The living dead: acknowledging life after tree death to stop forest degradation

Simon Thorn[1,*], Sebastian Seibold[2,3], Alexandro B Leverkus[1,†], Thomas Michler[4], Jörg Müller[1,4], Reed F Noss[5], Nigel Stork[6], Sebastian Vogel[1], and David B Lindenmayer[7]

Global sustainability agendas focus primarily on halting deforestation, yet the biodiversity crisis resulting from the degradation of remaining forests is going largely unnoticed. Forest degradation occurs through the loss of key ecological structures, such as dying trees and deadwood, even in the absence of deforestation. One of the main drivers of forest degradation is limited awareness by policy makers and the public on the importance of these structures for supporting forest biodiversity and ecosystem function. Here, we outline management strategies to protect forest health and biodiversity by maintaining and promoting deadwood, and propose environmental education initiatives to improve the general awareness of the importance of deadwood. Finally, we call for major reforms to forest management to maintain and restore deadwood; large, old trees; and other key ecological structures.

Front Ecol Environ 2020; doi:10.1002/fee.2252

The world's forests not only provide essential ecosystem services to humans, including the storage of vast amounts of carbon, but also support most of the planet's terrestrial biodiversity. Approximately 1.6 billion people directly depend on forests for their lives and livelihoods. The UN recognizes the unique importance of forests through major global policy initiatives, such as the Aichi targets (https://www.cbd.int/sp/targets) and REDD+ (https://redd.unfccc.int). Policy attention directed toward deforestation is well justified, given that forest loss is a major threat to terrestrial biodiversity, including mammals, amphibians, and birds (Betts *et al.* 2017). However, as important carbon sinks and habitat for species, dying trees and deadwood – both of which can decline even in the absence of obvious changes in the amount of forest cover – are largely ignored by these initiatives (Stokland *et al.* 2012). Deforestation is typically initiated when hunting and gathering societies shift to agricultural systems. For example, in Central Europe, large-scale deforestation began in the Bronze Age (2000–1000 BCE; Stokland *et al.* 2012). In the early 18th century CE, when European forests had been reduced to their smallest extent due to overexploitation, wood production declined. Early concepts of sustainable forest management then began to evolve to end deforestation and ensure a long-term supply of timber (von Carlowitz 1713). Historically, large, old trees and deadwood were widespread, but "sustainable" forest management practices that were popular at that time called for their removal, as their presence was considered a waste of economic resources and a source of forest diseases (Hartig 1808). The economic rationale of not wasting timber resources remains a major reason why deadwood is still routinely removed, even under so-called ecologically sustainable forest management. In contrast to deforestation, forest degradation due to the removal of dying and dead trees is often legal and goes unnoticed by the public (Müller *et al.* 2015). Unfortunately, the pervasive effects of forest degradation may magnify biodiversity loss well beyond that caused by deforestation (Barlow *et al.* 2016).

In a nutshell:

- Public awareness about the importance of deadwood for biodiversity is lacking
- Removal of dead and dying trees often results in major losses of forest biodiversity, but elicits little or no public response
- Halting forest degradation requires protecting and restoring key attributes of forest structure, especially large deadwood structures with long persistence times
- Enhancing public understanding of the ecological importance of deadwood is critical

[1]*Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Rauhenebrach, Germany* *(simon@thornonline.de); [†]*current address: Department of Ecology, University of Granada, Granada, Spain;* [2]*Ecosystem Dynamics and Forest Management Group, Department of Ecology and Ecosystem Management, Technical University of Munich, Freising, Germany;* [3]*Berchtesgaden National Park, Berchtesgaden, Germany;* [4]*Bavarian Forest National Park, Grafenau, Germany;* [5]*Florida Institute for Conservation Science, Melrose, FL;* [6]*Environmental Futures Research Institute, Griffith School of Environment and Science, Griffith University, Nathan, Australia;* [7]*Fenner School of Environment and Society, The Australian National University, Canberra, Australia*

In this review, we outline the importance of deadwood for biodiversity, illustrate several examples of where deadwood is commonly removed from forest ecosystems, and discuss the ways in which deadwood could be promoted through passive and active management to restore degraded forest ecosystems. Finally, we briefly review scientific evidence to explain why deadwood and associated biodiversity has a low public profile and elaborate on how awareness can be improved through targeted environmental education.

