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Evaluation of an integrative strategy in forests: does deadwood enrichment work and increase biodiversity?

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It all came together then, you see—all the various isolated bits—and made a coherent pattern.
Miss Marple, Agatha Christie 1950, A murder is announced

Widmen möchte ich diese Arbeit einer ganzen Menge an Menschen. Dazu gehören zum Glück meine großartigen Eltern die immer für alles ein offenes Ohr haben. Aber auch meinen Geschwistern, mit denen ich viel Glück habe.

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Content

Zusammenfassung

Der starke weltweite Rückgang der Artenvielfalt, macht es notwendig, dass neue und praktikable Naturschutzstrategien entwickelt werden. Integrative Strategien, die die Produktion von Gütern und Naturschutz auf einer Fläche vereinen, könnten dabei bereits existierende Strategien erweitern. Da ein hoher Anteil der Artenvielfalt auf Wälder angewiesen ist und darin besonders auf das Habitat Totholz, wird die Anreicherung von Totholz im Wirtschaftswald häufig als wichtige integrative Naturschutzmaßnahme empfohlen. Integrative Maßnahmen können dabei nicht nur das natürlich entstandene Totholz bewahren, sondern auch aktiv Totholz schaffen. Die Bayerischen Staatsforsten, die seit dem Jahr 2005 29,8 Prozent der Bayerischen Wälder bewirtschaften, haben ihren Bewirtschaftungsplan vor zehn Jahren auf eine integrative Strategie umgestellt. Ihre Strategie beinhaltet den Erhalt von natürlich entstandenem Totholz und die aktive Anreicherung von Totholz mit Ernteresten. Der Erfolg von Strategien dieser Art ist bisher nicht evaluiert und der Nutzen für die Artenvielfalt daher unklar. Das Ziel dieser Studie war es, zu der Evaluierung von integrativen Naturschutzmaßnahmen, die durch Forstbetriebe auf Landschaftsebene eingesetzt werden, beizutragen. Für diese Evaluierung wurden Datensätze verwendet, in denen Totholzmengen und die Diversität von Käfern, Pilzen, Vögeln, Pflanzen und Wanzen vor und nach der Einführung der Strategie erhoben wurden. Diese Datensätze enthielten detaillierte Informationen über die Totholzmengen vor und nach der Anreicherung, die Totholzcharakteristika sowie eine ausführliche Aufnahme der fünf Artengruppen vor und nach der Totholzanreicherung. Die Ergebnisse zeigen, dass es möglich ist, Totholzmengen in einem forstlich kurzen Zeitraum von zehn Jahren zu verdoppeln. Die Anreicherung war dabei stark von der Bewirtschaftungsintensität und der natürlichen Mortalität bestimmt. Die Mengen, die liegen blieben, standen jedoch zusätzlich stark im Zusammenhang mit Charakteristika des Lebendbestandes, wie zum Beispiel der Baumartenzusammensetzung. Die Totholzanreicherung hatte einen positiven Einfluss auf die allgemeine Biodiversität. Insbesondere die Artenzahlen totholzabhängiger Käfer und Pilze stiegen mit einer Totholzanreicherung. Die Ergebnisse zeigen jedoch auch, dass die gesamte aufgenommene Biodiversität starken jährlichen Schwankungen unterliegt. Des Weiteren wird bei der Auswertung von funktionell-phylogenetischen Ähnlichkeiten deutlich, dass die Artengemeinschaft der totholzabhängigen Käfer diverser wird, was auf eine Vergrößerung des Nischenangebots hinweist. Integrative Maßnahmen mit Totholzanreicherungen in Wirtschaftswäldern sind somit eine gute Möglichkeit die Biodiversität von intensiv genutzten Wälder zu schützen und zu fördern. Integrative Strategien wie die hier untersuchte sind somit eine gute Ergänzung für die Einrichtung von Naturschutzgebieten für einen umfassenden Schutz der Artenvielfalt.

Summary

The strong pressure on global biodiversity makes new and achievable nature conservation strategies inevitably. Integrative approaches that combine production of goods and conservation within the same area are considered to complement existing conservation strategies. With a considerable proportion of biodiversity being dependent on forests and therein on deadwood structures, an enrichment of deadwood is often proposed as important integrative measure. The integrative measures can not only include the retention of deadwood but also its active creation. The Bavarian State forestry that manages since the year 2005 29.8 percent of the Bavarian forest, implemented an integrative strategy for ten years. The strategy includes the retention of naturally developed deadwood and the active enrichment of deadwood with harvest remnants. However, a scientific evaluation of strategies like this is missing so far. The success of the strategy in promoting biodiversity is therefore uncertain. The objective of this study is to contribute with a detailed evaluation of this nature conservation strategy to the evaluation of integrative strategies implemented in practice on a large scale. This evaluation was based on comparisons of deadwood amounts and diversity of five taxonomic groups (beetles, fungi, birds, plants and true bugs) before and after the implementation of the strategy. Therefore, we used two datasets, which were collected four and nine years after the strategies' implementation. These datasets contained detailed information of deadwood amounts and characteristics as well as a comprehensive assessment of the five taxonomic groups. The study shows a doubling of deadwood amounts, within this short time-span, considering rotation times in forests. The enrichment was strongly increasing with harvesting intensity and natural mortality. For the actual amount, however the type of stand, especially the tree species composition remained an important driver for the amounts that accumulate. It also shows that the enrichment of deadwood had a positive influence on biodiversity and therein especially deadwood dependent taxa profited, i.e. saproxylic beetles and fungi. It revealed however, that the examined species groups are subject to considerable interannual variations. Furthermore, the evaluation of functional-phylogenetic distance shows that the community of saproxylic beetles became less clustered, i.e. less equal than expected, whereas the other taxonomic groups showed no changes in their assembly with increasing deadwood amounts. Since most of the forests in Central Europe but also worldwide are intensely managed, integrative approaches like the one examined here are a good way to protect and promote biodiversity. The strategy is therefore a good extension to the protection in reserves.

1. Introduction

1.1 Global threats to biodiversity

The loss of biodiversity has been recognized for centuries (Dirzo and Raven 2003). Despite increasing awareness towards the topic, the decrease of species is still persistent and often even intensified (Butchart, Walpole et al. 2010). This loss of biodiversity is considered to impair essential life-supporting processes and ecosystem functions, such as primary production or provision of clean water (Bengtsson, Nilsson et al. 2000).

The main threats to biodiversity are: climate change, excessive nutrient loads, invasive alien species, habitat loss and degradation, alongside over-exploitation and unsustainable management (Secretariat of the Convention on Biological Diversity 2010). Whereas, in many tropical ecosystems the destruction of natural habitats is still ongoing, temperate regions have been altered since millennia leaving nearly no natural habitats (Hannah, Carr et al. 1995).

1.1.1 Conservation agreements in Germany

Germany, as one of the most Central European countries, has only a very small proportion of natural habitats left. Only 28 percent of the 863 existing habitat types are considered as not endangered (with 28 already being classified as near threatened) (Fink, Heinze et al. 2017). About 30 percent of Germanys biodiversity, including animals, plants and fungi, are considered as endangered and 6 percent already extinct (Haupt 2009, Matzke-Hajek, Hofbauer et al. 2016). Therefore, based on the Convention on Biological Diversity of the UN and the agreements of the ministerial conference of Europe, the German government developed in 2007 the ‘Strategie zur Biologischen Vielfalt’ (Strategy for biological diversity) (Bundesministerium für Umwelt Naturschutz und Reaktorsicherheit 2007). The goal of this strategy was to decelerate biodiversity losses until 2010. The measures of this strategy include the implementation of the European Flora-Fauna-Habitat Directive for the protection of rare and mainly in Germany distributed habitats and species along with the establishment of a coherent network of protected areas under the Natura 2000 directive. However, concerns have arisen that the intended segregation of biodiversity protection and production in separate areas, i.e. the creation of some protected areas, and intensive management in the remaining area might not be sufficient for a comprehensive conservation and promotion of biodiversity (Bollmann and Braunisch 2013). Setting areas aside for conservation allows for the recovery of natural dynamics and associated species communities. However, this is only possible if the size and spatial distribution of the reserves is adequate, otherwise species will be vulnerable to extinction (Lindenmayer and Franklin 2002). Currently, national parks, which represent the largest conservation areas with process conservation in Germany, cover 214,588 ha (without marine areas), representing about 0.6 percent of the German landscape (Bundesamt für Naturschutz 2017a). Additionally, 4 percent of the landscape (1,376,989 ha, 8757 areas) are protected in nature reserve.

Whereas the national parks are quite far apart, the vast majority of nature reserves is small, comprising a mean area of 156 ha, with about 60 percent of the single reserves being smaller than 50 ha and only 13 percent bigger than 200 ha or more (Bundesamt für Naturschutz 2017b). Therefore, many of the small areas are strongly influenced by the intense management of the surrounding area facing e.g. eutrophication, drainage or the introduction of invasive species (Bundesamt für Naturschutz 2017b). Additionally, the intensely used areas surrounding reserves often forms barriers for the distribution of species, e.g. roads for the ground beetle *Carabus violaceus* (Keller and Largiadèr 2003).

In Germany, a strong focus lies on conservation in forests, because they are considered as the main potential natural habitat in Germany, with about 90 percent of the natural conditions being suitable for forest growth (Ellenberg and Leuschner 1996). The specific goal for forests in the biodiversity strategy of the German government is the exclusion of management on 5 percent of the forested area in Germany (about 1,786,880 ha), to promote the development of natural forests (Bundesministerium für Umwelt Naturschutz und Reaktorsicherheit 2007). Considering the recent forest cover this is 1.5 percent of Germanys land surface what could be insufficient for the protection of forest biodiversity, especially for species with special habitat requirements or species which are slow dispersers and need a suitable habitat in an accessible distance. This includes for example Urwald relict beetles or ancient forest plants (Hermy, Honnay et al. 1999, Müller, Bußler et al. 2005). Dunning (1995) found that even for common species like the Bachman's sparrow (*Peucaea aestivalis*) densities decline with increasing isolation and decreasing connectivity by corridors. Therefore, even if suitable habitats exist but the patches are too small, too far away from source populations or blocked by barriers such as roads they can be missing the respective species. This is for example shown for the European wildcat (*Felis silvestris*) and its repopulation of forest patches in a human shaped landscape after extinction (Klar, Fernández et al. 2008). The lack in exchange of individuals of populations can then result in inbreeding, connected to the accumulations of unfavourable genes and the possible the extinctions of local populations.

1.1.2 Improvement of current conservation actions

To overcome this difficulty of small and poorly connected habitats, the German government agreed on improving the habitat quality in forests in general by integrating certain measures in managed forests. The governmental aim is to promote naturally occurring forest communities with a natural vegetation and a high diversity in structures and dynamics. Monocultures of spruce and pine are planned to be replaced by tree mixtures (Bundesministerium für Umwelt Naturschutz und Reaktorsicherheit 2007). Natural processes should be promoted through a close to nature management and large unfragmented forest areas will be preserved. Therefore, deadwood and old trees are expected to become present in adequate quantity and quality (Bundesministerium für Umwelt Naturschutz und Reaktorsicherheit 2007). The aim is to create sustainable multifunctional forests, which serve not only for wood production but also for the provisioning of ecosystem services and biodiversity conservation while facing climate change.

1.2 Biodiversity and threat of saproxylic species

Within forest ecosystems deadwood dependent, i.e. saproxylic species (Stokland, Siitonen et al. 2012) are extensively considered as seriously endangered and in need of protection. Saproxylic species are defined as: "*any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weekend or dead trees*" (Stokland, Siitonen et al. 2012). Different attempts have been made to estimate the species richness of saproxylics, reporting numbers of about 30 percent of all forest dwelling species to be saproxylic (Speight 1989, Jonsell, Weslien et al. 1998, Stokland, Siitonen et al. 2012, Seibold, Brandl et al. 2015). This includes many insects (e.g. beetles and diptera), fungi, bryophytes, nematodes but also vertebrates (Stokland, Siitonen et al. 2012).

1.2.1 Properties of saproxylics' habitat

The diverse evolution of species of so many different taxonomic groups associated with deadwood is proposed to result from the special characteristics of deadwood as a habitat. High amounts of deadwood can accumulate in natural forests, representing a large habitat and a major source of energy. According to the species-energy hypothesis large amounts of energy enable the coexistence of species (Wright 1983) and promote a high speciation (Stokland, Siitonen et al. 2012). Several studies confirmed this hypothesis and showed a strong relationship between deadwood amount and the biodiversity of many taxonomic groups, e.g. saproxylic beetles (Müller and Bussler 2008, Bouget, Larrieu et al. 2013) or fungi (Berglund, Hottola et al. 2011). Deadwood amounts in natural forests are a product of many factors like the growing stock that can range around 600 to 800 m³ ha^{-1} (Slovenia, virgin forest remnant and reserves (Boncina 2000, Rugani, Diaci et al. 2013), but also the mortality which can comprise 1.5 percent of the present trees per year (Holzwarth, Kahl et al. 2013).

In natural forest communities, which are often dominated by beech in Central Europe, deadwood amounts can range from 44.7 (German reserve, Minimum diameter in cm (*MinDm*): 7 (Meyer 1999)) to 220 m³ ha^{-1} (European reserves, *MinDm*: 5 (Christensen, Hahn et al. 2005)) and up to 256 m³ ha^{-1} (French reserve, *MinDm*: 5 (Mountford 2002)).

The deadwood amounts vary strongly with the agents of mortality. Wind, insects or fire can create large scale, i.e. stand replacing disturbance pattern which occur mainly in coniferous forests (Angelstam and Kuuluvainen 2004). However, small scale disturbance patterns are far more common, especially in broadleaf forests. These patterns result from mortality by competition and diseases of trees. The mortality in forests dominated by mortality by diseases and competition is therefore strongly influenced by the stand age, with the probability of mortality with age resembling a U-shaped curve (Laarmann, Korjus et al. 2009). The highest amounts of deadwood can therefore be found in early and late developmental phases of beech forests (Sefidi and Marvie Mohadjer 2010). For young trees the main mortality reason is competition, commonly causing death while trees are still standing. With ageing the mortality due to infections with fungi or other agents increases (Laarmann, Korjus et al. 2009). Therefore, old trees often display a variety of growth structures and damages, such as cavities, fruiting bodies of fungi, and bark damages which are coined as microhabitats (Kraus, Bütler et al. 2016). Nearly 100 percent of trees > 90 cm diameter at breast height (1.3 m, DBH) were found to exhibiting some kind of microhabitat (Larrieu and Cabanettes 2012), resulting in a frequency of trees with cavities ranging from 7 to 20 in unharvested montane forests in Europe (Larrieu, Cabanettes et al. 2014). However, with ageing also the vulnerability to wind damages increases, leading to a growing probability of snapping or uprooting for old trees (Laarmann, Korjus et al. 2009, Holzwarth, Kahl et al. 2013). This causes, besides high deadwood amounts considerable changes in the canopy cover. In beech forests, average gaps created by wind induced mortality vary around a size of 60 m² (Kenderes, Mihok et al. 2008) to 117 m² (Rugani, Diaci et al. 2013). After large storm events deadwood amounts can be very high, e.g. 260 m³ ha^{-1} even ten years after a storm in Swiss mixed forests (*MinDm*: 10 and Minimum length: 10 cm (Priewasser, Brang et al. 2012)). In a French beech dominated reserve the amounts were on average 199 m³ ha^{-1} one year after the storm (*MinDm*: 5 (Mountford 2002)) but deadwood amounts can even reach 400 m^{3} ha^{-1} 11 years after a storm, as shown in a British beech dominated reserve (Minimum height: 1.3 m (Mountford and Peterken 2000)).

However, deadwood is a highly variable habitat not only in terms of amount but also in persistence and the conditions within the habitat (Stokland, Siitonen et al. 2012). Deadwood shows strongly varying properties resulting from factors influencing the tree during its life e.g. regeneration and growth, its death and decomposition (Stokland 2001). These varying properties produce a high diversity within deadwood as a habitat. According to the habitat heterogeneity hypothesis, the high variability in deadwood habitats promotes the coexistence, persistence and diversification of species (Seibold, Bässler et al. 2016). The specialisation of many species to a certain type of deadwood make the properties of deadwood an important factor that determines biodiversity (Jonsell, Weslien et al. 1998). During the progressing decomposition, the deadwood habitats also continuously change, resulting from a distinct succession of species. The properties of deadwood, i.e. the way the decomposition proceeds is influenced by the properties of the wood, e.g. slow decomposition of hard wood with small growth rings which develop due to slow growth (Stokland, Siitonen et al. 2012), but also by the mortality agent determining the condition of the tree at its day of death. Trees with a sudden death due to e.g. wind are very nutrient rich when starting the decay. Death due to competition or senesces however, proceeds slowly and over a much longer time span. When trees die slowly they can become hard and dry, especially for young and small trees dying of a lack of nutrients and light due to a high competition. However, old and often large trees decay gradually over decades due to senescence processes (Stokland, Siitonen et al. 2012). Further on the orientation and type of the deadwood object, i.e. if it is lying (log) or standing (snag), determines its moisture level and exposition to sun and with that strongly the way of decay (Vanderwel, Malcolm et al. 2006).

The succession of species within deadwood can therefore take many ways. In fresh deadwood where the varying secondary compounds created by the trees species are still present very tree species specific decomposer communities are present. The early colonizing communities of fungi and insects rapidly consume the inner bark and cause the bark to detach, creating again a large habitat for fungi. Subsequently, fungi spread their mycelia into the wood and insects bore tunnels into it, causing the wood to become soft and finally break up into small pieces which are then available as habitat for e.g. earthworms or springtails (Stokland, Siitonen et al. 2012).

The adaption to a certain type of deadwood in distinct decay phases requires the presence of the habitats in a suitable dispersal distance to promote stable populations of saproxylic species. Meyer, Tabaku et al. (2003) found 19 deadwood logs and 8.3 deadwood snags in Albanian virgin beech forest reserves. In old-growth Picea abies forests 684 deadwood logs bigger 10 cm were found on a 200 m x 300 m area (Edman and Jonsson 2001). Importantly, spatial pattern of deadwood in natural forests are not random (Commarmot, Bachofen et al. 2005). Edman and Jonsson (2001) found an aggregated distribution up until 45 m radius. This non-random spatial distribution results most likely from the non-random distribution of living trees and should therefore occur especially in natural beech forests where small scale disturbances govern the stand characteristics. However, when deadwood connectivity is addressed not only the spatial but also the temporal distribution needs to be taken into account (Peltoniemi, Penttilä et al. 2013). The temporally changing physical and chemical properties of the deadwood object make some of the developmental stages of deadwood objects rather ephemeral habitats, forcing species to adapt. Therefore, species need to be able to distribute and colonize new habitats sometimes after only a few month (Lachat, Bouget et al. 2013). However, not all saproxylic species are adapted in this way. Some of the saproxylic habitats such as large tree cavities are lasting over decades and are inhabited by species such as *Osmoderma eremita* that are poor dispersers (Lachat, Bouget et al. 2013), making them vulnerable to habitat destruction.

1.2.2 Influences of forest management on saproxylics' habitat and their biodiversity

Due to the dependency of saproxylic organisms on wood these species are in direct competition with human wood extraction making them prone to extinction. Only considering saproxylic beetles, already 28 percent are listed as threatened or regionally extinct in the German Red List (Nieto and Alexander 2010, Seibold, Brandl et al. 2015). Also, more than half of saproxylic bryophyte species in Hungary are considered as rare (62 saproxylic species, 37 treated as regionally rare) (Ódor and Standovár 2001). For saproxylic beetles especially those of lowland forests, those that rely on large diameter deadwood, broadleaf trees and open canopies are endangered, reflecting well the influences of the century long intense forest management (Seibold, Brandl et al. 2015).

The removal of living wood and the removal of dead trees, e.g. by salvage logging in coniferous forests but also as energy source, e.g. fire wood in temperate regions, reduces the amount of deadwood in production forests. The harvest prohibits the development of old trees and changes therefore the mortality pattern of the forest (Debeljak 2006). Managed beech forest in Slovenia show only 12 percent of the deadwood amount of a virgin forest remnant (managed: 41–67 m³ ha^{-1}, reserve: 248–626 m³ ha^{-1}, *MinDm*: 5) (Debeljak 2006). Also, Central Swedish spruce clear-cut forests showed distinct lower amounts (13.6 m³ ha^{-1} (Gibb, Ball et al. 2005), young: 9.3–14.2, old: 9–16 (Ekbom, Schroeder et al. 2006)) than mature managed (23 m³ ha^{-1}) or unmanaged old-growth forests (72.6 m³ ha^{-1} (Gibb, Ball et al. 2005), set aside: 27.1, reserve: 34.3 (Ekbom, Schroeder et al. 2006)).

However, also the continuous conversion of forests to efficient, habitat poor high forests threatens saproxylic species because it additionally changes the characteristics of the existing habitat and with that reducing not only the amount of deadwood but also the diversity within deadwood. The applied short rotation times reduce the presence of old and large trees which are required for the formation of microhabitats such as tree cavities (Larrieu and Cabanettes 2012). Besides that the promotion of coniferous monocultures has a negative effect with conifers exhibiting lower abundances of cavities (Larrieu and Cabanettes 2012). In addition, monocultures only provide deadwood of a single tree species. Moreover, the even-aged structure with rather small trees promotes mainly the mortality of small deadwood affecting also the size of deadwood objects (Gore and Patterson 1986, Karjalainen and Kuuluvainen 2002). Therefore, managed forests often display a low variety of deadwood. The assessment of a ‘deadwood profile’ that takes the orientation, diameter and decay class into account shows distinct gaps of old and large diameter objects in intensely managed stands (Stokland 2001). Due to the reduction of the absolute amount and the reduction of certain types of deadwood and microhabitats the distance between ‘islands’ of deadwood habitats become very large resulting into a low connectivity between deadwood habitats in managed forests (Morrissey, Jenkins et al. 2014).

The deadwood that is present in managed forests consist mainly of harvest remnants (Montes, Cañellas et al. 2005), which are often small pieces of deadwood that decay fast and do not provide sufficient habitat for the variety of saproxylic organisms present. After abandonment of management deadwood accumulates over time (Christensen, Hahn et al. 2005). However, due to the changes of the forests’ age structure and mortality pattern and the accumulation of deadwood after harvests in production forests, recently established reserves can have even lower amounts of deadwood than production forests. A study of 12–46 years unmanaged and managed high beech forests in Switzerland showed that the amounts in managed forests are higher (3.7–6.3) than in unmanaged forests (0.7–28.2), resulting from a very high variation within deadwood amounts in reserves (Guby and Dobbertin 1996). Even salvage-logging on clear-cuts in Swiss coniferous forests leaves around 75 m³ ha^{-1} ten years after a storm in Swiss coniferous forests (Priewasser, Brang et al. 2012). However, this is only about 30 percent of the deadwood amounts on unlogged sites. A study in Germany found that deadwood amounts in coniferous age-class forests were considerably higher (25.1 ± 5.3) than in broadleaf age-class forests (17.5 ± 3.2) or unmanaged forests (9.7 ± 2.5). However, the reserve included in this study has only been unmanaged 10 to 30 years and deadwood might not have accumulated yet (Blaser, Prati et al. 2013). Therefore, even after a considerable time of abandonment natural conditions and deadwood amounts might not be restored in forests.

1.3 Integrative management for deadwood enrichment

Due to the long history of forest utilization and the rather slow accumulation of deadwood, the often small and isolated nature conservation areas are proposed to be insufficient to conserve stable populations of saproxylic species (Abrego, Bässler et al. 2015). It is already shown that the retention of old growth islands and single structures such as old trees or the accumulation of harvest remnants can promote biodiversity (Jonsell, Hansson et al. 2007, Gustafsson, Baker et al. 2012). Therefore, the integration of nature conservation measures in production forests to enhance biodiversity conservation are often proposed as a strategy for a comprehensive conservation (Bauhus, Puettmann et al. 2009). The aim of integrative conservation measures is to improve the conditions for biodiversity in managed forests to make them more suitable habitats for species. This should not only increase the population sizes but also mediate the dispersal between source populations. Measures in managed forests can not only influence a larger proportion of the forest area compared to exclusive protection in reserves it also allows for a variety of measures, including active approaches of habitat creation that might not be possible in reserves destined for natural development (Bollmann and Braunisch 2013). The enrichment of deadwood is considered to be an important part of integrative measures.

Several approaches on how deadwood enrichment can be practices as integrative measure are proposed. Integrative conservation measures can be differentiated into: (i) the passive retention of habitats and, (ii) the active creation of habitats.

1.3.1 Passive approaches

Passive approaches include variable retention, group retention, green tree retention or retention of so called woodland key habitats. These terms include many different measures ranging from the retention of whole forest patches to single elements like large or dead trees. The aim is to conserve biological legacies, i.e. preharvest elements, to guarantee a continuous supply of habitats for the preservation of spatial and temporal forest continuity and complexity to promote biodiversity (Gustafsson, Baker et al. 2012).

Retention forestry is common practice in Canada, the US and Scandinavia since the 1980ies. In these regions, coniferous forests, with regular large disturbances by insect, fire or wind dominate. The main harvesting practice in these forests are clear-cuts. In temperate forests with continuous cover, retention forestry includes mainly the promotion of old large trees, microhabitats, old growth islands and deadwood. In Germany the application of retention approaches is not very common yet (Gustafsson, Baker et al. 2012). The most comprehensive approach concerning the retention of structural elements is the ‘Alt- und Totholzkonzept’ (Old growth and deadwood concept) applied by the State Forest Company of the Federal-State of Baden Württemberg (ForstBW 2010). This includes predominantly selective felling and the retention of five habitat trees per hectare, in addition to all known trees with cavities or trees which are used by various species for reproduction or resting. Furthermore, habitat tree groups are conserved to cover at least 5 percent of the forest in mature stands. Besides that, so called ‘forest refuges’ which are areas > 1ha with old forests are preserved (Gustafsson, Kouki et al. 2010).

Retention measures are often proven to be beneficial for forests biodiversity especially in clear-cut areas (Rosenvald and Lõhmus 2008). Also, in continuous cover forestry retention was proven to be successful (Bollmann and Müller 2012). The success in preserving species in green tree retention is determined by the patch size (Rosenvald and Lõhmus 2008) and, especially in continuous cover forests the time patches are retained, because saproxylic species can take considerable time to recolonize habitats (Bouget, Parmain et al. 2014). The retention of large patches is a successful measure to promote biodiversity (Gustafsson, Kouki et al. 2010). However, even large retention groups cannot maintain typical species of mature and old-growth forests (Gustafsson, Kouki et al. 2010). Nonetheless, for saproxylic beetles the conditions in retention patches can be still favourable due to a high mortality of retained trees that provide a high amount of habitat (Jönsson and Jonsson 2007). Also the preservation of certain elements like trees with microhabitats is an important aspect for biodiversity conservation (Bütler, Lachat et al. 2013). For cavity depending species the preservation of trees with hollows and broken branches is a relevant measure and especially trees with a high number of cavities are likely to be occupied (Gibbons, Lindenmayer et al. 2002). Cavities with a larger entrance widths are in general more often occupied by mammals in Australian temperate eucalypt forests. Therefore, a pre selection of trees that have the possibility to develop hollows is necessary to guarantee a continuous supply of this slow developing habitats (Gibbons and Lindenmayer 1996).

1.3.2 Active approaches

Next to the retention of habitats that develop naturally also the active creation of habitats is a possibility for integrative nature conservation. Whereas the retention can only retain existing structures or retain trees with a potential to develop certain habitats, active approaches can create these structures and with that are expected to increase habitats faster and towards specific quantities.

Experimental studies show that deadwood can be created in various ways using e.g. forestry machinery (Lilja, De Chantal et al. 2005, Fossestol and Sverdrup-Thygeson 2009, Arnett, Kroll et al. 2010, Kroll, Duke et al. 2012), cutting or girdling of trees with an axe (Brandeis, Newton et al. 2002, Shea, Laudenslayer Jr. et al. 2002), or by killing trees with explosives (Bull, Partridge et al. 1981). A very comprehensive review on measures taken in the Bosco de la

Fontana reserve in Italy shows how much interventions cost, including machinery and labour (Cavalli and Mason 2003). The most expensive operation is the production of fallen snags using a winch (38.73 €/tree), whereas standing dead trees produced by debarking a ring at the bottom of the stem are the cheapest (9.57 €/tree). Artificially uprooted or leaning (half uprooted) trees are cheaper then fallen snags (23.07, 33.74 €/tree) because they do not require a preceding cutting of a notch. The usage of explosives however is complicated because of legal requirements (Cavalli and Mason 2003).

Next to the production of deadwood by killing a whole tree also the creation of microhabitats, especially cavities can be considered in integrative management. There are several different ways to approach the creation of microhabitats. It is possible to promote management techniques such as pollarding of willows, where in regular time spans branches are cut off for the creation of crafts (e.g. baskets), what promotes a rapid formation of tree hollows in these trees (Sebek, Altman et al. 2013). Also the active creation of trunk cavities can be practiced such as in Italy where invasive London plane trees (*Platanus hybrida*) were used to actively create habitat trees (Cavalli and Mason 2003, Zapponi, Minari et al. 2015). Besides that, the installation of nesting boxes for birds and arthropods is another active approach to promote biodiversity in managed forests.

A comprehensive review of the effect of experimental deadwood enrichment by Seibold, Bässler et al. (2015) shows that additional deadwood has an overall positive effect on saproxylic species (e.g. Gossner, Floren et al. 2013, Hekkala, Päätalo et al. 2014). Additionally, many species considered as non-saproxylics are positively affected by additional amounts of deadwood (e.g. Toivanen and Kotiaho 2007). The effects of deadwood enrichment can also differ between taxonomic groups. Beetle richness is in general positively influenced by deadwood enrichment (Barton, Manning et al. 2011), especially the richness of saproxylic species (Gossner, Floren et al. 2013, Hekkala, Päätalo et al. 2014) but also the richness of non-saproxylic species (Toivanen and Kotiaho 2007). The same positive effect was found for fungi (Brazee, Lindner et al. 2014), birds (activity: Caine and Marion 1991, richness: Mac Nally, Horrocks et al. 2002, Mac Nally 2006), bryophytes, lichen (Laarmann, Korjus et al. 2013) and flat bugs (Seibold, Bässler et al. 2014). However, the effect of deadwood enrichment on plants was negative, but shown only once (Laarmann, Korjus et al. 2013). Nevertheless, the positive response of the here mentioned taxonomic groups towards deadwood enrichment cannot be confirmed by all studies. Berglund, Hottola et al. (2011) showed that the richness of pioneer fungi did not change considerably with deadwood enrichment and burning. However, burning promoted a very distinct fungal community. Birds do also not always respond to deadwood enrichment. The studies of Arnett, Kroll et al. (2010) and Kroll, Duke et al. (2012) show that the creation of snags in clear-cuts of Douglas-fir does not primarily increase the nesting activity by birds. However, they could show that within intensely managed landscapes these snags were an important nesting habitat and that they were increasingly used for foraging with increasing age of the snag.

