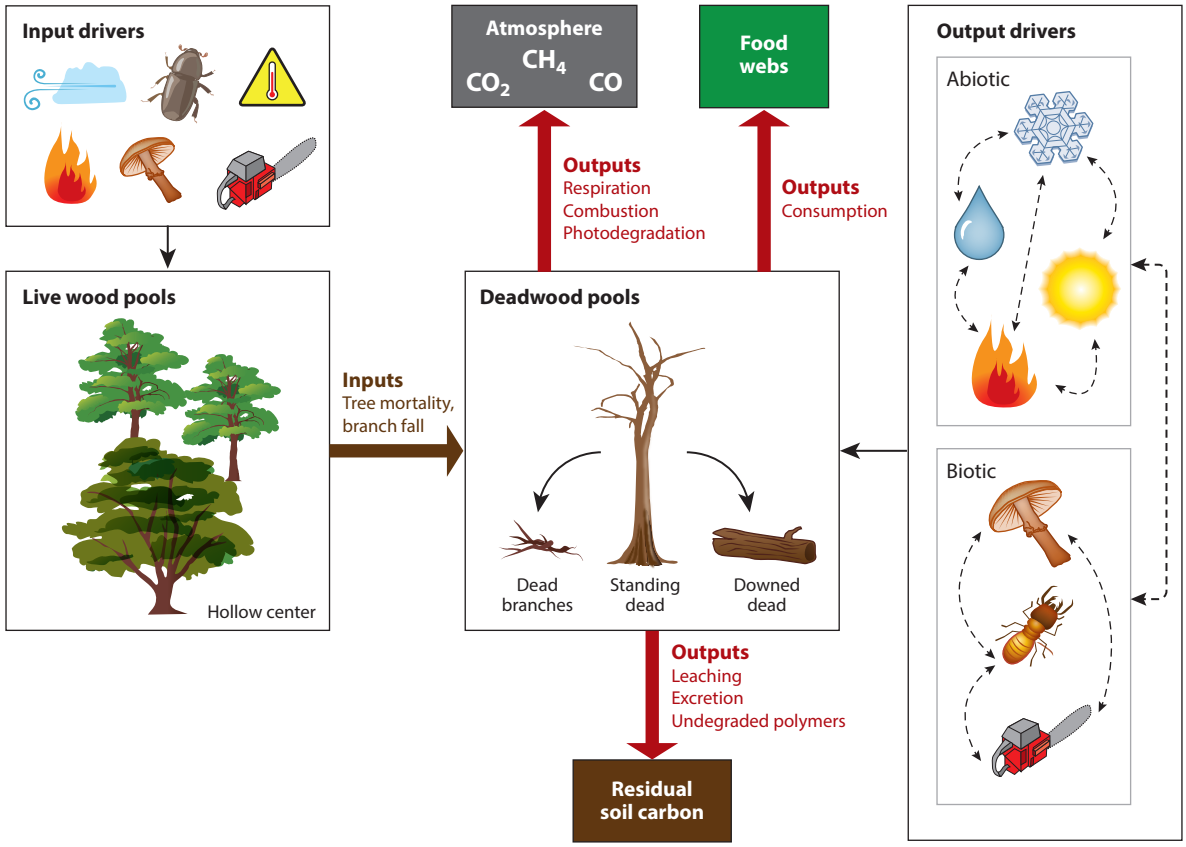

Figure 1

Inputs into and outputs from deadwood pools, separated into standing dead, dead branches, and downed dead. Outputs are regulated by biotic (animals and microbes) and abiotic (solar radiation, freeze–thaw, and fire) output drivers and their interactions (depicted by *dashed arrows* between the output drivers). The output drivers mineralize carbon into the atmosphere by breaking down carbon polymers and releasing them as gases including CO_2 and CH_4. The remaining carbon polymers are transferred to the soil carbon pool. Biotic consumers such as invertebrates and fungi also make deadwood carbon available to organisms higher up in the food webs.

1.1. How Much Deadwood Is There?

Deadwood pool sizes are determined by plant inputs and outputs (**Figure 1**). The majority of studies on deadwood carbon pools and their inputs and outputs have been carried out in forest ecosystems, with forests defined as areas spanning >0.5 ha with trees ≥5 m tall and tree canopy cover of ≥10% (Pan et al. 2011). These studies employ standardized deadwood biomass surveys and create conversions to carbon pools (Russell et al. 2015). Approximately 8% (73 ± 6 Pg C) of all carbon pools in forests are thought to be deadwood (Pan et al. 2011), but these carbon pools are not evenly distributed around the globe, and the intensity of management (plantation, logging, and deadwood removal) causes further spatial variation. An average of 58.7 Pg (~80%) of deadwood is found in tropical rainforests, equating to ~17.6 Mg C/ha (Anderson-Teixeira et al. 2016), while 16.1 Pg (~15%) are found in boreal forests and 3.3 Pg (~5%) in temperate and subtropical forests. Deadwood is found in a variety of sizes and positions; for instance, a study from the Amazon rainforest found that half of all deadwood biomass is standing trees, while the

TERMS

- **Pools:** deadwood stores or stocks of biomass or carbon; biomass pools are usually expressed as mass per area, and carbon pools are usually expressed as mass of carbon per area.
- **Inputs:** processes leading to fluxes of biomass or carbon into deadwood pools, including dead branch fall and tree death (both standing and downed); biomass input rates to deadwood pools are usually expressed as mass per area per time, and carbon input rates to deadwood pools are usually expressed as mass of carbon per area per time.
- **Outputs:** processes leading to fluxes of biomass or carbon out of deadwood pools including through fragmentation, decomposition, combustion and transformation. Biomass output rates from deadwood pools are usually expressed as mass loss through time (i.e., decomposition rates) and presented as % mass loss or as parameters from functional forms capturing the decay process, such as shape and scale parameters from the Weibull equation or k parameter from the negative exponential equation. Carbon output rates from deadwood are estimated by either converting biomass to carbon or directly measuring respiration rates as CO_2.

other half is downed broken and uprooted trees, with the latter pool having larger areas of contact with the soil (Esquivel-Muelbert et al. 2020).

