The role of deadwood in the carbon cycle: Implications for models, forest management, and future climates

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Summary:

Deadwood represents a significant carbon pool in forests and savannas. Although previous research has focused mainly on forests, we synthesise deadwood studies across all ecosystems with woody vegetation. Storage and release of carbon from deadwood is controlled by interacting decomposition drivers including biotic consumers (animals, microbes) and abiotic factors (water, fire, sunlight, freeze-thaw). 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 recognise the importance of deadwood for controlling forest dynamics, biodiversity and carbon emissions. Together, emerging knowledge from modelling and management suggests a dire need for additional knowledge on deadwood contributions to carbon storage and greenhouse gas emissions.

Keywords:
Carbon Cycle, Deadwood, Global Change, Management, Modelling, Pools

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, stem, root, and reproductive tissues. Plant carbon is returned to the atmosphere and released into the soil through decomposition drivers 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. Woody plants are found across ecosystems around the globe (Crowther et al. 2015), although woody species increase in relative abundance towards 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. Throughout this review, we synthesise the 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 wood) respond to global change processes.

We begin by summarising (1) the basics of the global importance of deadwood pools (i.e., stocks) including their distributions globally, processes driving their inputs (i.e. the biomass of woody vegetation within the ecosystem and the tissue senescence and mortality rates of woody plants) and rate and forms of outputs. Then, we focus on (2) how inputs and outputs from deadwood pools are driven by different abiotic and biotic decomposition drivers acting across spatial and temporal scales; (3) how these inputs and outputs are likely to respond to future changes in climate and land use; (4) how to model the contributions of deadwood to the carbon cycle and better predict changes therein; and (5) what lessons can be learned from the current state of knowledge on deadwood and the carbon cycle to inform land management with a view to reducing the output rates and maximising moving outputs into the soil of carbon from deadwood, rather than the atmosphere.

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 forest defined as areas spanning >0.5 ha with trees ≥5 m tall and tree canopy cover of ≥10% (Pan et al. 2011). 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, 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 (~15%) Pg are found in boreal forests and 3.3 Pg in temperate and subtropical forests (~5%). 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 other half is downed broken and uprooted trees with the latter pool having increased area of contact with the soil (Esquivel-Muelbert et al. 2020).

To date, drier ecosystems such as savannas and semi-arid 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 they 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 in 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 wood biomass; Cook et al. 2020), which equates to 2 Mg C/ha assuming that deadwood is 48.5% carbon (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 of carbon, which is more than three times what has been found in temperate ecosystems (Table S1, Figure 2). Setting aside deadwood sampling strategies (e.g., line-intersect, fixed-area, or LiDAR-based), 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 inputs into deadwood carbon 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 (Table 1; 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 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 biomass of carbon entering deadwood pools around the globe (Figure 2, Table S1). While mortality of trees is the main source of deadwood, it is also important to note that deadwood 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. Abiotic and biotic drivers of tree mortality are often thought to be interlinked but the consequences of these interactions for deadwood formation 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 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 % mass loss or as the exponent *k* of an exponential curve of mass remaining over time, although non-exponential functions may be more appropriate in certain tree species or environmental contexts (Freschet et al. 2012b). In one data synthesis of such values (Harmon et al. 2020), most studies were from the temperate (61%) followed by 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 wood 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 (change in the rate of decomposition for a 10°C increase in temperature) of 2.5-2.6 on average (Harmon et al. 2020). Decomposition rates were consistently less strongly related to moisture than temperature (Harmon et al. 2020; Hu et al. 2018; Seibold et al. 2021; Zanne et al. 2022), especially when measured as precipitation, although other representations of moisture such as relative humidity may improve predictions. To better understand 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 above) 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 during the decomposition process they are released (Harmon et al. 1986; Swift et al. 1979). Carbon also has different fates, leaving the wood in various forms depending on interactions among the wood structure, carbon polymers and decomposition drivers (Figure 1).

Wood 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 or lower trophic levels when entering the detrital pool (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 mineralised (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 in 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 smouldering process (Cornwell et al. 2009). Carbon from smouldering wood is mainly mineralized as CH_4 and CO, while combustion releases only trace amounts of these compounds. Finally, photodegradation can also lead to the mineralisation 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, termite mounds or nests (Rückamp et al. 2011).

Only a few studies explicitly investigated the contribution of deadwood respiration to ecosystem fluxes. Studies from temperate ecosystems suggest that deadwood decomposition can represent between 1 and 16% of total annual ecosystem heterotrophic respiration (Table S1). In boreal ecosystems, a study found that deadwood respiration represented ~7.6%, although another study found this estimate increased to 30% after windthrow events (Table S1). For tropical and subtropical ecosystems, estimates ranged between 6.4% and 20% of annual ecosystem respiration (Table S1). Taken together, these estimates show high variability in the relative contributions of deadwood respiration within and across ecosystems. This uncertainty highlights the need for further studies, especially in tropical ecosystems, which contain the vast 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 wood decomposition (Figure 1). Fungal pathogens, especially non-native 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 *O. 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 wood 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 2012). Fungal hyphae penetrate wood 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 wood decomposition. Some ascomycetes in the Xylariaceae can degrade wood through a soft rot mechanism, including lignin, even without significant oxidative enzyme production (Liers et al. 2006). Soft rot fungi have broad environmental tolerances, allowing them to carry out wood 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 2012). Although they are not as well studied, bacteria likely contribute to wood 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 wood decomposition and requires further attention. For example, mycorrhizal fungi colonising leaf litter can reduce decomposition by fungi through extraction of water and nutrients. Some mycorrhizal fungi may colonise wood 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 tradeoff 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 United States 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. 2023).

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 wood decomposition, for example, as they physically fragment wood in search of insects. When consuming wood, 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. 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 within their nests, capable of degrading lignin; examples include fungus-growing termites and ambrosia beetles. Other clades of invertebrates are also indirect feeders on deadwood. For example, in the beetles, there are a host of families (e.g. Ptiliidae, Ciidae, Erotylidae) that feed on the spores, mycelium 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 wood than other invertebrates; because of their ability to resist desiccation via their social behaviour (Zanne et al. 2022), termites are thought to contribute most in hot dry locations, as compared to wood-dwelling microbes. In one global study, the effective Q_{10} when termites accessed the wood 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 with 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 wood decomposition (Ulyshen 2016).

2.3 Fires

Large-scale episodic disturbances are key drivers of deadwood dynamics (Woodall et al. 2021), and fire ranks high 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, 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 determines the amount of standing deadwood (Burton et al. 2021). For example, in eucalypt forests of southeastern Australia, the proportion of standing deadwood increased due to topkill of resprouting trees from 5-12% at low severity burn sites to 24-46% at high severity sites (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 post-fire 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 increases 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 (Cornwell et al. 2009). 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

There is evidence that 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 are a significant contributor to inputs into the deadwood pool. They are highly variable in severity and type including thunderstorm downbursts, hurricanes (aka cyclones, 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-shape 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 for leaf litter of woody species (Austin et al. 2016). Given the demonstrated importance of lignin as a light absorbing compound and its degradation 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 mineralisation by sunlight upon exposure. This solar radiation 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 or clear-cut or deciduous forests, the direct effect of solar radiation exposure and increased temperatures could increase microbial activity and carbon outputs.

The effect 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 realised 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 (Cornwell et al. 2009) and transport of fragmented wood. Collectively, these abiotic factors affecting mechanical and chemical composition of deadwood likely accelerate and increase outputs of deadwood in terrestrial ecosystems, although mechanistic evidence for their relative importance is lacking. There is a clear need for improved understanding of these factors and their interactions with biotic decomposition drivers during deadwood decomposition.

