Deadwood as a driver of forest functions

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Introduction

For generations, people have looked on deadwood as something to be removed from forests, either to be used as a fuel, or simply as a necessary part of "correct" forest management. Deadwood is supposed to harbour disease and even veteran trees are often regarded as a sign that a forest is being poorly managed. Breaking up these myths will be essential to preserve healthy forest ecosystems and the environmental services they provide. In international and European political processes, deadwood is increasingly being accepted as a key indicator of naturalness in forest ecosystems (MCPFE and EfE/PEBLDS, 2004). Forest policies have recognized the need to preserve a wide range of forest ecosystem services, such as the conservation of biodiversity (Nelson *et al*., 2009). This can be done by including deadwood in national biodiversity and forest strategies, monitoring deadwood, removing subsidies that pay for its undifferentiated removal, introducing supportive legislation and raising awareness.

The importance of deadwood in forests has been partially documented, and can be divided into the following inter-related categories (Harmon *et al*., 1986):
- Forest productivity;
- Providing habitat and structure to maintain biological diversity;
- Geomorphology of streams and slopes;
- Long-term carbon storage.

The importance of each abovementioned parts varies throughout the bio-geographical areas due to natural disturbance type, climatic zones and moisture regime.

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The ecological role of deadwood

Deadwood may add a significant amount of organic matter to the soil, provide habitat for decomposer organisms, retain moisture through dry periods, offer a refuge for ectomycorrhizal roots and their associated soil organisms, provide a site for asymbiotic or associative nitrogen-fixing bacteria, represent a capital pool of nutrients for the ecosystem, provide a site for the regeneration and contribute to soil acidification and podsolization (Christensen *et al*., 2003; Kruys and Jonsson, 1999).

All size classes of decaying pieces of wood contribute to the long-term accumulation of soil organic matter because the lignin and humus of well-decayed wood are rich in carbon constituents (Maser *et al*., 1988). Deadwood improves the water holding capacity and structure of the soil. In order to protect the productive potential of a forest soil, a continuous supply of organic materials is preferable.

Deadwood can also contribute to nutrient storage, which includes the nutrients accumulated in the woody bole, large branches, roots and stumps during tree growth and the nutrients added from litterfall and throughfall (rain falling through the forest canopy) being intercepted by a down log rather than falling on the forest floor. If the nutrients are added faster than they are leached by rain, the result is positive nutrient storage. As the wood decays, the nutrients are added to the available pool. Mechanisms for removing the nutrients from deadwood and adding them to the available pool vary in relation to climatic conditions, forest structure and soil characteristics (Laiho and Prescott, 2004). When these mushrooms fall off the logs and decay, they are returning nutrients from the downed wood into the available nutrient pool. Arthropods and earthworms digest the complex, organic molecules in down wood with the help of microorganisms in their digestive systems and return the nutrients to the forest in their frass. Thus, deadwood can be a reliable and steady source of nutrients over more than 100 years. When coarse woody debris is added to the ecosystem at regular intervals and is well distributed, it represents a long-term source of nutrients (Keenan *et al*., 1993).

In some wet ecosystems, the tree seedlings with the best chance of success are those that germinate on large pieces of woody debris (Harmon *et al*., 1986). The understorey is dense, so no light reaches seedlings on the forest floor. The decaying woody boles provide a platform for successful germination and growth (Lambert *et al*., 1980).

Deadwood also contributes to the soil formation and stabilization, supporting biological organisms and interactions that are precious for the forest ecosystem health. This involves soil arthropods, fungi, bacteria, animal waste and among other things, decaying wood.

There is no doubt that deadwood plays an important part in creating habitat for many plant and animal species in forests ecosystems. Particularly, deadwood provides sites for nests, dens and burrows; habitat for microbial decomposers (*e.g.*, bacteria, fungi and actinomycetes); a primary energy source for a complex food web; hiding cover for predators and protective cover for their prey; moist microsites *(e.g.*, for amphibians, insects, worms, plants, ectomycorrhizal fungi and tree roots); travel-ways across streams, across the forest floor, beneath and through the snow; refugia during disturbance and environmental stress (*e.g.*, low moisture and temperature extremes).

Deadwood represents a structural link with the previous stand form in some natural disturbance types, and continuity of habitats for some species (Hansen *et al*., 1991). Carey and Johnson (1995) reported that along with understorey vegetation, coarse woody debris is the most important habitat factor for small mammals. These latter help to sustain the ecological processes in which they are an integral part (*e.g.*, the dispersal of seeds and mycorrhizal fungi spores, the maintenance of healthy predator populations, and the control of potentially harmful invertebrate populations) (Hanski, 1998).

Arthropods are one of the most diverse groups of animals and one of the least understood. Soil microarthropods, although largely unidentified, are the most important arthropods in terms of their impact on nutrient cycling. Groups of them associated with deadwood have been shown to increase the availability and suitability of organic particles for decomposer communities, and contribute to nutrient cycling and soil formation (Setälä and Marshall, 1994).

Many nonvascular plant species and fungi are associated with deadwood. The diversity of these species is related to the diversity of substrates, including a variety of decay stages, and has been linked to forest health (Amaranthus *et al*., 1994; Stelfox, 1995). Variability in piece size contributes to this diversity. Some bryophytes and fungi are restricted to very large pieces (Soderstrom, 1988).