Deadwood in natural forests

In forests subject to natural dynamics, deadwood is commonly created by the complete or partial die-off of large, old trees (Holzwarth *et al.* 2013), as well as by natural disturbances, which can affect single trees up to entire landscapes (Kulakowski *et al.* 2017). Forests are characterized by natural tree death (Figure 1), which typically creates a high diversity of deadwood ranging from branches to standing stems and downed logs (Stokland *et al.* 2012). However, the diversity of tree species, each of which may exhibit varying vulnerability to different mortality sources, serves as an important proxy for the diversity of deadwood (Holzwarth *et al.* 2013). Deadwood-dependent taxa are associated with numerous microhabitats such as dead branches (Seibold *et al.* 2018) or cavities (Müller *et al.* 2014) provided by the gradual death of large, old trees – often called "veteran trees". In addition to single-tree dieback, natural disturbances can leave behind disturbance-specific deadwood structures, including snags and downed deadwood, and can also generate the spatially heterogeneous recovery of vegetation (Swanson *et al.* 2011). These so-called biological legacies can be crucial for biodiversity and forest recovery following major disturbances, such as the Mount St Helens volcanic eruption in 1980 (Franklin *et al.* 2000). Natural deadwood amounts are variable and range from a few cubic meters per hectare (m^3 ha^{-1}) up to more than 1000 m^3 ha^{-1} (Lindenmayer *et al.* 1999). Following stand-replacing natural disturbances, the amount of deadwood can even exceed the amount of living tree biomass, making deadwood a characteristic and abundant resource in natural forest ecosystems (Seibold and Thorn 2018).

The reduction of deadwood

At present, deadwood removal includes, for instance, fuel wood and stump biomass extraction (Jonsell 2007), selective logging of high-value large old trees (Ahrends *et al.*

Figure 1. Deadwood structures characteristic of old intact forests include (a) fallen logs with large numbers of fruiting bodies of wood-inhabiting fungi; (b) large logs in an advanced state of decay, which facilitate the regrowth of natural vegetation, such as in old-growth forests in the US Pacific Northwest; and (c) standing dead old trees created by natural disturbances like bark-beetle outbreaks. Such dead trees can persist for decades and are often sun-exposed ecological islands in otherwise closed canopies, such as in (d) old-growth mountain ash (*Eucalyptus regnans*) forests in Victoria, Australia.

2010), and deadwood collection for firewood and charcoal production (Ulyshen 2018). The removal of deadwood has been accelerated by forest exploitation for biomass-based fuels during recent decades (Jonsell 2007). Furthermore, deadwood is created by natural (Thorn *et al.* 2018) and anthropogenic disturbances, and is routinely removed in both cases in an effort to reduce the risk of further disturbances (eg the creation of firebreaks or the reduction of fuel loads) (Donato *et al.* 2006). Current levels of deadwood in large parts of the world, for example in European temperate and boreal forests, Douglas fir (*Pseudotsuga menziesii*) forests of western North America, and Australian mountain ash (*Eucalyptus regnans*) forests, are far below those typical of primeval stands (Figure 1). The diversity of saproxylic species (ie species that depend on the decay of dying and dead trees), such as saproxylic arthropods and wood-inhabiting fungi (Grove 2002), is positively related to the amount of available deadwood, and therefore a reduction in deadwood results in a decline of associated biodiversity. Not surprisingly, saproxylic insects and fungi feature prominently in lists of endangered forest species (Seibold *et al.* 2015b).