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 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 only focus on a single driver.

Of the studies with multiple decomposition drivers, interactions with microbes are probably best studied. Often these studies involve adding or removing non-microbial 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) summarised findings from studies investigating how wood-dwelling fungi affect termite behaviour after inoculating wood with specific fungal cultures or sterilising fungal-colonised wood. All but one of the studies in the meta-analysis were conducted under laboratory conditions. The presence of fungi in wood increased termite wood feeding (by 120%), survival (by 136%), aggregation (by 81%) and trail-following (by 200%). Interestingly, consumption by termites increased for wood colonised 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 metagenomic 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 wood as a substrate for wood-decomposing fungi, affecting the outcomes of fungal interactions while colonising that wood (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 wood (Lustenhouwer et al. 2020). Additionally, controlled burning of boreal forest plots where fire had previously been suppressed led to 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 colonisation of wood by airborne spores may be limited due to mortality caused by solar radiation exposure, particularly for wood that is not under a forest canopy (e.g., savannas, semi-arid 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 two 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 wood 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 the susceptibility to mortality and branch loss, as well as decomposition by different abiotic and biotic drivers. However, these contributions will not be reviewed here, as they were covered extensively in previous papers (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 likely to be affected by global change. In the coming decades, a changing climate is predicted to increase global temperatures and shift rainfall patterns with increases in the frequency and intensity of episodic events such as droughts, windstorms and storm surges (Lee et al. 2023). In addition, changes in land use are modifying ecosystems through shifts in vegetation types also affecting soil composition, microclimatic conditions and more. 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 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 (Lee et al. 2023). However, there are still large uncertainties in these models 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). There will also be an increased frequency, intensity and extent of fires (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 also 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 lead to an increase in deadwood biomass. However, logging can result in large dead biomass input of branches and can create damage to live unharvested trees, increasing their chances of 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 simultaneous changes in rainfall will also 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 would expect their impacts to increase both within the tropics and extra-tropically as the climate changes (Figure 3). Additionally, warmer and drier conditions may promote more frequent and intense fires consuming increased amounts of deadwood. These changing effects of fire are expected to be more marked 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 these outputs. For instance, biotic decomposers are dependent on the positioning of the deadwood which itself is influenced by global change. The output rates of wood increase when trees fall, with deadwood having direct contact with the soil, as compared to when dead trees remain standing as snags (standing dead trees) or are suspended off the ground (Song et al. 2017). Taking this into account, one study from the Eastern USA found that warmer climates are predicted to increase the rate of snag fall, speeding up deadwood 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 biotic pressures (see Section 3.1); such events will create patches of high deadwood density. In these instances, 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 favour some invertebrate animals over microbes as decomposition drivers. Mass mortality events may also increase exposure to solar radiation, with the result of greater lignin removal.

While global change will shift the output rates of wood, 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 will likely 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 carbon released. It should be noted that greater CH_4 emissions will depend on the 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 emission 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 will likely 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 wood (Austin 2011).

The complete removal of deadwood through direct harvesting may also shift the contribution of different decomposers to deadwood outputs as the deadwood pools build up again. The destructive nature of logging significantly reduces the function and activity of both wood-decomposing fungi and wood feeding invertebrates (Chen et al. 2019; Luke et al. 2014). As the forest recovers, interactions between both abiotic and biotic decomposition drivers will be altered. For instance, termites can recolonise 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. 2021). Decomposing fungi also decline in abundance following logging, with impacts potentially lasting for decades (Chen et al. 2019). As interactions shift among wood 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 on 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 Analysis (FIA) plots. In these, pool sizes have been highly variable and hard to predict across the landscape (Woodall et al. 2021). Future research should better explore the links between the deadwood inputs and outputs as influenced by global change to better inform Earth system models (see Section 4), which can predict changes in deadwood carbon emissions across local to global scales.

4. Modelling 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 wood 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 chemical quality, temperature, and moisture as drivers of wood decay. Similar to Yasso, other soil biogeochemical models also account for mechanisms of deadwood inputs and outputs. The Community Land Model, which incorporates the BiomeBGC soil model, represents wood 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 (classification of plants into different categories, such as needleleaf versus broadleaf and evergreen versus deciduous). The forest sub-model of Century (Parton et al. 1988) also represents explicit pools of deadwood. In that model, output rates depend on wood size, temperature, and moisture while carbon transfer to soil pools depends on wood lignin:nitrogen ratios.

Recently, Dai et al. (2021) developed a detailed process-based model of wood output rates known as the Coarse Woody Debris Decomposition Assessment Tool (CWDDAT). Based on literature data and conceptual theory, CWDDAT simulates wood 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 wood size and position (e.g. downed or standing dead). The model represents physical fragmentation and the flux of dissolved organic carbon that moves from wood into soil through leaching. CWDDAT simulations of wood 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 wood dynamics at ecosystem to global scales where variation in wood inputs and disturbance regimes affects wood pools and their outputs. Currently, the representation of wood dynamics in global models is rudimentary. Most Earth system models lack a mechanistic representation of deadwood pool sizes, inputs and outputs. In the 5th Coupled Model Intercomparison Project (CMIP5), only two models--CCSM4 and NorESM-- explicitly represented deadwood pools; both used the BiomeBGC/CLM approach (Todd-Brown et al. 2013). Other global models treat wood as a type of litter which does not account for the unique chemistry, size structure, positioning, and biological communities that influence wood outputs. Likewise, disturbances such as fire, insect outbreaks, and windstorms that uniquely impact wood inputs and outputs are poorly represented in Earth system models. It is possible that improvements have been made in the representation of wood dynamics in Earth system models included in CMIP6 (Ito et al. 2020; Lovato et al. 2022), but the model outputs only recently became available and have not yet been fully analysed.

Future Earth system model development could incorporate more mechanistic approaches such as CWDDAT. Doing so would require additional efforts to couple the wood output mechanisms with other processes such as drivers of tree mortality, soil microclimate conditions, and the production of trace gases from wood. For example, no wood 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 emphasised long-term observations of forest dynamics to maximise 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 recognised that reducing individual tree mortality was central to achieving production objectives. An unintended consequence of minimising 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 1970's. 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 loss of deadwood substrates on which they depend (Stokland et al. 2012). In North America, ecologists began to recognise the critical services provided by deadwood including nutrient cycling, water retention and tree regeneration (Harmon et al. 1986).

Although minimising 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 states, "At the time a tree dies, it has only partially fulfilled its potential ecological function." 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 recognised 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 recognised that deadwood resulting from harvest activities (i.e., unutilised 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 stumps and below ground 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

Burgeoning work on adaptive forest management advocates for increasing tree species diversity and forest structural complexity, with explicit incorporation of deadwood creation or retention. 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 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 minimising 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 reconfiguring the structure and precedents of markets themselves.

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 worldwide. Likewise, the apparent increase in windstorms, such as hurricanes, and drought has created deadwood management challenges, particularly evident in controversies over post-disturbance salvage logging (Leverkus et al. 2020). These issues have heightened the importance of deadwood such that US Congressional Acts (e.g USDA Forest Service 2022) now explicitly identify deadwood’s role in future forests.