Deadwood is also important in the geomorphology of terrestrial ecosystems, due to the physical properties of large pieces of wood. Upland sources of deadwood contribute to slope stability, soil surface stability, prevention of erosion and control of storm surface runoff. Particularly, on a steep slope, deadwood plays a crucial role in soil stabilization, controlling the flow of water, soil and litter across the forest floor. Material in any decay class, lying across the slope will reduce soil movement down-slope.

Finally, deadwood plays also a wider role by storing carbon to mitigate global warming as efficiently as many young timber plantations (Stevens, 1997).

As the reality of climate change is widely recognised, carbon sequestration (the storing of carbon in ecosystems) is gaining attention as one way of reducing greenhouses gases (Dixon *et al*., 1994). Major forest carbon pools include trees, understorey vegetation, deadwood, litter, and soil. Deadwood is important as it is both a store and source of carbon but is generally the less studied of the carbon pools. This will now change because national carbon inventories are required under the Kyoto Protocol of the 1992 United Nations Framework Convention on Climate Change (Woldendorp *et al*., 2002). Initial discussion on carbon storage focused on fast-growing rotations of exotic plantations.

However, while these can quickly accumulate carbon, storage is very temporary: average retention time of carbon in plantation trees is only a few years because most of the fibre is used in paper and other short life products that are either burned or degrade quickly in landfill. Deadwood itself releases carbon to the atmosphere -becoming a carbon source- during microbial respiration from decomposer organisms. But in terrestrial ecosystems in cool climates, microbial activity is restricted and decomposition very slow, so that deadwood tends to act as a long-term storage site (Angers *et al*., 2010).

Deadwood in forest ecosystems

In forests, a deadwood biomass, which is mostly result of the mortality (natural and human-induced), is composed of different types of dead and dying woody material, occurring in numerous forms with various decaying rates. Although deadwood has been a subject of many studies, there is a large variability of definitions for deadwood, which manly depend on the aim for which the study is carried out (Rondeux and Sanches, 2010). While some authors distinguish only two types of deadwood (standing and lying deadwood), a more detailed classification with four or five deadwood components is used by others (Merganičová *et al*., 2012). There are also differences concerning the use of terminology. In English-speaking countries most often the term woody detritus or debris instead of deadwood is used to describe dead and decaying pieces of wood. For example, in earlier studies by the term coarse woody debris (CWD) was meant snags, logs, chunks of wood, large branches and coarse roots with variable minimum diameters (Harmon *et al*., 1986). However, some other studies defined CWD as a total woody necromass found in the forest, including the woody fruits, buried wood and stumps (Pyle and Brown, 1999). There also exists a discrepancy in the understanding of snags and stumps between some authors (Merganičová *et al*., 2012). Beside the difficulties with definitions and terminology, another important issue refers to methods employed for deadwood assessment.

A wide range of sampling techniques exists, such as sample plot inventory, strip surveying, line intercept sampling, adaptive cluster sampling, point and transect relascope sampling, and guided transect sampling (Ståhl *et al*., 2001; Ritter and Saborowski, 2012). As there is no unique international standard for terms, definitions and methods for deadwood, the estimates are generally not comparable between different countries (Harmon and Sexton, 1996; Rondeux and Sanchez, 2010), although it may be achieved using two possible approaches, standardization or harmonization (Rondeux *et al*., 2012).

Different quantitative and qualitative indicators may assess deadwood. In Europe, deadwood volume is used as one of the most important indicators of forest biodiversity and is a focal component of forest monitoring (Lassauce *et al*., 2011). The volume of deadwood share is generally smaller in managed forests than in natural forests (Lombardi *et al*., 2008; Jonsson and Siitonen, 2012a). Some studies have reported that quantity of deadwood in managed forest ranges between 2 and 8 m^3 ha^{-1} (Lombardi *et al*., 2008), representing only values of 2÷30% of the quantity in unmanaged forests (Fridman and Walheim, 2000; Siitonen, 2001; Lombardi *et al*., 2008). While the amount of deadwood in managed forest depends mostly on the history and type of forest management (Green and Peterken, 1997; Bobiec, 2002; Banaś *et al*., 2014), the amount of deadwood in unmanaged forests is determined by stand productivity and mortality. In these forest stands, the volume of deadwood is usually higher. As example, in natural and semi-natural temperate forests, estimates of deadwood volume are often in the range of 14÷222 m^3 ha^{-1} (Bretz Guby and Dobbertin, 1996). The most important primary mortality factor in young stands entering the stem-exclusion stage is competition, whereas in old-growth stands the mortality is mostly governed by the natural disturbances (Jonsson and Siitonen, 2012a). According to the review of Schelhaas *et al*. (2003) natural disturbances in the European forest caused in the period 1950-2000 a damage of 35 million m^3 of trees. In addition to the influence of different forest management and disturbance regimes, the amount of deadwood in forests depends on variables, such as forest type, its developmental stage, local soil and climatic characteristics (Lombardi *et al*., 2008). Opposite to this, Böhl and Brändli (2007) reported that little evidence of correlations between deadwood volume and such parameters as management, site or stand attributes is evident.

At the stand scale, a high amount of deadwood under natural conditions not only leads to a larger diversity of substrates, but also to a higher deadwood surface area (Lachat *et al*., 2013). At first, higher amounts of available deadwood lead to more dead-wood surface area that according to the island theory therefore a higher species number on sampling units with a larger surface can be expected. Secondly, larger surface areas lead to more different available habitats (Müller and Bütler, 2010). Not only the volume, but also maintaining diverse qualities of deadwood in terms of tree species, decomposition stage, diameter, decay class, and type has a positive effect on the conservation of saproxylic species assemblages (Lachat *et al*., 2013).

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