Naturally developed tree holes are demonstrably hotspots of biodiversity (Müller, Jarzabek-Müller et al. 2014). But also actively created holes and nesting boxes are proven to be a suitable habitat for certain species. In the Italian reserve, more than 50 percent of artificial cut holes are shown to be occupied by breeding birds in the first season after creation, with an increase in number after two years (Longo 2003). Nesting boxes filled with sawdust and leaves combined with water are shown to have almost identical thermal conditions to natural tree cavities offering conditions which allow a high survival of the endangered beetle *Osmoderma barnabita* (Hilszczański, Jaworski et al. 2014). Other types of nesting boxes filled with various types of substrate (e.g. dead chicken or flour) are also shown to promote saproxylic beetles (Jansson, Ranius et al. 2009).

Experiments on deadwood enrichment show that the success of deadwood enrichment in conserving biodiversity can be influenced by various factor, i.e. the way it is created, where it is placed and by the wood used. Comparisons of artificially created and naturally developed deadwood show that, although deadwood enrichment increases biodiversity in general, the artificially created objects display different characteristics than the naturally developed ones, with varying effects on the colonizing species. Abundance of species, i.e. birds and beetles, can be higher in naturally developed deadwood, such as bark beetle trees, stumps or wind felled trees, than in artificially produced deadwood, like girdled trees, cut stumps or cut logs (Shea, Laudenslayer Jr. et al. 2002, Jonsell 2004, Eriksson, Neuvonen et al. 2008). However, other experiments show that artificially created deadwood, e.g. freshly girdled trees, stumps or cut logs are colonized better by these species than natural deadwood, i.e. bark beetle trees, snags or logs (Walter and Maguire 2005, Jacobs, Spence et al. 2007, Komonen, Halme et al. 2014).

The local amounts, the distribution and densities of deadwood are a very important factor for the colonization by saproxylic biodiversity. In a study combining the effects of grazing and deadwood enrichment Barton, Manning et al. (2011) showed that at low grazing levels clumped arranged logs were most beneficial for beetles. However, by showing that several small deadwood patches had a higher diversity of beetles than single large patches Seibold, Bässler et al. (2017) were able to point out that in forested habitats the amount matters more than the actual patch size. The enrichment of wood of different tree species also determines the colonizing biodiversity. Different tree species promote different assemblages, e.g. for foraging of birds (Hallett, Lopez et al. 2001), fungi (Brazee, Lindner et al. 2014), or saproxylic beetles (Lindhe, Lindelöw et al. 2005, Gossner, Floren et al. 2013). Wood with more similar properties promotes more similar assemblages of species, e.g. for fungi on broadleaf deadwood vs. fungi on coniferous deadwood. Also, the richness of species can be influenced by the tree species. Saproxylic beetles, for example are best promoted by hornbeam in the early decomposition stages (Gossner, Wende et al. 2016). Long term experiments also reveal the importance of ageing deadwood. With increasing age e.g. the nesting and foraging of birds increases on snags (Hallett, Lopez et al. 2001, Arnett, Kroll et al. 2010) and also fungi increase with time on burned logs (Penttilä, Junninen et al. 2013). In experiments, the addition of explicitly large diameter deadwood has mainly a positive effect on biodiversity and richness on e.g. flat bug abundance (Seibold, Bässler et al. 2014), fungi richness (Edman, Kruys et al. 2004, Lindhe, Åsenblad et al. 2004) and saproxylic beetle abundance (Shea, Laudenslayer Jr. et al. 2002, Lindhe and Lindelöw 2004). However, in non-experimental studies also the occurrence of small diameter deadwood increases biodiversity of fungi (Heilmann-Clausen and Christensen 2004). The type of deadwood, i.e. if it is a log or a snag, influences less the species diversity but strongly the community. Fungi tend to have a higher diversity on logs (Olsson, Jonsson et al. 2011, Brazee, Lindner et al. 2014). Saproxylic beetles on the other hand, do not show distinct differences in richness when different object types are compared but very distinct communities on different object types (Abrahamsson and Lindbladh 2006, Gibb, Pettersson et al. 2006, Hjältén, Johansson et al. 2007, Fossestol and Sverdrup-Thygeson 2009). However, in experiments the handling between snags and downed deadwood is very different. Whereas many studies transport downed deadwood to the plot to avoid confounding factors (Gibb, Pettersson et al. 2006, Johansson, Gibb et al. 2006, Mac Nally 2006, Hjältén, Johansson et al. 2007, Barton, Manning et al. 2011, Cornelissen, Sass-Klaassen et al. 2012, Gossner, Wende et al. 2016), snags have to be created on the plot (e.g. Hallett, Lopez et al. 2001, Brandeis, Newton et al. 2002, Jonsell 2004).

Next to the properties of the wood also the climate, i.e. sunny or shady conditions determines the effect of the enrichment. Especially invertebrates like beetles or flat bugs show often higher abundances in deadwood lying in the sun (e.g. Fossestol and Sverdrup-Thygeson 2009, Vodka, Konvicka et al. 2009, Seibold, Bässler et al. 2014). Sunny conditions also have a positive influence on the diversity of vascular plants and lichen (Laarmann, Korjus et al. 2013) and on richness of ferns and vascular plants (Laarmann, Korjus et al. 2013, Sharpe and Shiels 2014). For fungi it is not always definite where deadwood should be placed to promote high biodiversity. Brazee, Lindner et al. (2014) found higher abundances in the sun, whereas Olsson, Jonsson et al. (2011) found that diversity of fungi was higher in the shade.

Therefore, experiments show that active and passive integrative measures are largely successful in promoting biodiversity but that several factors can influence their effectiveness.

1.4 Integrative conservation in German beech forests

The implementation of integrative measures in production forests becomes more common practice, however, the evaluation of the success of the measures that aim at promoting forest biodiversity is lacking behind. The success of deadwood enrichment is therefore only shown by experiments but not by the evaluation of implemented strategies. In Germany, nature conservation in forests has a strong focus on beech forests since they are defined as the main potential vegetation type in the temperate zone of Central Europe. Germany, with a potential natural cover of 90 percent of woodland dominated by beech forests, is considered as the core area of the occurrence of beech forests and thus the government has a special responsibility to protect this habitat type. The protection of natural beech forests in Germany is difficult not only because the creation of protected areas is shown to be demanding but also because virgin beech forests are not existing anymore in Germany. Also, forest with old growth character, which are important for saproxylic biodiversity are rare.

Of the existing forest (10,887,990 ha) 43 percent are broadleaf forest (4,727,260 ha) but only 15.4 percent actually beech (1,680,072 ha) and 2.5 percent old broadleaf forest with trees older 160 years (270,155 ha) (Bundeswaldinventur 2012). Also in other European countries the remnants of virgin beech forests are very small with only 0.4 percent of the total forested area being covered with virgin forest (0.3 million ha, mainly in Slovak Republic, Bulgaria, Albania, Slovenia and the Czech Republic) (Parviainen 2005). Therefore, even though beech forests could spread extensively due to their natural demands they are defined to be in critical status (Moning and Müller 2009).

A long history of changes by human land-use created the present forests (Bengtsson, Nilsson et al. 2000). The utilisation and therefore transformation and reduction of beech forests dates centuries back and make the restoration of natural conditions difficult. In Germany the forests experienced an intense time of deforestation in the middle ages (8th–9th and 12th–13th century) (Röhrig, Bartsch et al. 2006). Wood was used for ore smelting, salt production, as fire wood or for metal extraction. Remaining forests were used as wood pasture, coppice, for sod cutting or litter use (Röhrig, Bartsch et al. 2006). In the late 18th till the early 19th century the forest law was reformed, resulting in a stronger separation of forestry and agriculture and the promotion of high forests. Subsequently, in the 19th and 20th century coniferous forests were promoted, consisting mainly of monocultures of spruce (*Picea abies*) and pine (*Pinus sylvestris*) (Röhrig, Bartsch et al. 2006). In the last decades the total cover of forest in Germany is increasing, with present forest covering about 30 percent of the land surface (10.9 million ha) (Bundeswaldinventur 2012). Today, the main function of forests is the production of wood, whereas other forest products (e.g. Christmas trees) are of minor importance (Röhrig, Bartsch et al. 2006). About 95 percent (10,809,870 ha) of the present forests are managed as high forest. The dominant practice is cutting blocks (10,783,477 ha, 98 percent of high forests), whereas selection cutting (26,393, 0.2 percent of high forests) plays a small role. The regrown forests are therefore strongly characterised by human management and thus distinctly different to virgin and old growth beech forests.

The intense management in high forests leads to uniform cohort of even-aged trees (Kenderes, Mihok et al. 2008) making them distinctly denser and darker compared to old growth and virgin beech forests. Old growth and virgin forests are dominated by small scale disturbances, e.g. by death of single trees due to senescence or small groups killed by wind, producing small canopy gaps which allow small patches of rejuvenation. They have a spatial and temporal continuous cover of wood and are characterized by a patchy system of trees in different age classes. Also the maximum age of trees becomes distinctly lower in production forests, from a possible maximum of about 300 years to about 100 years, which is considered as optimum rotation time for beech (Knoke 2002). Therefore, also the natural development of senescent trees, trees with microhabitats and deadwood amounts become distinctly lower in managed beech forests. The interventions in production forests change the structure of the forests, especially the occurrences of canopy gaps, old and senescent trees and trees with microhabitats.

These old growth structures are considered to be key structures for forest biodiversity. Integrative management approaches that aim at restoring and maintaining key structures of natural forests in production forests are therefore considered to conserve and promote biodiversity in production forests (Bauhus, Puettmann et al. 2009). Therefore, these strategies could be a complement in conservation to the establishment of reserves.

However, since these integrative measures are competing with the human needs and the development of old growth elements can take a considerable time (Larrieu, Cabanettes et al. 2014) the measures should be as cost-effective as possible. A combination of passive retention and active creation of deadwood habitats could result into a comprehensive increase of structures while allowing for wood production in the same area (Jonsson, Ranius et al. 2006, Bollmann and Braunisch 2013). For habitats with very specific characteristics like woodpecker- or mould filled cavities and structures that are difficult and laborious to create, passive retention would be the most cost-efficient strategy. The active creation of habitats however should be considered where large amounts and certain thresholds are needed as for deadwood. This could also enable a fast increase in deadwood amounts. Since measures in production forests do not need to be as careful as the presented approaches in the Bosco de la Fontana reserve (Cavalli and Mason 2003), the enrichment of deadwood with harvest remnants is be a promising approach to rapidly increase deadwood amounts in production forests while still being able to produce wood.

The Bavarian State Forest Company, that manages 29.8 percent of the Bavarian forest (Bundeswaldinventur 2012), implemented an integrative nature conservation strategy in 2006, with a strong focus on beech forests. The key element of this strategy is to enrich the structural diversity of the managed forest, by (i) increasing deadwood amounts, and (ii) retention of ‘habitat trees’ that provide special structures which serve as microhabitats for various forest taxa. The deadwood enrichment is implemented by leaving crowns and large diameter parts of trunks actively after harvests and additionally preserving existing, naturally developed deadwood. The deadwood enrichment is oriented along age classes of the forests, targeting higher amounts in older stands. The retention of habitat trees is implemented by preserving ten trees with microhabitats per hectare. These provide habitats while they are still alive and can later develop to deadwood. To further improve the forest matrix, small reserves, created in the 80ies where deadwood accumulates naturally, are preserved and enlarged. This integrative strategy is considered to increase the deadwood amounts and directly target thresholds that are needed for the conservation of particular species (Müller and Bütler 2010).

Integrative nature conservation strategies that aim to increase deadwood amounts, like the one of the Bavarian State Forest Company have been implemented in many managed forests in Europe and beyond. However, a scientific evaluation of the success of these strategies is generally lacking. Therefore, we aim at a comprehensive evaluation of a landscape wide implementation of an integrative nature conservation strategy with a focus on deadwood enrichment in beech forests. This includes descriptions of deadwood amounts and the determination of their drivers (Chapter A), the description of biodiversity before and after the implementation of the strategy (Chapter B), as well as the evaluation of the dependency of biodiversity changes on deadwood enrichment (Chapter C), and furthermore an evaluation if deadwood changes affect the mechanisms determining species' assemblies (Chapter D).

1.5 Single chapters of the manuscript

A) Evaluation of the changes in deadwood amounts and their drivers

The evaluation of integrative management with an assessment of quantities of deadwood amounts, if the amounts meet specific targets aimed at by the forest department and what determines the quantity of deadwood amounts and enrichment is largely missing. It is assumed that a strict implementation of an integrative strategy can significantly increase deadwood amounts, even in a short time-period. However, it can also change the drives of deadwood amounts. Deadwood amounts in even-aged managed forest are commonly related to stand type features such as stand age and tree species composition. They are increasing with increasing stand age (Ekbom, Schroeder et al. 2006) and with increasing natural tree mortality (Laarmann, Korjus et al. 2009). They are influenced by the occurring tree species, due to higher mortality rates of certain species (Laarmann, Korjus et al. 2009), or varying decay rates of the deadwood of different tree species (Weedon, Cornwell et al. 2009, Kahl, Baber et al. 2015). Deadwood amounts could also be influenced by the fear of managers that the presence of deadwood amounts of certain tree species might attract insects, such as bark beetles, which can cause substantial damage to the living stand (Eriksson, Lilja et al. 2006). Additionally, harvesting practices strongly influence deadwood amounts. Although harvesting often destroys deadwood, especially of late decay stages, due to the use of heavy machines (Hautala, Jalonen et al. 2004), harvest remnants can still enrich deadwood amounts (Ódor and Standovár 2001).

It is important to evaluate drivers of deadwood amounts in forests managed with an integrative conservation strategy because they can affect the success of the strategy. The implementation of the strategy could decrease the influence of stand type variables such as stand age and tree species composition if the deadwood enrichment is applied regularly during thinning and harvest. However, if deadwood enrichment is only implemented in certain stand types, e.g. age classes or stands with the dominance of certain tree species it could also increase the influence of the importance of the stand type variables. Therefore, also a high diversity in the tree layer could result in lower deadwood amounts because of an increasing potential occurrence of high valuable tree species such as maple or cherry that would be less left as harvest remnants. Since the growing stock determines thinning and harvesting operations (Ahlström and Lundqvist 2015) but is rather low in production forests and reduced by harvest operations this might be a factor determining the actual deadwood amount and their enrichment. Unlike the general negative influence of harvests in production forests, harvest and thinning operations with an integrative strategy should have in total a positive influence on deadwood amounts. Therefore, deadwood amounts in a forest managed with a deadwood enrichment strategy should become more equal to amounts in remote or protected areas. However, the final success of the strategy is strongly dependent on the strict execution of the planned strategy and will therefore strongly rely on people who are responsible for the implementation of the strategy on a local scale, especially the managers of districts within the department.

We expect therefore increasing deadwood amounts that come closer to the goals set by the forestry department but also the changes in drivers to change towards an increasing positive influence of harvests and an increasing influence of age classes and broadleaf stands. The results of this part of the study are already published (Doerfler, Müller et al. 2017), however for a comprehensive representation of the evaluation of the strategy a shortened and partly modified version is given here.

B) Description of biodiversity before and after the implementation of the strategy

The integrative strategy aims at increasing forest biodiversity. It is shown that many species groups increase with nature conservation in reserves (Paillet, Berges et al. 2010) and that also many species groups increase with deadwood enrichment (Seibold, Bässler et al. 2015). The evaluation on the response of biodiversity onto integrative nature conservation strategies is however lacking widely. Additionally, the evaluation relies often only on the assessment of structures as indicators, without or with a limited assessment of actual biodiversity (Spielmann, Bücking et al. 2013). For the evaluation of forest biodiversity taxonomic groups need to be selected that are suitable indicators for various aspects of forestry. The selected species groups should cover a wide variety of functions in the ecosystem, e.g. from primary producers to primary and secondary consumer, from short to long lived and deadwood dependent to independent species to be good indicators for the forest biodiversity. Invertebrates and fungi constitute the major part of the biodiversity in forests (Schuck, Meyer et al. 2005). Therefore, fungi and especially beetles are often used to assess the impact of forests management and deadwood reduction. Both groups include a large number of species and comprise many saproxylics (Schuck, Meyer et al. 2005). Besides these two groups, birds are often considered when assessing the naturalness of forests, although they have distinctly lower species numbers. The strong relationship of, e.g. woodpeckers to certain habitats occurring only in certain trees or with certain amounts of deadwood (Bütler, Angelstam et al. 2004) and their relative straightforward assessment makes them a valuable indicator of forest conditions, old growth status and management intensity (Müller 2005, Begehold, Rzanny et al. 2015). Additionally, birds are quite long living and the individuals are not dispersal limited, enabling them to react fast onto changes in their environment. Another important, quite large and easy to assess taxonomic group are plant species in forests. In temperate beech forests they are considered as primarily independent of deadwood (Burrascano, Lombardi et al. 2008). The diversity of plants is shown to respond quickly to disturbance, e.g. by forest machines promoting the immigration of non-forest species into forests. This makes plants important when assessing disturbance but also for the evaluation of the light regime and the tree species mixture. True bugs are, compared to the before mentioned groups rather poor studied in their habitat requirements. However, they are shown to be strongly affected by the forest structure, the light availability in the forest and the tree species composition, making them a valuable additional indicator for the effects of an integrative conservation strategy (Gossner 2009, Sobek, Gossner et al. 2009).

The combined assessment of different taxonomic groups, being dependent on different habitats can therefore give a good overview of the overall effects of integrative management. We expect the Gamma- and Alpha-diversity to increase, with a distinct addition but a low extinction of species. Rare species should become more frequent due to a promotion of habitats rare in regular production forests. However, the changes will mainly concern saproxylic species since the strategy focuses on the promotion of these. Further on, the strategy can also affect the abundances of species due to a higher amount of habitat and niche availability.

C) Relation between changes in biodiversity and deadwood enrichment

Deadwood enrichment has been shown to promote diversity of saproxylic, i.e., obligatory deadwood dependent, taxonomic groups such as saproxylic beetles and fungi (Jonsell 2004, Lassauce, Paillet et al. 2011, Gossner, Lachat et al. 2013, Seibold, Bässler et al. 2015) and is similarly effective in stands with previously low and high deadwood amount, at least for saproxylic beetles (Seibold, Bässler et al. 2017). Deadwood enrichment was also shown to increase non-target organisms, i.e. taxonomic groups not obligatorily depending on deadwood, i.e. birds (e.g. Brandeis, Newton et al. 2002, Kroll, Duke et al. 2012). However, it can also negatively affect species, i.e. plants (Laarmann, Korjus et al. 2013). Therefore, the active creation of deadwood by a forestry department should strongly increase saproxylic species but might also affect other species groups.

Additionally to deadwood, saproxylic species are also dependent on living, microhabitat bearing trees, especially those with cavities, this concerns e.g. beetles (Bouget, Larrieu et al. 2014, Müller, Jarzabek-Müller et al. 2014) and birds (Johnsson, Nilsson et al. 1993). Therefore, the retention of habitat trees should promote especially these species. Since, the active creation of these habitats is elaborate (Zapponi, Minari et al. 2015) they can mainly be promoted by retention of trees carrying these structures. However, a passive retention of trees also means that the actual number of cavity bearing trees relies on natural dynamics and can be less controlled by the forest department.

Next to actual deadwood amount the response of species on deadwood enrichment in forests is strongly linked to the openness of the canopy (Seibold, Bässler et al. 2016). Sun exposed deadwood can promote a higher diversity, especially of beetles (Seibold, Bässler et al. 2016), but harbors in general a different community than deadwood under shady conditions (Seibold, Bässler et al. 2016). However, sun exposure can also have negative effects on e.g. saproxylic fungi (Bässler, Müller et al. 2010). Besides that also non-saproxylic taxa such as plants (Burrascano, Lombardi et al. 2008) are positively influenced by canopy gaps because of an increased light availability. Although, effects of canopy openness on forest species are a common finding, the actual underlying mechanism is not clear. Besides that, it is often difficult to keep apart the effect of deadwood enrichment and canopy openness in non-experimental approaches, since the dead of a tree usually leaves a gap in the canopy. The size of the gap, however can vary very strongly between different agents of natural mortality (e.g. small-scale disturbance by age related senescence or large-scale disturbance by fire, wind or bark beetles) and different management approaches (e.g. selection cutting or clear-cuts). Therefore, it is important to consider potential effects of the canopy openness when evaluating deadwood enrichment.

Existing evaluations of deadwood enrichment strategies are strongly based on experimental treatments (Seibold, Bässler et al. 2015). The drawback of experiments is that they are often implemented on a small spatial scale and that they often focus on single taxonomic groups. The large-scale evaluation of deadwood enrichment as applied by forest management companies on a landscape scale is still lacking.

However, we expect a similar positive result of deadwood enrichment on overall biodiversity, but that the responses are most pronounced in saproxylic taxa, but neutral or even negative for birds and plants. Similarly, a decrease in canopy cover should be related to an increase in deadwood amounts and mainly influences the diversity of saproxylic beetles and plants.

D) Relationship of assembly mechanisms and deadwood enrichment

Species diversity and ecosystem functions are often strongly linked and also the diversity of a community and the range of functions provided by this are closely correlated. Land use changes can strongly affect ecosystem functions and services provided by natural communities. Land use intensification cannot just decrease species diversity but also the functions a community provides. Since community assembly is assumed to be mediated by functional traits, changes in these can also change the mechanisms how communities assemble. This is shown for several species groups, both in forests and agricultural land (Flynn, Gogol-Prokurat et al. 2009, Gossner, Lachat et al. 2013). The intensification of land use is often connected to habitat destruction or degradation and leads to the reduction of certain resources such as deadwood. The reduction of resources has been shown to change but not to increase the dominant assembly mechanism, especially for species depending directly on this resource (Thorn, Bässler et al. 2015). However, for habitat restoration, i.e. an enrichment of resource it is unclear if and how species assemblies might change.

Two main theories exist how communities are shaped. The first one is competition, causing communities to be overdispersed, i.e. more different than in a random assembly. The second one is environmental filtering, causing communities to be more clustered, i.e. more similar than expected. The increase of a resource such as deadwood is likely to affect saproxylic and non-saproxylic species different. For saproxylic species it is either possible that the addition of deadwood could lead to a change in the assembly mechanism. Saproxylic beetle communities, which tend to be more clustered and shaped by environmental filtering would therefore become more overdispersed. Saproxylic fungi, which tend to be more overdispersed and shaped by competitive exclusion would therefore become more clustered. However, communities could also become less clustered due to an increase in niche diversity with deadwood enrichment. Finally, species could also become first less clustered with increasing niche diversity and, with a certain amount of deadwood enrichment become again more clustered due to a stagnation in niche addition. For non-saproxylic species groups like plants or species groups which are attached only slightly to deadwood, like birds, deadwood enrichment will most probably not influence the assembly mechanisms.

However, also the changes in light availability could strongly influence the species assembly, either directly for, e.g. plants or indirectly by effects on deadwood, since e.g. beetle communities show very distinct communities on sunny and shaded deadwood and possibly also different assembly mechanisms (Seibold, Bässler et al. 2016).

1.6 Specific aims and Questions

Within this study, we aim at a comprehensive evaluation of an integrative strategy that is implemented in the forest department Ebrach in southern Germany to increase our understanding of the factors that influence the success of such strategies in means of its implementation and its promotion of biodiversity. By the assessment of deadwood amounts and their drivers we can assess the success and what might influence it to give recommendations for an improvement of the here examined strategy but also for other, similar strategies. Furthermore, we can assess the success of the strategy to promote and conserve biodiversity and whether the enrichment in habitat possibly leads to changes in the community and the mechanisms shaping its assembly. To structure the results, we separated the single steps of the evaluation into four Chapters (A–D). The specific questions in this study were:

A) Evaluation of the changes in deadwood amounts and their drivers
1: Are deadwood amounts increasing and do they meet the expected targets after the implementation of the strategy?
2: Are the drivers of deadwood amounts changing after the implementation of the strategy?

B) Description of biodiversity before and after the implementation of the strategy
1: Are Gamma- and Alpha-diversity higher after the implementation of the strategy?
2: Does the potential increase in diversity affect saproxylic species stronger than non-saproxylic species?

C) Relation between changes in biodiversity and deadwood enrichment

1: Does the deadwood enrichment promote overall biodiversity?
2: Are the responses to deadwood enrichment more pronounced in saproxylic taxa than in non-saproxylic taxa?
3: Can other factors like the canopy cover or the previous diversity additionally affect the changes in biodiversity?

D) Relationship of assembly mechanisms and deadwood enrichment
1: Are the mechanisms shaping the assembly of different species group change with deadwood enrichment?
2: Are the changes in species assembly rather related to competitive exclusion or to environmental filtering?
3: Are other factors like the canopy cover affecting the assembly mechanisms?

2. Methods

The aim of this study is to investigate the impact of integrative nature conservation on both the targeted structures and biodiversity. For this purpose, a forest department has been chosen which has both a strict execution of an integrative strategy as well as data that allow a comparison of management with and without the integrative nature conservation strategy.

2.1 Research Area

The study area is located in the ‘Steigerwald’-region (N 49° 50' 53 E 10° 29' 41) in southern Germany (Bavaria). It is a low mountain range area with a size of about 1,000 km² which is bounded by the rivers Main in the North, Regnitz in the East and Aisch in the South (Figure 1).

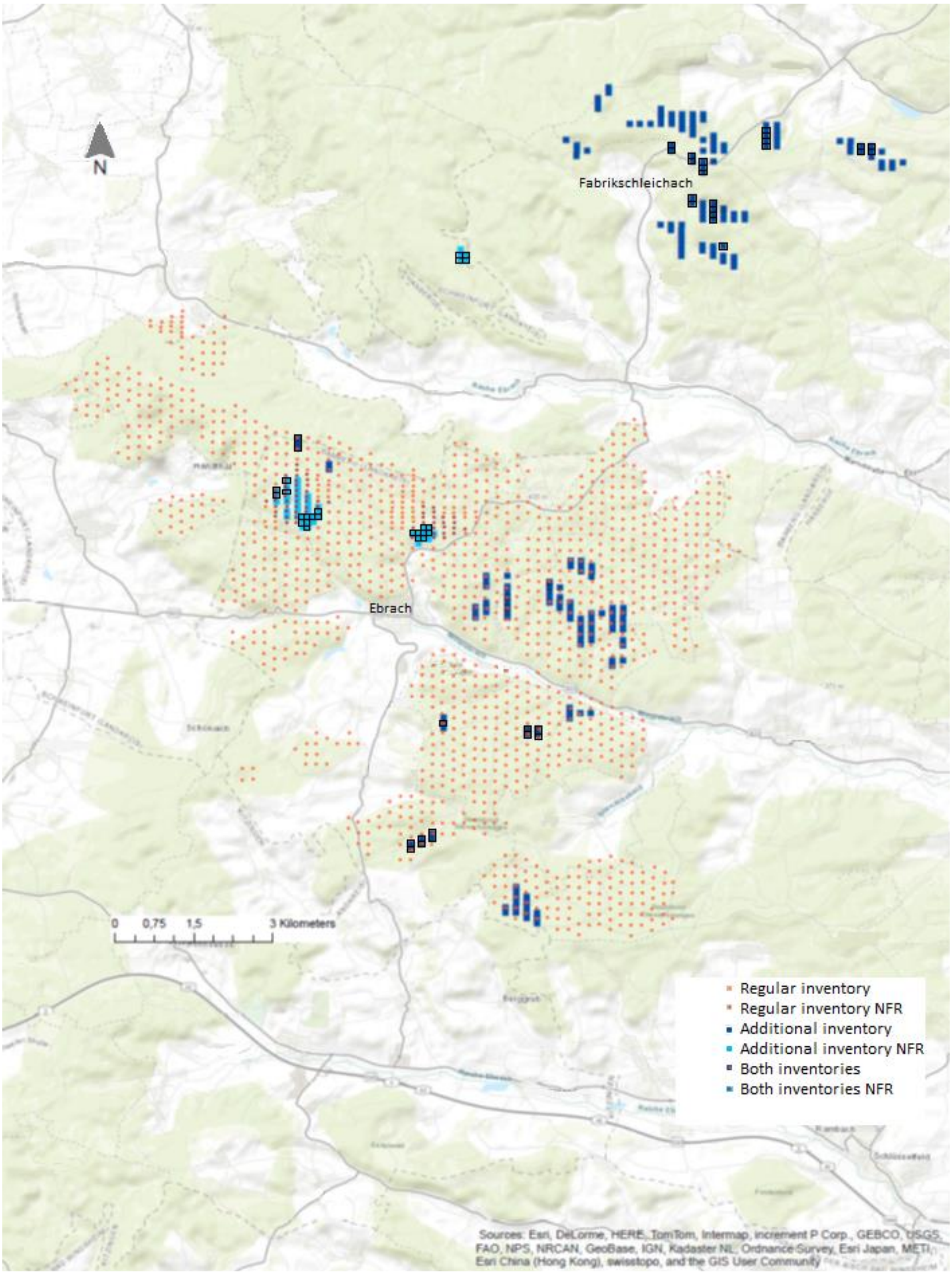
2.1.1 Climate and soil conditions

The Steigerwald is placed in a region in the transition between sub-Atlantic moderate climate zone with mild winters and cool summers, with precipitation all year round and the sub continental climate with more cold winters, warmer summers and lower precipitation (Welss 1985). Additionally, the relief promotes precipitation at the steeper slopes due to air masses that cool down when moving from lower to higher elevation.