The lack of resources in many countries may preclude them from establishing and regularly monitoring forest inventories to assess deadwood carbon stocks and accurately estimate greenhouse gas emissions, e.g., CO_2 and CH_4 (Umemiya & White 2023). 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 in the accuracy of their inventories (Woodall et al. 2019), many other regions still lack critical basic information. Given many of these countries are found in the tropics where most deadwood biomass is found (Figure 2), it is imperative to build and support their capabilities of carrying out regular deadwood assessments. Support to maintain regular deadwood assessments in countries which lack resources can be achieved through the continued establishment and maintenance of global, on the ground, forest inventory networks in collaboration with local governments, non-governmental organisations, and scientists. Additionally, it will be crucial to increase data storage and sharing capacities between carbon inventory networks and government inventories to encourage and improve the accuracy and use 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 a better management of deadwood resources.

We anticipate that future forest management will balance the varying benefits and challenges associated with deadwood resources in the 21st century. While there are a few challenges such as wildfire risk, there are many benefits including microclimates buffered against climate change, maintenance of biodiversity, retained structural legacy, carbon credits sold in a market, natural capital, and serving as a “lifeboat” for fungal/microbial communities in forests affected by global change. Further work is needed to quantify deadwood carbon pools, and their inputs to and outputs from, including measures of uncertainty, in a wider range of forest types (Russell et al. 2015). However, the more daunting challenge for 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 applying this information can 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 non-tree woody plants (e.g. shrubs, lianas) and trees from non-forest ecosystems (e.g. savanna) into our understanding of deadwood pool sizes, inputs, and outputs under current and future climates?
5) What is the magnitude of carbon pools below ground in deadwood derived from coarse roots and rhizomes, and what are the drivers of the inputs and outputs rates and forms compared with aboveground deadwood?
6) Should there be a distinction between output rates of naturally senesced deadwood versus "fresh" deadwood derived from anthropogenic or natural disturbances?
7) How can we use evolutionary relationships of tree lineages to predict and 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 in the world more climate-resilient and climate friendly (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, and how should we integrate deadwood into carbon markets?

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.

References

Acanakwo EF, Sheil D, Moe SR. 2019. Wood decomposition is more rapid on than off termite mounds in an African savanna. *Ecosphere*. 10(1):e02554
Ahlström A, Raupach MR, Schurgers G, Smith B, Arneth A, et al. 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink. *Science*. 348(6237):895–99
Anderegg WRL, Trugman AT, Badgley G, Anderson CM, Bartuska A, et al. 2020. Climate-driven risks to the climate mitigation potential of forests. *Science*. 368(6497):eaaz7005
Anderson-Teixeira KJ, Wang MMH, McGarvey JC, LeBauer DS. 2016. Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). *Glob. Change Biol.* 22(5):1690–1709

Austin AT. 2011. Has water limited our imagination for aridland biogeochemistry? *Trends Ecol. Evol.* 26(5):229–35

Austin AT, Ballaré CL. 2023. Attackers gain the upper hand over plants in the face of rapid global change. *Curr. Biol.* 33(11):R611–20

Austin AT, Méndez MS, Ballaré CL. 2016. Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proc. Natl. Acad. Sci.* 113(16):4392–97

Austin AT, Vivanco L. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*. 442(7102):555–58

Bar-On YM, Phillips R, Milo R. 2018. The biomass distribution on Earth. *Proc. Natl. Acad. Sci.* 115(25):6506–11

Bauman D, Fortunel C, Delhaye G, Malhi Y, Cernusak LA, et al. 2022. Tropical tree mortality has increased with rising atmospheric water stress. *Nature*. 608(7923):528–33

Bennett LT, Bruce MJ, MacHunter J, Kohout M, Tanase MA, Aponte C. 2016. Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire. *For. Ecol. Manag.* 380:107–17

Berzaghi F, Longo M, Ciais P, Blake S, Bretagnolle F, et al. 2019. Carbon stocks in central African forests enhanced by elephant disturbance. *Nat. Geosci.* 12(9):725–29

Bowman DMJS, Kolden CA, Abatzoglou JT, Johnston FH, van der Werf GR, Flannigan M. 2020. Vegetation fires in the Anthropocene. *Nat. Rev. Earth Environ.* 1(10):500–515

Bradford MA, Veen GFC, Bradford EM, Covey KR, Crowther TW, et al. 2023. Coarse woody debris accelerates the decomposition of deadwood inputs across temperate forest. *Biogeochemistry*

Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, et al. 2014. Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proc. Natl. Acad. Sci.* 111(17):6347–52

Burton JE, Bennett LT, Kasel S, Nitschke CR, Tanase MA, et al. 2021. Fire, drought and productivity as drivers of dead wood biomass in eucalypt forests of south-eastern Australia. *For. Ecol. Manag.* 482:118859

Campbell JL, Fontaine JB, Donato DC. 2016. Carbon emissions from decomposition of fire-killed trees following a large wildfire in Oregon, United States. *J. Geophys. Res. Biogeosciences*. 121(3):718–30

Campbell JL, Green MB, Yanai RD, Woodall CW, Fraver S, et al. 2019. Estimating uncertainty in the volume and carbon storage of downed coarse woody debris. *Ecol. Appl.* 29(2):e01844

Carmichael MJ, Bernhardt ES, Bräuer SL, Smith WK. 2014. The role of vegetation in methane flux to the atmosphere: should vegetation be included as a distinct category in the global methane budget? *Biogeochemistry*. 119(1):1–24

Chen J, Xu H, He D, Li Y, Luo T, et al. 2019. Historical logging alters soil fungal community composition and network in a tropical rainforest. *For. Ecol. Manag.* 433:228–39

Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE. 2018. Triggers of tree mortality under drought. *Nature*. 558(7711):531–39

Clausen CA. 1996. Bacterial associations with decaying wood: a review. *Int. Biodeterior. Biodegrad.* 37(1):101–7

Cook GD, Liedloff AC, Meyer CP (Mick), Richards AE, Bray SG, et al. 2020. Standing dead trees contribute significantly to carbon budgets in Australian savannas. *Int. J. Wildland Fire*. 29(3):215–28

Cornelissen JHC, Grootemaat S, Verheijen LM, Cornwell WK, van Bodegom PM, et al. 2017. Are litter decomposition and fire linked through plant species traits? *New Phytol.* 216(3):653–69

Cornwell WK, Cornelissen JHC, Allison SD, BAUHUS J, Eggleton P, et al. 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? *Glob. Change Biol.* 15(10):2431–49

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 11(10):1065–71

Crowther TW, Thomas SM, Maynard DS, Baldrian P, Covey K, et al. 2015. Biotic interactions mediate soil microbial feedbacks to climate change. *Proc. Natl. Acad. Sci.* 112(22):7033–38

Dai Z, Trettin CC, Burton AJ, Jurgensen MF, Page-Dumroese DS, et al. 2021. Coarse woody debris decomposition assessment tool: Model development and sensitivity analysis. *PLOS ONE*. 16(6):e0251893

Dix NJ. 2012. *Fungal Ecology*. Springer Science & Business Media

Dossa GGO, Schaefer D, Zhang J-L, Tao J-P, Cao K-F, et al. 2018. The cover uncovered: Bark control over wood decomposition. *J. Ecol.* 106(6):2147–60

Driscoll DA, Armenteras D, Bennett AF, Brotons L, Clarke MF, et al. 2021. How fire interacts with habitat loss and fragmentation. *Biol. Rev.* 96(3):976–98

Edman M, Eriksson A-M. 2016. Competitive outcomes between wood-decaying fungi are altered in burnt wood. *FEMS Microbiol. Ecol.* 92(6):fiw068

Esquivel-Muelbert A, Phillips OL, Brienen RJW, Fauset S, Sullivan MJP, et al. 2020. Tree mode of death and mortality risk factors across Amazon forests. *Nat. Commun.* 11(1):5515

Fei S, Morin RS, Oswalt CM, Liebhold AM. 2019. Biomass losses resulting from insect and disease invasions in US forests. *Proc. Natl. Acad. Sci.* 116(35):17371–76

Flores-Moreno H, Yatsko AR, Cheeseman AW, Allison SD, Cernusak LA, et al. 2023. Higher internal stem damage in dry compared to wet tropics: where are we overestimating forest biomass?