To date, drier ecosystems such as savannas and semiarid lands have largely been ignored in deadwood surveys, despite their significant contributions to carbon cycling (Ahlström et al. 2015). The dearth of such studies is problematic, given that these ecosystems cover larger areas than tropical rainforests (Grace et al. 2006). Savannas, which are found in tropical and subtropical regions, can contain significant amounts of fallen deadwood (Cook et al. 2020); droughts, herbivore attacks, and fires are constantly adding inputs into these deadwood pools. Attempts have been made to estimate total primary productivity in savanna ecosystems (Grace et al. 2006), but little has been done to quantify deadwood carbon pools. The prevalence of episodic events such as fires within savanna ecosystems can lead to stochasticity in deadwood inputs and outputs, and time since the last fire may be critical for accurately estimating deadwood presence on the landscape. A study from northern Australian savannas, using 10 sites and incorporating time since fire, found an average of 3.9 Mg/ha of deadwood biomass (~12% of total aboveground biomass) (Cook et al. 2020), which equates to 2 Mg C/ha, assuming that deadwood is 48.5% carbon (**Supplemental Table 1**) (Martin et al. 2021). When accounting for the area of tropical savanna around the world, we found that deadwood stores within these ecosystems represented 9.5 Pg C, which is more than three times what has been found in temperate ecosystems (**Figure 2**, **Supplemental Table 1**). Setting aside deadwood sampling strategies (e.g., line-intersect, fixed-area, or LiDAR-based methods), perhaps one of the largest sources of uncertainty for deadwood pool sizes (Campbell et al. 2019) comes from the assumed allometry, wood density, and carbon fractions (Martin et al. 2021) associated with any given piece of deadwood across the diversity of global ecosystems and determinants of global change leading to increased novel mortality and combinations of disturbance regimes.

1.2. What Are the Input Rates of Carbon into Deadwood Pools?

Carbon enters the deadwood pool through tree death and the falling of branches from live trees. The background rate at which trees die varies across regions. Studies from the Amazon rainforest observe tree mortality rates of ~2% per year (Esquivel-Muelbert et al. 2020). A study from Australian tropical ecosystems shows mortality rates ranging from 0.1% to 7.4%, depending on the year considered (Bauman et al. 2022), while studies from temperate forest ecosystems in the

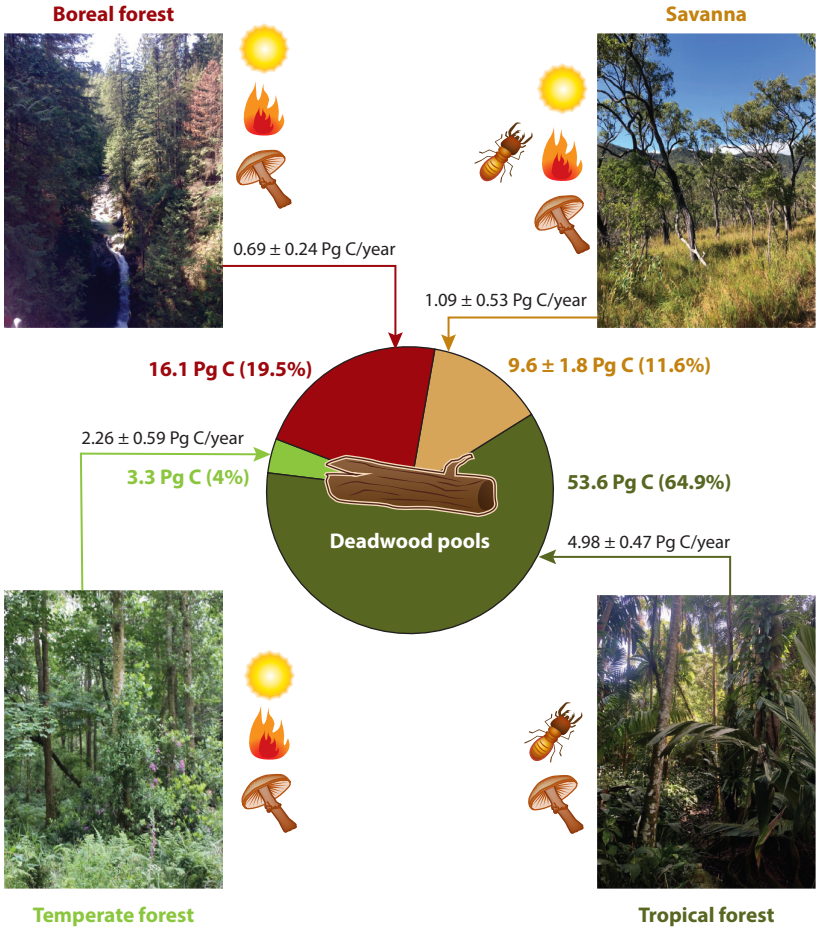

Figure 2

Input rates of deadwood in Pg C/year (*black text* above *colored arrows*) within boreal, temperate, and tropical forests and savannas calculated from the studies compiled in **Supplemental Table 1**. The deadwood pool sizes (i.e., biomass; Pg) found across boreal (*red*), temperate (*light green*), and tropical (*dark green*) forests were extracted from Pan et al. (2011) and compared with deadwood pool sizes found in savannas (*orange*), from the compiled studies listed in **Supplemental Table 1**. The icons indicate the main decomposers within each biome. Photographs provided by Baptiste J. Wijas.

USA and Europe show mortality rates between 0.5% and 2% (Senf et al. 2018, van Mantgem et al. 2009). Mortality rates can be equated to the biomass of carbon entering deadwood pools around the globe (**Figure 2**, **Supplemental Table 1**). While mortality of trees is the main source of deadwood, it is important to note that deadwood also comes from damage to live trees. For instance, Zuleta et al. (2023) showed that 41.5% of all biomass entering the deadwood pool in tropical forest ecosystems originated from branches falling from live trees.

Tree death has multiple causes, including extreme climatic events such as droughts (Choat et al. 2018), associated wildfires (reviewed in Cornwell et al. 2009), windstorms (Zeng et al. 2009), and biotic disturbances, such as microbial pathogens, invertebrate and vertebrate pests, and herbivores (Seidl et al. 2017). The multiple drivers of tree death (detailed throughout Section 2) lead to inputs of deadwood to the landscape. These abiotic and biotic drivers are often thought to be

interlinked, but the consequences of these interactions for deadwood input and output rates are poorly understood (McDowell et al. 2020). Tree species' traits, e.g., wood chemistry, anatomy, and morphology, may lead to certain species being particularly vulnerable to particular drivers (Cornwell et al. 2009). Similarly, the death of different sized trees contributes unevenly to necromass gains in the deadwood pool, with larger trees contributing more than smaller trees (Gora & Esquivel-Muelbert 2021), which can affect how fast carbon is lost from this pool.

1.3. What Are the Output Rates of Carbon from Deadwood Pools?

Our knowledge of the output rates of deadwood varies around the world (Harmon et al. 2020, Hu et al. 2018, Seibold et al. 2021, Zanne et al. 2022). These rates are typically measured as a loss of wood mass through time (i.e., decomposition rates) and presented as the percentage mass lost or as the exponent k of an exponential curve of mass remaining over time, although nonexponential functions may be more appropriate in certain tree species or environmental contexts (Freschet et al. 2012b). In one synthesis of such values (Harmon et al. 2020), most studies were from temperate (61%) and boreal (25%) climates in the northern hemisphere; much less work has been done in the tropics (14%) and southern hemisphere. Recent globally distributed experiments have begun to address some of these data gaps (Seibold et al. 2021, Zanne et al. 2022), although much more work is needed.