The importance of deadwood for biodiversity

The importance of deadwood as habitat for insects was recognized early on, including by naturalists searching for previously undescribed species in the late 19th century (Wallace 1869) and ecologists in the early 20th century (Graham 1925). By the end of the 20th century, the historical ranges of several species had been greatly reduced due to overexploitation of deadwood (Figure 2). For instance, the wrinkled bark beetle (*Rhysodes sulcatus*) has been extirpated from large parts of Europe for more than

H Bussler
L Haselberger

Figure 2. Species inhabiting deadwood structures include (a) the Rosalia longicorn (*Rosalia alpina*), which is protected by the European Commission's Habitats Directive and breeds in large, sun-exposed, dead deciduous trees; (b) the rare wrinkled bark beetle (*Rhysodes sulcatus*) inhabiting advanced brown-rot decay stages of large-diameter trees; (c) the rare wood-inhabiting fungus (*Hericium coralloides*), which is now restricted to old-growth forest reserves; and (d) the bark-gnawing beetle (*Peltis grossa*), which is strongly dependent on wood subject to fungal decay.

two centuries because of the lack of decayed, large-diameter deadwood (Palm 1959), whereas the dead log bark beetle (*Pytho kolwensis*) is now restricted to remnant primary spruce (*Picea abies*) forests where there has been a continuous supply of deadwood for at least 300 years (Siitonen and Saaristo 2000). The importance of deadwood for biodiversity is underpinned by complex interactions between the amount and diversity of deadwood, along with the microclimatic environment. For instance, some specialized insects require the occurrence of particular fungal species that are in turn associated with specific types of deadwood (Weslien *et al.* 2011), or dead trees of particular species and a certain diameter and decay stage (Kostanjsek *et al.* 2018). Deadwood is particularly critical for biodiversity because certain deadwood habitats (especially large structures) may be utilized by numerous species and/or individuals over long time periods, such as hermit beetles (*Osmoderma eremita*) colonizing tree cavities (Ranius and Hedin 2001).

Deadwood can promote diversity at higher trophic levels by increasing food resources, facilitating accessibility to those resources, and providing shelter and resting sites (Kortmann *et al.* 2018). For instance, the white-backed woodpecker (*Dendrocopos leucotos*) and threatened species of saproxylic beetles utilize the same types of deadwood (Martikainen *et al.* 1998), and bat species richness is higher in forests with larger amounts of deadwood (Tillon *et al.* 2016). In addition to food resources, deadwood and large, old trees provide shelter, nesting, and roosting habitat for many birds and mammals (Lindenmayer and Ough 2006); bats even occasionally use the galleries created by wood-boring beetles as hibernation sites (Gottfried *et al.* 2019), which qualifies these insects as ecosystem engineers (Buse *et al.* 2008).

Managing forests for deadwood

Speight (1989) first initiated consideration of dead and dying trees as important habitat features for threatened species in the EU. Since the late 1990s, conservation programs with a special focus on deadwood (eg deadwood enrichment strategies) have been implemented in an increasing number of countries, including Sweden, Finland, and Germany (Vítková *et al.* 2018). Ecologically sustainable forest management requires the recovery of the full range of natural deadwood amounts and variability in deadwood conditions, such as decay stage, wood diameter, sun exposure, standing versus downed deadwood, and tree species (reviewed in Seibold *et al.* [2015a]). Two different strategies can help achieve this. The first consists of passive enrichment of deadwood through the exclusion of logging from forest stands or the protection of large, old trees and clumps of trees, with deadwood created via natural processes, such as disturbance or the maturation of trees (Figure 3, a and b). However, rates of deadwood creation may initially be slow in young, formerly managed stands, and cessation of timber harvesting is not practicable or desirable in all regions because of commercial interests and societal demand for timber and fuelwood (Lassauce *et al.* 2011). Nevertheless, protected areas with no human intervention and without deadwood removal are crucial for protecting biodiversity in all biomes, including the tropics (Laurance *et al.* 2012), and temperate (Phalan *et al.* 2019) and boreal (Moen *et al.* 2014) forests. The second strategy, applicable to forests in which most of the natural deadwood has been lost, consists of active enrichment of deadwood during harvest operations, with deadwood created primarily by leaving tree parts, such as crowns or stem sections, within harvest units (Ranius *et al.* 2014).