Frank J, Castle ME, Westfall JA, Weiskittel AR, MacFarlane DW, et al. 2018. Variation in occurrence and extent of internal stem decay in standing trees across the eastern US and Canada: evaluation of alternative modelling approaches and influential factors. *For. Int. J. For. Res.* 91(3):382–99

Freschet GT, Aerts R, Cornelissen JHC. 2012a. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *J. Ecol.* 100(3):619–30

Freschet GT, Weedon JT, Aerts R, van Hal JR, Cornelissen JHC. 2012b. Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. *J. Ecol.* 100(1):161–70

García-Palacios P, Maestre FT, Kattge J, Wall DH. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecol. Lett.* 16(8):1045–53

Gora EM, Esquivel-Muelbert A. 2021. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nat. Plants*. 7(4):384–91

Grace J, José JS, Meir P, Miranda HS, Montes RA. 2006. Productivity and carbon fluxes of tropical savannas. *J. Biogeogr.* 33(3):387–400

Griffiths HM, Eggleton P, Hemming-Schroeder N, Swinfield T, Woon JS, et al. 2021. Carbon flux and forest dynamics: Increased deadwood decomposition in tropical rainforest tree-fall canopy gaps. *Glob. Change Biol.* 27(8):1601–13

Guo C, Tuo B, Ci H, Yan E-R, Cornelissen JHC. 2021. Dynamic feedbacks among tree functional traits, termite populations and deadwood turnover. *J. Ecol.* 109(4):1578–90

Guo C, Yan E-R, Cornelissen JHC. 2022. Size matters for linking traits to ecosystem multifunctionality. *Trends Ecol. Evol.* 37(9):803–13

Harmon ME. 2001. Moving Towards a New Paradigm for Woody Detritus Management. *Ecol. Bull.* (49):269–78

Harmon ME, Fasth BG, Yatskov M, Kastendick D, Rock J, Woodall CW. 2020. Release of coarse woody detritus-related carbon: a synthesis across forest biomes. *Carbon Balance Manag.* 15(1):1

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, et al. 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems. In *Advances in Ecological Research*, Vol. 15, eds. A MacFadyen, ED Ford, pp. 133–302. Academic Press

Hartmann H, Bastos A, Das AJ, Esquivel-Muelbert A, Hammond WM, et al. 2022. Climate Change Risks to Global Forest Health: Emergence of Unexpected Events of Elevated Tree Mortality Worldwide. *Annu. Rev. Plant Biol.* 73(1):673–702

Hlásny T, König L, Krokene P, Lindner M, Montagné-Huck C, et al. 2021. Bark Beetle Outbreaks in Europe: State of Knowledge and Ways Forward for Management. *Curr. For. Rep.* 7(3):138–65

Hu Z, Michaletz ST, Johnson DJ, McDowell NG, Huang Z, et al. 2018. Traits drive global wood decomposition rates more than climate. *Glob. Change Biol.* 24(11):5259–69

Hyvärinen E, Kouki J, Martikainen P. 2006. Fire and Green-Tree Retention in Conservation of Red-Listed and Rare Deadwood-Dependent Beetles in Finnish Boreal Forests. *Conserv. Biol.* 20(6):1710–19

Ibanez T, Platt WJ, Bellingham PJ, Vieilledent G, Franklin J, et al. 2022. Altered cyclone–fire interactions are changing ecosystems. *Trends Plant Sci.* 27(12):1218–30

Ito A, Hajima T, Lawrence DM, Brovkin V, Delire C, et al. 2020. Soil carbon sequestration simulated in CMIP6-LUMIP models: implications for climatic mitigation. *Environ. Res. Lett.* 15(12):124061

Jeffrey LC, Reithmaier G, Sippo JZ, Johnston SG, Tait DR, et al. 2019. Are methane emissions from mangrove stems a cryptic carbon loss pathway? Insights from a catastrophic forest mortality. *New Phytol.* 224(1):146–54

Junninen K, Kouki J, Renvall P. 2008. Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. *Can. J. For. Res.* 38(2):202–15

Keenan T, Williams C. 2018. The terrestrial carbon sink. *Annu. Rev. Environ. Resour.* 43:219–43

Kim YS, Singh AP. 2000. MICROMORPHOLOGICAL CHARACTERISTICS OF WOOD BIODEGRADATION IN WET ENVIRONMENTS: A REVIEW. *IAWA J.* 21(2):135–55

Krishna MP, Mohan M. 2017. Litter decomposition in forest ecosystems: a review. *Energy Ecol. Environ.* 2(4):236–49

Le Breton TD, Lyons MB, Nolan RH, Penman T, Williamson GJ, Ooi MK. 2022. Megafire-induced interval squeeze threatens vegetation at landscape scales. *Front. Ecol. Environ.* 20(5):327–34

Lee H, Calvin K, Dasgupta D, Krinner G, Mukherji A, et al. 2023. Synthesis Report of the IPCC Sixth Assessment Report (AR6): Summary for Policymakers. Intergovernmental Panel on Climate Change

Lee H, Rahn T, Throop H. 2012. An accounting of C-based trace gas release during abiotic plant litter degradation. *Glob. Change Biol.* 18(3):1185–95

Leverkus AB, Gustafsson L, Lindenmayer DB, Castro J, Rey Benayas JM, et al. 2020. Salvage logging effects on regulating ecosystem services and fuel loads. *Front. Ecol. Environ.* 18(7):391–400

Liers C, Ullrich R, Steffen KT, Hatakka A, Hofrichter M. 2006. Mineralization of 14C-labelled synthetic lignin and extracellular enzyme activities of the wood-colonizing ascomycetes Xylaria hypoxylon and Xylaria polymorpha. *Appl. Microbiol. Biotechnol.* 69(5):573–79

Liski J, Palosuo T, Peltoniemi M, Sievänen R. 2005. Carbon and decomposition model Yasso for forest soils. *Ecol. Model.* 189(1):168–82

Liu G, Cornwell WK, Cao K, Hu Y, Van Logtestijn RSP, et al. 2015. Termites amplify the effects of wood traits on decomposition rates among multiple bamboo and dicot woody species. *J. Ecol.* 103(5):1214–23

Lovato T, Peano D, Butenschön M, Materia S, Iovino D, et al. 2022. CMIP6 Simulations With the CMCC Earth System Model (CMCC-ESM2). *J. Adv. Model. Earth Syst.* 14(3):e2021MS002814

Luke SH, Fayle TM, Eggleton P, Turner EC, Davies RG. 2014. Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodivers. Conserv.* 23(11):2817–32

Lunde LF, Boddy L, Sverdrup-Thygeson A, Jacobsen RM, Kauserud H, Birkemoe T. 2023. Beetles provide directed dispersal of viable spores of a keystone wood decay fungus. *Fungal Ecol.* 63:101232

Lustenhouwer N, Maynard DS, Bradford MA, Lindner DL, Oberle B, et al. 2020. A trait-based understanding of wood decomposition by fungi. *Proc. Natl. Acad. Sci.* 117(21):11551–58