In Harmon et al. (2020), decomposition rates were estimated to vary 244-fold, with deadwood remaining on the ground for periods ranging from 3 to 750 years. Across different global syntheses and distributed experimental studies (Harmon et al. 2020, Hu et al. 2018, Seibold et al. 2021, Zanne et al. 2022), decomposition rates consistently increased with increasing temperatures. Harmon et al. (2020) found effective Q_{10} values, changes in the rate of decomposition with a 10°C increase in temperature, of 2.5–2.6 on average (Harmon et al. 2020). Decomposition rates were consistently associated less strongly with moisture than temperature (Harmon et al. 2020, Hu et al. 2018, Seibold et al. 2021, Zanne et al. 2022), especially when moisture was measured as precipitation, although other representations of moisture, such as relative humidity or deadwood moisture content, may improve predictions. To better understand the biogeographic differences and climate drivers, more data are especially needed from tropical and subtropical biomes, in addition to temperate dry sites (Harmon et al. 2020).

1.4. In What Forms Is Carbon Leaving Deadwood Pools?

Wood is almost 50% carbon (Martin et al. 2021) (see Section 1.1), with this carbon found in various forms, including pectin, hemicellulose, cellulose, and lignin (Swift et al. 1979), as well as suberin and resinous compounds in bark. These carbon polymers vary in how readily degradable they are, depending on which driver is causing the wood to decompose and when they are released during the decomposition process (Harmon et al. 1986, Swift et al. 1979) (see Section 2). Carbon also has different fates, leaving the deadwood in various forms depending on interactions among the wood structure, carbon polymers, and decomposition drivers (**Figure 1**).

Deadwood often begins decomposing by physical fragmentation via both abiotic and biotic processes (Cornwell et al. 2009, Harmon et al. 2020). Through the activity of microbes and macrofauna, some of the carbon is incorporated into new biomass, which subsequently is consumed by organisms in higher trophic levels via predation (Moore et al. 2004). Carbon is lost via the transfer of soluble materials through water into the soil, i.e., leaching (Cornwell et al. 2009, Harmon et al. 2020). Other carbon transformed during biotic decomposition is mineralized (converted to inorganic forms) as CO_2 (carbon dioxide) when organisms respire aerobically or as CH_4 (methane) under anaerobic conditions via methanogenic archaea. Anoxic conditions may be found in the

guts of insects, such as termites, which are thought to contribute as much as 3% to the annual CH_4 budget (Carmichael et al. 2014). However, we lack measures for other wood-feeding insects. When wood burns, CO_2 is released mainly through combustion but also through the smoldering process (Cornwell et al. 2009). Carbon from smoldering wood is mainly mineralized as CH_4 and CO, while combustion releases only trace amounts of these compounds. In addition, photodegradation can also lead to the mineralization of CO_2, CH_4, or CO from wood, especially in drier sites where solar irradiance is high (Austin & Vivanco 2006, Lee et al. 2012). As complex carbon polymers, such as lignin, persist, they often become incorporated into the soil and termite mounds and nests (Rückamp et al. 2011).

Only a few studies explicitly investigated the contribution of heterotrophic respiration from deadwood to ecosystem fluxes. Studies from temperate ecosystems suggest that deadwood decomposition can represent between 1 and 16% of total annual ecosystem heterotrophic respiration (**Supplemental Table 1**). In boreal ecosystems, a study found that respiration from deadwood represented ~7.6%, although another study found this estimate increased to 30% after windthrow events (**Supplemental Table 1**). For tropical and subtropical ecosystems, estimates ranged between 6.4% and 20% of annual ecosystem respiration (**Supplemental Table 1**). Taken together, these estimates show high variability in the relative contributions of respiration from deadwood within and across ecosystems. This uncertainty highlights the need for further studies, especially in tropical ecosystems, which contain the majority of global deadwood pools (**Figure 1**).

2. WHAT CONTROLS CARBON DEADWOOD POOLS, INCLUDING DRIVERS OF CARBON INPUTS AND OUTPUTS?

2.1. Microbes, Including Fungi and Bacteria

Microbes contribute to deadwood inputs through pathogenic activity and to outputs through deadwood decomposition (**Figure 1**). Fungal pathogens, especially nonnative species, have the potential to cause mass tree die-offs, thereby generating a pulse of deadwood input to ecosystems. Well-known examples include Chestnut Blight (*Cryphonectria parasitica*) and Dutch Elm Disease (*Ophiostoma ulmi* and *Ophiostoma novo-ulmi*), which led to mass die-offs of American chestnut and North American and European elm trees, respectively. Epidemics caused by fungal pathogens continue to occur, such as Sudden Oak Death, caused by *Phytophthora ramorum*, and European Ash Dieback, resulting from *Hymenoscyphus fraxineus*. Dead heartwood in living trees is also susceptible to decomposition by microbes, which can affect the structural integrity and survival of trees, depending on its extent (Frank et al. 2018).

Once trees die, wood-dwelling microbes, especially fungi, are the primary decomposition drivers around the globe (Cornwell et al. 2009), although they decompose deadwood most quickly in warm sites with sufficient water availability (Seibold et al. 2021, Zanne et al. 2022). One study found that the effective Q_{10} when microbes are the main decomposers is 1.7 (Zanne et al. 2022). The main fungal decomposers are the basidiomycetes, which include white-rot and brown-rot fungi (Dix & Webster 1995). Fungal hyphae penetrate deadwood through vessels or insect tunnels and secrete cellulases, hemicellulases, and oxidases that degrade wood polymers such as cellulose and hemicellulose. White-rot fungi also produce extracellular oxidases and peroxidases that degrade lignin via free radical mechanisms (ten Have & Teunissen 2001); brown-rot fungi lack these enzyme systems to decompose lignin.

Other microbes may also play a role in deadwood decomposition. Some ascomycetes in the Xylariaceae can degrade deadwood, including lignin, through a soft rot mechanism even without significant oxidative enzyme production (Liers et al. 2006). Soft rot fungi have broad

environmental tolerances, allowing them to carry out deadwood decomposition in moist and cold locations (Kim & Singh 2000). Zygomycetes, commonly known as sugar fungi, may be involved with the decomposition of sugars and other low molecular weight compounds early in the decomposition process (Dix & Webster 1995). Although they are not as well studied, bacteria likely contribute to deadwood decomposition as well, especially early in decomposition and in association with fungi (Clausen 1996). Microbes also likely indirectly influence decomposition rates, although this is poorly studied in the context of deadwood decomposition and requires further attention. For example, mycorrhizal fungi colonizing leaf litter can reduce decomposition by fungi through their extraction of water and nutrients. Some mycorrhizal fungi may colonize deadwood during later decomposition stages and enhance decomposition by translocating nitrogen to the site of decomposition (Rinne et al. 2017).