The application of such strategies can increase deadwood amounts on a landscape scale, even in young, formerly managed stands, and ultimately enhance biodiversity (Roth *et al.* 2019). Another enrichment strategy consists of the creation of damaged and dying trees by various techniques, including the use of explosives and partial cutting of tree crowns (Speight 1989). Active and passive enrichment strategies can be applied in the tropics, where deadwood amounts increase if logging residues remain after selective logging (Carlson *et al.* 2017), as well as in temperate and boreal forests (Gustafsson *et al.* 2012).

Public perception of deadwood

The perception of landscape aesthetics is a cultural ecosystem service that can help raise public support for protecting ecosystems. Humans often perceive ecological sustainability and the value of landscapes as a function of scenic beauty, and they expect forests to look "beautiful" and diverse (Gobster *et al.* 2007). Landscape aesthetics in forests is strongly affected by the densities and size of trees, and the diversity of tree species (Daniel *et al.* 2012). In contrast, forests affected by natural disturbances – those associated with large amounts of deadwood – are commonly perceived as chaotic, untidy, and "destroyed" (Flint *et al.* 2009). For instance, in the Bavarian Forest National Park, in Germany, appreciation of large-scale forest disturbances was strongly related to the regeneration of young spruce trees, which were perceived as benchmarks of healthy and natural forest ecosystems (Michler *et al.* 2019). Similarly, studies addressing visual preferences of visitors in forest landscapes in the US and Germany also indicated predominantly negative perspectives of large volumes of deadwood (Arnberger *et al.* 2018). In undisturbed forests, deadwood is barely noticed by forest visitors and the general public. For instance, only one out of 479 visitors to a national park in Germany mentioned deadwood as a reason for selecting a specific hiking trail (Meyer *et al.* 2019). These local findings match the results of an expert-based study across Europe, where respondents rated large, old trees as the most important forest feature but deadwood was ranked only tenth out of

12 possible positions on a scale (Edwards *et al.* 2012). Tourists generally expressed a preference for forests without deadwood (Stachová 2018) even when they were aware of the importance of deadwood for forest biodiversity (Pelyukh *et al.* 2019). These examples illustrate a need to increase public understanding of deadwood's importance in forests.

Figure 3. Deadwood creation in managed forests may encompass passive methods, such as (a) the retention of tree crowns with low economic value in selective-logging systems and (b) the partial or complete set-aside of areas affected by natural disturbances for natural succession; and active methods, such as (c) girdling a vital tree to initiate tree death and (d) topping of trees to create sun-exposed high stumps.

Improving public awareness of the importance of deadwood

Many environmental education programs mention the importance of deadwood for biodiversity in only general and superficial ways. This is possibly because most invertebrate species found in deadwood have a low public profile, are small and inconspicuous, lack appealing characteristics for a non-scientific audience, and are rarely represented in conservation efforts (Barua *et al.* 2012; Eckelt *et al.* 2018). In contrast, some species perceived as forest pests, such as bark beetles, receive substantial (and largely negative) attention by a broad audience (Flint *et al.* 2009). This underscores the challenge for environmental education in raising awareness of the importance of deadwood, not only among the general public but also among land managers, policy makers, and even scientists. Environmental education programs that target different groups are needed to overcome centuries of negative perceptions about deadwood and natural forest dynamics, and to foster greater awareness of the critical importance of deadwood for forest biodiversity. A large proportion of the few existing deadwood education programs in Europe are based on guided forest visits with groups of people and rely on informative outdoor displays (Figure 4c) that focus on species found in deadwood, nutrient cycles, and the natural decay of large, old trees. Such educational forest visits can enhance conservation-related knowledge and long-term retention of gained knowledge (Kuhar *et al.* 2010). Another promising approach is to adapt the flagship-species concept to environmental education programs (Eckelt *et al.* 2018), in which particular taxa are highlighted and used to stimulate interest in the ecological importance of deadwood. Selecting flagship species from higher trophic levels in saproxylic food webs, such as birds or mammals, might help to foster positive attitudes toward deadwood. One potential example is the barbastelle bat (*Barbastella barbastellus*), which uses deadwood and forest stands decimated by bark beetles as nesting, roosting, and foraging sites (Kortmann *et al.* 2018). Likewise, the white-backed woodpecker is a charismatic species that forages on dry snags, and therefore could be selected both as a flagship species for deciduous forest conservation and as a tool for communicating deadwood conservation (Roberge *et al.* 2008).