Martin AR, Domke GM, Doraisami M, Thomas SC. 2021. Carbon fractions in the world's dead wood. *Nat. Commun.* 12(1):889

McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, et al. 2020. Pervasive shifts in forest dynamics in a changing world. *Science*. 368(6494):eaaz9463

Mitchell SJ. 2013. Wind as a natural disturbance agent in forests: a synthesis. *For. Int. J. For. Res.* 86(2):147–57

Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, et al. 2004. Detritus, trophic dynamics and biodiversity. *Ecol. Lett.* 7(7):584–600

Norros V, Karhu E, Nordén J, Vähätalo AV, Ovaskainen O. 2015. Spore sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. *Ecol. Evol.* 5(16):3312–26

Oberle B, Ogle K, Zanne AE, Woodall CW. 2018. When a tree falls: Controls on wood decay predict standing dead tree fall and new risks in changing forests. *PLOS ONE*. 13(5):e0196712

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, et al. 2011. A Large and Persistent Carbon Sink in the World's Forests. *Science*. 333(6045):988–93

Parton WJ, Stewart JWB, Cole CV. 1988. Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry*. 5(1):109–31

Pausas JG, Ribeiro E. 2013. The global fire–productivity relationship. *Glob. Ecol. Biogeogr.* 22(6):728–36

Pfeifer M, Lefebvre V, Turner E, Cusack J, Khoo M, et al. 2015. Deadwood biomass: an underestimated carbon stock in degraded tropical forests? *Environ. Res. Lett.* 10(4):044019

Pietsch KA, Ogle K, Cornelissen JHC, Cornwell WK, Bönisch G, et al. 2014. Global relationship of wood and leaf litter decomposability: the role of functional traits within and across plant organs. *Glob. Ecol. Biogeogr.* 23(9):1046–57

Preston CM, Schmidt MWI. 2006. Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences*. 3(4):397–420

Pugh TAM, Rademacher T, Shafer SL, Steinkamp J, Barichivich J, et al. 2020. Understanding the uncertainty in global forest carbon turnover. *Biogeosciences*. 17(15):3961–89

Reineke LH. 1933. Perfecting a stand-density index for even-aged forests

Renne RR, Schlaepfer DR, Palmquist KA, Bradford JB, Burke IC, Lauenroth WK. 2019. Soil and stand structure explain shrub mortality patterns following global change–type drought and extreme precipitation. *Ecology*. 100(12):e02889

Rinne KT, Rajala T, Peltoniemi K, Chen J, Smolander A, Mäkipää R. 2017. Accumulation rates and sources of external nitrogen in decaying wood in a Norway spruce dominated forest. *Funct. Ecol.* 31(2):530–41

Rückamp D, Martius C, Bragança MAL, Amelung W. 2011. Lignin patterns in soil and termite nests of the Brazilian Cerrado. *Appl. Soil Ecol.* 48(1):45–52

Russell MB, Fraver S, Aakala T, Gove JH, Woodall CW, et al. 2015. Quantifying carbon stores and decomposition in dead wood: A review. *For. Ecol. Manag.* 350:107–28

Sandström J, Bernes C, Junninen K, Lõhmus A, Macdonald E, et al. 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. *J. Appl. Ecol.* 56(7):1770–81

Seibold S, Rammer W, Hothorn T, Seidl R, Ulyshen MD, et al. 2021. The contribution of insects to global forest deadwood decomposition. *Nature*. 597(7874):77–81

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, et al. 2017. Forest disturbances under climate change. *Nat. Clim. Change*. 7(6):395–402

Senande-Rivera M, Insua-Costa D, Miguez-Macho G. 2022. Spatial and temporal expansion of global wildland fire activity in response to climate change. *Nat. Commun.* 13(1):1208

Senf C, Pflugmacher D, Zhiqiang Y, Sebald J, Knorn J, et al. 2018. Canopy mortality has doubled in Europe’s temperate forests over the last three decades. *Nat. Commun.* 9(1):4978

Sippo JZ, Lovelock CE, Santos IR, Sanders CJ, Maher DT. 2018. Mangrove mortality in a changing climate: An overview. *Estuar. Coast. Shelf Sci.* 215:241–49

Song Z, Dunn C, Lü X-T, Qiao L, Pang J-P, Tang J-W. 2017. Coarse woody decay rates vary by physical position in tropical seasonal rainforests of SW China. *For. Ecol. Manag.* 385:206–13

Stokland JN, Siitonen J, Jonsson BG. 2012. *Biodiversity in Dead Wood*. Cambridge university press

Swanson ME, Magee MI, Nelson AS, Engstrom R, Adams HD. 2023. Experimental downed woody debris-created microsites enhance tree survival and growth in extreme summer heat. *Front. For. Glob. Change*. 6:

Swift MJ, Heal OW, Anderson JM, Anderson JM. 1979. *Decomposition in Terrestrial Ecosystems*. University of California Press

ten Have R, Teunissen PJM. 2001. Oxidative Mechanisms Involved in Lignin Degradation by White-Rot Fungi. *Chem. Rev.* 101(11):3397–3414

Thornton PE, Rosenbloom NA. 2005. Ecosystem model spin-up: Estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. *Ecol. Model.* 189(1):25–48

Thorpe HC, Thomas SC, Caspersen JP. 2008. Tree Mortality Following Partial Harvests Is Determined by Skidding Proximity. *Ecol. Appl.* 18(7):1652–63

Todd-Brown KEO, Randerson JT, Post WM, Hoffman FM, Tarnocai C, et al. 2013. Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences*. 10(3):1717–36

Trenberth KE, Dai A, van der Schrier G, Jones PD, Barichivich J, et al. 2014. Global warming and changes in drought. *Nat. Clim. Change*. 4(1):17–22

Ulyshen MD. 2016. Wood decomposition as influenced by invertebrates. *Biol. Rev.* 91(1):70–85

Ulyshen MD, Diehl SV, Jeremic D. 2016. Termites and flooding affect microbial communities in decomposing wood. *Int. Biodeterior. Biodegrad.* 115:83–89

Umemiya C, White MK. 2023. National GHG inventory capacity in developing countries – a global assessment of progress. *Clim. Policy*. 0(0):1–13

USDA, Forest Service. 2022. CONFRONTING THE WILDFIRE CRISIS A Strategy for Protecting Communities and Improving Resilience in America’s Forests

van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, et al. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. *Science*. 323(5913):521–24

Viana-Junior AB, Côrtes MO, Cornelissen TG, Neves F de S. 2018. Interactions between wood-inhabiting fungi and termites: a meta-analytical review. *Arthropod-Plant Interact.* 12(2):229–35

Wijas B, Atkinson J. 2021. Termites in restoration: the forgotten insect? *Restor. Ecol.* 29(8):e13511

Woodall CW, Fraver S, Oswalt SN, Goeking SA, Domke GM, Russell MB. 2021. Decadal dead wood biomass dynamics of coterminous US forests. *Environ. Res. Lett.* 16(10):104034

Woodall CW, Monleon VJ, Fraver S, Russell MB, Hatfield MH, et al. 2019. The downed and dead wood inventory of forests in the United States. *Sci. Data*. 6(1):180303

Woodall CW, Rondeux J, Verkerk PJ, Ståhl G. 2009. Estimating Dead Wood During National Forest Inventories: A Review of Inventory Methodologies and Suggestions for Harmonization. *Environ. Manage.* 44(4):624–31