Emerging trait-based approaches are proving useful for identifying the ecological roles of wood-decomposing microbes. A study of 34 North American species showed that decomposition rates were related to a life history trade-off between drought-tolerant, slow-decomposing strategies and fast-growing strategies with high decomposition rates (Lustenhouwer et al. 2020).

2.2. Animals

A wide range of vertebrate and invertebrate animals contribute to deadwood inputs and outputs (**Figure 1**). Mammals are important in toppling or disturbing living trees (Berzaghi et al. 2019), while insect outbreaks lead to extensive tree mortality. For instance, bark beetles cause 5.53 Tg C of inputs to deadwood pools in the USA every year (Fei et al. 2019). In tropical ecosystems, internal damage to trees from termites reduces their structural integrity and survival while also impacting the amount of carbon stored in living trees (Flores-Moreno et al. 2024, Yatsko et al. 2024).

Once woody stems die, most of the animals that feed on them are invertebrates. Perhaps the only vertebrate dependent on deadwood is the South American catfish of the genus *Panaque*; however, vertebrates may indirectly promote deadwood decomposition, for example, as they physically fragment deadwood in search of insects. When consuming deadwood, exceptionally few animals are capable of digesting cellulose on their own. Wood-feeding termites, some Isopoda, and *Teredo* (ship worms) are the best-known examples of animals that produce their own cellulases (Griffiths et al. 2021a); they all provide at least part of the suite of enzymes needed to fully digest cellulose (the digestome). Invertebrates are incapable of digesting lignin. Some, though, farm white-rot fungi, which are capable of degrading lignin, within their nests; examples include fungus-growing termites and ambrosia beetles. Other clades of invertebrates are also indirect feeders on deadwood. For example, a host of beetle families (e.g., Ptiliidae, Ciidae, Erotylidae) feed on the spores, mycelia, or fruiting bodies of wood-feeding fungi (Birkemoe et al. 2018). Some beetles (e.g., Scolytinae) are also important vectors of wood-decomposing fungi (Lunde et al. 2023).

Global experiments show that termites consume far more deadwood than other invertebrates (Zanne et al. 2022); because of their ability to resist desiccation via their social behavior, termites are thought to contribute most in hot, dry locations, unlike wood-dwelling microbes. In one global study, the effective Q_{10} when termites accessed the deadwood in addition to microbes was 6.9 (Zanne et al. 2022). Most of these experiments used a common woody substrate stripped of bark. However, multi-species experiments on tree logs with bark attached showed that termites also contribute up to half of deadwood outputs in humid tropical (Liu et al. 2015) and subtropical forests (Guo et al. 2021). Many other invertebrates, particularly beetles, feed on the cambium layer of deadwood, under the bark. In cooler locations, where termites are absent, beetles contribute to deadwood decomposition (Ulyshen 2016).

2.3. Fires

Large-scale episodic disturbances are key drivers of deadwood dynamics (Woodall et al. 2021), and fire ranks highly among natural processes for causing deadwood inputs and outputs (Campbell et al. 2016) (**Figure 1**). Fires are more prevalent in ecosystems that show clear seasonal trends in rainfall; these include productive systems, such as tropical savannas, and less productive systems that slowly accumulate large biomass, such as coniferous forests (Pausas & Ribeiro 2013). In recent years, severe fires have become increasingly common, with record-breaking megafires throughout Brazil, the western USA, Australia, and Eurasia (Le Breton et al. 2022).

Immediately after fires, the proportion of standing deadwood increases sharply due to fire-induced mortality (Burton et al. 2021). Different components of the fire regime, including fire severity, season, frequency, and extent, can all influence tree mortality rates. Fire severity mediated by interactions with climate, forest type, and topography determine the amount of standing deadwood (Burton et al. 2021). For example, in eucalypt forests of southeastern Australia, the proportion of standing deadwood increased from 5% to 12% at low severity burn sites to 24–46% at high severity sites due to topkill of resprouting trees (Bennett et al. 2016).

Fire also affects outputs from the deadwood pool by consuming deadwood directly through combustion. The proportion of fallen deadwood typically declines immediately postfire and slowly increases over time, indicating that this deadwood pool is most readily consumed by fire and builds through standing deadwood thinning and treefall. Consumption of deadwood can increase with fire severity (Volkova et al. 2019); however, deadwood inputs from a fire can also persist in ecosystems for decades. For instance, Campbell et al. (2016) found that 85% of fire-killed necromass (primarily trees) remained in the forest 10 years after a wildfire in Oregon, USA. During incomplete combustion, e.g., under oxygen limitation, substantial amounts of char can be formed, consisting of a concentrated form of carbon that has lost its water-holding capacity and volatiles (Bird et al. 2015). Char tends to be more recalcitrant to decomposition than unburnt deadwood of the same tree species (Preston & Schmidt 2006).

2.4. Other Abiotic Output Drivers

In addition to fire, other abiotic factors, including windstorms, solar radiation, water, and freeze–thaw cycles, play significant roles affecting the inputs and outputs of deadwood in terrestrial ecosystems (**Figure 1**). Windstorms can be important for inputs into the deadwood pool. They are highly variable in severity and type, including thunderstorm downbursts, hurricanes (also known as cyclones and typhoons), derechos, and tornados. Storms also span a wide range of spatial scales and severities, from individual treefalls forming canopy gaps to extensive stand-replacing events (Mitchell 2013). Deadwood pool sizes following severe windstorms follow a U-shaped pattern (high–low–relatively high) over time (Harmon et al. 1986). The pattern results from the abundant initial wind-caused inputs, followed by a period of low abundance as this input decomposes, followed in turn by an increase as the recovering stand reaches maturity and natural canopy mortality occurs.

Solar radiation, particularly in open or sun-exposed environments, affects deadwood outputs directly through photodegradation (Lee et al. 2012) and indirectly by stimulating microbial decomposition (Wu et al. 2018), which has been observed to occur in the leaf litter of woody species (Austin et al. 2016). Given lignin is an important light-absorbing compound and that it degrades when exposed to sunlight (Austin et al. 2016), the relatively high lignin concentrations found in most deadwood tissue (Cornwell et al. 2009) may be very susceptible to photochemical mineralization by sunlight exposure. This solar radiation–induced degradation of lignin may have important consequences for the lignin bottleneck that constrains early stages of deadwood decomposition

by microbes. In high-light environments such as arid zones and clear-cut or deciduous forests, the direct effect of solar radiation exposure and increased temperatures could increase microbial activity and deadwood carbon outputs.