Flagship species can be utilized in education programs, for instance via richly illustrated children's books (Figure 4), which can help trigger interest in and greater appreciation of the value of deadwood by a broad audience. Yet because the effectiveness of deadwood-specific environmental education programs is largely unknown, such programs must be subject to quantitative evaluation, measuring success via the presence and quality of deadwood and associated biodiversity, in addition to the human dimensions of forest ecosystems. A greater focus on interdisciplinary research is also needed to identify knowledge gaps and diverging conceptions, which could be targeted through an array of educational programs encompassing various teaching methods, including novel approaches like video games (Chang 2019).

Conclusions

Deforestation imperils biodiversity worldwide, but forest degradation through the removal of deadwood and old trees is a widely neglected threat that results in considerable additional loss of biodiversity and alterations in ecosystem processes. Minimizing forest degradation in the future will require not only the maintenance and restoration of deadwood in forests, but also environmental education programs that emphasize the critical value of deadwood for forest biodiversity and ecosystem processes to policy makers, land managers,

Figure 4. Environmental education programs may emphasize the importance of deadwood through illustrated children's books about (a) the life history of relict species within primary forests and the important role of saproxylic invertebrates as food resources for higher trophic level species, such as (b) the white-backed woodpecker (*Dendrocopos leucotos*) feeding on larvae of the wood borer (*Ptilinus pectinicornis*). These programs may also rely on resources such as (c) information panels posted in forests describing the importance of deadwood for forest biodiversity and the interactions between wood-inhabiting fungi and saproxylic beetles, and (d) stickers of "Berti" the bark beetle highlighting the natural dynamics that lead to the creation of deadwood.

scientists, and the general public. To limit forest degradation and to promote ecologically sustainable forest management, we recommend specific policy reforms, including the (1) development of ecosystem-specific minimum thresholds for large, old trees and amounts of deadwood that are benchmarked against levels in natural forests; (2) promotion of management practices that recruit particularly large, old trees and increase natural amounts of deadwood by natural tree dieback; (3) introduction of educational programs that improve understanding of the ecological importance of deadwood among forest managers as well as the general public; and (4) implementation of compensation schemes for forest owners to offset possible financial losses associated with deadwood retention and restoration programs.

Acknowledgements

ABL and SV received funding from the Alexander von Humboldt Foundation and the German Environmental Foundation, respectively. Open access funding enabled and organized by Projekt DEAL.

References

Ahrends A, Burgess ND, Milledge SAH, *et al*. 2010. Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. *P Natl Acad Sci USA* **107**: 14556–61.

Arnberger A, Ebenberger M, Schneider IE, *et al*. 2018. Visitor preferences for visual changes in bark beetle-impacted forest recreation settings in the United States and Germany. *Environ Manage* **61**: 209–23.

Barlow J, Lennox GD, Ferreira J, *et al*. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**: 144–47.

Barua M, Gurdak DJ, Ahmed RA, and Tamuly J. 2012. Selecting flagships for invertebrate conservation. *Biodivers Conserv* **21**: 1457–76.

Betts MG, Wolf C, Ripple WJ, *et al*. 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**: 441–44.

Buse J, Ranius T, and Assmann T. 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. *Conserv Biol* **22**: 329–37.

Carlson BS, Koerner SE, Medjibe VP, *et al*. 2017. Deadwood stocks increase with selective logging and large tree frequency in Gabon. *Glob Change Biol* **23**: 1648–60.

Chang AY. 2019. Playing nature: ecology in video games. Minneapolis, MN: University of Minnesota Press.

Daniel TC, Muhar A, Arnberger A, *et al*. 2012. Contributions of cultural services to the ecosystem services agenda. *P Natl Acad Sci USA* **109**: 8812–19.

Donato DC, Fontaine JB, Campbell JL, *et al*. 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* **311**: 352.