Wu C, Zhang Z, Wang H, Li C, Mo Q, Liu Y. 2018. Photodegradation accelerates coarse woody debris decomposition in subtropical Chinese forests. *For. Ecol. Manag.* 409:225–32

Yin X. 1999. The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. *Oecologia*. 121(1):81–98

Zanne AE, Flores-Moreno H, Powell JR, Cornwell WK, Dalling JW, et al. 2022. Termite sensitivity to temperature affects global wood decay rates. *Science*. 377(6613):1440–44

Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature*. 506(7486):89–92

Zeng H, Chambers JQ, Negrón-Juárez RI, Hurtt GC, Baker DB, Powell MD. 2009. Impacts of tropical cyclones on U.S. forest tree mortality and carbon flux from 1851 to 2000. *Proc. Natl. Acad. Sci.* 106(19):7888–92

Zhao W, van Logtestijn RSP, van der Werf GR, van Hal JR, Cornelissen JHC. 2018. Disentangling effects of key coarse woody debris fuel properties on its combustion, consumption and carbon gas emissions during experimental laboratory fire. *For. Ecol. Manag.* 427:275–88

Zhu Q, Riley WJ, Iversen CM, Kattge J. 2020. Assessing Impacts of Plant Stoichiometric Traits on Terrestrial Ecosystem Carbon Accumulation Using the E3SM Land Model. *J. Adv. Model. Earth Syst.* 12(4):e2019MS001841

Zuleta D, Arellano G, McMahon SM, Aguilar S, Bunyavejchewin S, et al. 2023. Damage to living trees contributes to almost half of the biomass losses in tropical forests. *Glob. Change Biol.* 29(12):3409–20

Figures

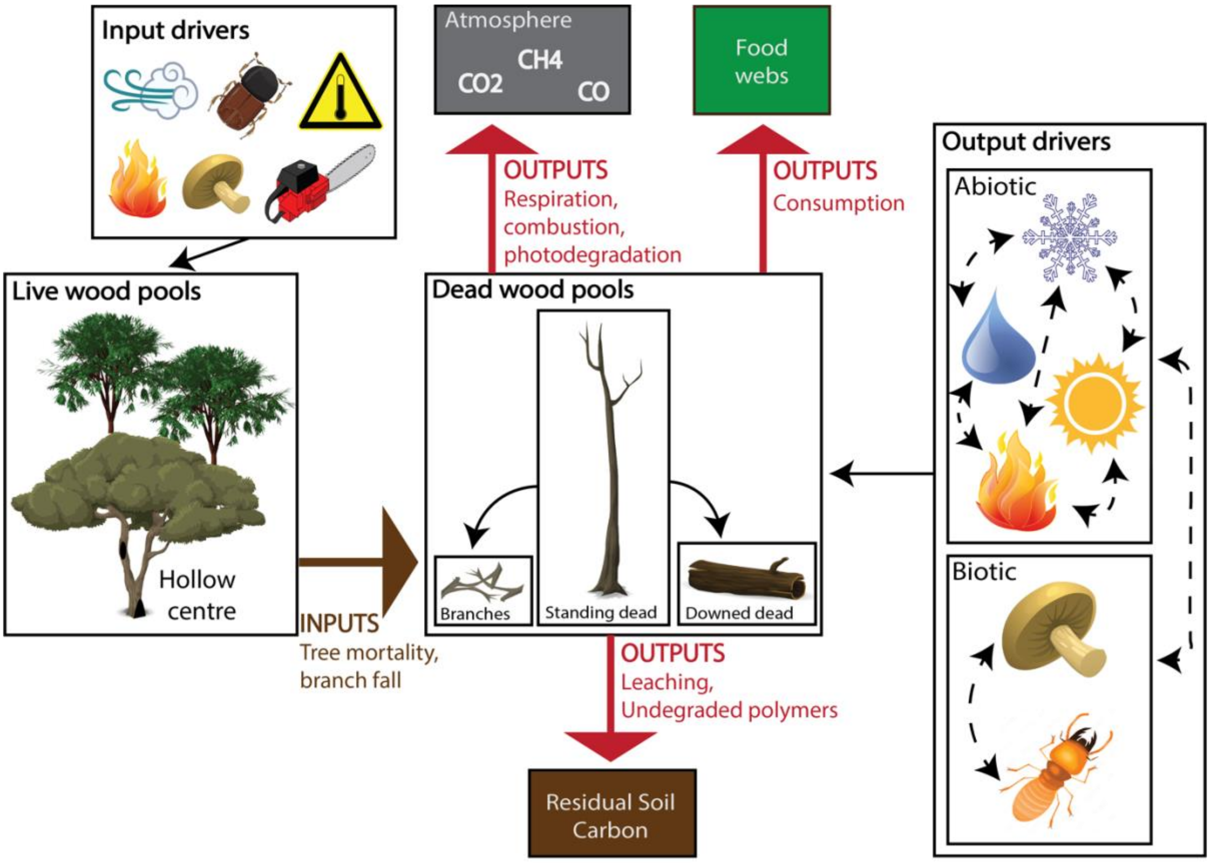

Figure 1 - Inputs into and outputs from deadwood pools separated as standing deadwood, branches, or logs. Outputs are regulated by biotic (animals and microbes) and abiotic output drivers (solar radiation, freeze-thaw, fire) and their interactions. The decomposers mineralize carbon into the atmosphere 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 will also make deadwood carbon available to organisms up the food webs.