Within the time span of our study (2003-2015) the mean annual temperature was 8.6 °C, with a standard deviance of 0.6 °C between the years. The annual temperatures range from -14 °C to 26.8 °C. The mean temperature in winter (December till February) is 0.45 °C and 17 °C in summer (June till August). The mean annual rainfall in this period was 2.2 mm per day with a standard deviance of 0.34 mm between the years. The daily rainfall ranged from 0 mm to 60.3 mm within these twelve years. The precipitation between the months had a standard deviation of 0.44 mm. The month with the highest precipitation was July with 2.9 mm. In winter (December till February) the precipitation is a little lower with 2.14 mm than in summer (June till August) with 2.5 mm (Appendix A, Figure A1).

Relief and soil

The Steigerwald area is part of the Franconian Keuper-Lias Land which belongs to the South German Scarplands. This geological region is characterised by changing layers of hard sand- and soft claystones forming steep slopes and flat ridges (Bayerisches Landesamt für Umwelt 2017a). The elevation ranges from 300 to 450 m. The Steigerwald region is forming a distinct silvicultural growth area (WB 5.5) with clayey-sandy two layered soils (Welss 1985). The soil profile is brown soil developed from loess clay.



Sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, and the GIS User Community

Figure 1: Map of the plots used in this study. Orange: regular forest inventory in production forests, red: regular forest inventory in reserves, dark blue: additional forest inventory in production forest, light blue: additional forest inventory in reserves. Plots present in both inventories are bicolored. Plots of the subset of the additional inventory are black framed.

Growth conditions – natural plant associations

The soil is dominantly acidic and therefore a typical forest site in Germany. Whereas sites which are influenced by clay layers are water logged, exposed sites with sandy soils that develop directly from the bedrock are prone to desiccation (Welss 1985). The main plant sociologies are the ‘Luzulo-Fagetum’’ and ‘Galio odorati-Fagetum’, (Ellenberg and Leuschner 1996). The area is located in a FFH-protected landscape („Buchentäler und Wiesentäler des Nordsteigerwaldes“, FFH-Gebiet 6029-371), comprising typical habitats of broadleaf forests (Bayerisches Landesamt für Umwelt 2017b).

2.1.2 Bavarian state forest company and department Ebrach

This study was realised in a part of the Bavarian state forest which is managed by the Bavarian state forest company. This is an institution which is authorized to perform public tasks and therefore underlies directly decisions made by the Bavarian government. It was founded in 2005 and is managing 755,000 hectares of forests in Bavaria making it the biggest forest company in Germany (Bayerische Staatsforsten 2016a). With their founding they also published a conservation strategy that aims on sustainable management and promotion of certain types of habitats that are important for forest biodiversity (e.g. aeries or deadwood) (Bayerische Staatsforsten 2009).

Department Ebrach

The department Ebrach, where the study took place, comprises 17,000 ha of state forest. Management activities are executed on 97 percent (16,494.2 ha) of the forestry area. The remaining area is protected in nature reserves of different sizes.

Historic management

Until the year 2005 the area of the recent forestry department was divided in three forestry departments, in the North (Eltmann), in the South (Ebrach) and in the West (Gerolzhofen). Until the 18th century coppice, with high proportions of oak and hornbeam was the main management practice in this region. The conversion into a high forest with a higher proportion of beech started from the beginning of the 19th century on. The main harvesting practice from 1880 until 1930 was shelter wood cutting. In 1930 this practice was replaced by selective cutting of tree groups combined with a stronger promotion of spruce. Until the 1970ies high intensity logging was practiced. However, management practices during and after the Second World War were very different in the South and North still influencing recent stand features. In the South close to nature management was introduced in the 1980ies, resulting into a promotion of the rejuvenation of broadleaf trees. In the northern region, especially around the village Fabrikschleichach (Figure 1), the management concentrated on the cultivation of high-value timber. The increased cutting of sylvicultural less valuable trees that bear structures like fungi brackets or cavities led to an impoverishment in biodiversity (Müller, Bußler et al. 2007, Müller, Hothorn et al. 2007, Müller and Bussler 2008).

Recent management

The forest management was reformed in 2005 when the Bavarian state forest company was founded. The Bavarian state forest company increasingly promotes permanent forest cover and selective logging with a high tree species diversity, using indigenous tree species, in particular beech (*Fagus sylvatica*), pine (*Pinus sylvestris*), spruce (*Picea abies*) and oak (*Quercus petraea*).

Nature conservation strategy

In 2006, additionally a ‘nature conservation strategy’ was introduced in the forestry department Ebrach (Bayerische Staatsforsten 2016b). In addition to the creation of small protected areas, a key element of this strategy is to enrich structural diversity of the managed forests, by:

(1) Increasing deadwood amounts in forests with target values of 20 m^3ha^{-1} in broadleaf stands older than 100 years, and 40 m^3ha^{-1} in broadleaf stands older than 140 years. Stands above 180 years are under special protection to conserve existing stand structures. In practice, deadwood enrichment is realised by active creation of deadwood during harvest operations, by leaving crowns and parts of the stem in the forest and by passive retention of naturally developed deadwood (Appendix B, Figure B1). The intended deadwood profile consists of 50 percent logs (diameter threshold 20 cm) and branches, 38 percent snags and 12 percent stumps.

(2) The strategy also includes the retention of 10 ‘habitat trees’ per hectare, i.e. trees providing microhabitats (e.g. cavities, bark damage, fungal fruiting bodies) which are important habitats for a number of forest animals (Kraus, Bütler et al. 2016). These trees are marked during forest inspections and spared during thinning and harvest operations.

2.2 Data

For the evaluation of the integrative nature conservation strategy we aimed at comparing deadwood amounts and drivers of deadwood amounts as well as biodiversity before and after the implementation of the integrative nature conservation strategy. Therefore, we collected repeated data from before and after the implementation on exactly relocatable plots and included deadwood amounts, local composition of stand structure, information on management and biodiversity.

To obtain all these data, we used two different datasets. The first one is derived from the regular forest inventory implemented by the Bavarian state forest company, which comprise repeated inventories of the living stand and deadwood amounts on a regular grid in the state forestry. The second dataset is a deadwood and biodiversity inventory that was realised by Müller (2005) and repeated in the framework of this study.

The data from the first dataset, derived from the regular forest inventory, are here termed as ‘regular inventory’. From this regular inventory, we used data from the deadwood inventory, and data from the living stand inventory in the chapter A) of the manuscript.

The data from the second dataset, derived from the inventory by Müller (2005) and in the framework of this study are termed as ‘additional inventory’. From this additional inventory, we used data from the deadwood inventory in the chapter A) of the manuscript, data from the biodiversity inventory for the chapter B) and both, deadwood and biodiversity data, for the chapters C) and D).

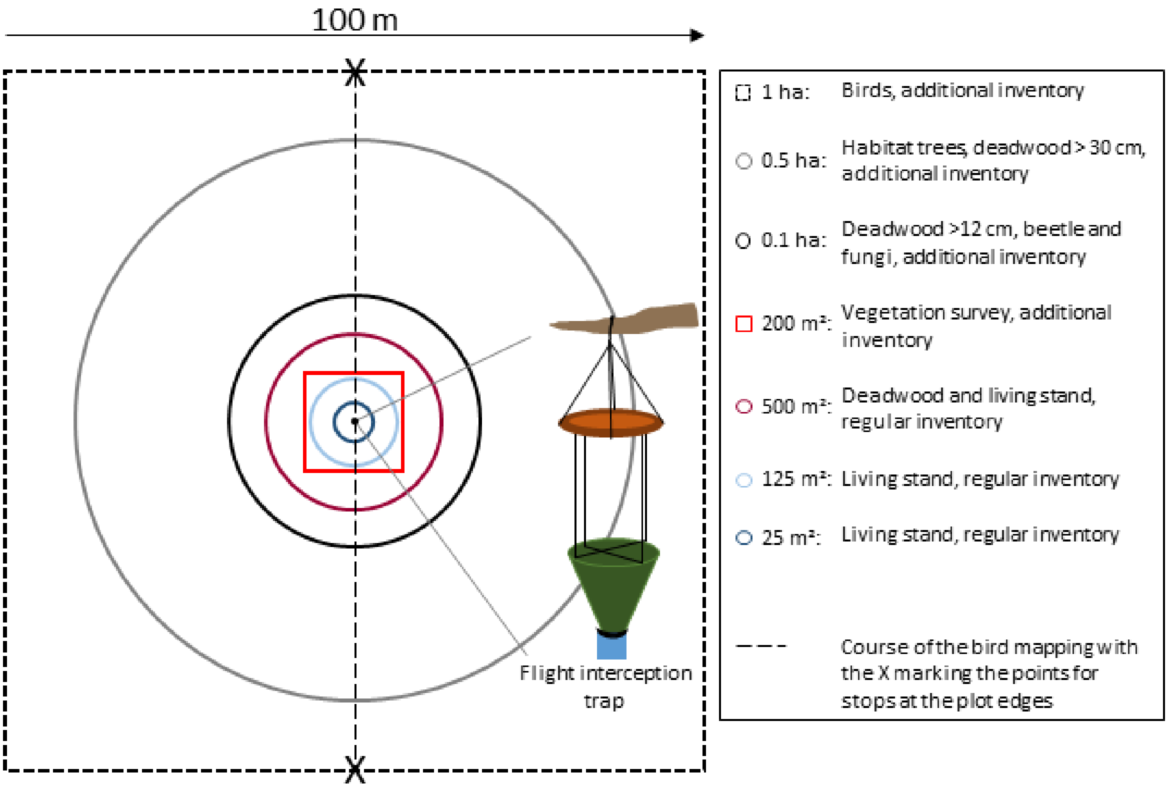


Figure 2: design of the sampling plots ranging from 1 ha plot for birds in the additional inventory to a 25 m² plot for the assessment of small diameter trees in the regular inventory. The inset depicts a schematic drawing of a flight interception trap. Further descriptions to plot sizes can be found in the text.

2.2.1 Regular forest inventory

The main dataset for the analysis of deadwood amounts and their drivers is taken from the database of the regular forest inventory. The regular forest inventory includes all state forests in Bavaria and thus also the forestry department Ebrach. The inventories of the regular forest inventory are conducted about every ten years. In the department Ebrach, the last two inventories, which were used in this study, were conducted in 1997 and 2010, i.e. eight years before the implementation of the strategy, and four years after the implementation of the strategy. Both inventories (1997 and 2010) included detailed records of the living stand and deadwood amounts.

Plots

The inventory in 1997 originally included 2,579 plots and was conducted only in the south of the Steigerwald. The inventory in 2010 covered 4,532 plots in the entire Steigerwald area. For this study, we used only plots that were assessed in both years. These were 1,348 plots in total. After verifying the data, we could conduct our analysis with 1,345 plots.

The sample plots in the regular inventory are arranged in a regular grid across the area of the forestry department. The center is a permanently buried magnet, making an exact relocation possible. The grid size is 200 to 200 m in both directions. In forest nature reserve the grid size for both inventories is smaller with a distance of 100 m in both directions (Figure 1). 1,282 plots were located in managed forests and 63 plots in two forest nature reserves. These reserves were established in 1978 with a size of 5 and 10 ha, respectively and were extended to 50 and 92.4 ha, respectively, in 1997/98 (i.e. after the first inventory). The here studied reserves were enlarged shortly after the first inventory in 1997. Therefore, all plots that were designated as forest nature reserves in 2010 were treated as plots in reserves for both datasets.

The inventory takes place in concentric circular sampling plots with graded DBH thresholds for tree assessment with the permanent buried magnet as center. The smallest circle has a size of 25 m² (radius = 2.82 m), the next bigger circle has a size of 125 m² (radius = 6.31 m) and the biggest circle has a size of 500 m² (radius = 12.62 m). The DBH threshold in the small circle is 0 cm (it includes therefore rejuvenating trees), in the next bigger circle 11 cm, and in the biggest circle 30 cm. Only trees above the threshold are measured in the particular circle.

Measurements at the sample plot

The measurements at the plot level includes site features, the living stand (termed as: living stand inventory) and deadwood (termed as: deadwood inventory). Only those that are used for this study or for the calculation of variables used in this study are described here.

The site features that are registered when a permanent plot is set up are slope (measured in degree) and the location within a nature forest reserve or within the production forest.

Living stand inventory

Within the plots of the permanent inventory all trees ≥ 0.2 m height are measured. For trees with a DBH > 11 cm also the azimuth and distance to the center are recorded. This precise location within the permanently marked plot allows assumptions of changes in the dimension of tree specific features e.g. height, DBH and mortality.

Whereas the DBH is measured for each tree individually, the height is measured for one tree in a group of trees which is formed by tree species, stratum and diameter class (Appendix C, Table

C1). Trees with broken crowns are not used for height measurements. For permanent sample plots, as in our inventory, the trees that were used for the height measurement in the inventory before are used if possible.

The stratum per tree is also recorded in classes. These are: top layer (trees which reach at least 2/3 of the stand height at the plot), second layer (trees which reach maximal 2/3 of the stand height and are above 5 m height) and regeneration layer (trees ≤ 5 m height if the stand height is distinctly above 5 m). Single trees which are older than the stand because they were left during shelter wood cutting and cannot be classified into a distinct layer are classified extra. If a plot has only trees in the top layer it is classified as unstratified. If a plot has only trees ≤ 5 m height these are not classified as either second or regeneration layer but as top layer or unstratified.

The age of the single trees in all layers and for all sizes is determined by counting branches, counting growth rings at stumps or drillings during the first inventory and then updated in the following.

The regular inventory allows an assessment of mortality by different agents. Trees with a DBH > 11 cm that were measured in the inventory before but do not exist in the actual inventory are uphold in the data table of the actual inventory. During the recent inventory, the cause for death is examined and classified into: standing or lying dead or harvested.

Deadwood inventory

In the forestry department Ebrach the regular inventory was extended in the 1990s to also include a deadwood assessment. Deadwood is recorded on the 500 m² plot of the living stand inventory (radius = 12.62 m). Recorded are deadwood objects ≥ 20 cm diameter and ≥ 1.3 m height or length, that are evidently not designated for use. The objects are categorized into lying deadwood (logs), broken standing trees (broken snags) and complete standing dead trees (snags). If objects cross the border of the plot, only the parts within the circle are recorded, provided that they fulfill the above-mentioned size criteria. If the upper part of a broken stem is still connected to the standing part these are measured as logs and broken snag. The diameter of logs is measured at 1.3 m from the thicker end. The diameter for snags and broken snags is measured at DBH. The height of snags and broken snags and the length of logs is measured. All deadwood objects are categorized into 3 decay classes. 1: not decayed, bark still attached, 2: slightly until heavily decayed, bark resolving till gone, branches more or less broken, 3: heavily decayed, stem breaks when stepped on or easy to knock over for snags. The following groups of tree species are distinguished: coniferous wood, oak, other broadleaf tree species, not determinable (the last category only in the inventory in 2010).

2.2.2 Additional forest inventory

The *additional inventory* was used in this study to assess habitat quality in more detail compared to the regular forestry and for the evaluation of the effects of deadwood enrichment on biodiversity. The plots are based on the grid of the forest inventory in 1997 and were originally selected by Müller (2005), who compared the forest structure of beech stands along a stand age gradient.

Plots

The dataset in 2014 included 263 plots, whereas in the study of Müller (2005) only 258 plots were included because not all plots matched the previous selection criteria. However, since the aim of this study was to compare deadwood amounts throughout the whole department and not in relation to age classes we included all originally selected plots to increase the sample size.

For the assessment of biodiversity 68 plots, evenly distributed on the original age classes of the 263 plots of the *additional inventory*, were selected.

The plots of the additional inventory were placed in the North and the South of the department Ebrach, whereas the regular inventory was conducted only in the South (Figure 1).

The plots of the additional inventory were located on the grid of the regular forest inventory in 1997. Therefore, we were able to relocate the plots using the magnet in the centre.

The dataset of the additional inventory included 214 production forest and 49 in three forest nature reserves (Figure 1). The reserves include the two reserves represented in the regular inventory and additionally one reserve in the northern Steigerwald. This northern reserve was established in 1995 with 5.4 ha and extended to 53.7 ha in 2010.

The subset of 68 plots included 44 plots that were located in managed areas and 24 in forest nature reserves, including all three reserves represented in the complete additional inventory (Figure 1). In the reserves in the south we examine 8 and 12 plots and 4 plots in the northern reserve.

With 0.1 ha (1,000 m^2, radius = 17.84 m), the plot size in the additional inventory was larger than in the regular forest inventory. Snags and 'habitat trees' were assessed within an extended circle of 0.5 ha (40 m radius, Table 1). The plots for the measurements of biodiversity were partly smaller and bigger than the plots for the deadwood assessment, also centred at the magnet for all biodiversity assessments (Figure 2). The plot sizes differed, depending on the methodological standard for each taxonomic group, which are described further down below in the specific paragraphs for the sampling of the different taxonomic groups.

Table 1: Overview of the structures recorded on 'habitat trees' in the additional inventory, along with plot size on which the structures were recorded, whether they were recorded on living or dead trees and the reference in Kraus, Bütler et al. (2016).

Structure	Description	Code in Kraus, Bütler et al. (2016)	Plot size (ha)	Record tree
Fungi bracket	Perennial fungi that use the trees as substrate	EP 12	0.1	Only on living trees
Stem rot	Moist holes and rotting wood	IN 31-32		
Large woodpecker hole, i.e. black woodpecker	Woodpecker cavities > 54 mm	CV 13	0.5	Living and dead trees
Medium woodpecker hole, i.e. great spotted woodpecker	Woodpecker cavities ca. 35-53 mm	CV 12		
Similar woodpecker hole, i.e. lesser spotted woodpecker	Woodpecker cavities < 34 mm	CV 11		
Natural cavities	Cavities that can be used as nesting holes but show no marks of bird activity. They originate from e.g. rotten or broken branches	CV 31/32		
Nesting boxes	Anthropogenic nesting holes	None		
Mould-filled cavities	Cavities filled with mould, with or without connection to the soil	CV 21/22 and 23/24		

Deadwood and habitat tree assessment

The deadwood inventory was conducted as in the regular inventory, with the following deviations: in addition to logs, snags, and broken snags we measured stumps resulting from harvest and natural developed stumps, complete lying dead trees, root plates and branches. Additionally, in 2014, we noted whether deadwood logs originated from stems/branches or tree crowns to derive information on the management and retention of tree crowns in forests. The minimum diameter for the measurements was 12 cm. The diameter of logs, crowns and stumps (< 1.3 m, naturally developed and resulting from harvest) was measured in the middle, for snags and natural stumps (> 1.3 m height) we measured the DBH. For root plates, we measured the horizontal and vertical diameter in the middle. The amount of piled and scattered fine woody debris (FWD, diameter < 12 cm) was recorded as the percentage cover on the 0.1 ha plots. In 2004 the height of complete standing dead trees was calculated with the Pettersson curve (Appendix D). In 2014 the height was measured using an ultrasonic rangefinder (Vertex IV, Haglöf). The decay stages in the additional inventory were assessed as in Albrecht (1990), Müller (2005).

The inventory included the record of microhabitat structures that occurred in snags or living trees and were visible from the ground. We counted the number of habitat trees with saproxylic microhabitats within the extended circle of 0.5 ha (40 m radius) (Table 1). Only structures that are most likely to find and included both saproxylic and epixylic microhabitats were selected

(Table 1). Additionally, we recorded nesting boxes. We describe the microhabitats here following the approach of (Kraus, Bütler et al. 2016) and added additional characteristics. We recorded 'habitat trees' with cavities of woodpeckers (CV11-13), trunk and mould filled cavities (CV21/22, CV 23/24, CV 31/32: not separated by size), injuries and wounds when the wood was rotten (IN 31/32) and perennial polypores (EP12) (Table 1).

2.2.3 Species records

We examined five taxonomic groups in 2004 and 2014. We ensured that, when the people recording species were different within or between the years, the methods were the same to make the data comparable between the years.

Beetles

Beetles were sampled by combining two methods. We used flight-interception traps to sample flying individuals. Traps consisted of two transparent plastic windows (40 cm x 60 cm) with a funnel and a jar filled with copper sulphate attached to the bottom, and a roof attached to the top (Figure 2). The traps were installed in the centre of each plot at 1.5 m height using a rope that was hung over large off-standing branches of trees, between two trees or if the stand was too open on a wood construction. The traps were operated from March to October. Sampling vials were replaced once a month. Trapping was supplemented by time-standardised (45 min per plot) hand-collection by the same expert in both years (Heinz Bußler), with a special focus on deadwood habitats to represent also less mobile species. The sampling was conducted three times per year in both years, in spring (April/June), summer (July/August) and autumn (September). On the 1000 m² circular plot that was also used for the deadwood inventory in the additional inventory. For analysis of beetle species sampled with both methods were joined in one dataset. We identified all specimen to species level in 2014 (Ludger Schmidt, Johannes Bail). All beetle families that were not identified to species level in 2004 were excluded from the analysis. The final beetle data set included all saproxylics (Schmidl and Bußler 2004), in total 52 families and the non-saproxylic families Curculionidae, Chrysomelidae and Elateridae (Appendix E, Table E1) (provided by Nicolas Roth).

Fungi

Fungi were assessed by two different experts in the two years on circular plots covering an area of 1,000 m², simultaneously to the expert sampling of beetles, i.e. three times per year. We used a time-standardised method with 45 min spent within the plot area. During this time, the expert examined the ground and deadwood objects (Markus Blaschke, Heinz Engel). Only deadwood fungi that could be determined in the field without microscopic analysis (macroscopic) were recorded. Since different experts examined the fungi in the two years we separated the fungi into three classes to ensure their comparability (provided by Markus Blaschke). The three classes were: 1) Irregularly fructifying, very rare, or very small and therefore easy to overlook (total 310 species) 2) Usually regularly fructifying, easily determinable, sufficiently frequently found and sufficiently large fruit bodies, which should regularly be found again, but mostly with a certain seasonal effect (total 117 species), 3) Mostly long-lasting or long-standing, easily determinable species (total 18 species). For the analysis, we included only species that were in group 2 and 3 and therefore comparable between the years.

Birds

Birds were recorded within a 10,000 m² square at five times in regular intervals (5-8 days) between March and June, using point-stop grid sampling. The surveyor recorded for a fixed time of 7 min, passing the grid along a central line (Figure 2) mapping also during the walk. To record undisturbed activities the mapper spent 1 min at each edge and about 5 min in the centre. All birds that could be seen (also using binoculars) or heard in the plot were recorded. In cases of vague calls, the surveyor used tape lures with a low volume to exclude attraction. The abilities of surveyors were tested in predecessor projects. The mapping was conducted during the morning (from dawn, i.e. between 6.00/7.00 am, until 11 am) and in the evening (5 until 7 pm), and only on days without rain or wind. Several people were employed in the records (Rico Michaelis, Niclas Böhm, Jörg Müller, Volker Zahner, Christine Franz), to account for differences between surveys the order of grid fields was changed.

Plants

Plants were mapped on a 200 m² square (Inken Doerfler, Holger Hastreiter, Michael Seuß). To avoid errors due to different people conducting the mapping we classified the cover of single species according to Braun-Blanquet (Wikum and Shanholtzer 1978). This scale gives only rough estimates for high covers but fine scale estimates for low covers avoiding therefore an overestimation of high covers. We only used species of the herb layer (< 1.5 m height) for this analysis. Two surveys were conducted, one in April and one in June.

True bugs

True bugs were sampled in flight interception traps simultaneously to beetles and determined by the same expert in both years (Martin Gossner) We were not able to complete the sampling with an expert searching for saproxylic species as for the beetles.

Separation into saproxylics and non-saproxylics

We separated the taxonomic groups into subgroups depending on their deadwood dependency, i.e. species living in deadwood and species which are independent from that resource (saproxylic, non-saproxylic). We used the definition of Stokland, Siitonen et al. (2012): "*any species that depends, during some part of its life cycle, upon wounded or decaying woody* *material from living, weakened or dead trees*". Therefore, cavity breeding birds, all fungi living on deadwood and beetle species listed as saproxylic in Schmidl and Bußler (2004) were considered as saproxylic. All plants, soil-saprotrophic fungi and mycorrhiza fungi, non-cavity breeding birds and phytophagous beetles were considered as non-saproxylics in the analysis. Among the sampled true bugs only the genus *Aradus* can be considered saproxylic (Gossner, Engel et al. 2007, Heiss and Péricart 2007). Species of this genus were included in the analysis of the total species number, but not analyzed separately as saproxylics because of only few detections (six individuals of two species in the entire inventory).

2.3 Statistics

2.3.1 General statistics

All statistical analyses were conducted in R (R CoreTeam 2015). For pairwise comparison of plot-wise data between years, e.g. deadwood amounts or species numbers we tested the distribution of the data by graphical examining and the Shapiro-Wilk Test. For normal distributed data, we used a Student's t-test for paired samples, for non-normal data distribution we used the nonparametric paired Wilcoxon Signed-Rank Test, for binomial data we used the McNemar's chi-squared test. For comparisons within years, e.g. between plots within production forests and reserves we used a linear model with the different categories of plots as factor. Results are given as the test statistic (pairwise tests: t, V or Chi^2; linear model: t) and the p-value (p). We used a significance level of 0.05.

2.3.2 Chapter A) Evaluation of the changes in deadwood amounts and their drivers

To assess amounts of deadwood and their drivers we used the data from the regular inventory including the deadwood and the living stand inventory and the additional deadwood inventory.

Extrapolation to plot level and variable calculation

All measures from the deadwood assessments in the regular and additional inventory were standardized to an area of one hectare. Therefore, all values were multiplied with the factors 400 (25 m^2 circle), 80 (125 m^2) and 20 (500 m^2) to account for the graded sample plot sizes in the assessment of the living stand. For the data from the deadwood inventory the values were multiplied with 20 (500 m^2) in the regular inventory and with 10 (1,000 m^2 circle) in the additional inventory.

For statistical analysis, we used different values derived from the measurements from the living stand inventory at the plot level. This included the *basal area* g (in m^2) and the *volume* of trees V (in m^3). The equations how these values are calculated by the Bavarian State Forest Company are given in Appendix C. With these two calculated variables and the further data assessed at the plot level we calculated twelve variables which were used to calculate models to determine drivers of deadwood amounts (Table 2).

Models to identify the main drivers of deadwood amounts and deadwood enrichment

To analyse which variables affected the amount of deadwood in the forests, we had the challenges that a) there was a large number of potentially important predictor variables, yet the total sample size was limited, and b) that the data were potentially spatially auto-correlated. Thus, a simple multiple regression model to identify the factors that influenced deadwood amounts may be inappropriate, unreliable or even biased. We thus used a technique called component-wise gradient boosting (Hofner, Mayr et al. 2014), implemented in the R-package mboost (Hothorn, Bühlmann et al. 2010, Hothorn, Buehlmann et al. 2015) (Appendix F).

In boosting, one defines simple regression models for each of the explanatory variables, so called base-learners. In our model, categorical variables (e.g. *forest nature reserve*) were defined as categorical effects. Continuous variables (e.g. *stand age*) were defined as smooth effects. The smooth base-learner uses penalized B-splines (Eilers and Marx 1996, Schmid and Hothorn 2008) to fit smooth, non-linear curves. A radial basis function of the plot location was used to account for spatial autocorrelation (Hofner 2011). This function interpolates values by estimating a weighted average of the measured values in the surrounding area of the point as in Kriging (Oliver and Webster 1990) and hence can interpolate the measured data on a continuous map. Here, we used low-rank Kriging (Nychka and Saltzman 1998, Kammann and Wand 2003). For model optimization, we defined the loss function as the squared error of the Gaussian model (Appendix F).

We calculated three models to explain deadwood amount in 1997, the amount in 2010, as well as temporal changes in deadwood. For these models, we used the data from the regular inventory only, to have a sufficient number of observations. The response variables in the three models were:

Model 1 (Deadwood 1997): the log-transformed deadwood amount in 1997, before the implementation of the strategy,

Model 2 (Deadwood 2010): the log-transformed deadwood amount in 2010, after the implementation of the strategy,

Model 3 (Deadwood enrichment): the relative change in deadwood amounts between 1997 and 2010, which we accounted for by using the log-transformed deadwood amount in 2010 as outcome and appointing the log-transformed deadwood amount in 1997 as offset variable.

The candidate set of explanatory variables was chosen from the data of the forest inventory for their ecological and sylvicultural relevance which can be assigned to stand type or management (Table 2). Each model had the similar set of predictor variables (Table 2) with the model 1 including values from 1997 and model 2 and 3 values from 2010. The final set of variables presented in the results is the one chosen via the boosting approach. Finally, we computed 95 percent bootstrap confidence intervals for the effects in all three models (Hofner, Kneib et al. 2016).

Assessment of deadwood profile

We used the data of the additional inventory to evaluate deadwood qualities, and analysed the deadwood profile in both years as proposed by Stokland (2001). For the analysis of the deadwood profile we included the comparable characteristics of deadwood objects, i.e. the decay stage, aggregated to fresh and decayed deadwood objects, the object type (snags, logs and stumps) and size of the object (larger and smaller than 30 cm diameter). The type of tree species was omitted because of an extra category of ‘unknown’ tree species in 2014 making the absolute amount of deadwood between the years difficult to compare. The deadwood volume of different tree species was therefore analysed separately.

2.3.3 Chapter B) Description of biodiversity before and after the implementation of the strategy

To evaluate changes in biodiversity before and after the implementation we compared absolute species numbers and abundances per year. Since, the abundances are measured for most of the examined groups in different ways we report the results for each group separately. We compared how many species per group were present in both years and how many were occurring only within one year. To assess how the distribution of abundances changed we looked at singletons - species occurring only once per sample period, and common species per year. To test if the changes in biodiversity were significant between the years we calculated rarefaction-extrapolation curves as proposed in (Chao, Gotelli et al. 2014) and additionally used pairwise comparison of species numbers per plot. For the assessment of management effects, we compared species numbers in forest reserves and production within the respective years.