The effects of mechanical stress can also accelerate output rates from deadwood. For example, freeze–thaw cycles in boreal or temperate climates may have a large impact on weakening of woody tissues, with the realized effect determined by hydraulic adaptations of tree species to freezing environments (Cornwell et al. 2009, Zanne et al. 2014). Water moving across deadwood can lead to losses through leaching of dissolved organic compounds (Błońska et al. 2019) and transport of fragmented deadwood. Collectively, these abiotic factors affecting the mechanical and chemical composition of deadwood likely accelerate outputs of deadwood in terrestrial ecosystems, although mechanistic evidence for their relative importance is lacking. An improved understanding of these factors and their interactions with biotic decomposition drivers during deadwood decomposition is clearly needed.

2.5. Interactions Among Output Drivers

Much remains to be learned about how different drivers of deadwood inputs and outputs interact with one another to affect deadwood pool sizes. Multiple studies have explicitly examined interactions among tree mortality drivers, such as biotic attack and drought (McDowell et al. 2020). On the other hand, most studies of decomposition focus on only one or two drivers.

Of the studies with multiple decomposition drivers, interactions with microbes are probably best examined. Often these studies involved adding or removing nonmicrobial decomposition drivers because it is difficult to exclude microbes, especially under field conditions (Seibold et al. 2021, Zanne et al. 2022). That said, a meta-analysis by Viana-Junior et al. (2018) summarized findings from studies investigating how wood-dwelling fungi affect termite behavior after inoculating deadwood with specific fungal cultures or sterilizing fungal-colonized deadwood. All but one of the studies in the meta-analysis were conducted under laboratory conditions. The presence of fungi in deadwood increased termite deadwood feeding (by 120%), survival (by 136%), aggregation (by 81%), and trail following (by 200%). Interestingly, consumption by termites increased in deadwood colonized by wood-decomposing and sap-stain fungi but not molds. Further, Ulyshen et al. (2016) observed compositional shifts in bacterial, but not fungal, communities in association with increasing termite damage. Their methods did not allow identification of the specific microbial taxa associated with those shifts, but metabarcoding and metagenomics make such identification possible for future studies.

Abiotic decomposition drivers, such as fire and photodegradation, may also interact with biota to influence output rates from deadwood. Fire chemically changes deadwood as a substrate for wood-decomposing fungi, affecting the outcomes of fungal interactions while colonizing that deadwood (Edman & Eriksson 2016). Although the consequences of these interactions for decomposition have not been assessed, fungi do vary in their ability to break down unburned deadwood (Lustenhouwer et al. 2020). Additionally, controlled burning of boreal forest plots where fire had previously been suppressed led to an increased abundance of wood-decomposing fungi after four years (Junninen et al. 2008). Increased activity and abundance of wood-feeding beetles were observed just prior to fire and up to two years after burning (Hyvärinen et al. 2006). Additionally, fungal colonization of deadwood by airborne spores may be limited due to mortality caused by solar radiation exposure, particularly for deadwood that is not under a forest canopy (e.g., savannas, semiarid drylands, forest edges). Norros et al. (2015) found that spores of wood-decomposing fungi exposed to solar radiation exhibited high mortality, with 14 of 17 species having a half-life of less than 2 hours of exposure. Solar radiation exposure may also reduce the

activity of invertebrate detritivores such as termites, which prefer shadier conditions, and hence slow outputs from deadwood where termites are major consumers (Acanakwo et al. 2019).

2.6. Deadwood Traits

Across woody species, chemical, anatomical, structural, and architectural traits are important determinants of their susceptibility to mortality and branch loss, as well as decomposition by different abiotic and biotic drivers. However, these contributions are not reviewed here, as they have been covered extensively in previous articles (Cornelissen et al. 2017, Cornwell et al. 2009, Dossa et al. 2018, Liu et al. 2015, Pietsch et al. 2014, Zhao et al. 2018).

3. GLOBAL CHANGE IMPACTS ON DEADWOOD AND THE CARBON CYCLE

Deadwood inputs and outputs are expected to be affected by global change, with outcomes including shifts in climate; pest and disease outbreaks; invasive species colonization and establishment; and land-use changes, such as urbanization. In the coming decades, global temperatures will increase and rainfall patterns will shift with increases in the frequency and intensity of episodic events such as droughts, windstorms, and storm surges (IPCC 2023). In addition, changes in land use are modifying ecosystems through shifts in vegetation types, soil composition, and microclimatic conditions, to name a few. It is important to understand how global change will influence deadwood pools, especially if forests shift from sinks to sources of carbon.

3.1. Global Change Is Influencing Rates of Input into Deadwood Pools

Inputs into the deadwood pool at landscape scales are expected to increase due to global change through greater living biomass pools (more trees) and higher mortality rates of those trees (McDowell et al. 2020). Terrestrial biosphere models largely agree that carbon tied up in living plants, such as trees, will increase in the coming decades (IPCC 2023). However, these models still contain large uncertainties as to whether the turnover rates of live vegetation (i.e., seedling recruitment and tree mortality) will be higher (Pugh et al. 2020). Empirically, studies from various ecosystems, including tropical rainforests and temperate forests, show that background tree mortality rates have increased in recent decades (Bauman et al. 2022, Hartmann et al. 2022, Senf et al. 2018, van Mantgem et al. 2009). As the climate warms, it is predicted that extreme weather events such as windstorms and droughts will become more intense (Trenberth et al. 2014). Fires will also increase in frequency, intensity, and extent (Bowman et al. 2020). Together, these extreme events can lead to higher incidences of mass tree mortality (Hartmann et al. 2022) and branch fall. These abiotic events may also interact to amplify their effects on tree mortality (Seidl et al. 2017). For instance, a study by Brando et al. (2014) found that fire-induced tree mortality increased by 200–400% after an extreme drought in the Amazon. Alternatively, windstorms can lead to more intense fires, which increases the likelihood of mass mortality events (Ibanez et al. 2022). Simultaneously, global warming, especially combined with increased severity and intensity of drought is expected to increase the likelihood of pest outbreaks such as bark beetles and pathogen attacks (Hlásny et al. 2021), which have cascading effects for massive tree mortality (Austin & Ballaré 2023) and subsequent large sudden pulses of deadwood into ecosystems.

In addition to climate change, land-use change may influence the mortality rate of trees. The main activity causing direct tree mortality is deforestation through logging, which leads to the death and harvesting of trees. Most trunks of logged trees are removed from the ecosystem and do not result in an increase in deadwood biomass. However, logging can increase dead biomass input of branches and create damage to live, unharvested trees, followed by greater mortality

(Thorpe et al. 2008), with resulting elevated rates of deadwood pool sizes across disturbance gradients (Pfeifer et al. 2015). Further, impacts can be indirect, such as increases in woody biomass due to shrub encroachment driven, in part, by alterations in grazing and fire regimes. These increases will generate inputs of woody-shrub living and dead biomass in formerly herbaceous-dominated ecosystems. Such woody plants may be more vulnerable to droughts and other climate extremes than the original vegetation, resulting in elevated mortality rates (Renne et al. 2019).