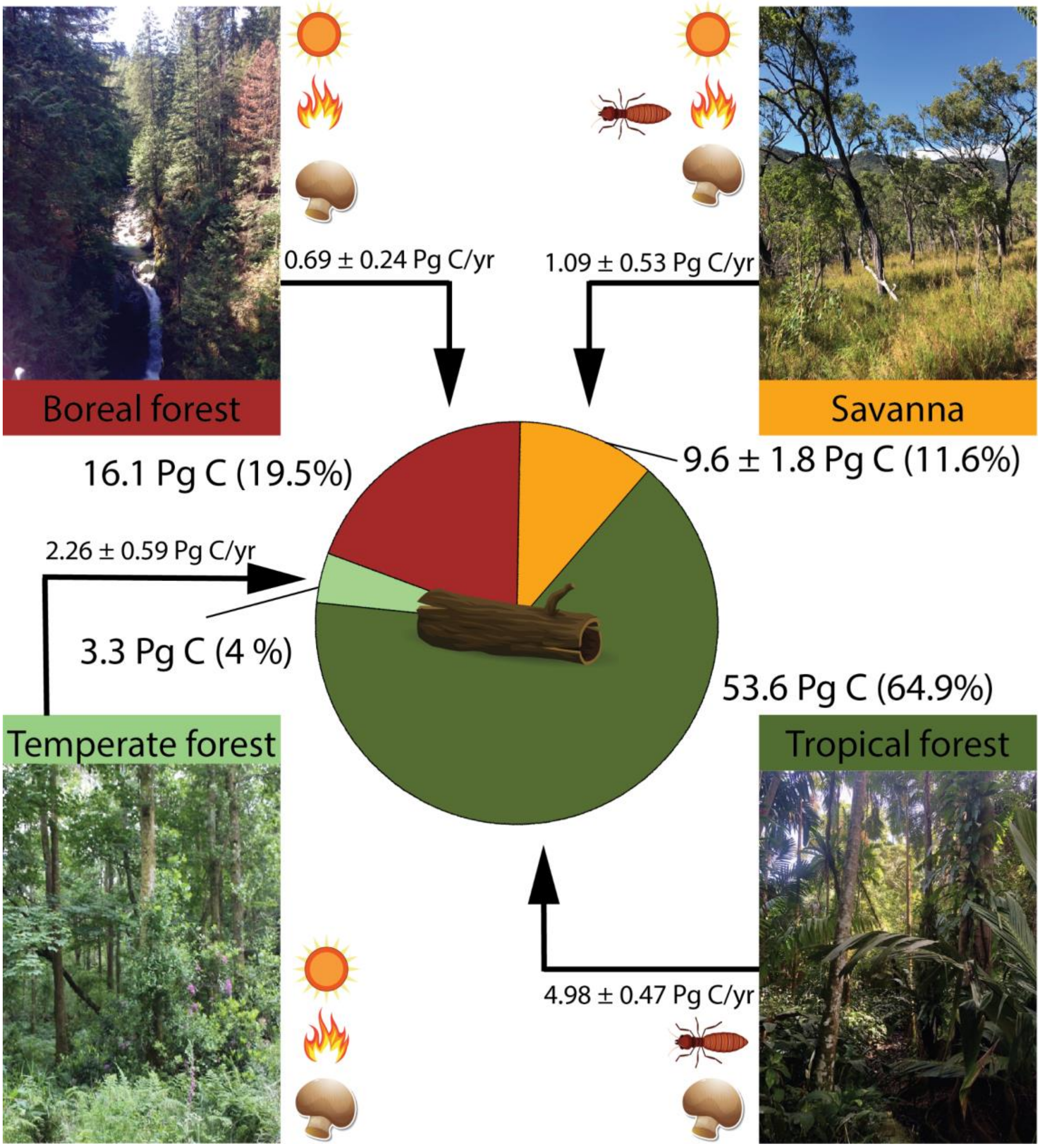

Figure 2 - Inputs of deadwood (Pg C/yr) within different biomes calculated from study compilation in Table S1. Biomass of deadwood (Pg) found across boreal, temperate and tropical forests extracted from Pan et al. (2011) compared with that found in savannas as compiled from studies in Table S1. The cartoons indicate the main decomposers within each biome.

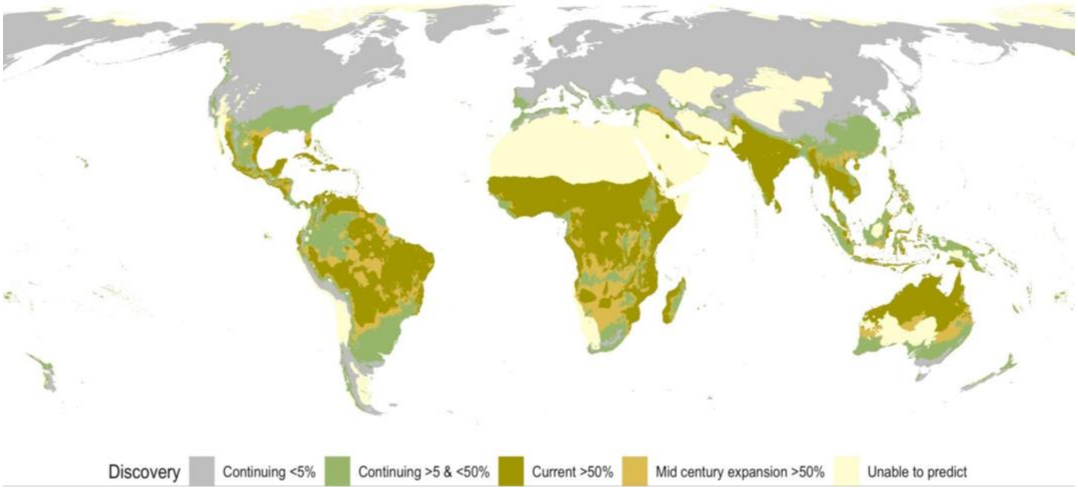

Figure 3 - Discovery rates as predicted by climatic variables (mean annual temperature and precipitation) were modelled from a large wood decomposer experiment by Zanne et al. (2022). This map indicates the expansion in the activity of termites with climate change scenario 585 for 2041-2060 from the GISS-E2-1-H model, which forecasts close to the median level of expansion among the models considered by Lee et al. (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 colour shows areas that do not currently have high rates but where rates are forecast to increase to greater than 50% by mid-century.

Supplemental Table

Table S1 - Compilation of studies measuring deadwood carbon pools across boreal, temperate, and tropical forests in addition to savanna ecosystems. Input of carbon to deadwood pools across all ecosystems and percentage of total ecosystem respiration attributed to deadwood outputs.

Biome	Area (million km^2)	Region	Deadwood carbon pools (Mg C/ha for savannas and Pg C for other biomes)	Input of carbon to deadwood carbon pools (Mg C/ha/yr)	Percentage of total ecosystem respiration represented by deadwood outputs
Boreal	15.4	All	16.1 (1)	0.38-1 (2)	7.6% (3)
				0.29 ± 0.21 (4)	30% (5)
Temperate	16.2	All	3.3 (1)	0.54 (6)	10-16% (7)
				1.31 (8)	2.2% (9)
				0.61 (7)	37% (10)
				0.8 (11)	1.4% (12)
				1.31 (13)	20% (14)
				0.8 (15)	

				1.2 (16) 0.8 (17) 0.54 ± 0.47 (18) 2.8 (19) 4.9 ± 0.71 (20) 0.8 (21) 0.92 (9)	
Tropical savanna and grasslands	4	Brazil	1.39 ± 1.26 (22) 0.87 (23)	N/A	N/A
	15	Africa	1.36 (24) 0.31 (25) 5.85 ± 3.7 (27) 2.47 (29)	0.67 (24) 0.18 ± 0.05 (26) 2.13 (28)	N/A

	2.2	Australia	1.9 (30)	0.47 (30)	N/A
Tropical Rainforest	23.4	All	53.6 (1)	4.23 (31) 2.7 ± 0.42 (32) 2.57 ± 0.08 (34) 2.81 (35) 1.84 (36) 1.93 ± 0.83 (37) 1.72 ± 0.52 (38) 1.1 ± 0.5 (39) 2.4 (40) 4 (41)	16% (32) 6.4% (33)

1. Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, et al. A Large and Persistent Carbon Sink in the World's Forests. Science. 2011;333(6045):988-93.
2. Krankina ON, Harmon ME. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air, and Soil Pollution. 1995;82(1):227-38.
3. Karelin DV, Zamolodchikov DG, Shilkin AV, Popov SY, Kumanyaev AS, de Gerenyu VOL, et al. The effect of tree mortality on CO2 fluxes in an old-growth spruce forest. European Journal of Forest Research. 2021;140(2):287-305.
4. Bond-Lamberty B, Gower ST. Decomposition and Fragmentation of Coarse Woody Debris: Re-visiting a Boreal Black Spruce Chronosequence. Ecosystems. 2008;11(6):831-40.
5. Knohl A, Kolle O, Minayeva TY, Milyukova IM, Vygodskaya NN, Foken T, et al. Carbon dioxide exchange of a Russian boreal forest after disturbance by wind throw. Glob Change Biol. 2002;8(3):231-46.
6. Brown SL, Schroeder PE. Spatial patterns of aboveground production and mortality of woody biomass for Eastern U.S. forests. Ecol Appl. 1999;9(3):968-80.
7. Jomura M, Kominami Y, Tamai K, Miyama T, Goto Y, Dannoura M, et al. The carbon budget of coarse woody debris in a temperate broad-leaved secondary forest in Japan. Tellus B: Chemical and Physical Meteorology. 2007;59(2):211-22.
8. Gonzalez-Akre E, Meakem V, Eng C-Y, Tepley AJ, Bourg NA, McShea W, et al. Patterns of tree mortality in a temperate deciduous forest derived from a large forest dynamics plot. Ecosphere. 2016;7(12):e01595.
9. Hollinger DY, Davidson EA, Fraver S, Hughes H, Lee JT, Richardson AD, et al. Multi-Decadal Carbon Cycle Measurements Indicate Resistance to External Drivers of Change at the Howland Forest AmeriFlux Site. Journal of Geophysical Research: Biogeosciences. 2021;126(8):e2021JG006276.
10. Harmon ME, Bible K, Ryan MG, Shaw DC, Chen H, Klopatek J, et al. Production, Respiration, and Overall Carbon Balance in an Old-growth Pseudotsuga-Tsuga Forest Ecosystem. Ecosystems. 2004;7(5):498-512.
11. Ohtsuka T, Shizu Y, Hirota M, Yashiro Y, Shugang J, Iimura Y, et al. Role of coarse woody debris in the carbon cycle of Takayama forest, central Japan. Ecol Res. 2014;29(1):91-101.
12. Gough CM, Vogel CS, Kazanski C, Nagel L, Flower CE, Curtis PS. Coarse woody debris and the carbon balance of a north temperate forest. For Ecol Manage. 2007;244(1):60-7.
13. Sollins P. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research. 1982;12(1):18-28.
14. Guo J, Chen G, Xie J, Yang Z, Yang Y. Respiration of downed logs in four natural evergreen broad-leaved forests in subtropical China. Plant and Soil. 2014;385(1):149-63.

15. Hudiburg T, Law B, Turner DP, Campbell J, Donato D, Duane M. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecol Appl. 2009;19(1):163-80.

16. Köhl M, Stümer W, Kenter B, Riedel T. Effect of the estimation of forest management and decay of dead woody material on the reliability of carbon stock and carbon stock changes—A simulation study. For Ecol Manage. 2008;256(3):229-36.

17. Kimberley MO, Beets PN, Paul TSH. Comparison of measured and modelled change in coarse woody debris carbon stocks in New Zealand's natural forest. For Ecol Manage. 2019;434:18-28.

18. Harmon ME, Hua C. Coarse Woody Debris Dynamics in Two Old-Growth Ecosystems. Bioscience. 1991;41(9):604-10.

19. Harcombe PA, Harmon ME, Greene SE. Changes in biomass and production over 53 years in a coastal Piceasitchensis – Tsugaheterophylla forest approaching maturity. Canadian Journal of Forest Research. 1990;20(10):1602-10.

20. Šebeň V, Konôpka B, Pajtík J. Quantifying carbon in dead and living trees; a case study in young beech and spruce stand over 9 years. Central European Forestry Journal. 2017;63(2-3):133-41.

21. Meyer P, Nagel R, Feldmann E. Limited sink but large storage: Biomass dynamics in naturally developing beech (Fagus sylvatica) and oak (Quercus robur, Quercus petraea) forests of north-western Germany. Journal of Ecology. 2021;109(10):3602-16.

22. Ottmar RD. Stereo photo series for quantifying cerrado fuels in central Brazil: United States Department of Agriculture, Forest Service, Pacific Northwest …; 2001.

23. De Castro EA, Kauffman JB. Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. J Trop Ecol. 1998;14(3):263-83.

24. Collins NM. The role of termites in the decomposition of wood and leaf litter in the Southern Guinea savanna of Nigeria. Oecologia. 1981;51(3):389-99.

25. Komposch A, Ensslin A, Fischer M, Hemp A. Aboveground Deadwood Biomass and Composition Along Elevation and Land-Use Gradients at Mount Kilimanjaro. Frontiers in ecology and evolution. 2022;9:732092.

26. Shackleton CM. Annual production of harvestable deadwood in semi-arid savannas, South Africa. For Ecol Manage. 1998;112(1):139-44.

27. Awé DV, Noiha NV, Zapfack L. Carbon management for savannah ecosystems in Central Africa: a case study from Cameroon. International Journal of Low-Carbon Technologies. 2021;16(4):1290-8.

28. Malaisse F, Freson R, Goffinet G, Malaisse-Mousset M. Litter fall and litter breakdown in miombo. Tropical ecological systems-Trends in terrestrial and aquatic research. 1975;11:137-52.

29. Willcock S, Phillips OL, Platts PJ, Balmford A, Burgess ND, Lovett JC, et al. Towards Regional, Error-Bounded Landscape Carbon Storage Estimates for Data-Deficient Areas of the World. PLoS One. 2012;7(9):e44795.

30. Cook GD, Liedloff AC, Meyer CP, Richards AE, Bray SG. Standing dead trees contribute significantly to carbon budgets in Australian savannas. International Journal of Wildland Fire. 2020;29(3):215-28.

31. Zuleta D, Arellano G, McMahon SM, Aguilar S, Bunyavejchewin S, Castaño N, et al. Damage to living trees contributes to almost half of the biomass losses in tropical forests. Glob Change Biol.n/a(n/a).

32. Hutyra LR, Munger JW, Hammond-Pyle E, Saleska SR, Restrepo-Coupe N, Daube BC, et al. Resolving systematic errors in estimates of net ecosystem exchange of CO2 and ecosystem respiration in a tropical forest biome. Agricultural and Forest Meteorology. 2008;148(8):1266-79.

33. Chambers JQ, Tribuzy ES, Toledo LC, Crispim BF, Higuchi N, Santos Jd, et al. Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. Ecol Appl. 2004;14(sp4):72-88.

34. Chave J, Condit R, Lao S, Caspersen JP, Foster RB, Hubbell SP. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. Journal of Ecology. 2003;91(2):240-52.

35. Gora EM, Kneale RC, Larjavaara M, Muller-Landau HC. Dead Wood Necromass in a Moist Tropical Forest: Stocks, Fluxes, and Spatiotemporal Variability. Ecosystems. 2019;22(6):1189-205.

36. Baker TR, Honorio Coronado EN, Phillips OL, Martin J, van der Heijden GMF, Garcia M, et al. Low stocks of coarse woody debris in a southwest Amazonian forest. Oecologia. 2007;152(3):495-504.

37. Chao KJ, Phillips OL, Baker TR, Peacock J, Lopez-Gonzalez G, Vásquez Martínez R, et al. After trees die: quantities and determinants of necromass across Amazonia. Biogeosciences. 2009;6(8):1615-26.

38. Gurdak DJ, Aragão LEOC, Rozas-Dávila A, Huasco WH, Cabrera KG, Doughty CE, et al. Assessing above-ground woody debris dynamics along a gradient of elevation in Amazonian cloud forests in Peru: balancing above-ground inputs and respiration outputs. Plant Ecology & Diversity. 2014;7(1-2):143-60.

39. Aryal DR, De Jong BHJ, Gaona SO, Vega JM, Olguín LE, Cruz SL. Fine Wood Decomposition Rates Decline with the Age of Tropical Successional Forests in Southern Mexico: Implications to Ecosystem Carbon Storage. Ecosystems. 2022;25(3):661-77.

40. Clark DB, Clark DA, Brown S, Oberbauer SF, Veldkamp E. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. For Ecol Manage. 2002;164(1):237-48.

41. Sato T, Yagihashi T, Niiyama K, Rahman KA, Azizi R. Coarse woody debris stocks and inputs in a primary hill dipterocarp forest, peninsular Malaysia. Journal of Tropical Forest Science. 2016;28:382-91.