Calculating Multidiversity

The major goal was to evaluate effects of integrative forest management on overall biodiversity. We therefore calculated an index of multidiversity (Allan, Bossdorf et al. 2014) (function ‘multidiv’) that combines the species richness (total number of species identified per plot) of all studied taxonomic groups. We calculated the average proportional species richness over all of the examined groups. This was done by scaling the species richness per group to the maximum value found per study year across plots (‘sc = max’). By using this approach, the function divides the species number per taxonomic group, found at each plot in the single years separately, by the maximum species number of the individual taxonomic group found in the total sampling. We used the function without thresholds (‘threshold = FALSE’) which calculates the mean of the scaled species numbers of the five taxonomic groups. The function enables the comparison between taxonomic groups with different total species numbers such as birds and fungi. In our approach, all groups were weighted equally ("weights" = 1). In addition, we calculated multidiversity of saproxylic and non-saproxylic species separately.

2.3.4 Chapter C) Relation between changes in biodiversity and deadwood enrichment

To test effects of changes in deadwood amount and canopy cover on overall multidiversity, multidiversity of saproxylic and non-saproxylics, and species numbers of each taxonomic group, we calculated generalized linear models (glm, package stats). We used a gaussian error term distribution for multidiversity. For the analysis of species numbers of the single taxonomic groups we used poisson error term. If the deviance was > 1.5 times than the degrees of freedom, i.e. overdispersion we used the quasipoisson error term. As predictor variables, we used the 1) log-transformed ratio of deadwood change (log scaled amount 2014 divided by the log scaled amount 2004). Due to this transformation, small changes in deadwood amounts are weighted stronger than when using the actual difference of deadwood amount, reflecting the flattening increase of diversity with large amounts of deadwood. 2) The difference in canopy cover between the years. The data of canopy cover for both years were derived from the vegetation sampling (Methods: 2.2.3). We calculated the difference between the cover in both years and used this value without transformation since this is measured as a percentage. 3) The log-transformed ratio of the change in the number of cavity bearing trees (log scaled number 2014 divided by the log scaled number 2004) to account for the count data. Cavity bearing trees included trees with woodpecker cavities, natural and mould filled cavities since these are the most important structures which are priorities by the strategy and are comparatively assessable. We ensured beforehand that these variables were not correlated (Appendix G, Table G1). To account for the fact that diversity of 2004 may influence the biodiversity change from 2004 to 2014, we used multidiversity or the log-transformed number of species before the implementation of the strategy as offset variables. A constant value of one was added to each value before log-transformation. The standard model for analysis was therefore:

$$\begin{gathered}\text{(Multi-)Diversity 2014} \sim \\ (\log(\text{deadwood volume 2014}) / \log(\text{deadwood volume 2004})) \\ + (\log(\text{number of cavity bearing trees 2014}) - \log(\text{number of cavity bearing trees 2004})) \\ + (\text{canopy openness 2014} - \text{canopy openness 2004}), \\ \text{offset=(Multi-)Diversity 2004}\end{gathered}$$

To account for the fact, that the integrative strategy might have different outcomes for areas with different management in the past (e.g. nature forest reserves: no harvest, production forests: with harvest) we tested the differences of biodiversity in nature forest reserves and production forests (Appendix H). Additionally, we calculated the previous mentioned models using an interaction between the two predictors (log ratio deadwood and change in canopy cover) and the reserve vs. production forest (Appendix H, Table H1). Since these models only serve for the exploration of the effect of active enrichment, but do not have a sufficient sample size we report here the relationships between biodiversity and the predictor variables of all plots to describe the effects of the implementation of the strategy in total.

2.3.5 Chapter D) Relationship of assembly mechanisms and deadwood enrichment

Functional-phylogenetic distance measure

The analysis of assembly pattern is proven to give a better insight into changes in the species communities that cannot be seen if only species richness is analyzed (Bässler, Ernst et al. 2014). To assess species ecological differences and similarities two major approaches are usually used to summarize the degree to which the single species differ in terms of their function, niche or evolutionary history. The first one is the phylogenetic approach that assesses the amount of evolutionary divergence. This approach assumes that the ecological differences between species are proportional to the amount of time since they diverged from a common ancestor. Therefore, more divergent species are more likely to become ecologically different (Cadotte, Albert et al. 2013). To describe this, a Brownian motion model of evolution is used that assumes that rates of trait evolution occur homogenously across the tree. However, ecological differences can also be distributed heterogeneously within a tree, when either ecological differences in sympatric species (species diverging without spatial isolation) rapidly increase or when distantly related lineages converge on similar traits or strategies (homoplasy - similar, corresponding traits without phylogenetic continuity). This approach relies therefore strongly on the correctness of the evolutionary model which is a hypothesis made on a suite of methodological assumptions and choices and cannot be tested to be correct (Cadotte, Albert et al. 2013). Therefore, the second common method uses a functional (-trait based) approach. In this approach, ecologically differences are estimated as distances between species' traits. In the case that the traits explain ecological patterns similarly to the phylogeny it is sensible to use the traits directly since they allow assumptions about potential candidate mechanisms (Cadotte, Cavender-Bares et al. 2009). However, this approach relies strongly on the selected traits. Due to lacking data of traits or the application of either unimportant traits or the exclusion of important traits this approach might not explain the pattern of community assembly appropriately (Cadotte, Albert et al. 2013).

Cadotte, Albert et al. (2013) proposed an approach that overcomes the difficulties of both approaches by considering both sources of information complementary. This approach takes both, the convergence and divergence of traits for the phylogenetic distances into account and the information from unmeasured, phylogenetically correlated traits for the functional distance. It does this by combining the phylogenetic distance of the phylogeny and the functional distance of the trait ordination into a new traitagram of a functional-phylogenetic distance (FPDist):

$$FPDist = (a\ PDist^{p} + (1-a)\ FDist^{p})^{1/p}$$

Whereas FDist ist the functional distance, PDist ist the phylogenetic distance, p determines the distance matrix used for FDist and PDist and a is a value between 0 and 1 determining the strength of the weighting of FDist or PDist. An a = 0 means this index takes only FDist into account, an a = 1 means this index takes only PDist into account. A p = 2, as used in this study, calculates an Euclidean distance matrix.

Trait characterization and phylogenetic trees

We acquired phylogenetic trees for saproxylic beetles, birds, fungi and plants. Since we were not able to build a phylogeny for non-saproxylic beetles or true bugs they were omitted from this analysis. Also non-saproxylic fungi were omitted since they contain relatively few species (50) that also belong to different ecological groups (soil saprotrophs and mycorrhiza) which are shown to assemble very differently (Bässler, Ernst et al. 2014). We used ultrametric, e.g. root weighted trees whose tips have the same depth, which therefore cannot be used to make assumptions on rates of evolution but reflect community changes well (Thorn, Bässler et al. 2015). Trees were beforehand checked for polytomies. For birds and beetles, we used published phylogenies (Hackett, Kimball et al. 2008, Seibold, Brandl et al. 2015), for fungi and plants we calculated them in the framework of this study. Therefore, we used plastid and mitochondrial sequences of the studied taxonomic groups that were derived from GenBank using the megaptera package (Heibl 2014). With these sequences, we calculated phylogenetic trees with a maximum likelihood approach (provided by Christoph Heibl).

For the selection of traits we focused on actually measurable traits that can strongly influences organismal performance (McGill, Enquist et al. 2006).

We acquired published data on ecological traits per species that reflect important ecological functions for beetles, birds, fungi and plants (Appendix I Table I1). We omitted those traits that are related only to habitat types and are therefore not distinctly measurable (e.g. preferred tree species of saproxylic beetles and fungi). We tested beforehand for co-linearity between the traits of each taxonomic group using the vifstep function (package usdm), which applies a stepwise variable selection based on variance inflation factors. The obtained traits included numeric and binary traits for all taxonomic groups. Categorical traits with more than two levels were decoded into binary traits. The selected traits included size of the examined species (e.g. size of fungal fruiting bodies, plant height, body size of beetles, and weight of birds). Traits related to dispersal and range of motion (e.g. specification of migratory birds, spore traits of fungi and dispersal mode of plants). Also, traits of life span (e.g. perennial plants, life span of birds), nutrition (e.g. feeding strategy of beetles and diet of birds), reproduction (e.g. clutch size of birds, asexual reproduction for fungi and plants), and on the appearance of the species (e.g. galert consistence of fungi or leaf forms of plants). The final datasets included five traits for beetles, ten for saproxylic fungi, eight for birds, and thirteen for plants (Appendix I, Table I1).

Calculation of distance matrix

To explain prevailing assembly mechanisms, we evaluated the convergence and divergence of traits as proposed by Cadotte, Albert et al. (2013) combining functional and phylogenetic distance matrices. We calculated therefore distances matrices for each taxonomic group. For functional distance, we used the function daisy (package cluster), which computes all pairwise dissimilarities between observations and can handle different types of data. Binary traits derived from categorical traits with more than two levels were assigned for using the function 'weights' within daisy. The phylogenetic distance was calculated using the function cophonetic (package stats) which also calculates a pairwise distance between pairs of tips of the phylogenetic tree.

These two distance matrices per taxonomic group were then combined to a functional-phylogenetic distance matrix using the function FPDist (package funphylocom). We set the p-value to 2, what implies a Euclidean distance for the combined functional-phylogenetic distance matrix (Cadotte, Albert et al. 2013). The weighting parameter (a) for the phylogenetic respective functional distance was set from 0 to 1 in 0.025 steps (total 41 steps), hence including with a = 1 only the phylogenetic distance and with a = 0 only the functional distance. For intermediate values of the a-value both distance matrices contribute to the functional-phylogenetic distance matrix.

With this functional-phylogenetic distance matrix, we calculated a null model to compare the observed pattern of co-occurrence within the four taxonomic groups against the expected levels when species are randomly assembled using the function ses.mpd (package picante) without abundance weighting and with 999 runs. The null model was set to 'taxa.labels', hence shuffling the distance matrix labels and with that randomly selecting species from the regional e.g. recorded species pool. The thus calculated null model provides a standardized effect size, representing the differences between observed mean similarities and expected similarities of 999 randomly selected, artificial assemblages. If the resulting standardized effect size is > 0 it indicates a trend towards overdispersed assemblies (species become more different than expected e.g. by adaptation to niches or competition), if the standardized effect size is < 0 it indicates a trend towards clustered assemblies (species become more similar than expected e.g. by environmental filtering).

Data analysis

To test the effect of deadwood enrichment on the standardized effect sizes of the mean functional-phylogenetic pairwise distance (ses mpd) we used linear models with the ses mpd in 2014 as dependent variable. The predictor variables were: 1) the log response ratio of deadwood (log (deadwood amount 2014) / log (deadwood amount 2004)), 2) the difference in tree cover (cover 2014 – cover 2004) and 3) the ses mpd in 2004. We calculated this model for all the functional-phylogenetic distance matrix with the 41 a-values (0-1) to find if unused traits were 'hidden' in the phylogeny. The model with the highest adjusted R^2 was selected as best model (Cadotte, Albert et al. 2013) and presented here. To test whether deadwood amount or diversity was the main driver of species assemblies we tested models with both variables. The deadwood diversity was calculated with the same characteristics used for the deadwood profile and deadwood objects with different combinations of these characteristics per plot were counted.

Description of traits

Additionally, to the assembly mechanism we looked at the traits that were used for the calculation of the assembly to see if they have a significant phylogenetic signal and if their weighted mean is related to deadwood enrichment.

Calculating the phylogenetic signal

Closely related species are assumed to be ecologically more similar, with similar niche dimensions and therefore similar traits. To see if the traits we used are phylogenetic patterned, i.e. conserved we calculated the phylogenetic signal. The phylogenetic signal measures if related species resemble each other more than they resemble species drawn randomly from a phylogenetic tree. A strong phylogenetic signal shows that close related species share similar traits and more distant related species are less similar.

For binary data, we used the function phylo.d (package: caper). This function calculates a D-value which gives a measure for phylogenetic signal strength. To calculate D the differences between each pair of sister clades, i.e. the closest relatives, are summed across the whole tree. This gives the sums of sister-clade differences and subsequently the mean of the values at the descendant nodes, i.e. any node in the path from a certain node to the tip node. This value is compared to a D-value developed under a random model and a Brownian motion model. For the calculation of D with a random model, the species-trait values are shuffled along the tips to create a random phylogenetic pattern. We used 1000 permutations for this randomization model. A Brownian motion model, describes the changes in a trait due to mutations and genetic drift by an undirected random movement. It assumes a trait change in which traits diverge independently over time analogous to a random walk. A random walk, in this case, means that a mean trait of an ancestor can develop in each direction with equal probability. In the Brownian model, it is additionally specified that changes from one time to the next are randomly drawn from a normal distribution with a mean of zero and a variance of $\sigma^2 * \Delta t$ (σ^2 = constant rate of change, Δt= change in time). Therefore, the variance, expected under this model increases linearly over time, with a rate of σ^2. It is used to transform the tip data of a tree into values that are statistically independent and normal distributed. With the Brownian motion model, a continuous trait is evolved along the phylogeny. This continuous trait is converted into a binary trait using a threshold approach. The final D-value is the observed D-value scaled to the means of the two expected distributions (random and Brownian motion).

If the D-value is equal to 1 the observed binary trait has a phylogenetically random distribution. If it becomes higher than 1 the trait is overdispersed.

To calculate the phylogenetic distance for numeric traits we used the function phylosignal (package: picante). This function calculates K statistics for the phylogenetic signal (Blomberg, Garland et al. 2003). This value indicates, as for the D-value for binary data, the strength of the signal relative to a Brownian motion model that assumes an independent divergence of traits over time (analogous to a random walk).

If K is > 1 it represents a Brownian motion model in which species are more similar in their trait values than predicted from the model. A K-value < 1 shows that relatives resemble each other less than expected under the Brownian motion model. This indicates a departure from the Brownian motion evolution, i.e. adaptive evolution (homoplasy).

Calculation of weighted means for single traits

To evaluate how single traits change with deadwood enrichment, we calculated the weighted mean for all traits used in the assembly analysis. We used the function weighted.mean (package stats). We then calculated a linear model with the weighted mean of a single trait in 2014 as dependent variable. To make this analysis comparable to the analysis of the assembly mechanisms we used the same predictor variables for the model which are: the log response ratio of deadwood, the difference in tree cover and in this case the weighted mean of the trait in 2004.

3. Results

3.1 Chapter A) Evaluation of the changes in deadwood amounts and their drivers

In the following paragraph, the results for the deadwood amounts from the regular and the additional inventory are reported complementary. For the analysis of drivers only the regular inventory was used, because of a higher number of plots. The regular inventory included also detailed data on stand structure and a well-documented management history. The additional inventory was used for the analysis of the deadwood profile, since it included many types of deadwood objects, a specific definition of their quality (e.g. tree species, decay stage) and deadwood objects were recorded on a larger area compared to the regular inventory. The following paragraphs concerning the deadwood amounts and drivers are slightly modified from Doerfler, Müller et al. (2017).

3.1.1 Description of deadwood amounts before and after the implementation of the deadwood enrichment strategy

In both examined datasets the deadwood amounts increased significantly by 55 percent in the regular inventory ($V = 137150$, p-value < 0.0001), assessing the amount four years after the implementation and 176 percent in the additional inventory ($V = 4851$, p-value < 0.0001), assessing the amount eight years after the implementation. In the regular inventory before the implementation of the strategy (1997) the deadwood amount was 8.7 ± 0.5 m^3 ha^{-1} (range: 0 - 160 m^3 ha^{-1}). Four years after the implementation (2010) the deadwood amount was 13.5 ± 0.6 m^3 ha^{-1} (range: 0–225.1 m^3 ha^{-1}). In the additional inventory before the implementation (2004) the deadwood amount was 24.6 ± 2 m^3 ha^{-1} (range: 0.2–235.5 m^3 ha^{-1}). Eight years after the implementation (2014) the amount was 67.9 ± 11.3 m^3 ha^{-1} (range: 0.9–2772 m^3 ha^{-1}) (Doerfler, Müller et al. 2017) (Appendix J, Figure J1).

3.1.2 Deadwood amounts in different areas

The deadwood amounts and their development were different for plots within production forests and nature forest reserves considered separately. The amounts in both, the regular and the additional inventory, were higher in reserves (Figure 3, Appendix J). However, the increase of the deadwood amount was stronger in the production forests for the regular inventory. In the plots in production forests we found an increase of 61 percent ($N = 1282$) in the regular inventory and an increase of 160 percent in the additional inventory ($N = 44$) (Appendix J). The deadwood amounts in reserves increase not significantly by 18 percent in the regular inventory ($N = 63$) and significantly by 201 percent in the additional inventory ($N = 24$) (Appendix J).

Within the regular inventory, we were able to assess very detailed data on the management history in production forests. This revealed a significant higher increase of deadwood on plots with management activity between 1997 and 2010. Plots with management between 1997 and

2010 (N = 922) showed an increase of 73 percent from 7.6 ± 0.5 m³ ha^{-1} to 13.2 ± 0.7 m³ ha^{-1} (range: 0–163.1; V = 63923, $p < 0.0001$). Plots without management (N = 360) showed a marginal significant increase of 34 percent from 9.1 ± 1m³ ha^{-1} (range: 0–144.7) to 12.2 ± 1.2 m³ ha^{-1} (range: 0–149.4; V = 8895, p-value = 0.0647).

The goal of deadwood enrichment within different age classes in beech dominated stands was only partly realised. The separate analysis of beech dominated plots with the mean stand age of the top layer in the regular inventory revealed that deadwood enrichment was realised in all age classes, except in class > 180 years, where the number of plots (N = 23) was too small to test the difference between the years. However, the specific goals of 20 and 40 m³ ha^{-1} in stands older than 100 years and older than 140 years were only realised partly (Figure 3). 14 percent of the plots between 100 and 140 years (N = 319) met the goal of amounts between 20 m³ ha^{-1} and 40 m³ ha^{-1}. However, 9 percent of the plots within this age class had already amounts above 40 m³ ha^{-1}. Of the plots above 140 years (N = 227) 6 percent met the goal of 40 m³ ha^{-1}. Additionally, plots without any specific deadwood goal (N = 776) had in 13 percent of the plots amounts above 20 m³ ha^{-1} (Figure 3).

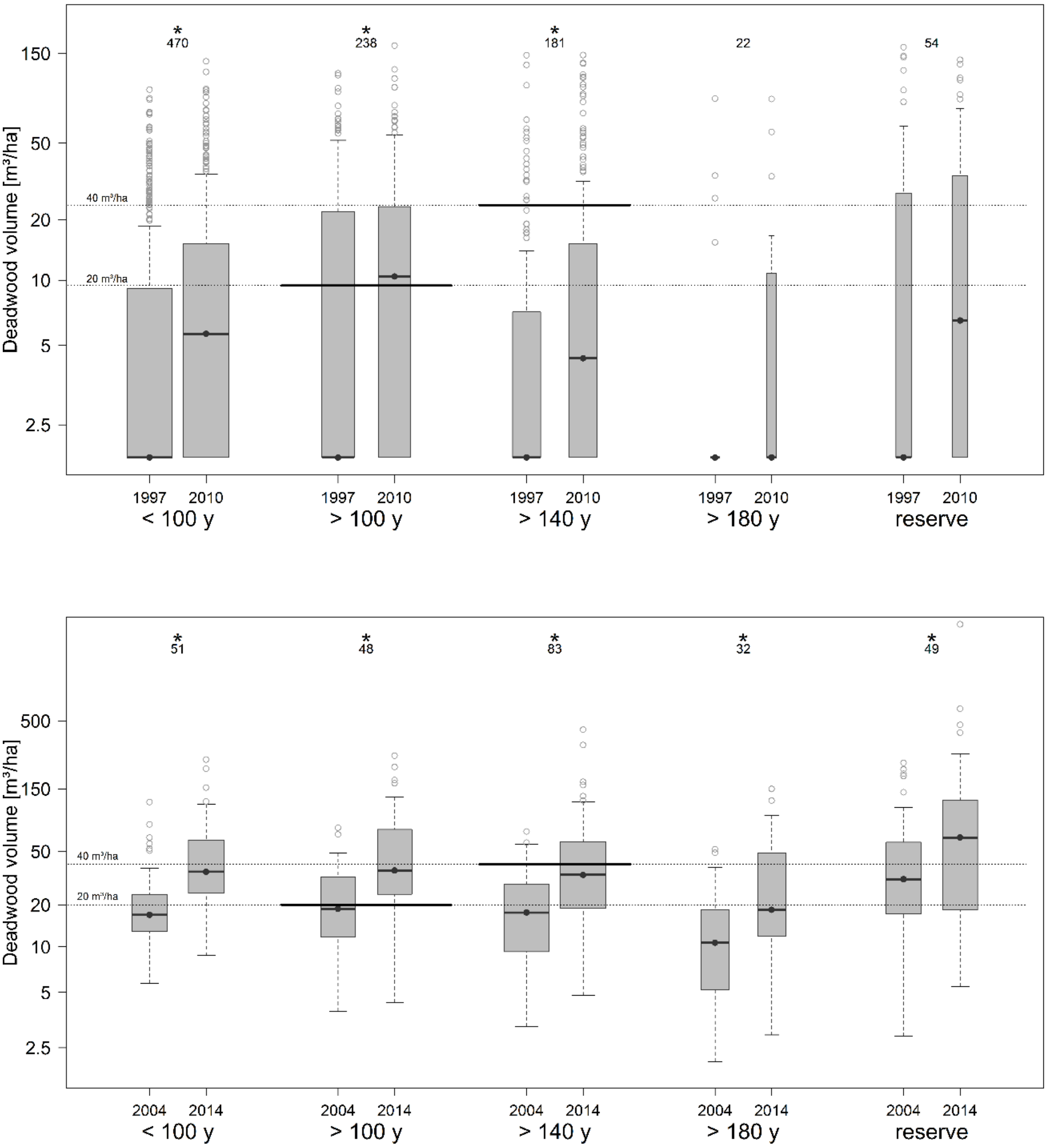


Figure 3: Deadwood amounts in the regular inventory (upper panel) and the additional inventory (lower panel) before (upper panel: 1997, lower panel: 2004) and after (upper panel: 2010, lower panel: 2014) the implementation of the deadwood enrichment strategy, considering the different targets for different age classes in stands dominated by broadleaf tree species (regular inventory: N = 965, additional inventory: N = 263). The deadwood targets are shown as dotted lines and the target for a particular age class is indicated by a thick horizontal line. Median deadwood amounts (Lines with dot in middle) and variation (Box: 25% / 75% percentiles, Whisker: Min. Max values excl. outliers) are given. For stands below 100 years (1997), no deadwood target exists and for stands above 180 years (1997) stable deadwood amounts are targeted. In the regular inventory, the targets are adjusted to the method of the forest inventory, adding the standard volume of deadwood till 5 cm and a standard value for stumps. Significant changes (Wilcoxon Signed-Rank Test, $p < 0.05$) between the years are marked with a star. The width of the boxes and numbers above represents the number of plots within a respective age class. The scale of the y-axis is log transformed. The upper panel is slightly modified from (Doerfler, Müller et al. 2017).

3.1.3 Living stand parameters before and after the implementation of the deadwood enrichment strategy

To assess drivers of deadwood amounts we first looked at characteristics in the living stand and management to detect if these changed between the years (Doerfler, Müller et al. 2017). We found that all characteristics of the stand type and management that we looked at changed after the implementation of the strategy (Table 2). The management was intensified, indicated by a strong increase in the basal area harvested between 1997 and 2010 (i.e. harvesting intensity) (Table 2). The main harvested tree in both years was beech. The harvest was intensified for all four main tree species (beech, spruce, pine and oak) (Appendix K, Table K1). The living stands changed towards a higher abundance of beech and a higher tree mixture (Table 2, Appendix K, Table K2). Despite the high amount of harvest the growing stock increased, including mainly broadleaf trees, and especially beech. Coniferous trees species (pine and spruce) were decreasing (Table 2). In total, we found an increasing diversity of tree species per plot (Table 2). The proportion of the plots in the age classes did not change significantly between 1997 and 2010. The class < 100 years accounted for 56 percent of all plots in 1997 and 58 percent in 2010. Stands > 100 years accounted for 24 percent in 1997 and 20 percent in 2010. Stands > 140 years accounted for 17 percent in 1997 and 18.5 percent in 2010 and stands > 180 years accounted for 2 percent in 1997 and 3.3 percent in 2010. The natural mortality, measured as the basal area of trees dead but not harvested, decreased significantly (Table 2).

Table 2: Overview of the stand type and management variables used in the models, their structure, unit, mean and standard error in both inventory years (1997, 2010). Additionally, results of the Wilcoxon Signed-Rank Test (V) for continuous or count data or the results of the McNemar's chi-squared test (Chi^2) for binomial data testing for differences between years and a description on how variables are calculated are given, slightly modified from (Doerfler, Müller et al. 2017).

	Explanatory variable	Type of variable	Mean ± SE 1997	Mean ± SE 2010	V or Chi^2, p	Description of variable calculation
Stand type:						
Living stand	Number of tree species	count data (1-8)	2.2 ± 0.03	2.4 ± 0.03	63164.5, < 0.0001	Number of tree species in the top layer
	Growing stock	continuous (0-986.7 $m^3 ha^{-1}$)	253.9 ± 3.7	303.2 ± 3.6	20690, < 0.0001	Sum of the volume of all living trees in all layers
	Percentage broadleaf trees	continuous (0-100%)	70.7 ± 1	76.4 ± 0.9	84887, < 0.0001	Percent basal area of broadleaf trees in the top layer
	Presence of spruce	binomial (1,0)	Plots with presence: 307 (23%)	Plots with presence: 272 (20%)	424.08, < 0.0001	Species is present if basal area > 0
	Presence of pine		Plots with presence: 435 (32%)	Plots with presence: 397 (30%)	189.55, < 0.0001	Species is present if basal area > 0
	Stand age	continuous (0-269 years)	90 ± 1.3	92 ± 1.4	201890, < 0.0001	Mean age of all trees in the top layer
	Natural mortality (across 13 years)	continuous (0-56.5 $m^2 ha^{-1}$)	3.5 ± 0.2	0.84 ± 0.06	201850, < 0.0001	Basal area of trees deceased between the inventories naturally or by harvest
Management and site:						
Management	Harvesting intensity (across13 years)	continuous (0-39.2 $m^2 ha^{-1}$)	3.5 ± 0.1	5.4 ± 0.2	209050, < 0.01	
	Forest nature reserve	binomial (1,0)	managed: 1282, reserve: 63			Data from the original data base
	Management district	categorical (1-3)	Number of plots: 1: 481, 2: 467, 3: 397			
Plot	Slope	continuous (0-34°)	7.027 ± 0.14			
	Gauss-Krueger coordinates	continuous				

Drivers of deadwood amounts before and after the implementation of the deadwood enrichment strategy

The final models specifying driving factors for deadwood amounts were complex for the single years and included linear, smooth and spatial effects (Figure 4). The model for the change of deadwood amount was less complex and included only smooth and spatial effects (Figure 4). The variables selected by the boosting approach of all three models characterize both, stand type and management.

Model 1 (deadwood amounts 1997)

In 1997 the stand type variables, natural mortality, and stand age explained most of the variance (Doerfler, Müller et al. 2017). However, also the spatial distribution explained considerable variance. The other six variables which were related to management and other stand type variables, including the tree species composition, explained less variance. We report here the drivers in the order of the size of their effect size, whereas in the figures they are sorted into stand type and management related variables for easier comparison between the models.

Deadwood amounts increased with increasing natural mortality (Figure 4; absolute range of effects: 1.57 log-units) (Appendix L, Table L1). Deadwood amounts were higher in older stands, but only until an age of 120 years. In old stands the confidence interval became very large due to a small number of observations (Figure 4; absolute range of effects: 0.84 log-units). These two stand type variables are explaining most of the variance in this model as shown by the absolute range of the effect estimates. The spatial distribution of plots (Gauss-Krueger coordinates) showed that plots in the North and South of the region had higher deadwood amounts and plots in the North West had lower amounts (Figure 5; absolute range of effects: 0.74 log-units). Besides that, plots on steep slopes and plots located in forest nature reserves had high amounts of deadwood (Figure 4; absolute ranges of effects: 0.46 and 0.31 log-units, respectively). Also, the growing stock determined deadwood amounts with a U-shaped correlation. Deadwood amounts were lowest at intermediate growing stock of about 200 $m^3 ha^{-1}$ (Figure 4; absolute range of effects: 0.14). Deadwood amounts increased also with increasing percentage of broadleaf trees (Figure 4; absolute ranges of effect: 0.1) in the top layer. Also, a high harvesting intensity resulted into higher deadwood amounts (Figure 4; absolute ranges of effects: 0.09). However, for harvesting intensities higher than a moderate intensity of 15 $m^2 ha^{-1}$ the deadwood amounts decreased. This effect is also related to the number of data points in these high intensities which results in a large confidence interval. Deadwood amounts were slightly different in the three management districts (Figure 4; absolute range of effects: 0.02). We could not detect effects of the presence of spruce, the presence of pine or the number of tree species in the model explaining deadwood amounts before the implementation of the strategy (Figure 4).

Model 2 (deadwood amounts 2010)

The deadwood amounts after the implementation of the strategy were partially driven by similar stand and management parameters compared to the deadwood amounts before the implementation, also with a similar order and trend of effect sizes of the variables. The main difference was that the nature forest reserve, management district, and the growing stock were not related to deadwood amounts anymore, whereas the number of tree species and the presence of spruce were identified as drivers. Additionally, the absolute extend of effect sizes of single variables was generally higher in 2010.

Stands with a high natural mortality still had the highest deadwood amounts in 2010. (Figure 4; absolute range of effects: 2.6 log-units; 66 percent higher as in 1997). Also the spatial effect affected the model. The deadwood amounts were still highest in the North and South of the region, but lowest in the West and East (Figure 5; absolute range of effects: 1.07). The higher deadwood amounts in old stands around 120 years were also present in 2010 (Figure 4; absolute range of effects: 0.96). Unlike to the model 1997, when this driver was not important, the deadwood amounts in 2010 were decreasing with an intermediate number of tree species (Figure 4; absolute range of effects: 0.39 log-units). The relationship between deadwood and the number of tree species was U-shaped, showing lowest deadwood amounts in stands with 4 tree species and highest in monocultures or stands with a high tree diversity. The deadwood amounts were still higher on plots with a steep slope (Figure 4; absolute range of effect size: 0.32). The higher deadwood amounts in stands with a higher percentage of broadleaf in the living stand were still present after four years of management with the strategy, with even lower amounts in non-broadleaf stands compared to the time before the implementation of the strategy (Figure 4; absolute range of effect size: 0.29). After the implementation of the strategy the deadwood amount was highest on plots with a harvesting intensity up to 25 m^2 ha^{-1}. The maximum deadwood amounts were therefore at higher harvesting intensities than in 1997. Additionally, the deadwood amounts decreased even stronger on very high intensities (Figure 4; absolute range of effect size: 0.24). Plots with the presence of spruce had also higher deadwood amounts (Figure 4; absolute range of effect size: 0.21). The model 2010 showed no difference between plots in forest nature reserve and in managed areas or between the three management districts (Figure 4).