3.2. Global Change Is Influencing Rates and Forms of Output from Deadwood Pools

Global change can directly affect biotic and abiotic decomposition drivers of deadwood. For instance, it is well known that higher temperatures increase the activity of both wood-dwelling microbes and invertebrate detritivores, leading to higher output rates from deadwood (Seibold et al. 2021, Zanne et al. 2022). However, it is uncertain how changes in rainfall influence outputs via effects on decomposition drivers. Zanne et al. (2022) found that termites are particularly well adapted to hot and dry conditions; therefore, we expect their impacts to increase both within the tropics and extratropically as ecosystems become warmer and drier (**Figure 3**). Additionally, such conditions may promote more frequent and intense fires, consuming increased amounts of deadwood, especially in temperate and boreal forests (Senande-Rivera et al. 2022).

While direct increases in temperature are likely to lead to faster deadwood outputs, indirect effects of climate change may also affect carbon outputs from deadwood. For instance, biotic decomposers are dependent on the positioning of the deadwood, e.g., on the soil, standing as snags, or suspended above the ground, which itself is influenced by global change. The output rates of carbon from deadwood increase when trees fall and deadwood has direct contact with the soil (Song et al. 2017). Taking this into account, one study from the eastern USA found that warmer climates are predicted to increase the rates of snag fall, speeding up deadwood carbon output rates via soil contact (Oberle et al. 2018). Another potential indirect influence on output rates is the expected higher incidence of mass mortality events via increased frequency of abiotic and

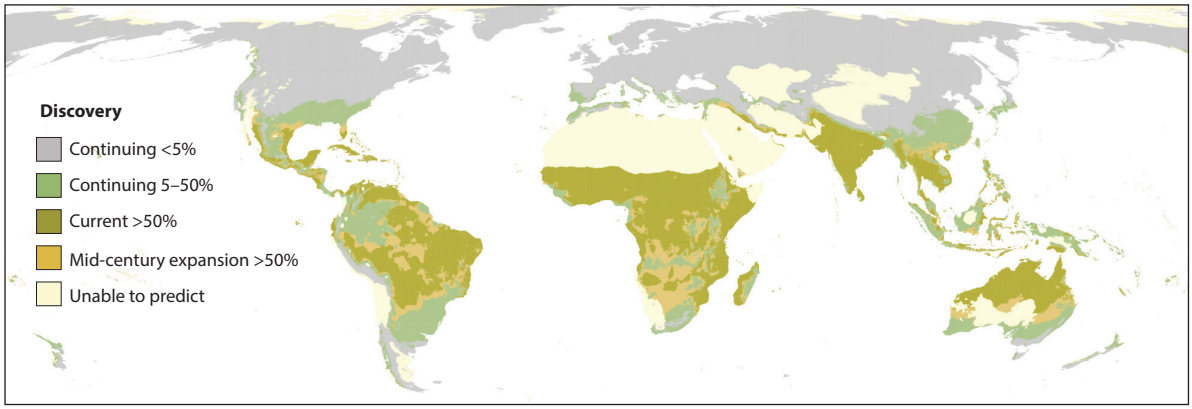

Figure 3

Discovery rates of deadwood by termites, as predicted by climatic variables (mean annual temperature and precipitation), were modeled from a large wood-decomposer experiment by Zanne et al. (2022). This map indicates the expansion in the activity of termites under climate change scenario 585 for 2041–2060 from the GISS-E2-1-H model, which forecasts close to the median level of expansion among the models considered by the IPCC (2023). The climate forecast was combined with the termite discovery model from Zanne et al. (2022). Most tropical regions are forecast to continue with high discovery rates. The orange color shows areas that do not currently have high rates but where rates are forecast to increase to greater than 50% by mid-century.

biotic pressures (see Section 3.1); such events will create patches of high deadwood density. In these instances, deadwood carbon output rates are likely to increase; one study found that snags closer together decompose more quickly (Bradford et al. 2023). On the other hand, mass mortality events may also alter environmental conditions leading to the desiccation of deadwood, which may favor some invertebrate animals over microbes as decomposition drivers. Mass mortality events may also increase exposure to solar radiation, resulting in greater lignin removal, as described in Section 2.4.

While global change will shift the output rates of deadwood, it may also alter the proportion of carbon forms released from deadwood. For instance, as termites, which are emitters of CH_4, are limited by cooler temperatures, they are likely to expand their ranges under global warming (**Figure 3**). These expansions could alter the balance between microbial- and termite-mediated decomposition at higher latitudes, with consequences for the fates of the released carbon. However, whether CH_4 emissions are larger in areas of high termite abundance will depend on the specific interactions between CH_4 release and methanotroph presence within the areas where termites process the deadwood. Wetland habitats such as mangroves are another major source of CH_4 emissions and are also at risk of disruptive events due to sea level rise, extreme weather, and increasing temperatures (Sippo et al. 2018). In one study, dead mangrove trees served as straws, transferring CH_4 from the soil to the atmosphere, leading to over eight times higher CH_4 emissions than those from live trees (Jeffrey et al. 2019).

As woody vegetated areas expand or contract with global change, novel interactions among abiotic and biotic decomposition drivers may occur. For instance, in grasslands experiencing woody plant encroachment, deadwood pools are likely to increase. As decomposer communities in grasslands are not functionally adapted to consume deadwood, output rates of deadwood, at least initially, may be slow (Freschet et al. 2012a). In these instances, especially when vegetative cover is altered by the wood–grass balance, other abiotic factors such as fire or photodegradation may become more prominent as the main cause of outputs from deadwood (Austin 2011).

The contribution of different decomposers to deadwood outputs may shift in response to forest management activities such as logging, which modify the deadwood inputs, decomposer communities, and microclimatic conditions of the forest floor. For instance, forest management activities can remove current and future deadwood inputs and alter the attributes of those inputs by changing the near-term input of small deadwood and long-term removal of large deadwood. Forest management activities can substantially alter the function and activity of both wood-decomposing fungi and wood-feeding invertebrates (Chen et al. 2019, Luke et al. 2014). As forest growth and related deadwood inputs return, interactions between both abiotic and biotic decomposition drivers will be altered. For instance, termites can recolonize disturbed habitats relatively quickly (Wijas & Atkinson 2021) and contribute more to decomposition than fungi, as they prefer drier microclimatic conditions found in open locations (Griffiths et al. 2021b). Decomposing fungi also decline in abundance following logging, with impacts potentially lasting for decades (Chen et al. 2019). As interactions shift among deadwood decomposition drivers, the fragmentation created by land use may increase the role of fire (Driscoll et al. 2021) and solar radiation in deadwood outputs.

