Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity?

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ABSTRACT

Modification of natural ecosystems has threatened biodiversity worldwide, with forests suffering especially. Strategies aimed at mitigating such loss in forests often include enrichment of deadwood, a critical resource for many decomposer species. However, it remains unclear how deadwood can best be enriched to most effectively promote the diversity of saproxylic species. In this study, we investigated saproxylic beetle diversity in experimentally exposed deadwood logs of 13 different tree species across 30 forests in three regions of Germany. We tested whether gamma-diversity differs between tree species and whether the alpha-diversity within an individual log depended on whether logs were placed in unmanaged beech forests, managed beech forests, or managed conifer forests. We found significant differences in gamma- and alpha-diversity of saproxylic beetles among tree species, but the ranking of tree species differed between regions, suggesting differences in regional beetle species pools. Randomization tests aiming to identify how many and which deadwood logs would need to be exposed to best conserve saproxylic beetle diversity, showed that the overall diversity of beetles increased with the number of tree species exposed, due to turnover of beetle species between tree species. However, some species (e.g. *Carpinus*) and species combinations (e.g. *Carpinus-Picea*) reached exceptionally high beetle diversity. Alpha-diversity was higher in conifer than in beech forests, but did not differ between managed and unmanaged beech forests. Canopy cover above logs and average stand temperature strongly influenced alpha-diversity, suggesting that environmental conditions that may be affected by management act as habitat filters for species assemblages. We conclude that deadwood enrichment strategies would be most effective when combining particular tree species that support highest diversity.

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1. Introduction

Modification of natural ecosystems has caused a loss of biodiversity worldwide (Newbold et al., 2015). In forests, management has led to a quantitative decrease of several constituents of old-growth forests, such as large reductions in the amount of deadwood and in the numbers of 'veterans' i.e. very old trees. This holds particularly true if management has been very intensive (Bauhus et al., 2009; Lindenmayer et al., 2012). As a consequence, animal communities in managed forests may differ from those of unmanaged forests (Bengtsson et al., 2000; Lassauce et al., 2012). Deadwood is important for forest biodiversity: one quarter of all forest species are saproxylic, i.e. depend on deadwood (Speight, 1989; Stokland et al., 2012). The lack of deadwood in managed

forests has hence repeatedly been shown to decrease biodiversity (Lassauce et al., 2011; Müller and Bütler, 2010) and to change the functional composition of communities (Gossner et al., 2013b; Seibold et al., 2015b). As an example, in Germany, 27% of saproxylic species are threatened (Seibold et al., 2015b).

Several conservation strategies consequently focus on the enrichment of deadwood in forests (Hutto, 2006; Hyvarinen et al., 2006). One strategy is to cease production in forests. However, setting aside enough and sufficiently large areas of forest is difficult if not entirely impossible due to economic interests and needs. This particularly concerns densely populated areas with limited forest reserves such as Central Europe, where cessation of logging would potentially result in an increased import of wood from other regions, causing conservation problems in those regions. In addition, managed forests may need a long time before pre-management levels of deadwood will be reached, due to the low natural tree mortality of medium aged-stands that are typical for most managed forests (Holzwarth et al., 2013; Sebek et al.,

2013) and due to rapid decomposition of most deciduous tree species (Pietsch et al., 2014). Another strategy to enrich deadwood is to use harvest operations to leave some of the crowns or stems in the forest. This is the strategy currently favored in several countries where large natural disturbances such as windthrow are rare or – as in the case of insect pest outbreaks and forest fire – are prevented by all means. However, this strategy is increasingly threatened due to the increasing demand for wood for energy production (Bouget et al., 2012). The amount of deadwood necessary to preserve the diversity of saproxylic species is still under discussion (Lassauce et al., 2011).

Several fundamental questions on the dependence of saproxylic beetles on deadwood are still open. One most basic question concerns the degree of specialization: Are they mostly generalists accepting a wide variety of host species, or do they resemble herbivores showing a similar degree of host specialization? Up to now, no reliable answer could have been given to this question.

Host specificity of saproxylic beetles has only rarely been studied, with inconclusive results. In boreal forests, studies on the occurrence patterns of threatened species suggested a great importance of particular tree species, e.g. from the genera *Populus*, *Picea* and *Pinus*, suggesting host specialization (Lindhe and Lindelöw, 2004; Tikkanen et al., 2007; Tikkanen et al., 2006). In contrast, studies on tree species preferences in boreal and temperate forests suggest a lower degree of specialization (Milberg et al., 2014; Toivanen and Kotiaho, 2010). A further common perception is that the importance of tree species identity for host choice of saproxylic species generally decreases with increasing wood decay, because of the convergence of physical and chemical properties. However, differences between broadleaved and coniferous trees are assumed to persist along the decomposition process (Stokland et al., 2012).

One potential limitation of most studies on host specialization of saproxylic species is that they are based on collections of existing deadwood pieces. Because managed temperate forests only contain a few tree species, the diversity of deadwood in these forests is very limited and hence the choice for beetles also very restricted. It is thus not possible to extrapolate beetle host range beyond the host species found in the forest. Furthermore, we know little about whether saproxylic species would accept a tree species that does not occur as a living tree in a particular forest, e.g. if they would also colonize deadwood from pine in a pure beech or oak stand. If saproxylic species are indeed very host-specific, then their diversity will be limited by deadwood species diversity and related to forest stand diversity and species composition.