Model 3 (deadwood change)

Deadwood enrichment was influenced only by a few variables, including the natural mortality, harvesting intensity, spatial effects, and stand age, which also had an effect on the deadwood amounts in both assessment times. The strongest influence on the change in deadwood was the natural mortality – with increasing natural mortality we found higher changes in deadwood (Figure 4, absolute range of effect size: 2.1). Besides that, this model showed a large effect of management. With high harvesting intensities, the change in deadwood amounts were highest, showing that active deadwood enrichment during harvest can lead to a significant increase in deadwood amounts (Figure 4, absolute range of effect size: 0.46). For the change in deadwood amounts from 1997 to 2010, there was still a strong effect of the spatial distribution of the plots (Figure 5, absolute range of effect size: 0.36). The changes in deadwood amounts were highest in the North / North-West and lower in the other parts. Additionally, high rates of changes were revealed for stands of about an age of 50 and 150 years (Figure 4, absolute range of effect size: 0.19).

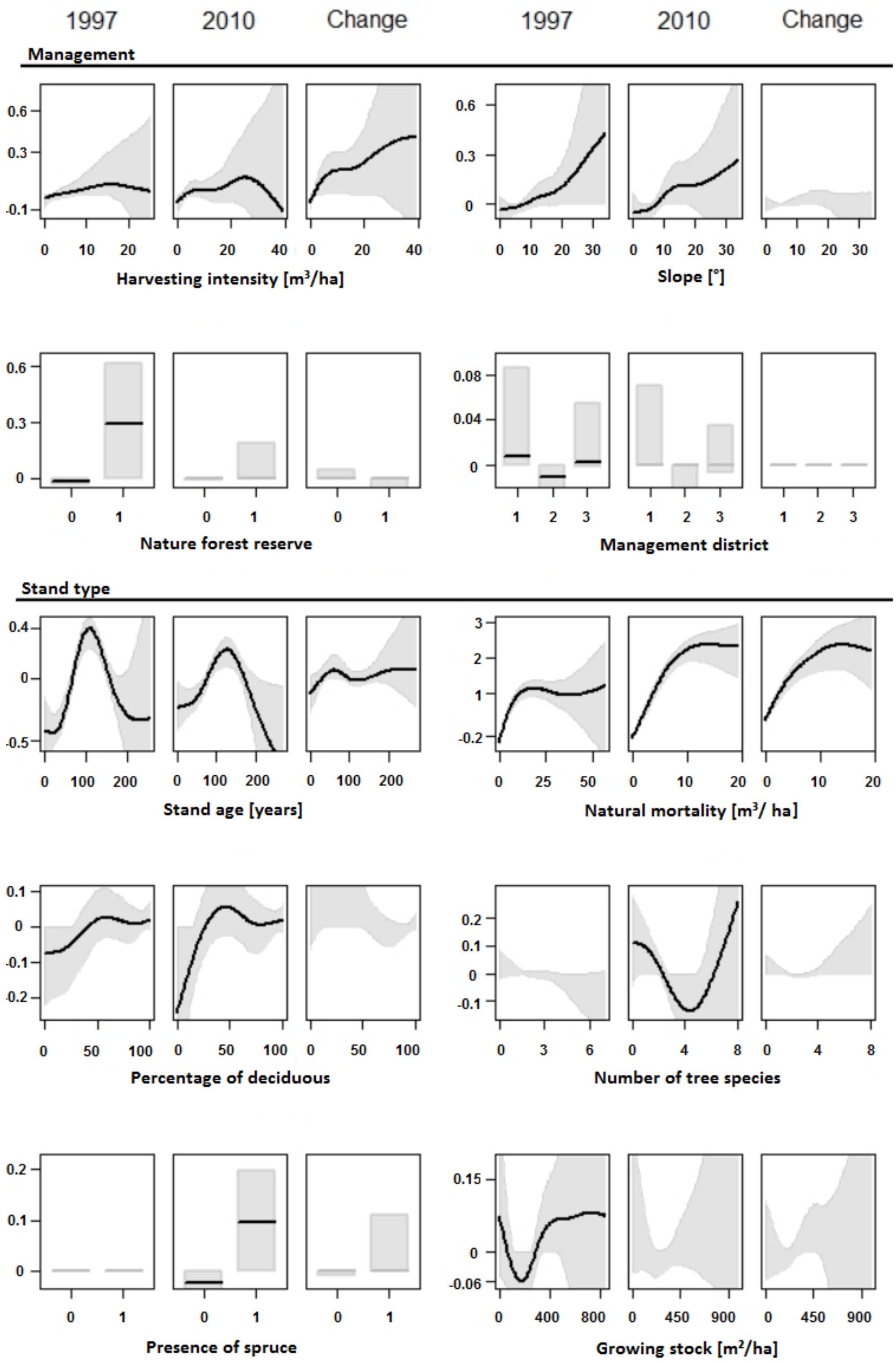


Figure 4: Effect of the ten included drivers found to have an effect in one of the three models, on deadwood amounts and deadwood change, separated into stand variables and management. The graphs show the results of the boosting models. Left panels: results from model 1 (deadwood amounts 1997); middle panels: results from model 2 (deadwood amount in 2010); right panels: results from model 3 (change in deadwood amounts from 1997 to 2010). For each graph, the y-axis displays the effect size on the logarithmic response variable, and the x-axis the range of the different explanatory variables. The black lines show the fitted effect size. Plots without black lines indicate variables that were not selected to contribute to the respective final model. The grey area shows the 95% confidence intervals. Slightly modified from Doerfler, Müller et al. (2017).

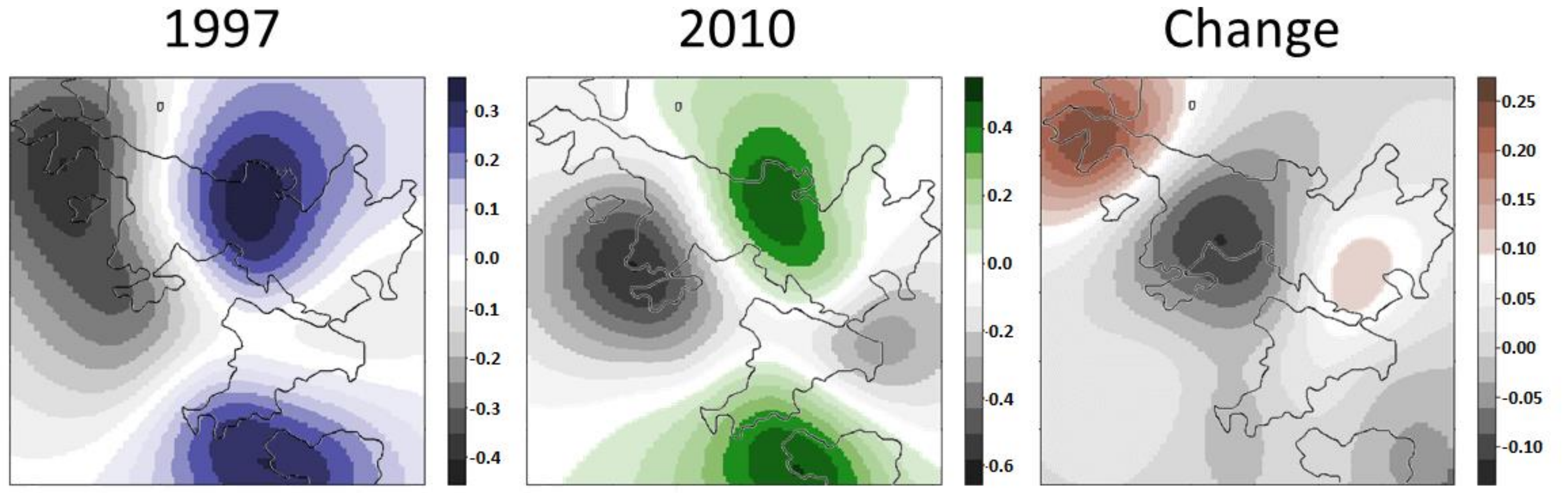


Figure 5: Spatial variability in deadwood amount and enrichment. The spatial position of each plot was fitted as explanatory variable in each of the three boosting models. Left: effect of space in model 1 (deadwood amounts 1997); middle: effect of space in model 2 (deadwood amount in 2010); right: effect of space in model 3 (change in deadwood amounts from 1997 to 2010). The shaded areas display the effect size. Darker areas show higher deadwood amounts or changes in these. The colored areas display the areas with a positive effect size, i.e., areas where the deadwood amounts were higher than the other variables used in the respective model can explain. The range of the effect size is displayed in the bar on the right side of the plot. The lines display the silhouette of the position of the sample plots. Slightly modified from Doerfler, Müller et al. (2017).

3.1.4 Change in Deadwood profile

The analysis of the deadwood profile using the additional inventory showed that especially logs of all sizes and decay stages, with highest effect on fresh, large logs, as well as fresh snags were promoted by the strategy (Figure 6). However, enrichment by purely passive management, i.e. in the reserves shows a more imbalanced increase of different object types then enrichment in production forests that includes also active enrichment (Appendix M, Figure M1).

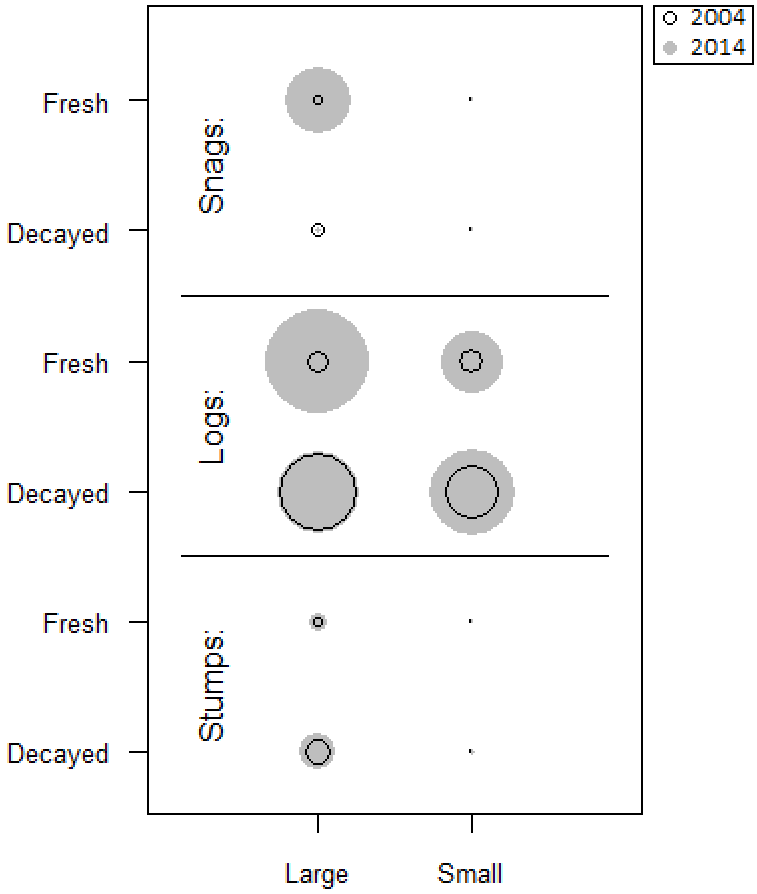


Figure 6: deadwood profile. The x-axis displays the object size (large > 30 cm diameter, small < 30 cm diameter), the y-axis displays the decay stages (fresh: decay stage 1 and 2, decayed: decay stage 3 and 4). The fields separated by horizontal lines display the volume of stumps, logs and snags separately. The size of the circles and rings display the deadwood volume for each category. The grey circles display the amount in 2014 and the black rings the volume in 2004.

Deadwood volumes of logs increased by 191 percent from 17.5 ± 1.7 m³ ha^{-1} (range: 0-207.7) in 2004 to 51 ± 11.2 m³ ha^{-1} (range: 0-2772) in 2014 ($V = 7453$, $p < 0.0001$), the volume of snags increased by 188 percent from 2.6 ± 0.4 m³ ha^{-1} (range: 0-50.1) in 2004 to 7.5 ± 1.3 m³ ha^{-1} (range: 0-196.3; $V = 3090$, $p < 0.0001$) and the volume of stumps increased by 50 percent from 4 ± 0.2 m³ ha^{-1} (range: 0-21.4) in 2004 to 6 ± 0.2 m³ ha^{-1} in 2014 (range: 0-19.8; $V = 5405$, $p < 0.0001$) in the additional inventory. Deadwood crowns were only recorded in the inventory of 2014 and cannot be compared to 1997, but they formed 6.6 percent of the total volume of lying objects (3.6 m³ ha^{-1}, range: 0-58.3) (Appendix N, Table N1).

We could not include the tree species in the deadwood profile because we included the category of unknown tree species in 2014, which makes the tree species between the years less comparable. In the additional inventory the deadwood of beech and other broadleaf trees increased significantly, apart from oak and hornbeam (Appendix N, Table N1). Coniferous trees (fir, spruce, pine and larch) were found in both years with a low percentage and did not increase. Results for the deadwood profile in the regular inventory are given in Appendix O.

Besides the volume, we also analysed the number of objects per hectare. We found a significant increase in the number of deadwood logs by 133 percent from 64.9 ± 3.6 ha^{-1} to 151.4 ± 7.7 ha^{-1} ($V = 2234.5$, $p < 0.0001$), in the number of snags by 88 percent from ha^{-1} 3.9 ± 0.4 in 2004 to ha^{-1} 7.3 ± 0.8 in 2014 ($V = 1794.5$, $p < 0.0001$) and in the number of stumps by 28 percent from 133.9 ± 5.6 ha^{-1} in 2004 to 171.6 ± 7.4 ha^{-1} in 2014 ($V = 5935.5$, $p < 0.0001$) (Appendix N, Table N2)2.

3.1.5 Habitat trees

In the additional inventory, we also assessed the number of living trees with habitat structures. The total number of living trees with habitat structures decreased significantly by 45 percent from 11.9 ± 0.88 to 6.5 ± 0.8 ($V = 10077$, $p < 0.0001$). However, looking at the single structures recorded, most of them decreased but not significantly (Table 3). Only trees with stem rot and small woodpecker holes decreased significantly, whereas medium woodpecker holes increased significantly (Table 3).

The comparison of habitat trees between production forests and reserves within the two years revealed that trees with stem rot and nesting boxes did not show a difference between production forests and reserves in both years. Large and small woodpecker holes and fungi were higher in reserves in 2004. No category of habitat trees was higher in production forests compared to reserves in 2004. In 2014 however, medium woodpecker holes, natural cavities and mould filled cavities were higher in reserves. Also after the implementation of the strategy none of the examined habitat structures were higher in production forests compared to reserves. However, we see that the number of habitat trees increased in production forests when 2004 and 2014 are compared (Appendix P, Table P1).

Table 3: Number of habitat trees of the additional inventory in both years (2004 and 2014): Mean number per plot and results of the Wilcoxon signed rank test of the comparison of both years. Slightly modified from Doerfler, Müller et al. (2017).

	2004		2014		Wilcoxon test	
	Number per ha	Standard error	Number	Standard error	V	p
Stem rot	9.1	0.7	0.7	0.16	**13912**	**< 0.001**
Large woodpecker holes	1.12	0.2	0.75	0.2	831	> 0.05
Medium woodpecker holes	4.3	0.7	5.88	0.7	**4008**	**< 0.01**
Small woodpecker holes	1.18	0.23	0.32	0.1	1415	**< 0.001**
Fungi brackets	0.4	0.14	0.3	0.11	90	> 0.05
Mould filled cavities	1.7	0.25	2	0.3	33126	> 0.05
Nesting boxes	0.4	0.1	0.34	0.09	83	> 0.05
Natural cavities	1.22	0.28	1.84	0.02	1245.5	> 0.05

3.2 Chapter B) Description of biodiversity before and after the implementation of the strategy

In the following paragraph, we report numbers of species and individuals per year. We do this separately for the five examined taxonomic groups since the groups were sampled in different ways and the number of individuals are assessed quite differently, which is important when doing a direct comparison between years.

Within the inventory of biodiversity, we found in total, 823 species within all five taxonomic groups, with 666 species before the implementation of the strategy and 625 species after the implementation of the strategy. Except for plants, the species of the taxonomic groups were not different in production forests and reserves (Appendix Q, Figure Q1).

3.2.1 Beetles

Beetles were the group with the overall highest species number. The total number of beetle species was 419 with 23,228 individuals. The number of species was 340 in 2004 and 283 in 2014 (Figure 7). The number of individuals decreased from 11,795 in 2004 to 11,698 in 2014. The number of species occurring only once per sampling years, so called singletons, decreased from 104 species in 2004 to 74 species in 2014. The most abundant species in 2004 was *Gyrophaena boleti* with 1,816 individuals, whereas in 2014 *Orchestes fagi* was the most abundant species with 4,634 individuals. We found 341 saproxylics beetle species. The number of saproxylic beetle species was 280 in 2004 and 237 in 2014. Respectively we found 59 non-saproxylic beetles in the comparable families in 2004 and 46 in 2014.

Species numbers of beetles were significantly lower in the second year (Figure 8). The distance between the rarefaction curves became even wider if abundances (q = 1 and 2) were considered, indicating that not only species numbers but also abundances became lower (Appendix R, Figure R1 and R2). Whereas the abundance based indices show a flattening with increasing sample size, the curve of the species numbers showed a continuous increase, indicating an incomplete sample size.

Additionally, the paired test of mean species numbers revealed a significantly lower number of species in 2014, with 34.29 ± 1.2 species in 2004 and 29.06 ± 1.3 species in 2014 (V = 1571.5, p-value < 0.01). Also, if only saproxylic beetles were considered they were significantly lower in the second sample year with 26.79 ± 1.1 species in 2004 and 21.9 ± 1.2 species in 2014 (V = 1528.5, p-value < 0.01). However, the species numbers of non-saproxylic beetles did not change significantly between the years with 7.5 ± 0.3 species in 2004 and 7.1 ± 0.3 species in 2014 (t = 1, p-value = 0.32).

3.2.2 Fungi

We report here the numbers of comparable fungi, which leaves out 310 species with 2110 occurrences but ensures that numbers reported are comparable between the years.

The number of comparable fungi species was 135 with 5,338 'individuals', measured as occurrences of fruiting bodies on different locations within the plot including all three sampling periods. The species number recorded in the first inventory was lower, with 117 species in 2004 and 126 species in 2014 (Figure 7). The number of 'individuals' was higher in 2014, with 2,258 fruiting bodies in 2004 and 3,080 in 2014. We found 13 species in 2004 and 10 species in 2014 that had only one occurrence in the respective year. The maximum number of 'individuals' were 285 in 2004 and 138 in 2014, with the most common fungi being *Hypoxylon fragiforme* in 2004 and *Ascodichaena rugosa* in 2014, which are both saproxylic fungi.

In total 85 species of fungi were saproxylics with 4,057 'individuals'. The species number was higher in 2014, with 75 species in 2004 and 80 species in 2014. Also, the number of fruiting bodies recorded as individuals were higher in 2014 with 1,894 'individuals' in 2004 and 2,163 in 2014. In total 50 species of fungi were non-saproxylic with 1,281 'individuals'. The non-saproxylic fungi of the comparable subset included mycorrhiza and soil saprotrophs. The respective percentage within non-saproxylic fungi species did not differ between the years. Of the 117 fungi species in 2004, 27 were mycorrhiza and 13 soil saprotrophs. Of the 126 fungi species in 2014, 33 were mycorrhiza and 11 soil saprotrophs. The number of fungi was significantly higher in 2014 (Figure 8; Appendix R, Figure R1 and R2). Also, the abundance based indices (q=1 and 2) were significantly higher. The rarefaction curves showed a distinct flattening, indicating that further sampling would increase the additional species only slightly (Figure 8). The pairwise comparison revealed that we found 21.06 ± 0.9 species in 2004 and 33.71 ± 0.8 species in 2014 (V = 52.2, p-value < 0.0001). The number of saproxylic fungi was also higher in 2014, with 15.54 ± 0.6 species in 2004 and 20.21 ± 0.6 species in 2014 (V = 413.5, p-value < 0.0001). The number of non-saproxylic fungi increased even stronger between the years, from 5.1 ± 0.4 in 2004 to 12.88 ± 0.5 in 2014 (V = 9, p-value < 0.0001).

3.2.3 Birds

Birds were the group with the lowest species number, with 50 species and 3,746 individuals in total. The number was distinctly lower in 2014, with 47 species in 2004 and 40 species in 2014 (Figure 7). The number of individuals decreased form 2,095 individuals in 2004 to 1,651 individuals in 2014. Species which occurred only once per year were 8 in 2004 and 7 in 2014. The maximum abundances per species were 274 individuals in 2004 and 283 individuals in 2014. The most common birds with abundances of > 200 individuals were *Fringilla coelebs* the Common chaffinch and *Parus major* the great tit, in both years and *Sitta europaea*, the Eurasian nuthatch in 2004. Saproxylic birds were found to be 21 species with 1,921 individuals. Species numbers of saproxylic birds decreased slightly from 19 species in 2004 to 16 species in 2014. The number of individuals also decreased from 1,119 to 802. The rarefaction curves only overlapped slightly with an increasing sampling size indicating that the species numbers of birds were significantly lower in 2014 (Figure 8, Appendix R, Figure R1 and R2). The pairwise comparison shows that the number of bird species was 13.59 ± 0.3 in 2004 and 10.57 ± 0.3 species in 2014 ($V = 1722$, p-value = < 0.0001). These lower numbers were independent from the ecological group. We found 6.62 ± saproxylic bird species in 2004 and 4.86 ± 0.2 species in 2014 ($V = 1595$, p-value < 0.0001). We found 6.97 ± 0.3 non-saproxylic bird species in 2004 and 5.71 ± 0.2 species in 2014 ($V = 1383.5$, p-value < 0.001).

3.2.4 Plants

The total number of plant species was 117. The number of species did not change strongly between the years, with 94 species in 2004 and 90 in 2014 (Figure 7). The total cover nearly tripled from 974 percent cover in 2004 to 2,860 percent cover in 2014.

The number of singleton was 15 in 2004 and decreased to 6 in 2014. The most common species in both years were beech *Fagus sylvatica* and the alpine grass *Carex brizoides*. The rarefaction curves overlapped strongly indicating similar species numbers in both years. However, this overlap decreased with increasing q (Figure 8, Appendix R, Figure R1 and R2). Also, the pairwise comparison revealed no significant change in species numbers with 9.71 ± 0.9 species in 2004 and 8.97 ± 1 species in 2014 ($V = 1028.5$, p-value = 0.4). Plants were the only taxonomic group that showed significant response to protection with significant lower species numbers in reserves than in managed areas for both years (2004: $t = -2.687$, $p < 0.01$; 2014: $t = -2.066$, $p < 0.05$) (Appendix Q, Figure Q1).

3.2.5 True bugs

The total number of true bug species was 89 with 1,237 individuals. The numbers increased from 57 in 2004 to 62 in 2014 (Figure 7). However, the numbers of individuals decreased from 789 in 2004 to 448 in 2014. Species which occurred only once per year were very common in both years with 25 species in 2004 and 30 species in 2014, making in both years about 45 percent of all recorded species singletons. The maximum abundances per species were 411 individuals in 2004 and 87 individuals in 2014. The most common true bugs were *Psallus varians* in 2004 and *Deraeocoris lutescens* in 2014. The rarefaction curves showed a strong overlap for bug species for all considered levels of q (Figure 8, Appendix R, Figure R1 and R2). However, the pairwise comparison revealed a significantly lower number in 2014, with 4.68 ± 0.3 species in 2004 and 3.9 ± 0.3 species in 2014 (t = 2.053, p-value = 0.044).

3.2.6 Multidiversity index

To assess to changes in overall biodiversity we calculated a multidiversity index. The multidiversity index, calculated on the species number per group, was not significant different in the sampling years, with a mean index value of 0.44 ± 0.01 in 2004 and 0.43 in 2014 ± 0.01 (t = 0.89, p = 0.4). We found that the multidiversity index differed between production forests (0.47 ± 0.01) and reserves (0.41 ± 0.01) in 2004 (t = -2.036, $p < 0.05$) but not any more in 2014 (production forest: 0.43 ± 0.01 and reserves: 0.43 ± 0.02; t = -0.07, p = 0.944).

The multidiversity index calculated separately for saproxylic species was higher in 2004, with 0.56 ± 0.01 in 2004 and 0.52 ± 0.01 in 2014 (t = 2.23, p-value = 0.0.3). The multidiversity of saproxylics in 2004 was not different in reserves (0.56 ± 0.02) compared to production forest (0.55 ± 0.02; t = 0.275, p = 0.785). However, in 2014 the multidiversity of saproxylic was significantly higher in reserves, with an index of 0.55 ± 0.02 in reserves and 0.49 ± 0.01 in production forest (t = 2.444, $p < 0.05$).

The multidiversity of non-saproxylic species was significantly higher in 2014 with values of 0.38 ± 0.01 in 2004 and 0.41 ± 0.01 in 2014 (V = 698, p-value = 0.0037). The multidiversity of non-saproxylics was significantly higher in production forests in 2004, with an index of 0.4 ± 0.01 in production forests and 0.34 ± 0.02 in reserves (t = -2.489, p-value = 0.0153). In 2014 the index was 0.42 ± 0.01 in production forests and 0.39 ± 0.01 in reserves (t = -1.604, p-value = 0.113).

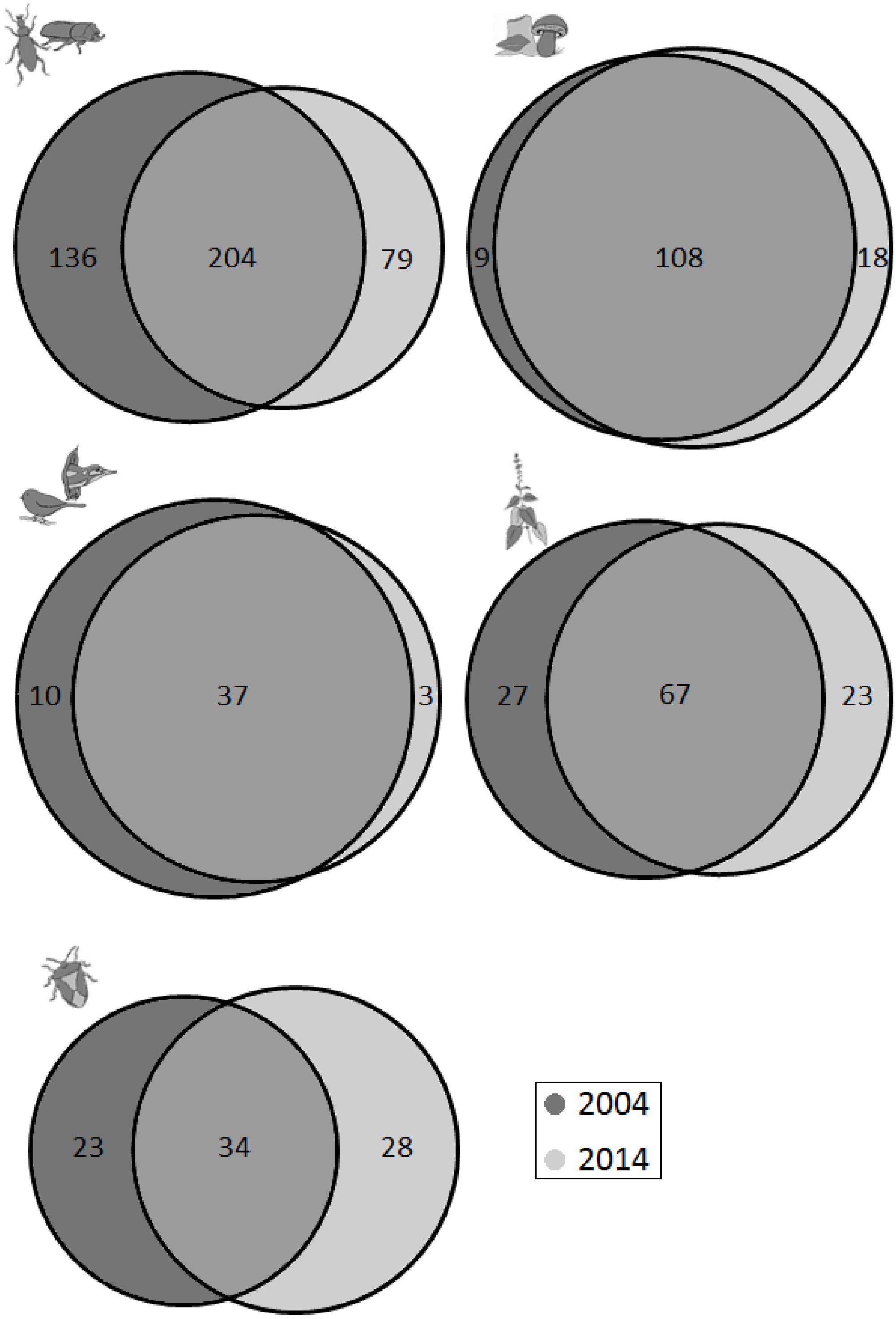


Figure 7: Venn-diagrams of species numbers of the five examined taxonomic groups in the two inventory years. Dark gray circles: species occurring exclusively in 2004, light gray: species occurring exclusively in 2014, medium gray: number of species overlapping in the two years. The numbers within the circles indicate the actual species numbers. Top left: beetles, top right: fungi, middle left: birds, middle right: plants, bottom left: true bugs.