3.3. Global Change and Deadwood Pool Sizes

Given the various impacts of global change on inputs to and outputs from deadwood pools and the relative lack of knowledge regarding how these will be influenced by global change both locally and globally, predicting changes in pool sizes remains challenging. Additionally, interactions among different global change components may contribute to large uncertainties in such estimates. Few studies on deadwood pools have been conducted across time and space to document the effects

of global change. Perhaps one of the best has been the long-term monitoring by the US Forest Service via their Forest Inventory and Analysis Program. In these plots, deadwood pool sizes have been highly variable and hard to predict across the landscape (Woodall et al. 2021). Due to the complexity and variability of estimating and predicting deadwood dynamics, we recommend that future research focus on exploring the links between deadwood inputs and outputs, as influenced by global change, to better inform Earth system models (see Section 4) and achieve the greatest advancement in this topic area.

4. MODELING OF DEADWOOD AND THE CARBON CYCLE

At the site and ecosystem scales, several models have been developed to represent deadwood pools and dynamics. The simplest models are statistical, meaning that they fit a function such as a negative exponential to deadwood decomposition data (see Section 1.3) to infer or compare parameter values (Harmon et al. 2020). Such models are useful for obtaining site- and time-specific output rate parameters but may be of limited use in predicting output rates under varying conditions. More mechanistic models, such as Yasso (Liski et al. 2005) and a framework developed by Yin (1999), account for deadwood chemical quality, air temperature, and moisture as drivers of deadwood decay. Similar to Yasso, other soil biogeochemical models also account for mechanisms of deadwood inputs and outputs. The Community Land Model (CLM), which incorporates the Biome-BGC soil model, represents deadwood output rates as a first-order physical fragmentation process that transfers material into two litter pools (Thornton & Rosenbloom 2005). The fragmentation rate varies with surface soil moisture and temperature. A partition coefficient determines the fraction of deadwood entering each litter pool and depends on plant functional type (with classification of plants into different categories, such as needleleaf versus broadleaf and evergreen versus deciduous). The forest submodel of Century (Parton et al. 1988) also represents explicit pools of deadwood. In that model, output rates depend on deadwood size, temperature, and moisture, while carbon transfer to soil pools depends on deadwood lignin:nitrogen ratios.

Recently, Dai et al. (2021) developed a detailed process-based model of deadwood output rates known as the Coarse Woody Debris Decomposition Assessment Tool (CWDDAT). Based on data from the literature and conceptual theory, CWDDAT simulates deadwood outputs via an array of biotic and abiotic drivers. Output rates from fungi, beetles, termites, and bacteria depend on moisture and temperature. Output rates are also determined by deadwood size and position (e.g., downed or standing dead). The model represents physical fragmentation and the flux of dissolved organic carbon that moves from deadwood into soil through leaching. CWDDAT simulations of deadwood output rates across environmental gradients matched well with empirical data collected from 89 North American sites, lending confidence to the model's mechanistic approach.

Additional model development is required to simulate deadwood dynamics at ecosystem to global scales, where variation in deadwood inputs and disturbance regimes affect deadwood pools and their outputs. Currently, the representation of deadwood dynamics in global models is rudimentary. Most Earth system models lack a mechanistic representation of deadwood pool sizes or inputs and outputs (together as turnover). In the fifth Coupled Model Intercomparison Project (CMIP5), only two models—CCSM4 and NorESM—explicitly represented deadwood pools; both used the Biome-BGC/CLM approach (Todd-Brown et al. 2013). Other global models treat deadwood as a type of litter but do not account for the unique chemistry, size structure, positioning, and biological communities that influence deadwood outputs. Likewise, disturbances that uniquely impact deadwood inputs and outputs, such as fire, insect outbreaks, and windstorms, are poorly represented in Earth system models. It is possible that improvements have been made in the representation of deadwood dynamics in Earth system models included in CMIP6

(Ito et al. 2020, Lovato et al. 2022), but the model outputs became available only recently and have not yet been fully analyzed.

Future Earth system model development could incorporate more mechanistic approaches such as CWDDAT. Doing so would require additional efforts to couple the deadwood output mechanisms with other processes such as drivers of tree mortality, soil microclimate conditions, and the production of trace gases from deadwood. For example, no deadwood output rate models currently represent CH_4 production from termite activity or free-living methanogens. Global models could also benefit from representing a link between forest species composition and wood properties that influence output rates and losses due to fire. Earth system models are incorporating increasingly sophisticated representations of plant functional types and vegetation dynamics that would potentially provide a more accurate picture of the inputs entering deadwood pools (Zhu et al. 2020).

5. THE PAST AND FUTURE OF DEADWOOD RESOURCES IN THE CONTEXT OF FOREST MANAGEMENT

5.1. History of Deadwood Resource Management

Over a century ago, the early foundations of forest management emphasized long-term observations of forest dynamics to maximize live tree volume production, with little thought given to the deadwood dynamics associated with tree mortality (e.g., Reineke 1933). Although a major goal was the growth of merchantable tree volume, it was recognized that reducing individual tree mortality was central to achieving production objectives. An unintended consequence of minimizing tree mortality through controlling the stocking of live trees was the reduction of deadwood inputs to managed forest systems. A common belief aligned with these early management objectives was that a forest without deadwood represented a well-managed, healthy, productive forest.

The intensive and extensive forest management—based on these early objectives—which grew out of the industrial revolution may have reduced deadwood abundance in many parts of the world. The negative consequences of these potential deficits began to be recognized beginning in the 1970s. In Fenno-Scandinavia, conservation biologists drew attention to the risks to wood-feeding species of insects and fungi, as their populations were declining in response to the loss of deadwood substrates on which they depend (Stokland et al. 2012). In North America, ecologists began to recognize the critical services provided by deadwood, including nutrient cycling, water retention, and tree regeneration (Harmon et al. 1986).

Although minimizing tree mortality (i.e., indirectly reducing deadwood creation) is still an objective of many forest management operations, especially in even-aged silvicultural systems, recent decades have witnessed a dramatic shift in our view of deadwood, resulting in the incorporation of deadwood resources into forest management activities. For example, forest ecologist Jerry Franklin stated, "At the time a tree dies, it has only partially fulfilled its potential ecological function" (Franklin et al. 1987, p. 550). Starting in the 1970–80s, the role of deadwood in forest ecology rose to prominence such that for some forest ownerships, deadwood standards became included in management plans (e.g., minimum number of logs of a minimum diameter). Further, practices such as snag retention, morticulture (i.e., the purposeful creation of deadwood), and deadwood transplantation/restoration projects began to emerge as feasible solutions (Harmon 2001).

The recognized importance of deadwood has in turn given rise to innovations and improvements in deadwood field sampling and quantification. Early deadwood inventories focused on quantifying fire risks associated with deadwood (viewed as fuels). Practitioners recognized that

deadwood resulting from harvest activities (i.e., unutilized materials) could alter the future trajectory of stand development via increasing fire hazards. A variety of deadwood field sampling strategies were born during this era (e.g., line-intersect sampling) that are still widely used today, albeit with refinements (Russell et al. 2015). Most national forest inventories associated with some of the world's largest economies currently include deadwood (Woodall et al. 2019), with deadwood inventories now being viewed by working foresters as an essential component of stand structural assessments. In a related manner, the increased focus on objectively quantifying deadwood attributes has further strengthened the field of deadwood ecology, especially as it relates to forest management.