In addition to host specificity, it is known that the abiotic and biotic environment affects the community of saproxylic species in a particular forest. Large differences in the composition of saproxylic communities among forests and regions have been shown (Gossner et al., 2013a; Müller et al., 2013; Müller and Gossner, 2010), but the causes for this, independent of the availability of deadwood variation, are largely unclear. (Micro-)Climatic variables, such as temperature (e.g. sun-exposed vs. shaded substrates), influence the development of insect species and may affect their diversity (Gough et al., 2015; Lindhe and Lindelöw, 2004; Lindhe et al., 2005; Müller et al., 2015a; Sverdrup-Thygeson and Ims, 2002).

In this study, we investigated saproxylic beetle communities colonizing the deadwood of logs of 13 different tree species across 30 forests in three regions of Germany using a large-scale experiment. About 1150 logs of >20 cm diameter were exposed. We were interested in whether saproxylic species diversity during the early successional stage of deadwood decomposition depends on tree species identity, or on forest management, i.e. management intensity (managed vs. unmanaged) and forest type (coniferous vs. broad-leaved), which reflects the management decision of selecting a particular tree species. We tested this at different spatial diversity scales; within and across region gamma-diversity, which combines log-scale alpha-diversity as well as species turnover between logs (only tree species identity) and log-scale alpha-diversity (tree species identity, management, region).

Furthermore we used forest stand-based temperature and subplot-based canopy cover to test for the influence of microclimate on saproxylic beetle diversity. We addressed the following questions:

1) Does alpha- and gamma-diversity of saproxylic beetles differ between tree species?
2) Is beetle diversity on tree species consistent between regions?
3) Which tree species and tree species combinations promote the highest diversity of saproxylic beetles?
4) Does alpha-diversity depend on forest management and microclimate?

2. Material and methods

2.1. Study regions

The experiment was conducted in the framework of the Biodiversity Exploratories Project (www.biodiversity-exploratories.de; Fischer et al., 2010) comprising three regions; the UNESCO Biosphere Reserve Schorfheide-Chorin (henceforth "SCH") in the glacially formed lowlands in north-eastern Germany (52°47′25″-53°13′26″N/13°23′27″-14°08′53″E, about 1300 km² in size, 3–140 m a.s.l.), the National Park Hainich and surrounding area of the Hainich-Dün (henceforth "HAI") in the hilly lands of central Germany (50°56′14″-51°22′43″N/10°10′24″-10°46′45″E, about 1560 km², 285–550 m a.s.l.) and the UNESCO Biosphere Reserve Schwäbische Alb (henceforth "ALB") in the low mountain range in south-western Germany (48°20′28″-48°32′02″N/9°10′49″-09°35′54″E, about 420 km², 460–860 m a.s.l.). With an annual precipitation of about 520–580 mm, SCH is one of the driest parts of Germany and has a mean annual temperature of 8.0–8.5C°. Most of the region is covered by forests of pine *Pinus sylvestris* (39%), beech *Fagus sylvatica* (12%) and oak *Quercus petraea* (9%). HAI (6.5–8.0 °C; 500–800 mm) is one of the largest continuous forest areas in Germany and is dominated by broadleaf trees; conifers comprise only 12% of the forest (pine *Pinus sylvestris*; spruce *Picea abies*; larch *Larix decidua*). ALB (6.0–7.0 °C; 700–1000 mm) is a highly fragmented, mixed forest landscape dominated by beech *Fagus sylvatica* (46%) and spruce *Picea abies* (24%).

2.2. Deadwood experiment

The Biodiversity Exploratory Long-term Deadwood experiment ('BELongDead') was set up in 2009, in the framework of a long-term study on the relationships between land use, biodiversity and ecosystem processes (Fischer et al., 2010). In the study regions, nine (ALB), nine (SCH) and twelve (HAI) research plots (100 m × 100 m) were established, in total 30 plots. These were selected by a stratified random sampling design from a total of >300 candidate plots per region (for details see Appendix A1). The stratified random selection of plots was also used to reduce spatial autocorrelation problems. Each plot was in one of three differently managed forest types with different levels of management intensity: currently unmanaged beech forest stands, which were previously managed up to 20–70 years ago; managed beech forest stands; and managed conifer stands (spruce in HAI and ALB and pine in SCH). Three replicates of each forest management intensity in each region were studied, except in HAI, where three additional managed beech forests were investigated, separating between even-aged and uneven-aged management of beech forests. In this study, we only focused on two forest management decisions, i.e. not managing vs. management and tree species selection, i.e. beech vs. conifer-oriented management. Because no unmanaged conifer forests exist in the study regions, we combined these two decisions in one variable "forest management" with the three levels 'unmanaged beech', 'managed beech', 'managed conifer'.

On each plot deadwood logs of 13 tree genera (henceforth "tree species" for simplicity) were exposed in three replicates (subplots). Tree