Eckelt A, Müller J, Bense U, *et al*. 2018. "Primeval forest relict beetles" of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. *J Insect Conserv* **22**: 15–28.

Edwards D, Jay M, Jensen FS, *et al*. 2012. Public preferences for structural attributes of forests: towards a pan-European perspective. *Forest Policy Econ* **19**: 12–19.

Flint CG, McFarlane B, and Müller M. 2009. Human dimensions of forest disturbance by insects: an international synthesis. *Environ Manage* **43**: 1174–86.

Franklin JF, Lindenmayer D, Macmahon JA, *et al*. 2000. Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. *Conserv Biol Pract* **1**: 8–16.

Gobster PH, Nassauer JI, Daniel TC, and Fry G. 2007. The shared landscape: what does aesthetics have to do with ecology? *Landscape Ecol* **22**: 959–72.

Gottfried I, Gottfried T, and Zając K. 2019. Bats use larval galleries of the endangered beetle *Cerambyx cerdo* as hibernation sites. *Mamm Biol* **95**: 31–34.

Graham SA. 1925. The felled tree trunk as an ecological unit. *Ecology* **6**: 397–411.

Grove SJ. 2002. Saproxylic insect ecology and the sustainable management of forests. *Annu Rev Ecol Syst* **33**: 1–23.

Gustafsson L, Baker SC, Bauhus J, *et al*. 2012. Retention forestry to maintain multifunctional forests: a world perspective. *BioScience* **62**: 633–45.

Hartig GL. 1808. Anweisung zur Holzzucht für Förster. Marburg, Germany: Neue Akademische Buchhandlung.

Holzwarth F, Kahl A, Bauhus J, and Wirth C. 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *J Ecol* **101**: 220–30.

Jonsell M. 2007. Effects on biodiversity of forest fuel extraction, governed by processes working on a large scale. *Biomass Bioenerg* **31**: 726–32.

Kortmann M, Hurst J, Brinkmann R, *et al*. 2018. Beauty and the beast: how a bat utilizes forests shaped by outbreaks of an insect pest. *Anim Conserv* **21**: 21–30.

Kostanjsek F, Sebek P, Baranova B, *et al*. 2018. Size matters! Habitat preferences of the wrinkled bark beetle, *Rhysodes sulcatus*, the relict species of European primeval forests. *Insect Conserv Divers* **11**: 545–53.

Kuhar CW, Bettinger TL, Lehnhardt K, *et al*. 2010. Evaluating for long-term impact of an environmental education program at the Kalinzu Forest Reserve, Uganda. *Am J Primatol* **72**: 407–13.

Kulakowski D, Seidl R, Holeksa J, *et al*. 2017. A walk on the wild side: disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecol Manag* **388**: 120–31.

Lassauce A, Paillet Y, Jactel H, and Bouget C. 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol Indic* **11**: 1027–39.

Laurance WF, Useche DC, Rendeiro J, *et al*. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* **489**: 290–94.

Lindenmayer DB and Ough K. 2006. Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. *Conserv Biol* **20**: 1005–15.

Lindenmayer DB, Incoll RD, Cunningham RB, and Donnelly CF. 1999. Attributes of logs on the floor of Australian mountain ash (*Eucalyptus regnans*) forests of different ages. *Forest Ecol Manag* **123**: 195–203.

Martikainen P, Kaila L, and Haila Y. 1998. Threatened beetles in white-backed woodpecker habitats. *Conserv Biol* **12**: 293–301.

Meyer MA, Rathmann J, and Schulz C. 2019. Spatially-explicit mapping of forest benefits and analysis of motivations for everyday-life's visitors on forest pathways in urban and rural contexts. *Landscape Urban Plan* **185**: 83–95.

Michler T, Aschenbrand E, and Leibl F. 2019. Gestört, aber grün: 30 jahre Forschung zu Landschaftskonflikten im Nationalpark Bayerischer Wald. In: Berr K and Jenal C (Eds). Landschaftskonflikte. Springer Fachmedien Wiesbaden: Wiesbaden, Germany.

Moen J, Rist L, Bishop K, *et al*. 2014. Eye on the taiga: removing global policy impediments to safeguard the boreal forest. *Conserv Lett* **7**: 408–18.