The ecological awareness of the vital role of deadwood in forest processes and incorporation into management guidelines continues to this day. However, the emphasis has moved beyond biodiversity and nutrient cycling to include growing public concerns involving climate change, adaptive forest management, carbon storage, and apparent increases in the frequency and intensity of natural forest disturbances leading to inputs into the deadwood pool. Even managers conducting the most basic forest operation such as a short-rotation, monoculture plantation now often consider the carbon implications of the stumps and belowground coarse roots that are left behind with each harvest. Beyond these most basic management operations, the impetus and associated complexity of deadwood management can only be expected to increase in the future.

5.2. Contemporary Issues Influencing Deadwood Resource Management

Adaptive forest management often prescribes increasing tree species diversity and forest structural complexity to provide increased resilience to future climate perturbations such as droughts and episodic precipitation events. The explicit incorporation of deadwood creation or retention into adaptive management practices could increase structural diversity, potentially increasing a forest stand's resilience. Beyond climate resilience, such practices can have benefits for biodiversity (wood-feeding species as well as vertebrates) and tree regeneration (Sandström et al. 2019, Swanson et al. 2023). Further, the microclimates and/or microtopography afforded by deadwood are seen as vital components of adapting current forests for an uncertain future.

The rise of carbon markets has elevated the prominence of deadwood in forest ecosystems. In contrast to the past focus on wildlife habitat (i.e., number of large-sized downed deadwood or snags with a potential for cavity creation), an emphasis on reducing the atmospheric concentrations of CO_2 and CH_4 may call for minimizing the output rates of deadwood carbon before transfer to the atmosphere. Additional deadwood management paradigms may view deadwood as a critical transfer pool between living biomass and longer-lived recalcitrant pools, such as soil organic carbon. Although climate change may increase rates of inputs via tree mortality, emerging forest carbon management practices may call for both accelerating tree growth (increased sequestration of atmospheric carbon) and identifying methods of reducing rates of outputs from deadwood through consumption, combustion, or lateral transfer (fragmentation and leaching). For forest carbon credit and offset markets, rising risks of carbon emissions associated with increasing rates of deadwood decomposition and/or combustion may require the structure and precedents of the markets themselves to be reconfigured.

The projected increase in natural disturbance frequency and intensity resulting from climate change (Anderegg et al. 2020) may further shift attention to the fate of deadwood. The increase in forest fire frequency in many parts of the world has clearly increased the focus on deadwood (i.e., forest fuels) in forest management. Likewise, the apparent increases in windstorms (e.g., hurricanes) and droughts have created deadwood management challenges, particularly evident in controversies over postdisturbance salvage logging (Leverkus et al. 2020). These issues have

heightened the importance of deadwood such that national natural resource strategic plans (e.g., USDA Forest Service 2022) now explicitly identify deadwood's role in future forests (e.g., tree mortality and wildfire hazards).

A lack of resources in many countries may preclude them from establishing and regularly monitoring forest inventories to assess deadwood carbon pools and accurately estimate emissions of greenhouse gases, e.g., CO_2 and CH_4 (Umemiya & White 2024). A survey from over a decade ago documented this problem from both a methodological and pragmatic perspective (Woodall et al. 2009), and while certain regions of the world have greatly improved the accuracy of their inventories (Woodall et al. 2019), many other regions still lack critical basic information. Given many such countries are found in the tropics, where most deadwood biomass is found (**Figure 2**), it is imperative to build and support their capabilities to carry out regular deadwood assessments. Support to maintain regular deadwood assessments in countries that lack resources can be achieved through the continued establishment and maintenance of global, on the ground, forest inventory networks in collaboration with local governments, nongovernmental organizations, and scientists. Additionally, it is crucial to increase data storage and sharing capacities between carbon inventory networks and government inventories to encourage the use of and improve the accuracy of globally available emerging technologies, such as remote sensing. A more robust deadwood inventory capability at global scales will improve our understanding of inputs and outputs from deadwood pools and allow for better management of deadwood resources.

We anticipate that future forest management will balance the varying benefits and challenges associated with deadwood resources in the twenty-first century. While challenges exist, such as wildfire risk, so do many benefits, including microclimates buffered against climate change, maintenance of biodiversity, retained structural legacy, carbon credits sold in a market, natural capital, and the presence of a lifeboat for fungal and microbial communities in forests affected by global change. Further work is needed to quantify deadwood carbon pools, and their inputs and outputs, including measures of uncertainty, in a wider range of forest types (Russell et al. 2015). However, the more daunting challenge for the future management of deadwood is balancing the many potentially conflicting objectives, while considering an ever-changing climate and associated uncertain future.

6. CONCLUSIONS AND OUTSTANDING QUESTIONS

Much recent progress has been made in measuring the drivers of deadwood pool sizes, inputs, and outputs across the planet, and this information can now help to better model and manage ecosystems with woody vegetation. However, outstanding knowledge gaps highlight opportunities for future research on the following questions:

1. What is the role of interacting biotic and abiotic drivers of deadwood inputs and outputs (e.g., fire and decomposition via char, amount of substrate, different explanatory deadwood traits)?
2. How do the interactions affecting deadwood inputs and outputs under Question 1, in turn, depend on the wood and bark traits of different diameter classes, species, and functional types of trees?
3. How do we improve models of carbon inputs and outputs into ecosystem and global models by incorporating interacting drivers?
4. How do we incorporate deadwood inputs and outputs of nontree woody plants (e.g., shrubs, lianas) and trees from nonforest ecosystems (e.g., savannas) into our understanding of deadwood pool sizes, inputs, and outputs under current and future climates?

5. What is the magnitude of carbon pools belowground in deadwood derived from coarse roots and rhizomes, and what are the drivers of the input and output rates and forms compared with aboveground deadwood?
6. Are output rates of deadwood derived from different input forms and drivers distinct (e.g., from branch or stem senescence versus anthropogenic or natural disturbances), and if so, how do they differ?
7. How can we use evolutionary relationships of tree lineages to hindcast deadwood inputs and outputs from the distant geological past to predict the future?
8. How can deadwood management play a role in making different forests around the world more climate resilient (through carbon and water regulation) while maintaining other ecosystem services?
9. What role does deadwood have in slowing carbon from entering the atmosphere as greenhouse gases?
10. How can deadwood attributes and dynamics be better integrated into carbon markets and associated natural climate solutions to reflect their role in ecosystem processes and associated evolving lines of science?

Aside from reducing uncertainties in inputs to and outputs from the deadwood pool for prediction of the future global carbon cycle, answers to these outstanding questions will provide greater insight into the biology driving deadwood carbon storage on the planet.

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