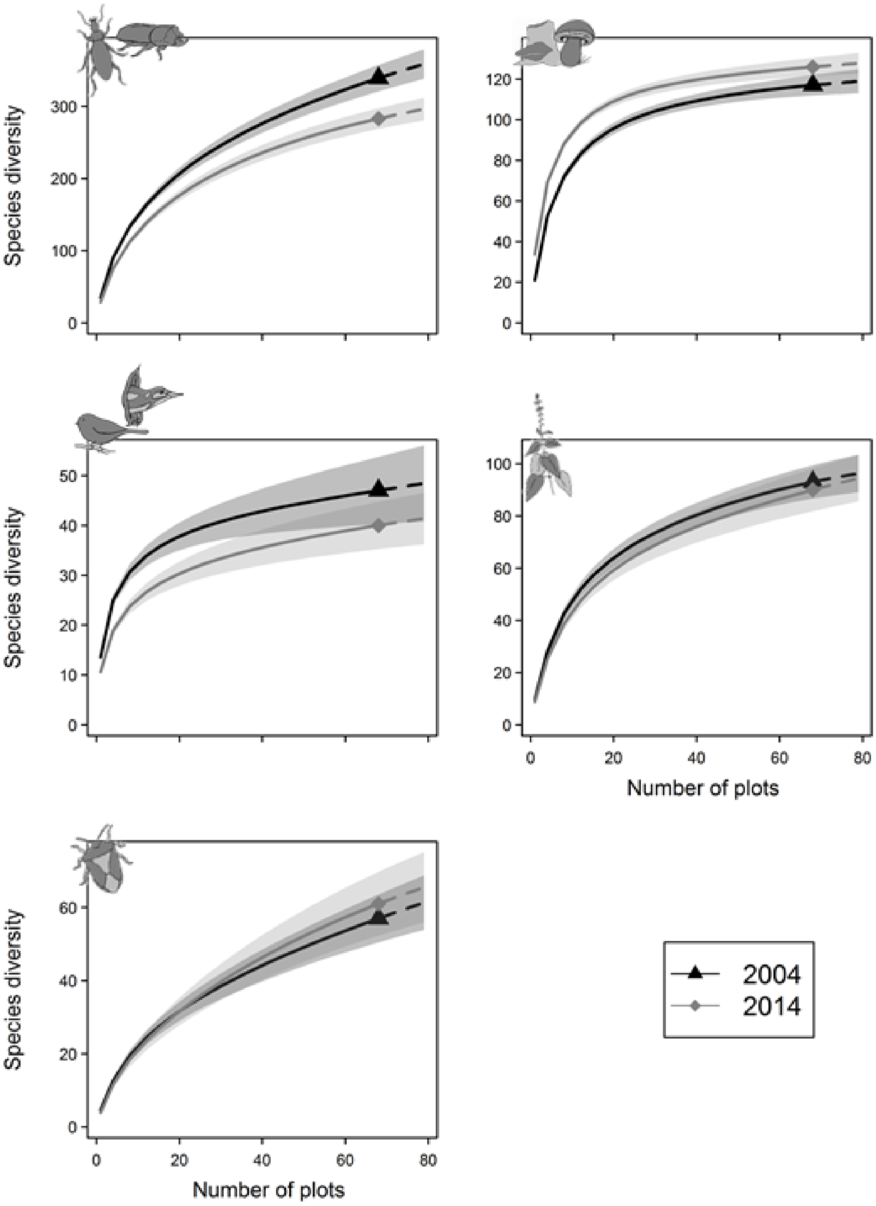


Figure 8: Rarefaction curves for the five examined taxa of q = 0. Species diversity in 2004 with a gray line and the confidence interval indicated in light gray, species diversity in 2014 with a black line and the confidence interval in dark gray. Top left: beetles, top right: fungi, middle left: birds, middle right: plants, bottom left: true bugs.

3.3 Chapter C) Relation between changes in biodiversity and deadwood enrichment

In this chapter, we analyze the influence of deadwood enrichment on overall biodiversity, calculated as a multidiversity index and for the species numbers of all taxonomic groups. We also separate the respective diversity indices into saproxylic species and non-saproxylic species if they are present in the respective group.

3.3.1 Environmental variables

Detailed analyses of changes in deadwood amounts on the scale of the forestry department can be found in the first chapter. However, since the here examined dataset comprises a subset of the previous analysed deadwood inventory, we briefly report deadwood amounts and other possibly confounding variables here and more detailed in Appendix N (Table N3). The deadwood amount increased significantly by 208.3 percent from 39.2 ± 5.9 (mean ± SE) in 2004 to 122.5 ± 41.2 m^3 ha^{-1} in 2014 ($V = 494$, $p < 0.001$). The increase was similar in production forests and reserves. The canopy cover decreased on average by 15 percent from 83 ± 2.9 percent cover to 69 ± 4.3 percent cover ($V = 1640.5$, p-value < 0.01, range = -90 - 85), with a higher number of plots (51) having decreasing cover than increasing cover (17). The log ratio of deadwood amounts was not significantly related to the change in canopy cover ($t = -1.571$, $p = 0.12$). The number of cavity bearing trees did not change significantly with a number of 15.2 ± 2.5 in 2004 and a number of 13.16 ± 1.8 trees in 2014 ($V = 884$, p-value = 0.83). We found that deadwood amount and diversity, calculated as the index proposed by Stokland (2001), were significantly correlated (Appendix N, Figure N1).

3.3.2 Drivers of biodiversity change

The model revealed that multidiversity was positively influenced by deadwood enrichment and but not by cavity bearing trees or the changes in the canopy. The multidiversity of saproxylics was also positively influenced by deadwood enrichment and marginally significant by an enrichment of cavity bearing trees but not by a change in canopy. The multidiversity of non-saproxylics was not influenced by any of the here tested variables (Figure 9, Table 4).

Deadwood enrichment had a positive influence on taxonomic groups that had a high percentage of deadwood dependent species, i.e. beetles and fungi.

For the species number of beetles both, all species and the saproxylic subgroup, responded positively to increasing deadwood amounts (Figure 10, Table 4). The species number of non-saproxylic beetles was not significantly influenced by deadwood enrichment (Figure 10, Table 4). Further on, none of the other tested variables had an effect on the species number of beetles (Appendix S, Figure S1 and S2).

The same results as for beetles can be seen for fungi: all species and saproxylic subgroups responded positively to increasing deadwood amounts. Non-saproxylic fungi did not respond significantly to deadwood enrichment (Figure 10, Table 4) and also the other variables were without influence (Appendix S, Figure S1 and S2).

Neither the overall number of birds nor the saproxylic or non-saproxylic subgroups responded to deadwood enrichment (Table 4, Figure 10). However, non-saproxylic birds were positively, even though statistically only marginally, influenced by an opening of the canopy cover.

For plants and true bugs, we also found no significant relationship between all species numbers or species numbers of the subgroups and deadwood enrichment (Table 4, Figure 10) and the other tested variables were also without influence (Appendix S, Figure S1 and S2).

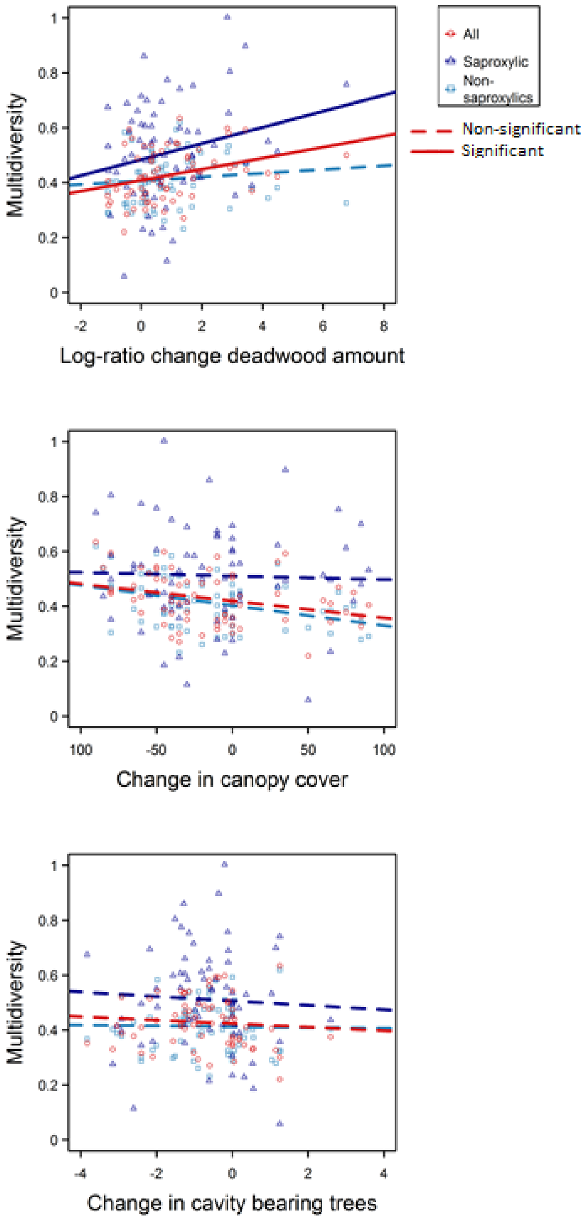


Figure 9: Results of the generalized linear model with multidiversity, multidiversity of saproxylic and non-saproxylics as dependent variables and the log-transformed ratio of deadwood change, the difference in canopy cover between the years and the log-transformed ratio of the change in the number of cavity bearing trees as predictor variables and the diversity before the implementation of the strategy as offset variables. Solid lines display significant results. Red lines display multidiversity of all species, dark blue only saproxylics and light blue only non-saproxylics.

Table 4: Summary of a generalized linear model with the multidiversity and the species numbers of the five examined taxonomic groups (beetles, fungi, birds, plants, true bugs) separated into saproxylic and non-saproxylic species as response variable; predictors are deadwood enrichment as log response ratio (log(amount 2014/amount2004)), the change in canopy cover (cover 2014 - cover 2004) and the enrichment of cavity bearing tress as log response ratio (log(number 2014/number 2004)). For each model the test statistic is given. The value behind the test statistic depends on the family term used in the model: poisson = z, quasipoisson = t, quasibinomial = F. Note that the results were calculated using the anova function which gives no positive or negative sign for the test statistic – these can be looked up in Figure 9 and Figure 10. The family term which was used in the model is indicated in "distribution". Variables in bold are significant. Taxonomic groups that had no or few saproxylic species were not analyzed separately.

		Changes canopy cover		Changes cavity-trees		Changes deadwood amounts		
		statistic	p	statistic	p	statistic	p	distribution
Multidiversity	all	0.02	0.88	0.06	0.81	**14.77**	**< 0.001**	gaussian
Multidiversity	saproxylic	0.77	0.38	3.04	0.09	**34.86**	**< 0.0001**	gaussian
Multidiversity	non-saproxylics	1.17	0.28	0.24	0.63	0.56	0.4576	gaussian
Beetles	all	0.3	0.59	0.19	0.67	**11.39**	**0.0013**	quasipoisson
Beetles	saproxylic	0.002	0.96	0.15	0.70	**14**	**< 0.001**	quasipoisson
Beetles	non-saproxylics	69.35	0.97	69.35	0.98	69.24	0.7468	poisson
Fungi	all	0.82	0.37	0.0003	0.99	**19.88**	**< 0.0001**	quasipoisson
Fungi	saproxylic	0.16	0.69	0.33	0.57	**34.15**	**< 0.000**	quasipoisson
Fungi	non-saproxylics	1.11	0.30	1.03	0.31	0.04	0.8425	quasipoisson
Birds	all	55.58	0.31	53.98	0.21	53.76	0.6335	poisson
Birds	saproxylic	33.83	0.68	33.42	0.52	33.24	0.6713	poisson
Birds	non-saproxylics	76.26	0.07	75.08	0.28	74.97	0.7372	poisson
Plants	all	1.79	0.19	2.3	0.13	0.63	0.4290	quasipoisson
Bugs	all	0.52	0.47	0.05	0.83	0.54	0.4647	quasipoisson
Bugs	non-saproxylics	0.46	0.50	0.04	0.84	0.42	0.5209	quasipoisson

Model with reserves

We also tested the effect of deadwood enrichment on biodiversity separately for production forests and reserves by defining an interaction term that separates the model for the two plot sets. These models have a distinct lower number of replicates (N = 24 in nature forest reserves and N = 44 in production forests) and are therefore less reliable. The results show in general similar results compared to the models without the reserve vs. production forest interaction term (Appendix H, Table H1), with a higher test statistic for deadwood enrichment in production forests. We found no distinct effect of the reserve on species number in the model. However, single effects changed if production forests and reserves were considered separately. An increase of cavity bearing trees had a significant positive influence on saproxylic multidiversity in production forests. Fungi and especially saproxylic species therein responded negatively to an opening of the crown in reserves. Additionally, the tendency of birds to increase with an opening of the canopy was found to be significant in reserves.

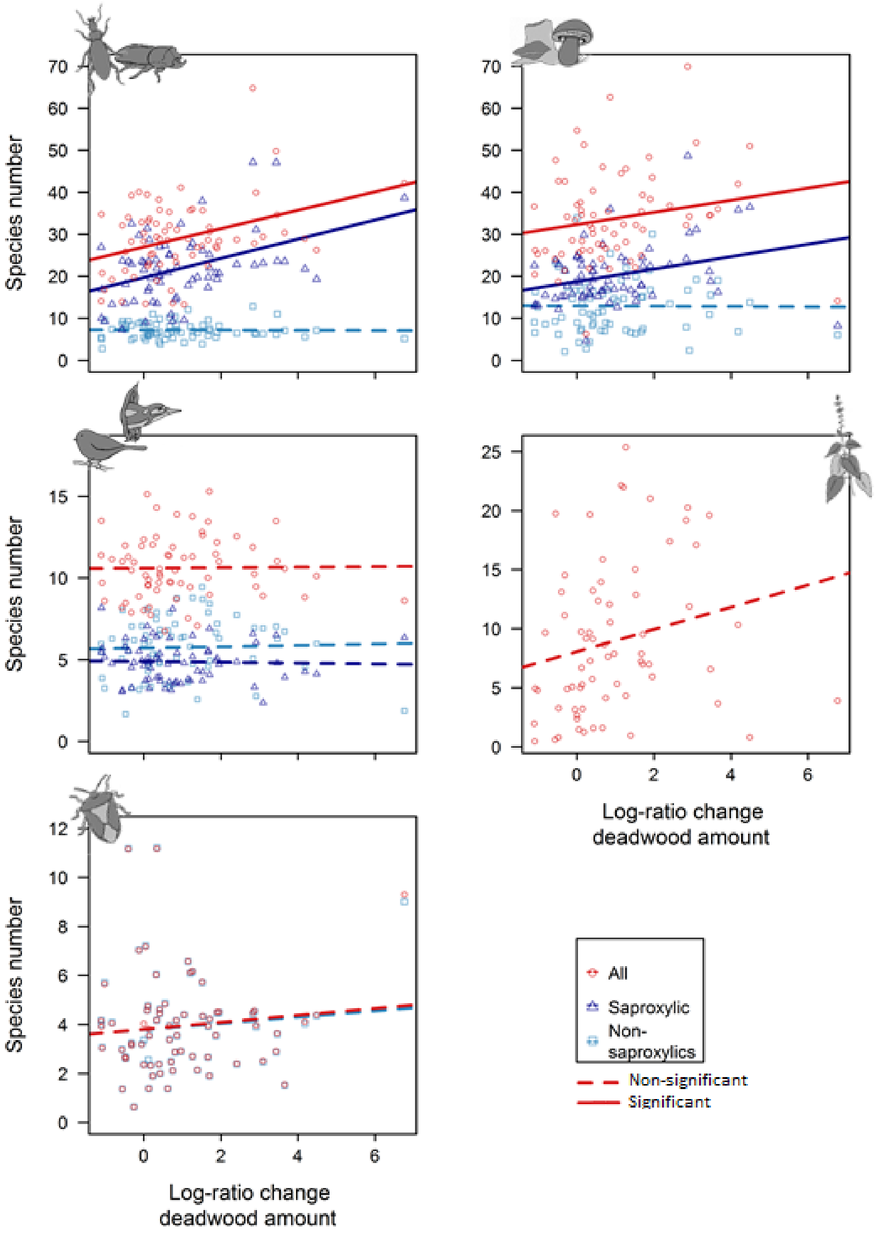


Figure 10: Results of the generalized linear model with the species numbers of the five taxonomic groups and the saproxylic and non-saproxylics species separate as dependent variables and the log-transformed ratio of deadwood change, the difference in canopy cover between the years and the log-transformed ratio of the change in the number of cavity bearing trees as predictor variables and the diversity before the implementation of the strategy as offset variables. The figures for the other two variables are given in Appendix S (Figure S1 and S2). Solid lines display significant results. Red lines display all species, dark blue only saproxylics and light blue only non-saproxylics. Top left: beetles, top right: fungi, middle left: birds, middle right: plants, bottom left: true bugs.

3.4 Chapter D) Relationship of assembly mechanisms and deadwood enrichment

In this paragraph, we summarize how the deadwood enrichment influences changes in species traits and how species assembly mechanisms are affected.

3.4.1 Description and phylogenetic signal of traits

Beetles

For beetles, we could use five traits of which four were binary for the calculation of species assembly (Appendix I, Table I1). Within the saproxylic beetles xylophagous species were most common (142 species), followed by predatory species (133) and mycetophagous species (112). The least species were detritivorous (19). The estimated D for these traits was low (-0.64– -0.78) indicating a non-random distribution in the phylogenetic tree. The mean body size of beetles was also not randomly distributed along the tree (K: 0.92). Both the percentage of mycetophagous species and larger species were promoted by deadwood enrichment (Figure 11). The change in canopy cover did not show an influence as well as the previous mean weighted trait (Appendix T, Figure T1 and T2).

Fungi

For saproxylic fungi we could use ten traits, of which seven were binary (Appendix I, Table I1). Saproxylic fungi were dominantly without ornamented spores (80) and without crustose cystidae and setae (79). These traits were clustered in the phylogeny (D: -0.23 and D: -0.08). About 30 percent of the species had resupinate fruiting bodies (25), only very few had persistent (7) or galert (7) fruiting bodies. These three fruiting body traits were also phylogenetically clustered (D: 0.08, D: -0.09, D: 0.63). Skeletal hyphae by contrast were quite common (22 species) also with phylogenetical clustering (D: -0.63), similar to asexual conidae (15 species, D: -1.18).

The numeric traits of saproxylic fungi showed only partly a high phylogenetic signal. The spore shape and volume were phylogenetically clustered (K: 0.44, K: 0.56) but the volume of fruiting bodies of saproxylic fungi was highly randomly distributed over the tree (K: 1.8).

The analysis of mean weighted traits of saproxylic fungi showed a significant increase of species with a larger spore volume and an increasing presence of species with asexual reproduction, whereas species with skeletal hyphae decreased significantly (Figure 11). The spore shape of saproxylic fungi was strongly positively related to the spore shape in the first inventory (Appendix T, Figure T2). The change in canopy cover did not show an influence on the mean weighted traits of fungi (Appendix T, Figure T1).

Birds

For birds, we could use eight traits of which five were binary. Species migrating and not migrating occurred to a similar percentage (not migrating: 23, migrating: 28). The estimated D was -0.66, indicating a non-random distribution in the tree. The trait determining the daytime of activity (nocturnal) was heavily influenced by our sampling method and included therefore only 1 nocturnal species (brown owl, *Strix aluco*). The estimated D was -0.06, and therefore not randomly distributed. The diet traits of birds reveal that most of the species feed on invertebrate (44), followed by species feeding on plants (17). Only eight species feed on vertebrates, including birds of prey like *Pernis apivorus* and *Buteo buteo* but also *Corvidae* like *Garrulus glandarius*, and one owl (*Strix aluco*). These traits were all distinctly not randomly distributed (D: -1.25 - -0.15, Appendix I, Table I1). The weight of birds was on average 164 g and clustered in the phylogeny (K: 0.88). The life span was 12 years on average and had a tendency towards random distribution (K: 0.43). The clutch size was 6 eggs on average and was not randomly distributed (K: 0.64). The linear model revealed a significant increase of species with a higher mean life span in communities with a formerly high lifespan and a marginal significant increase of the mean clutch size with an increase in canopy cover.

Plants

For the analysis of plants, we could use 13 traits of which ten were binary (Appendix I, Table I1). Most of the plants were annual or biennial (102 species) and dominantly propagating with seeds or mixed with seeds and vegetative (110 species). The trait of persistence was phylogenetically clustered within the tree (D: 0.31), whereas plants dominantly propagating vegetative was rather random (D: 0.85), indicating that the trait is not phylogenetically clustered. Besides that, about 30 percent (26 species) are woody. This trait is strongly clustered within the phylogeny (D: -0.46). The traits of seed dispersal revealed that several species are adapted to more than one type of seed dispersal mode but most are zoochorous, i.e. adapted to distribution with animals (96 species). 49 species are anemochorous, i.e. dispersed by wind and 59 species are autochorous, i.e. not adapted to a certain type of dispersal. Whereas zoochorous species are phylogenetically clustered (D: -0.03), anemo- and autochorous species are inclined towards random distribution within the phylogeny (D: 0.16, D: 0.26). The mean height of plants and the specific leaf area were not randomly distributed along the tree (K: 1.29, K: 0.18). However, the seed weight was also inclined towards random distribution (K: 0.31).

Whereas the deadwood changes did not affect plant traits, the change in canopy had an effect, with increasing dominantly vegetative propagating species in darker conditions (Appendix T, Figure T1). However, all plant traits were strongly and positively related to the weighted means in the first inventory (Appendix T, Figure T2).

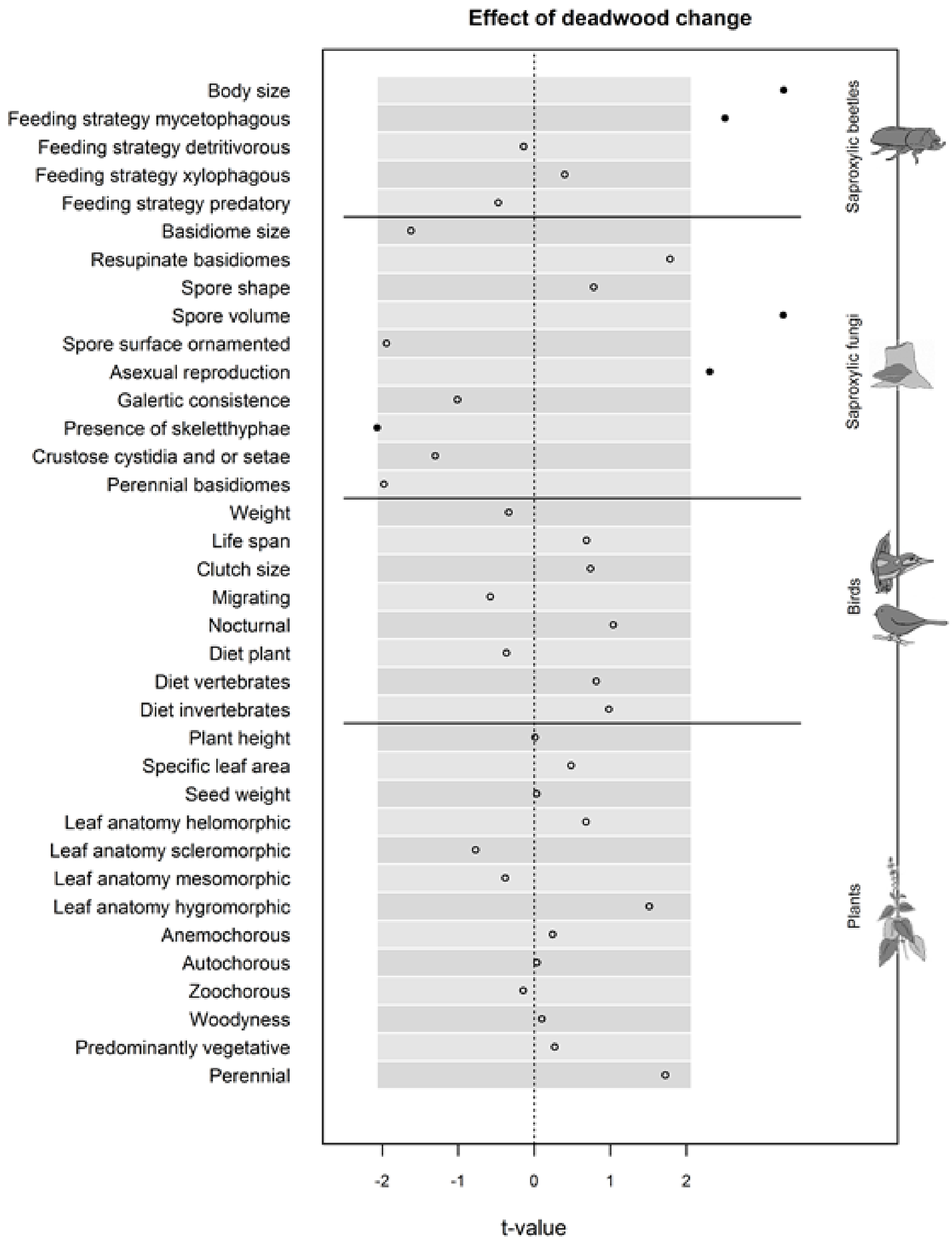


Figure 11: Results of linear model with the mean weighted traits in 2014 as dependent variable and the log ratio of deadwood volume, the change in canopy cover and the weighted mean of traits in 2004 as independent variables. The x-axis shows the t-value of the log ration of deadwood (results for the other two variables are in Appendix T, Figure T1 and T2). The gray bar marks the significance level: black points mark significant relationships; circles are not significant. The horizontal lines mark to which taxonomic group the trait belongs. Top: saproxylic beetles, upper middle: saproxylic fungi, lower middle: birds, bottom: plants.

3.4.2 Optimal a-value

The linear models showed that the optimal a-value varied between the examined taxonomic groups and that the assembly of groups was influenced by different variables. Saproxylic beetles had their optimal R² at a very low a-value (0.025) and birds at a = 0.175, indicating a major contribution of functional distance.

The highest adjusted R² for saproxylic fungi and plants were reached at high a-values (a = 1, a = 0.925) (Figure 12), i.e. when based mainly on phylogenetic distance. However, for plants the R²-values varied strongly creating rather a scatter than a clear pattern for optimal a-values. The explained variance was rather low for the optimal model of saproxylic fungi (adjusted R² = 0.06) and for birds (adjusted R² = 0.04). However, the models for plants and saproxylic beetles had a high explanatory power adjusted R² > 0.21 and 0.28).

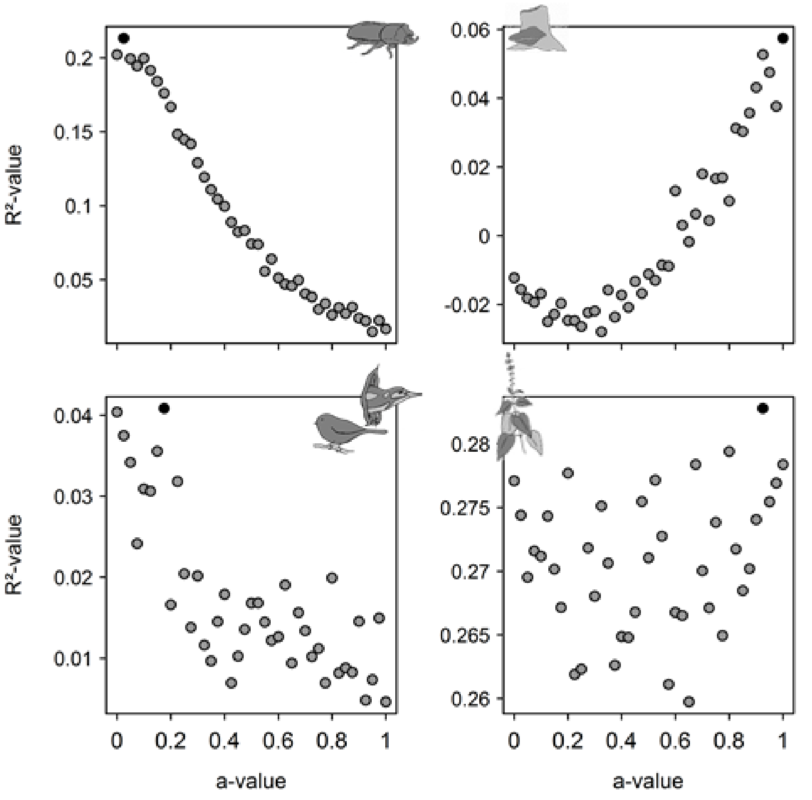


Figure 12: Trend of the adjusted R² of the linear models. These models included the standardized effect size of the mean pairwise functional-phylogenetic distance in 2014 as dependent variable and the deadwood volume, change in canopy cover and standardized effect size of mean pairwise distance in 2004 as independent variable. The models were calculated with the weighting parameter for the mean pairwise functional-phylogenetic distance ranging from 0 to 1 making it in total 41 models). The black point marks the optimal a. Top left: saproxylic beetles, top right: saproxylic fungi, bottom left: birds, bottom right: plants.

3.4.3 Changes in mean assembly mechanism per year.

The assembly differed between the groups. Whereas, saproxylic beetles and birds had a lower standardized effect sizes of the mean pairwise functional-phylogenetic distance (ses mpd), saproxylic fungi had in general a higher value (Figure 13). Comparisons between the inventories showed that the ses mpd of saproxylic fungi increase and that the ses mpd of plants decreased, but only marginally significant (Figure 13).