Müller J, Jarzabek-Müller A, Bussler H, and Gossner MM. 2014. Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Anim Conserv* **17**: 154–62.

Müller J, Thorn S, Baier R, *et al*. 2015. Protecting the forests while allowing removal of damaged trees may imperil saproxylic insect biodiversity in the Hyrcanian beech forests of Iran. *Conserv Lett* **9**: 1–23.

Palm T. 1959. Die Holz- und Rinden-Käfer der Süd- und Mittelschwedischen Laubbäume. *Opuscula Entomologica* **16**: 1–377.

Pelyukh O, Paletto A, and Zahvoyska L. 2019. People's attitudes towards deadwood in forest: evidence from the Ukrainian Carpathians. *J Forest Sci* **65**: 171–82.

Phalan BT, Northrup JM, Yang Z, *et al*. 2019. Impacts of the Northwest Forest Plan on forest composition and bird populations. *P Natl Acad Sci USA* **116**: 3322–27.

Ranius T and Hedin J. 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* **126**: 363–70.

Ranius T, Caruso A, Jonsell M, *et al*. 2014. Dead wood creation to compensate for habitat loss from intensive forestry. *Biol Conserv* **169**: 277–84.

Roberge J-M, Mikusiński G, and Svensson S. 2008. The white-backed woodpecker: umbrella species for forest conservation planning? *Biodivers Conserv* **17**: 2479–94.

Roth N, Doerfler I, Bässler C, *et al*. 2019. Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity. *Divers Distrib* **25**: 430–41.

Seibold S and Thorn S. 2018. The importance of dead-wood amount for saproxylic insects and how it interacts with dead-wood diversity and other habitat factors. In: Ulyshen MD (Ed). Saproxylic insects: diversity, ecology and conservation. Cham, Switzerland: Springer.

Seibold S, Bässler C, Brandl R, *et al*. 2015a. Experimental studies of dead-wood biodiversity – a review identifying global gaps in knowledge. *Biol Conserv* **191**: 139–49.

Seibold S, Brandl R, Buse J, *et al*. 2015b. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv Biol* **29**: 382–90.

Seibold S, Hagge J, Müller J, *et al*. 2018. Experiments with dead wood reveal the importance of dead branches in the canopy for saproxylic beetle conservation. *Forest Ecol Manag* **409**: 564–70.

Siitonen J and Saaristo L. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biol Conserv* **94**: 211–20.

Speight MCD. 1989. Saproxylic invertebrates and their conservation. Nature and environment. Series 42. Strasbourg, France: Council of Europe.

Stachová J. 2018. Forests in the Czech public discourse. *J Landscape Ecol* **11**: 33–44.

Stokland JN, Siitonen J, and Jonsson BG. 2012. Biodiversity in dead wood. Cambridge, UK: Cambridge University Press.

Swanson ME, Franklin JF, Beschta RL, *et al*. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front Ecol Environ* **9**: 117–25.

Thorn S, Bässler C, Burton PJ, *et al*. 2018. Impacts of salvage logging on biodiversity – a meta-analysis. *J Appl Ecol* **55**: 279–89.

Tillon L, Bouget C, Paillet Y, and Aulagnier S. 2016. How does deadwood structure temperate forest bat assemblages? *Eur J For Res* **135**: 433–49.

Ulyshen MD (Ed). 2018. Saproxylic insects: diversity, ecology and conservation. Cham, Switzerland: Springer.

Vítková L, Bace R, Kjucukov P, and Svoboda M. 2018. Deadwood management in Central European forests: key considerations for practical implementation. *Forest Ecol Manag* **429**: 394–405.

von Carlowitz HC. 1713. Sylvicultura oeconomica. Leipzig, Germany: Johann Friedrich Braun.

Wallace AR. 1869. The Malay Archipelago. London: Macmillan.

Weslien J, Djupström LB, Schroeder M, and Widenfalk O. 2011. Long-term priority effects among insects and fungi colonizing decaying wood. *J Anim Ecol* **80**: 1155–62.