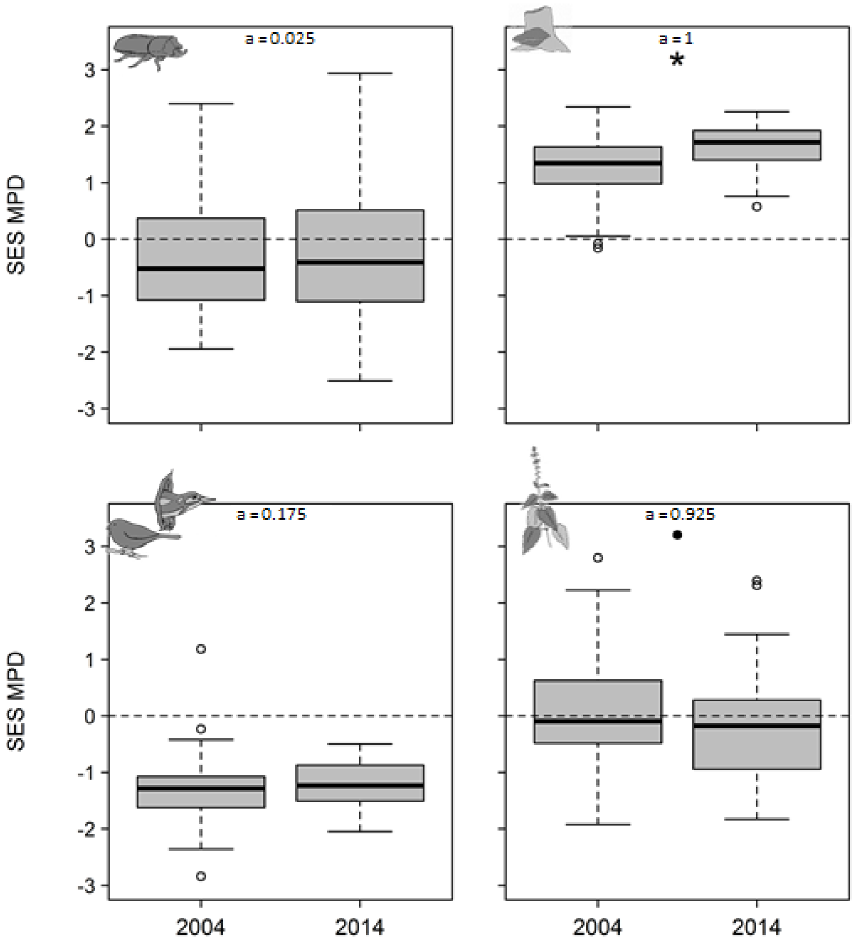


Figure 13: Standardized effect size of mean pairwise functional-phylogenetic distance of the examined species groups in both years for the a-value of the optimal model. A small a-value indicates that the phylogeny explains most, whereas a high a-value indicates a high explanatory value of the traits. The left boxplot displays 2004 and the right one 2014. Significant changes are marked with a star, marginal significant changes (p = 0.07) are marked with a dot. The dashed line displays zero. Values above zero indicate overdispersion (i.e. species are more different then in the Null model) whereas values below zero indicate clustering (i.e. species are more similar then in the Null model). Top left: saproxylic beetles, top right: saproxylic fungi, bottom left: birds, bottom right: plants.

3.4.4 Results of the optimal model

The linear model of the ses mpd with the optimal a-value revealed that deadwood enrichment influenced only the assembly of saproxylic beetles significantly. With increasing deadwood enrichment the ses mpd increased significantly (Table 5, Figure 14). None of the other examined groups, regardless if they are saproxylic or non-saproxylic, revealed a significant change in assembly pattern with deadwood enrichment (Table 5, Figure 14).

The changes in the canopy cover had no significant effect on the assemblies of the here examined groups. However, the ses mpd of the first inventory showed a significant relationship with the recent ses mpd of plants and birds. For both groups, a low ses mpd remained low and high ses mpd values remained high. Saproxylic beetles did not show a significant relationship with the previous ses mpd (Appendix U, Figure U1 and U2).

Table 5: Results of the optimal linear model. Giving the optimal a-value, and the t- and p-value for the three independent variables for the five models of the species groups. Significant results are indicated in bold.

		log ratio deadwood		difference cover		ses mpd 2004	
	a	t-value	p-value	t-value	p-value	t-value	p-value
Saproxylic beetles	0.025	**4.559**	**2.37e-05**	0.534	0.595	-0.395	0.694
Saproxylic fungi	1	-1.367	0.1765	0.778	0.4395	**2.235**	**0.0289**
Birds	0.175	0.534	0.5955	-0.218	0.8284	**2.056**	**0.0439**
Plants	0.925	-0.936	0.3535	-1.870	0.0672	**4.493**	**4.05e-05**

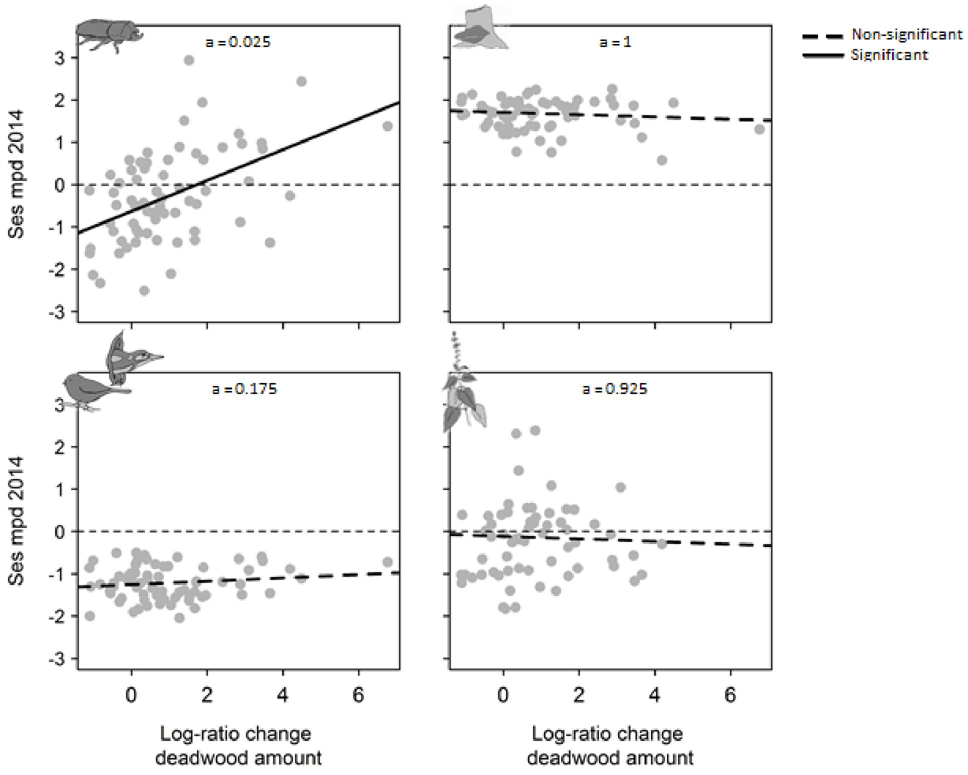


Figure 14: Results of the optimal linear model for the relationship of the standardized effect size of the mean pairwise phylogenetic-functional distance (ses mpd) for all examined five taxonomic groups with the change in deadwood amount. Solid lines display significant results. The figures for the other two variables are given in Appendix U (Figure U1 and U2). Top left: saproxylic beetles, top right: saproxylic fungi, bottom left: birds, bottom right: plants.

4. Discussion

Due to the strong pressure on global biodiversity new and achievable nature conservation strategies need to be developed and scientifically tested to assess their consequences. With a considerable proportion of biodiversity being dependent on forests and therein on deadwood structures these habitats should be key components for biodiversity conservation. In Central Europe where centuries of exploitation shape the recent forests it is not only necessary to establish reserves but to further improve the conditions in the surrounding landscape matrix to ensure stable populations of forest species. Consequently, integrative approaches are one of the considered strategy with many benefits, such as the large area on which they can be implemented, but also with many uncertainties compared to longer and more common applied and therefore better evaluated approaches. Deadwood enrichment is often proposed as a valuable tool for integrative management and a wide variety of proposed integrative approaches to enrich deadwood are available. These include both passive and active measures. However, these measures become limited when it comes to large scale implementation, since the measures must not only be financially viable but also practical. The here examined strategy of the Bavarian State forestry is implemented for ten years on a large landscape but a scientific evaluation is missing so far. It included active enrichment and passive retention of deadwood with the aim to increase structural diversity in production forests and hence promote biodiversity

The objective of this study is to contribute with a detailed evaluation of this nature conservation strategy to the evaluation of integrative strategies implemented in practice on a large scale. The study shows that it is possible to increase the intended habitat in a very short time-span considering rotation times in forests but that the type of stand remains an important driver for the amounts that accumulate (Chapter A). It also shows that, although harvest of wood is continued in this forest, the enrichment of the intended habitat had a positive influence on biodiversity and therein especially saproxylic taxa, i.e. saproxylic beetles and fungi (Chapter C). It revealed however that the examined species groups are subject to considerable annual variations which reveals the importance of continuous monitoring and the consideration of different species groups for the evaluation (Chapter B). The mechanisms determining the assembly of saproxylic beetle species changed considerable with deadwood enrichment but did not affect other examined taxonomic groups (Chapter D).

4.1 Chapter A) Evaluation of the changes in deadwood amounts and their drivers

The evaluation of deadwood amounts and enrichment revealed a strong increase in deadwood amounts in both datasets proving a successful implementation of the strategy in terms of deadwood enrichment.

Before the implementation of the integrative strategy the deadwood amounts of 8.7 ± 0.5 m^3 ha^{-1} (regular inventory, *MinDm*: 20) and 24.6 ± 2 m^3 ha^{-1} (additional inventory, *MinDm*: 12) were within the range of other temperate broadleaf forests, which show however highly variable deadwood amounts. In production forests, often low amounts of deadwood are reported, i.e. smaller than 10 m³ ha^{-1} (*MinDm*: 5 (Kruys, Fries et al. 1999), *MinDm*: 10 (Fridman and Walheim 2000, Lombardi, Lasserre et al. 2008)). However, they can also reach values of 41-67 m³ ha^{-1} (*MinDm*: 5 (Debeljak 2006)) or even 94 m³ ha^{-1} when the management intensity is low (*MinDm*: 7 (von Oheimb, Westphal et al. 2007)). Studies in German production forests show in general low amounts ranging from 3.3 m³ ha^{-1} (*MinDm*: 8 cm (Kühnel 1999)), to 33.1 m³ ha^{-1} (*MinDm*: 5 (Hessenmöller, Nieschulze et al. 2011), see also: (Erdmann and Wilke 1997, Gossner, Floren et al. 2013)).

The deadwood amount four years (regular inventory) and eight years (additional inventory) after the implementation of the deadwood enrichment strategy were distinctly higher than before the implementation of the strategy, with mean amounts of 13.5 ± 0.6 m³ ha^{-1} (regular inventory, *MinDm*: 20) and 67.9 ± 11.3 m³ ha^{-1} (additional inventory, *MinDm*: 12). These amounts, are therefore distinctly higher than in regular production forests and at single plots even reaching volumes comparable to European forest reserves (Christensen, Hahn et al. 2005) or virgin forest (Debeljak 2006). While the overall increase in deadwood at the level of the forestry district was quite remarkable, the success of meeting the specific targets differed between the stand ages. Whereas, in very old stands which were supposed to have the highest deadwood amounts the strategy mainly failed to reach the target of 40 m³ ha^{-1}, very young stands that were not part of the strategy showed a strong increase of deadwood amounts, often reaching the targets set for older stands.

The evaluation of the drivers of deadwood amounts revealed that the deadwood amounts in both years were found to be strongly influenced by stand type feature and management alike, whereas the change in deadwood amounts was only influenced by a small subset of the variables identified as drivers in both years. A comprehensive discussion of drivers with comparisons to findings in the literature can be found in Doerfler, Müller et al. (2017), here only a brief summary and discussion of the most crucial findings for the evaluation and further implementation of integrative nature conservation concepts will be given.

Deadwood amounts rely in both years strongly on the stand type and the therein occurring natural mortality, tree species composition and age structure. We see that in medium age, broadleaf forests with a high natural mortality high deadwood amounts accumulate. These findings are well supported by the literature and are related to increasing mortality with tree age (Christensen, Hahn et al. 2005, Seidling, Travaglini et al. 2014), the enrichment of deadwood at optimum rotation age, in our case 100 years (Jansson, Ranius et al. 2009), accumulation of high deadwood amounts with natural mortality (Debeljak 2006) and probably the avoidance of deadwood in stands which are susceptible to bark beetle outbreaks, in our case those dominated by spruce (Deuffic 2010). The high deadwood amounts on slopes, which can be quite steep in the research area and have often muddy conditions, can be related to a difficult management in these areas, resulting probably into less intense management compared to better accessible areas, as shown for mountainous regions (Castagneri, Garbarino et al. 2010).

Before the implementation of the strategy the reserves had a considerable effect on deadwood amounts showing the increasing development of deadwood with time of abandonment of forests (Christensen, Hahn et al. 2005). Before the implementation of the strategy the growing stock and deadwood amounts were mostly negatively correlated, however with an increase of deadwood amount at high stocks but also a large confidence interval. This relationship is therefore most probably related to a reduction of trees by harvest or natural mortality by management. Also, the management districts had a considerable effect on deadwood amounts, indicating that either the conditions of the forest, e.g. influences of historic management or the actual manager also determined deadwood amounts.

The implementation of the strategy decreased the influence of certain drivers, i.e. the management district and the reserve considerably, whereas other drivers like the stand age, tree composition and natural mortality were unaffected and remained important. The effect of the implementation of passive and active deadwood enrichment can be mainly seen in the strong influence of harvest on the changes in deadwood amounts and the increasing importance of the natural mortality as driver of deadwood amounts. In regular production forests, harvests have a negative long-term effect and a short-term positive effect on deadwood amounts (Boncina 2000, Siitonen, Martikainen et al. 2000). We see in both study years a positive influence of the harvesting intensity on deadwood amounts but only until a certain point which equals approximately the mean growing stock found in our study area. Therefore, harvests above a certain intensity seem to be leaving less deadwood compared to moderate harvests. However, the strong effect of harvest on the changes in deadwood amounts seem to reflect the implementation of the strategy much stronger than the actual deadwood amounts, indicating that the absolute amounts are still influenced by many other factors. The additionally remaining strong influence of natural mortality, despite an overall decrease and rather low rates of tree mortality compared to mature broadleaf forests (Holzwarth, Kahl et al. 2013), most likely indicates that an increasing percentage of naturally developed deadwood after the implementation of the strategy is preserved. Also, the missing effect of reserves on deadwood amounts are an indicator for the changes in the impact of the strategy. In regular managed forests the production sites show lower amounts than forests with natural development (Christensen, Hahn et al. 2005). However, in our study the deadwood amounts in production forests and reserves become more equal. We also see that the previous effect of the management districts was gone after the implementation of the strategy, indicating that all managers are contributing equally to deadwood enrichment.

4.1.2 Deadwood profile and habitat trees

The assessment of the deadwood profile gives us further insight into the success of the strategy, above the amount. It shows that the strategy promotes mainly deadwood logs which can be very easily created with harvest remnants. However, also snags, which develop only naturally and not by active creation in this strategy, were increasing. This indicates, additionally to the drivers, that a preservation of naturally developed deadwood objects was practiced.

This equal occurrence of different types of deadwood is an important finding. It shows that the strategy promotes equal habitat amounts for species that thrive on large deadwood objects, e.g. saproxylic beetles (Shea, Laudenslayer Jr. et al. 2002, Lindhe and Lindelöw 2004), or small object, e.g. fungi (Heilmann-Clausen and Christensen 2004). It also shows that after the implementation of the strategy all decay stages are represented which is important to promote fresh deadwood colonizing species but also the community of decayed deadwood. The combination of retention and active enrichment therefore promotes not only high amounts but also a large variety of deadwood structures which could have been missing if the enrichment would have focused only on fresh harvest remnants since a short time span (Stokland 2001).

However, we see that especially old snags and small diameter stumps and snags are missing within the profile. Whereas small cut stumps are rather rare because harvests occur more likely at larger diameters and small stumps decay fast, small snags are very prone to fall over. Old snags are nevertheless important habitats for breeding and foraging of birds (Hallett, Lopez et al. 2001, Arnett, Kroll et al. 2010), making the recent preservation of large habitat trees important since they develop towards more stable and long lasting habitat trees and snags.

Despite a very strong increase of deadwood amounts and their characteristics, with strong indicators of a sufficient contribution of naturally developed deadwood, living trees with microhabitats decline. The comparable assessment of trees with microhabitats is considered to be much more difficult than for deadwood amounts which are easier to detect and to quantify. However, we preselected structures which are easy to recognize, leaving out e.g. water filled holes or single deadwood branches to avoid sampling error. It is possible that some of these structures may have been overlooked in 2014, but this is unlikely to explain the decrease in habitat tree numbers. On the other side were we not able to identify possible other reasons for a decline in habitat trees, especially since many trees were lost in the reserves and not in the production forests, making harvests as cause for the declining number in habitat trees unlikely. The abundance of trees with cavities is increasing with a strong DBH and also higher on broadleaf trees (Larrieu, Cabanettes et al. 2014), both factors which are found to be increasingly present after the implementation of the strategy (Appendix K, Figure K1). Therefore, it is possible that the considerable lower number of habitat trees, as well as the natural mortality, which was also considerable lower in the second sampling period, were resulting from parameters, i.e. historic management or disturbance events that could not be covered without a real time series. Further on, it would be important to examine if the actual number of the single microhabitats, here summarized as habitat trees, are sufficient to support viable populations, especially of birds, which show distinct thresholds in their abundance towards the number of trees with cavities (Kanold, Rohrmann et al. 2008).

Overall, the implementation of the strategy results into an enrichment and more equal distribution of different types of deadwood objects. A longer implementation of this strategy should therefore result into a very even distribution of all kind of habitats necessary for saproxylic species. However, it would be important to analyse what influences the number of habitat trees and the tree mortality on a larger scale to control for factors possibly influencing the future outcome of the strategy.

4.2 Chapter B) Description of biodiversity before and after the implementation of the strategy

The here examined taxonomic groups developed differently between the years 2004 and 2014, with the overall results indicating that both the Gamma- and the Alpha-diversity were not increasing as expected but stagnating or decreasing.

Since this is not in line with the results of chapter C), that indicated a distinctly positive effect of deadwood enrichment on multidiversity and species numbers of saproxylic species, we assume that the negative development in single taxonomic groups is not related to the implementation of the management strategy but rather an effect related to the study year. The absolute species numbers from studies relying on only single-year sampling campaigns instead of a regular monitoring need to be considered carefully, especially if species groups with highly interannual variance in abundances and species numbers are examined, especially limiting the comparability to species numbers and abundances found by previous studies.

The higher abundances of beetles and lower abundances of fungi in the first sampling period with a reverse pattern in the second sampling period indicates an effect of the weather. Since the actual sampling years were quite comparable concerning temperature and precipitation (Appendix A, Figure A1), we assume that the dry and warm conditions in the summer before the first sampling year had an effect. Warm and dry conditions provide favorable conditions for the development of saproxylic beetles (Preisler, Hicke et al. 2012), whereas fungi develop better in moist conditions and are less influenced by the temperature (Bässler, Müller et al. 2010). In the year before to the second sampling period, higher precipitation and lower temperatures (Appendix A, Figure A1) provided good conditions for fungi but less favorable conditions for beetles.

The big differences in Alpha- and Gamma-diversity of beetles and fungi shows how important it is to compare not only one group but different groups to properly interpret what the single groups are responding to. The diverging development over the study period also indicates that the examined taxonomic groups might be suitable indicators for further evaluations of integrative management beyond deadwood enrichment.

Saproxylic beetles and fungi are often used to assess the impact of management (Gibb, Pettersson et al. 2006, Berglund, Jönsson et al. 2011, Blaser, Prati et al. 2013, Gossner, Lachat et al. 2013, Bouget, Parmain et al. 2014). Due to the high mobility of most species they can react quickly to changes in their habitat. However, they are also highly variable within and between years (Grove and Forster 2011), making direct comparisons of single sampling periods difficult.

Birds are often used to assess the naturalness of forests, e.g. the abundance of breeding holes or snags (Bütler, Angelstam et al. 2004, Kanold, Rohrmann et al. 2008, Moning and Müller 2009, Begehold, Rzanny et al. 2015). Due to a high number of studies concerning birds, detailed information on their breeding and feeding habitats and the dependence of single species on certain structures, e.g. nesting holes exists. However, studying their response to plot-wise assessed data is limited because of their high mobility making it possible for them to use larger areas as the other studied taxonomic groups, while also increasing the possibility of recording them by chance. Single bird species are also found to respond negatively towards management, e.g. forest roads, what could allow an indirect assessment of changes in disturbance intensity for a further evaluation of the strategy.

The use of plants as indicator has a long tradition, especially in Germany. The very detailed characterization of single species with Ellenberg indicator values (Ellenberg, Weber et al. 1992) make them a valuable tool to reveal changes in the abiotic environment. Plants display a rather large group of species with distinct habitat requirements. Especially in forests their diversity is strongly affected by local disturbances, e.g. by the use of heavy machines. A high plant richness in forests can therefore indicate influences by management practices considered as negative, i.e. the introduction of alien or non-native plants (Schmidt 2005). Although, our results indicate that plant diversity is independent from deadwood amounts a further analysis could reveal additional effects of the integrative management besides deadwood enrichment, including soil disturbance, change in light availability or nutrients by deadwood enrichment.

The use of true bugs as indicators is limited due to the restricted availability of information on them compared to the other studied groups. However, the analysis show that true bugs contribute strongly to biodiversity in the forests. Furthermore, they show high variation between 2004 and 2014, not as a result of a decrease in species but of a high turnover and many species occurring as singletons. True bugs are found to be strongly related to the structural diversity of the stand, the light availability, the abundance or patch size of certain tree species (Müller and Goßner 2007) and a high diversity of tree species (Sobek, Gossner et al. 2009). As for plants, a further analysis on the changes in the community of true bugs could reveal additional effects of the implementation of the integrative strategy, not by deadwood enrichment but by changes in the tree mixture or in the harvesting regime.

Despite some drawbacks concerning our methods the temporal close assessment (10 years) made it possible to coordinate the previous and the recent sampling procedures very precisely and even largely employ the same people as in the first sampling campaign or people very familiar with the sampling procedures of the experts in the first sampling campaign. This proved to be very valuable and underlines the importance of strict sampling protocols, a good documentation of sampling and permanently marked plots. The results also show how important regular monitoring is for the evaluation of certain taxonomic groups.

To assure that the findings, especially within birds and beetles are no legacies of the past and that Gamma diversity can recover when the key habitats exist a continuous monitoring of the here examined taxonomic groups would be advisable.

4.3 Chapter C) Relation between changes in biodiversity and deadwood enrichment

Our study confirms the overall positive effect of deadwood enrichment on biodiversity, found in experimental studies (Vanha-Majamaa, Lilja et al. 2007, Gossner, Floren et al. 2013, Seibold, Bässler et al. 2015). Especially, saproxylic multidiversity and saproxylic beetles and fungi showed a strong positive response to deadwood enrichment. This suggests that higher resource availability increases biodiversity, because more resources allow rare species to persist beside dominant species (More Individual Hypothesis (Srivastava, Cadotte et al. 2012)). In addition, to the positive effect of the increasing deadwood amounts, experiments also show that the responses of species can depend more on the enrichment of deadwood diversity than on the actual amount of deadwood because of an increase in niches (Seibold, Bässler et al. 2016, Seibold, Bässler et al. 2017). This is because more diverse resources provide more niches which increases biodiversity (Resource Heterogeneity Hypothesis (Hutchinson 1959)). As changes in deadwood amount and deadwood diversity highly correlate in our study (Appendix N, Figure N1), these effects cannot be disentangled. However, since both: the amount and the diversity of deadwood are found to influence forest biodiversity (Seibold, Bässler et al. 2016) an integrative strategy that includes the concurrent enrichment of both aspects of deadwood should be at any rate successful.

Cavity-breeding birds were the only saproxylic group that did not respond to deadwood enrichment in our study. Also other studies found deadwood amounts to be not the main drivers of bird richness (Thorn, Werner et al. 2016), either because other factors were important or because individuals operate on large scales compared to other taxonomic groups. However, experimental enrichment of deadwood in an Australian red gum forest shows that the enrichment of deadwood logs can increase the abundance of single bird species over long periods of time (Mac Nally, Horrocks et al. 2002, Mac Nally 2006). This indicates that an analysis of the development of single species could reveal a stronger insight into the effects of integrative management on birds. Most experimental studies examining the relationship between deadwood enrichment and birds focus on the enrichment of actively created snags, which are used for breeding or foraging. The enrichment of snags can increase the number of breeding events, especially in managed forests (Arnett, Kroll et al. 2010, Kroll, Duke et al. 2012). In our study, the main enrichment of deadwood is due to an enrichment of logs which is possible not the limiting resource for birds, which profit rather from increased potential nesting sites. Therefore, an enhanced creation of large snags and protection of old trees could be beneficial for the promotion of avian biodiversity.

Non-saproxylic species were not affected by deadwood enrichment. Hence, our findings are partly contradictory to experimental studies that found non-saproxylic taxa to respond positively (phytophagous beetles (Toivanen and Kotiaho 2007)) or negatively (plants (Laarmann, Korjus et al. 2013)) towards deadwood enrichment (Seibold, Bässler et al. 2015). The response of non-saproxylic species towards deadwood enrichment found in different experiments is often hypothesized to be not related to deadwood amounts directly, although deadwood could also be used as shelter (Toivanen and Kotiaho 2007). Deadwood enrichment is also often related to a change in light availability (Burrascano, Lombardi et al. 2008) or increasing resources such as litter that are related to tree mortality (e.g. Toivanen and Kotiaho 2007). Since the relationship of deadwood amount and light availability does not exist in our case this could explain the absent relationship of non-saproxylic taxa and deadwood enrichment.

4.3.1 Development related to other habitat variables

Not only in production forests but also in unmanaged old-growth forests, deadwood enrichment is usually associated with an increase in light availability due to gaps in the crown after harvest or due to natural tree death (Burrascano, Lombardi et al. 2008). Gaps in unmanaged beech forests are determined by small scale disturbances (Kenderes, Mihok et al. 2008, Rugani, Diaci et al. 2013) and beech is very effective in closing canopy gaps (Zeibig, Diaci et al. 2005). Therefore, the effects of single felled or naturally dead trees can be minor and short-termed in beech forests. The removal of single trees, as exclusively practiced since the implementation of the strategy, in combination with recently increasing growth trends (Pretzsch, Biber et al. 2014) should therefore lead to small numbers and sizes in gaps. The canopy cover here studied after ten years did not change much on average. Experimental studies and studies on old growth forests show that saproxylic taxa such as beetles (Seibold, Bässler et al. 2016) and fungi (Brazee, Lindner et al. 2014) and non-saproxylic taxa like plants (Burrascano, Lombardi et al. 2008) respond positively to canopy openings which could not be confirmed by our study. One reason for the lack of effect in our study could be that within the production forest the canopy openings resulted from recent disturbances by harvests (previous winter). The time periods after the canopy opening in the production forest were therefore very short which could be a reason why species could not react so far. Another reason could be that gaps, caused by the harvest of individual trees are generally small, which is why the amount of light arriving at the forest floor is too low to have an effect. In forest nature reserves, major gaps occurred through a windthrow in 2011. The affected area had very high deadwood amounts and a total disappearance of tree crowns. However, only one plot fell directly into the windthrow area. The other parts of the reserves were rather shaped by openings that occurred due to single senescent trees. Therefore, this one intensely sun affected plot, where no crown was left, might have very intense conditions which did not promote biodiversity outstandingly because the deadwood was too dry to foster a high biodiversity. The other two plots affect by the windthrow had still a certain amount of crown. However, these plots were not majorly outstanding in terms of biodiversity either, indicating possibly a maximum amount of deadwood for the increase in biodiversity. Canopy opening had a minor positive effect on birds, which are shown to respond quickly to creation of gaps with different communities occurring in gaps compared to forest with dense cover (Greenberg, Tomcho et al. 2007, Thorn, Werner et al. 2016). An increased availability of canopy gaps could therefore be beneficial for the diversity and species numbers of birds.

4.3.2 Effects of changes in cavity bearing trees

The number of cavity bearing trees decreased between the study years and we could only find a minor effect of the changes in habitat tree numbers per plot on saproxylic biodiversity. The numbers of cavity bearing trees resembles numbers found in French, Swiss and German unmanaged mountain mixed forests (Larrieu, Cabanettes et al. 2012). Since tree cavities harbor a high biodiversity ranging from several families of insects onto birds and even mammals (Stokland, Siitonen et al. 2012) they are proposed as indicators for forests naturalness (Winter and Möller 2008) and their promotion is therefore a necessary part of nature conservation strategies. Microhabitats such as rot holes, trunk cavities and woodpecker holes develop predominantly through damages that allow an infection with fungus and a further breakdown of woody material by insects (Stokland, Siitonen et al. 2012). Their formation is related to the characteristics of the tree, with e.g. large diameter trees and beech having higher number of cavities (Larrieu, Cabanettes et al. 2012). Therefore, ten years of implementing the strategy might not be enough time to promote cavities since it is not enough time to promote trees which can develop these. However, the small effect of cavity-bearing trees on saproxylic multidiversity, which becomes more pronounce where only production forests are considered, indicates a success also of the retention of habitat trees, which could become more pronounced when the implementation of the strategy is continued. Actively created holes by using a chainsaw can be a substitute for naturally developed holes for some species (Zapponi, Minari et al. 2015). However, this is a very time and labor intensive method and primarily unsuitable to be applied over a whole forestry department. The most applicable way to protect species which are dependent on cavity bearing trees would therefore be a continued long-term application of a careful selection of trees being preserved from harvest.

4.4 Chapter D) Relationship of assembly mechanisms and deadwood enrichment

The analysis of assembly pattern is proven to show impacts of management than cannot be seen if only species richness is analyzed (Bässler, Ernst et al. 2014). Furthermore, Assembly pattern can help to understand the mechanisms determining local species richness (Thorn, Bässler et al. 2015). Studies show that management intensity has a major impact on the assembly of species of different taxonomic groups. Practices like salvage logging and clear cuts significantly change assembly pattern (Thorn, Bässler et al. 2015, Heikkala, Seibold et al. 2016). Integrative measures with green tree retention and prescribed burning cannot distinctly diminish this (Heikkala, Seibold et al. 2016). This could be due to the fact that retention measures in clear-cuts still include a huge decrease in resources and a strong impact on the environment even when the retention patches are big (Gustafsson, Kouki et al. 2010). A significant increase in resources could therefore have a very different impact than retention forestry.

We found that the effect of deadwood enrichment on the assembly was dependent on the examined taxonomic group. Saproxylic beetles, which were in general inclined towards clustered assemblies, showed a significant development towards overdispersion with deadwood enrichment. The assembly of saproxylic fungi, birds or plants did not change with deadwood enrichment. The changes in the canopy cover did not have an influence. However, birds, plants and saproxylic fungi communities were strongly influenced by the assembly mechanism before the implementation of the strategy.

We expected the saproxylic species, i.e. beetles and fungi to react similarly towards deadwood enrichment due to their similar increase of species numbers with increasing deadwood amounts. The different response of saproxylic beetles and fungi communities could therefore be caused by the different mechanisms that shape their communities, i.e. competition or environmental filtering.

Fungi are shown to be able to utilize even small diameter deadwood very well (Heilmann-Clausen and Christensen 2004), making also harvest remnants a valuable habitat for them. This and the high values for the ses mpd could be an indicator that saproxylic fungi species cover wide niches. The wide niches should result into a stronger overlap of niches and higher competition in general, forcing the species in the community to become more different.

Saproxylic beetles however, tend towards a clustered assembly, indicating that at low deadwood volumes only species with certain functions exist and that niches are therefore not strongly overlapping. For example, a correlation between the, in this study omitted, niches traits and body size shows that large species live preferably in larger diameter deadwood. Thus, deadwood size and consequently amount, which increase the body size of beetles (Gossner, Lachat et al. 2013), can also be an environmental filter on the assembly of saproxylic beetles.

The response towards deadwood enrichment would therefore have a different influence on communities shaped by different mechanisms. Whereas saproxylic communities shaped by strong competition stay shaped by competition, communities which are more shaped by environmental filtering become more overdispersed and stronger shaped by competition.

Next to an indication for an increase of bigger deadwood objects the increase in larger saproxylic beetles could also show that the enrichment of deadwood influences the necessity for long distance dispersal. The body size is often related to the dispersal ability, e.g. with decreasing body size on intensely used grasslands (Simons, Weisser et al. 2016). The increase in larger species could therefore indicate that with deadwood enrichment the community of saproxylic beetles is less dependent on dispersal. The increase in mycetophagous beetles could then be related to a shift of the food resources by higher abundances of fungi with increasing deadwood amounts.

For saproxylic fungi, species with larger spores, asexual reproduction and without hardened, lasting skeletal hyphae increased with increasing deadwood amounts. These traits can indicate an increase of species which are less determined by dispersal but adapted to a fast colonization of habitat. Whereas, the spore volume can indicate species with lower dispersal ability (Bässler, Ernst et al. 2014), fruiting bodies of fungi without skeletal hyphae become less hard and are therefore probably short living. Additionally, asexual reproduction can enable fungi to colonize a large and uniform amount of habitat quickly (Pugh 1980). The increase in species with these traits could therefore indicate, as for the beetles, that with deadwood enrichment the necessity of dispersal decreases and that the communities shift towards species more adapted to large, better connected and long-lasting deadwood amounts.

The independence of plants and birds of the here applied deadwood enrichment which was already shown in Chapter C) is here supported.

The attempt to test an increasing niche diversity with increasing deadwood amount and diversity proved no additional explanation of the mechanisms shaping the community. We used the deadwood diversity calculated from decay categories, different types of objects, deadwood diameter, tree species and sun exposure as explanatory variable. This shows that the changes in deadwood diversity cannot explain considerably more variance than deadwood amount alone (Appendix V, Table V1). These results most probably indicate that the calculated deadwood diversity does not reflect the niche diversity present. The assessment of deadwood diversity is quite a difficult task. During extensive inventories of deadwood only characteristics per object, i.e. one decay stage or diameter per object can be assessed. However, a comprehensive analysis of the conditions of single deadwood objects would also include the heterogeneity of the object itself, resulting e.g. from the contact of the lower part to the soil or the growth of epiphytes on the upper surface.

Whereas saproxylic beetles responded strongly towards deadwood enrichment, saproxylic fungi, plants and birds showed a strong positive relation with the previous assembly mechanism and partly even an increase of the previous assembly mechanism. This could indicate that the assembly were quite stable on these plots and no additional filters are imposed on the communities, indicating long lasting individuals or site loyalty in this communities.

The effect of canopy changes which determine the changes in light availability had no influence on the assembly and only influenced the propagation of plants, with an increasing abundance of predominantly vegetative propagating plants in darker conditions. Since other studies found a strong difference of sun exposed and shaded deadwood (Seibold, Bässler et al. 2016) this is another indicator for the low impact of canopy gaps in the here studied forests. The gaps present in the here studied forests are possibly small and short living and a gap would therefore not necessarily mean the occurrence of sun exposed deadwood as in experiments (Seibold, Bässler et al. 2016).

The approach of the combination of functional and phylogenetic dissimilarities presents a good way to reveal the prevalent assembly mechanisms of communities by avoiding the pitfalls of using the single dissimilarity measures alone. However, most of the here examined groups did not show an intermediate but rather a low or a high value of a. Therefore, either functional or phylogenetic distance but not both explain the dissimilarities among species with deadwood enrichment best.

Whereas for the other groups the sampling design allowed a comparison of differences between the years the results of saproxylic fungi could also be influenced by the subset that was used to make the community of fungi more comparable. Due to the subset, the evaluated fungi comprise only a certain proportion of the actual assembly. Next to the drawback that the assessment of macroscopic fruiting bodies can already miss a considerable amount of the actual present but invisible diversity of fungi, the subset reduces the community further on. Although this actually enables the comparison of our fungi data it (1) might also exclude certain types of species which are short living and (2) exclude certain traits like the size of the fruiting body which might be important for the fast colonization of deadwood after its enrichment, since this is a trait being strongly related to short living habitats comprised by harvest remnants (Bässler, Ernst et al. 2014). Therefore, an additional evaluation of the possible exclusion or traits in the subset and what determines the assemblies in the single years would be important to strengthen the results.

4.5 Discussion on general drawbacks of the study

The datasets we analyzed offered a good opportunity to study the direct, short term effects of an integrative strategy, including the effect on an important part of the forests' biodiversity.

The continuous records of deadwood and the living stand by the assessment of single trees in the regular inventory were an important source of information with many replicates. However, the large number of replicates implied small sampling circles and large thresholds for the deadwood inventory which limits the possibility for a comprehensive analysis. However, the additional inventory also showed that a more comprehensive assessment is difficult for a set of plots used in the regular inventory. Although, the additional inventory proved to be much more detailed even here we see drawbacks of the assessment of deadwood diversity. Also, the assessment of habitat trees proved to be a difficult task, despite a training before the assessment. Since it is not definite if there was an error within the sampling we cannot rule out that the decline in habitat trees is present and might be, e.g. due to lower abundances of trees with microhabitats in general or if it is caused by a sampling error.

The here studied taxonomic groups cover only a small percentage of the actual forests' biodiversity. However, the different characters of the examined species groups offer good indicators for several possible effects of the strategy, complementing each other. It also shows that the examined species groups are not only influenced by deadwood amounts. Plants, although easy to assess are not be primarily influenced by the strategy. Beetles and fungi, which are targeted species groups seem to be very sensible towards fluctuating weather. Birds are possibly more influenced by changes in the landscape then at the plot level (Paillet, Berges et al. 2010). Additionally, the available information of the species groups, such as phylogenies and traits differed, which strongly limited their evaluation, especially for true bugs. Another strong drawback of this study was the singular assessment instead of a monitoring in shorter time periods, which proved to be a strong influencing factor, making a direct comparison difficult.

4.6 Implications for management

Given the low availability of deadwood-related habitats in many production forests the enrichment of deadwood is often suggested to promote biodiversity. Our results show that the enrichment of deadwood in the framework of an integrated conservation strategy is achievable within a short timeframe in production forests. Therefore, this strategy can substantially promote biodiversity when implemented on a larger scale. Our results also show that an increasing mosaic of gaps in the canopy and closed canopies could further improve the impact of deadwood enrichment. The analysis of drivers of deadwood amounts shows that a promotion of tree mixtures with a high percentage of broadleaf tree species and a high diversity in trees would strongly promote the success of strategies. We also have indication that some species rely more on the small-scale reserves which are by now not so different anymore in deadwood amounts but do not have any management. Therefore, a comprehensive nature conservation would still include areas reserved for the natural development of forest.

4.7 Future directions

In general, the evaluation of integrative strategies is lacking in many parts. This is strongly related to the big variety of existing strategies. Whereas certain types of strategies such as green tree retention are evaluated quite extensively, with large reviews summarizing the results of several studies (Gustafsson, Kouki et al. 2010, Gustafsson, Baker et al. 2012) other approaches, especially in temperate regions, are missing evaluation. In Germany, the organization into federal states, which determine the implementation of conservation concepts, complicates the evaluation further since the strategies vary in their proposed measures and are therefore difficult to compare. Additionally, the provision of the results for an international scientific community is also often lacking. Since Germany is one of the leading industrial nations the government should not only focus on a more comprehensive implementation of conservation measures but also on a better communication and evaluation of the existing strategies.

The here examined strategy is strongly focused on beech forests, but the main forest types in Germany are still spruce and pine forests, also on localities where it does not occur naturally. Therefore, it would be important to further on develop strategies for these forest types. These strategies would most probably look very different, since especially spruce is vulnerable to bark beetles which can be promoted by deadwood enrichment. However, the country wide effect of integrative management could strongly be influenced by a comprehensive implementation of integrative measures, since the success of integrative management is not only dependent on the successful implementation in one large department but on a landscape-wide improvement of forestry measures.

Another factor is that, although state forest companies manage a large proportion of the existing forest, especially in Bavaria, most of the forests is in private hand. A comprehensive implementation of integrative measures would therefore need to include those. This would bring the necessity to develop strategies how people can be motivated to implement integrative measures, how their fear towards possible negative influences can be countered and how possible compensatory payments can be organized. Additionally, the implementation of strategies in private owned forests would be difficult since the forests of single owners are often very small and the implementation could therefore be less effective. Further on, the monitoring of effects could be more difficult since private forests do not comprise such a close network of permanent study plots as in the state forests. Strong cooperation with forest owners would therefore be inevitably.

To further improve overall integrative strategies, it would be sensible to compare the effects of different strategies, i.e. retention, pure separation and the here combined active and passive enrichment of habitats. This could also contribute to the question how large reserves within a landscape with integrative management need to be to protect biodiversity, especially of those species which need special conditions and low disturbances.

5. Conclusion

Since most of the forests are intensely managed in Central Europe but also worldwide integrative approaches are a good extension of segregation approaches. The here examined strategy proved to be a fast and efficient way to enrich structures with integrative measures in a production forest. The promotion of broadleaf forests could further on substantially improve integrative measures focusing on deadwood enrichment. Due to the enrichment of a high diversity of deadwood characteristics the strategy substantially improves habitat conditions for saproxylic organisms, here represented by fungi and beetles and does not negatively affect the diversity or assemblies of non-saproxylic organisms. The strategy is therefore a valuable tool for biodiversity conservation and promotion in the respective forest. A further implementation can improve habitat conditions by an increase of the amount, diversity and connectivity of the habitat.

6. Literature

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Study Statement

This thesis contains four Chapters, with parts of part A) already published. Contributions of people to this thesis are given below:

A)
Inken Dörfler, Jörg Müller, Martin M. Gossner, Benjamin Hofner, Wolfgang W. Weisser
ID, WWW, JM and MMG conceived the idea for the manuscript, BH contributed to the statistics, those parts that were published were edited by WWW, JM and MMG. Statistics and writing was done by ID.

B)
Inken Dörfler, Wolfgang W. Weisser
ID and WWW conceived the idea. Statistics and writing was done by ID.

C)
Inken Dörfler, Jörg Müller, Martin M. Gossner, Sebastian Seibold, Wolfgang W. Weisser
ID, WWW, JM and MMG conceived the idea for the manuscript, WWW, MMG and SS contributed to the statistics. Statistics and writing was done by ID.

D)
Inken Dörfler, Jörg Müller, Martin M. Gossner, Wolfgang W. Weisser, Sebastian Seibold
ID and SS conceived the idea and compiled the statistics. Statistics and writing was done by ID.

Appendix Index

Appendix U: Results of the optimal linear model with the standardized effect size of the mean pairwise functional-phylogenetic distance for the difference in canopy cover and the previous assembly

Appendix V: Results of the optimal linear model for the standardized effect size of the mean pairwise functional-phylogenetic distance testing the effect of deadwood diversity

Appendix A: Weather in Ebrach

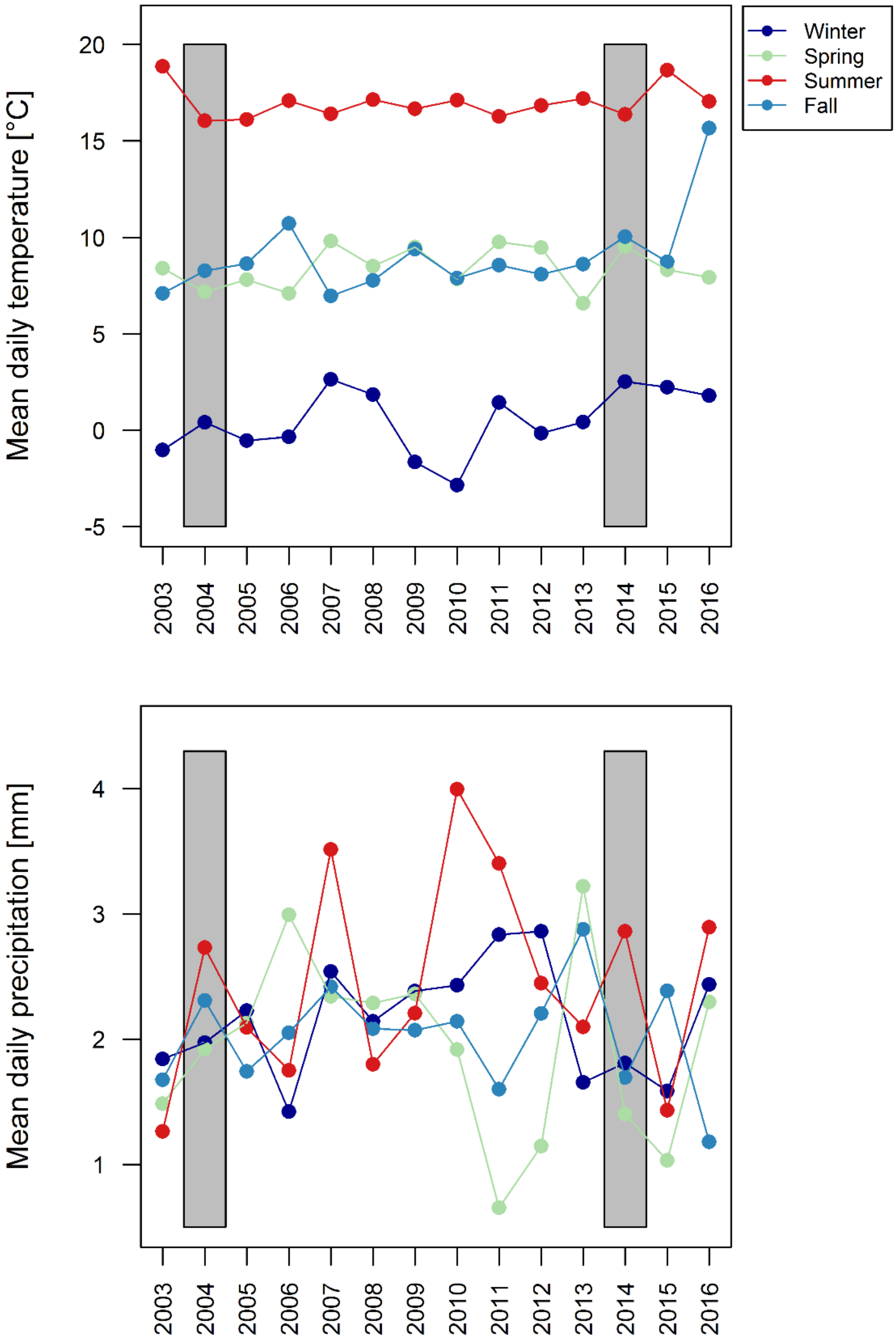

Figure A1: Mean daily temperature and precipitation in the years 2003 until 2016. The points mark the respective mean temperatures per season and year. The grey bars mark the sampling periods.

Appendix B: Illustration of the nature conservation strategy

Figure B1: Illustrations of the deadwood enrichment strategy in the forestry district Ebrach, Germany. The upper pictures show a stem and tree crown left as deadwood in the forest after harvest, i.e. active enrichment with harvest remnants. The lower pictures show enrichment by retention and the windthrow area in the nature forest reserve.

Appendix C: Details on the measurements and calculation of variables in the living stand and deadwood inventories

Table C1: Diameter classes used for the grouping which is applied for height measurements in the forest inventory data table per plots

Class	DBH
1	0 - 6.9
2	7 - 11.9
3	12 - 17.9
4	18 - 23.9
5	24 - 29.9
6	30 - 35.9
7	36 - 41.9
8	42 - 47.9
9	48 - 53.9
10	54 - 59.9
11	≥ 60.0

Calculation of basal area per tree in the regular inventory

For each tree, the basal area g (in m^2) was calculated using the DBH (Zöhrer 1980). The factor 0.01 accounts for the fact that the DBH is measured in cm.

(C-Eq. 1) $$g = (\pi * DBH * 0.01)^2 / 4$$

Calculation of volume per tree in the regular inventory

The volume V (in m^3) of a tree was calculated based on its DBH, the height (taken from the measurement of the respected tree per class) and diametral quotients (C1-C9) (Kennel 1973). The diametral quotients we used are specific for solid wood and were established by Kennel (1973), based on measurements of trees in Bavaria. These quotients are specifying the taper of the stem while correcting the volume of a cylinder-shaped tree. They are species-specific and given for different diameter and heights. We used this quotients implemented in the R-function v.GRI by Biber (Personal communication). This function calculates the form height (fh) using the nine given timber wood factors by Kennel (1973) for the specific tree species, the DBH and the height of the tree (C-Eq. 2 – C-Eq. 4).

(C-Eq. 2a) $$A1 = C1 + C4 * \log(DBH) + C7 * \log(DBH)^2$$

(C-Eq. 2b) $$A2 = C2 + C5 * \log(DBH) + C8 * \log(DBH)^2$$

(C-Eq. 2c) $$A3 = C3 + C6 * \log(DBH) + C9 * \log(DBH)^2$$

(C-Eq. 3) $$fh = \exp(A1 + A2 * \log(height) + A3 * \log(height)^2$$

(C-Eq. 4) $V\ [m^3] = (\pi / 4 * 10{,}000) * DBH^2 * fh$

The denominator is multiplied with 10,000 to account for the DBH in cm and the height in m.

Literature Appendix C:

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Appendix D: Deadwood assessment in the regular and the additional inventory

Plausibility checks

For the data of the deadwood inventory within the regular inventory we controlled for valid values. All objects with measured values below the minimum that was defined for the measurement (diameter < 20 cm and height < 1.3 m) were deleted. All plots that showed measured values above a possible limit of the height (45 m) were deleted. Trees with a height/diameter relationship below 0.3 were classified as broken snags even if they were classified as snags in the inventory data. To make sure that the deadwood volume in the regular and additional inventory, in both years was calculated in the same way, we recalculated the deadwood volume using the same method for all object types, as described in the main methods part.

Volume calculation snags

The standardized method of the Bavarian State forestry uses diametral quotients to calculate the volume V (in m^3) of snags. Therefore, the volume for snags in the regular inventories (DBH ≥ 20 cm, height ≥ 1.3m) and snags, complete lying trees and living trees which are recorded as habitat trees in the additional inventory (DBH ≥ 12 cm) were calculated as for living trees (C-Eq. 2 – C-Eq. 4, Appendix C). The diametral quotients were taken from Kennel (1973). These quotients are implemented in a R-function by Biber (Personal communication). This function uses the quotient of Kennel (1973) to calculate the volume of a stem specific for the tree species, the diameter and the height of the tree (Appendix C). Since spruce and beech are the most common coniferous and broadleaf tree species we used the quotients for these species for coniferous and broadleaf deadwood.

Volume calculation logs, broken snags, stumps, scattered FWD and crowns

To calculate the volume (V, m^3) of logs and broken snags in the regular and additional inventory (regular: DBH ≥ 20 cm, height ≥ 1.3m, additional: D_m or DBH ≥ 12 cm) as well as stumps, scattered FWD and crowns ($D_m \geq 12$ cm) in the additional inventory, we used the formula for the volume of a cylinder, based on the diameter in the middle of the object (D_m, cm) and the height (H, cm).

(D-Eq. 1) $$V\,[m^3] = (\pi * (D_m * 0.01)^2) / 4 * (H * 0.01)$$

The diameter in the middle of the object (D_m, cm) was calculated from the DBH. Logs (regular inventory) and broken snags (regular and additional inventory) were measured at 1.3 m length. Therefore, we first calculated the diameter at the bottom of the stem (D_b, cm) by adding 1.3 cm to the measured DBH using the assumption that the diameter of the stem decreases by 1 cm at 1 m height or length to the top.

(D-Eq. 2) $D_b = DBH + 1.3$

With the D_b we calculated the D_m subtracting half of the height or length of the stem from the D_b. To account for the loss of 1 cm in diameter per 1 m height or length we converted the Height (H, cm) to meter.

(D-Eq. 3) $D_m = D_b – (H * 0.01) * 0.5$

Volume calculation root plates

The volume of root plates in the additional inventory was calculated with the formula of a disc.

(D-Eq. 4) $V = (\pi * (D_m * 0.01)^2) / 4$

Deadwood volume for the models

Deadwood volume per plot was calculated by adding up the volume values for the single deadwood objects and extrapolate those to one hectare.

Height of dead trees in the additional inventory in 2004

In the additional inventory in 2004 the height of complete standing dead trees was calculated with the Pettersson curve (Kramer and Akça 2008). The regression coefficient a_0 and a_1 are values derived from a form factor for the stand height specific for the Steigerwald.

(D-Eq. 5) $H\,[m] = 1.3 + (DBH\,[cm] / (a_0 + a_1 * DBH\,[cm])^3$

Literature Appendix D:

Biber, P., Personal communication 2016. R-function v.GRI, personal communication. In, Freising.

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Appendix E: Species list

Table E1: List of species used in the study, with their taxonomic group, species name and abundances per sampling year. Species in bold are considered as saproxylic in this study.

Taxon		Species	2004	2014
Beetles	1	Agriotes acuminatus	23	15
Beetles	2	Agriotes obscurus	1	0
Beetles	3	Agriotes pallidulus	13	11
Beetles	4	Agriotes pilosellus	43	32
Beetles	5	Agriotes sputator	1	0
Beetles	6	Agrypnus murinus	1	3
Beetles	7	Altica lythri	0	1
Beetles	8	Anthonomus phyllocola	1	7
Beetles	9	Anthonomus rectirostris	1	0
Beetles	10	Athous haemorrhoidalis	13	36
Beetles	11	Athous subfuscus	171	138
Beetles	12	Athous vittatus	109	62
Beetles	13	Aulacobaris coerulescens	0	1
Beetles	14	Brachonyx pineti	1	0
Beetles	15	Bradybatus kellneri	0	2
Beetles	16	Cardiophorus ruficollis	1	0
Beetles	17	Cassida vibex	0	1
Beetles	18	Ceutorhynchus napi	2	0
Beetles	19	Ceutorhynchus pallidactylus	9	0
Beetles	20	Ceutorhynchus typhae	1	0
Beetles	21	Chaetocnema concinna	1	2
Beetles	22	Chaetocnema hortensis	0	4
Beetles	23	Cionus tuberculosus	0	5
Beetles	24	Coeliodes rana	0	1
Beetles	25	Cryptocephalus pusillus	0	1
Beetles	26	Cryptocephalus sexpunctatus	0	1
Beetles	27	Curculio betulae	0	1
Beetles	28	Curculio glandium	17	4
Beetles	29	Curculio venosus	1	0
Beetles	30	Curculio villosus	1	0
Beetles	31	Dalopius marginatus	114	140
Beetles	32	Ectinus aterrimus	5	0
Beetles	33	Gonioctena decemnotata	1	0
Beetles	34	Gonioctena interposita	8	0
Beetles	35	Gonioctena quinquepunctata	1	3
Beetles	36	Gonioctena viminalis	1	0
Beetles	37	Hemicrepidius hirtus	0	1
Beetles	38	Hypera meles	1	9
Beetles	39	Hypera nigrirostris	4	5
Beetles	40	Hypocassida subferruginea	0	1
Beetles	41	Longitarsus curtus	2	0
Beetles	42	Longitarsus pratensis	0	1
Beetles	43	Longitarsus tabidus	1	0
Beetles	44	Mogulones asperifoliarum	1	0
Beetles	45	Orchestes fagi	205	317
Beetles	46	Orchestes rusci	0	1
Beetles	47	Orchestes testaceus	0	1
Beetles	48	Orsodacne humeralis	1	0
Beetles	49	Otiorhynchus singularis	2	0
Beetles	50	Oulema gallaeciana	5	5
Beetles	51	Oulema melanopus	5	0
Beetles	52	Pheletes aeneoniger	3	6
Beetles	53	Phyllobius arborator	2	0
Beetles	54	Phyllobius argentatus	60	106
Beetles	55	Phyllobius glaucus	3	2
Beetles	56	Phyllobius pomaceus	1	0
Beetles	57	Phyllobius pyri	1	0
Beetles	58	Phyllotreta atra	2	3
Beetles	59	Phyllotreta christinae	1	0
Beetles	60	Phyllotreta vittula	2	0
Beetles	61	Plagiosterna aenea	2	0
Beetles	62	Polydrusus formosus	3	3
Beetles	63	Polydrusus fulvicornis	2	0
Beetles	64	Polydrusus impar	0	2
Beetles	65	Polydrusus marginatus	0	1
Beetles	66	Polydrusus planifrons	1	0
Beetles	67	Polydrusus tereticollis	6	7
Beetles	68	Prosternon tessellatum	2	2
Beetles	69	Rhinusa linariae	1	0
Beetles	70	Scleropteridius fallax	0	1
Beetles	71	Sericus brunneus	1	3
Beetles	72	Simo hirticornis	0	4
Beetles	73	Sitona lineatus	3	3
Beetles	74	Stereonychus fraxini	1	0
Beetles	75	Strophosoma capitatum	36	17
Beetles	76	Strophosoma melanogrammum	61	30
Beetles	77	Trichosirocalus troglodytes	1	0
Beetles	78	Tychius picirostris	2	0
Beetles	**79**	**Abdera flexuosa**	**2**	**2**
Beetles	**80**	**Abraeus granulum**	**2**	**1**
Beetles	**81**	**Abraeus perpusillus**	**7**	**5**
Beetles	**82**	**Acalles camelus**	**0**	**26**
Beetles	**83**	**Acalles echinatus**	**0**	**1**

Beetles	**84**	**Acrulia inflata**	**4**	**4**
Beetles	**85**	**Aderus populneus**	**2**	**0**
Beetles	**86**	**Agaricochara latissima**	**1**	**2**
Beetles	**87**	**Agathidium nigripenne**	**4**	**5**
Beetles	**88**	**Agrilus biguttatus**	**0**	**2**
Beetles	**89**	**Agrilus obscuricollis**	**1**	**0**
Beetles	**90**	**Agrilus olivicolor**	**1**	**0**
Beetles	**91**	**Agrilus viridis**	**3**	**1**
Beetles	**92**	**Allecula morio**	**6**	**2**
Beetles	**93**	**Allecula rhenana**	**1**	**1**
Beetles	**94**	**Alosterna tabacicolor**	**8**	**0**
Beetles	**95**	**Ampedus balteatus**	**3**	**12**
Beetles	**96**	**Ampedus erythrogonus**	**0**	**2**
Beetles	**97**	**Ampedus nigrinus**	**1**	**0**
Beetles	**98**	**Ampedus pomorum**	**27**	**30**
Beetles	**99**	**Ampedus sanguineus**	**1**	**0**
Beetles	**100**	**Anaglyptus mysticus**	**2**	**0**
Beetles	**101**	**Anaspis flava**	**1**	**0**
Beetles	**102**	**Anaspis frontalis**	**25**	**0**
Beetles	**103**	**Anaspis ruficollis**	**5**	**0**
Beetles	**104**	**Anaspis rufilabris**	**20**	**43**
Beetles	**105**	**Anaspis septentrionalis**	**0**	**6**
Beetles	**106**	**Anaspis thoracica**	**5**	**0**
Beetles	**107**	**Anisandrus dispar**	**14**	**4**
Beetles	**108**	**Anisotoma castanea**	**1**	**0**
Beetles	**109**	**Anisotoma humeralis**	**1**	**7**
Beetles	**110**	**Anisotoma orbicularis**	**2**	**0**
Beetles	**111**	**Anobium nitidum**	**1**	**0**
Beetles	**112**	**Anomognathus cuspidatus**	**5**	**0**
Beetles	**113**	**Anoplodera sexguttata**	**2**	**0**
Beetles	**114**	**Anostirus castaneus**	**6**	**5**
Beetles	**115**	**Anostirus purpureus**	**12**	**12**
Beetles	**116**	**Anthaxia quadripunctata**	**1**	**0**
Beetles	**117**	**Aplocnemus impressus**	**1**	**1**
Beetles	**118**	**Aplocnemus nigricornis**	**2**	**0**
Beetles	**119**	**Aspidiphorus orbiculatus**	**1**	**1**
Beetles	**120**	**Atheta picipes**	**1**	**0**
Beetles	**121**	**Atomaria longicornis**	**0**	**1**
Beetles	**122**	**Atomaria ornata**	**0**	**1**
Beetles	**123**	**Atomaria turgida**	**1**	**15**
Beetles	**124**	**Atrecus affinis**	**5**	**1**
Beetles	**125**	**Batrisodes delaporti**	**0**	**1**
Beetles	**126**	**Batrisus formicarius**	**0**	**2**
Beetles	**127**	**Bibloporus bicolor**	**7**	**22**
Beetles	**128**	**Bitoma crenata**	**8**	**3**
Beetles	**129**	**Bolitochara lucida**	**1**	**0**
Beetles	**130**	**Bolitochara obliqua**	**7**	**3**

Beetles	**131**	**Bolitophagus reticulatus**	**17**	**16**
Beetles	**132**	**Calambus bipustulatus**	**1**	**1**
Beetles	**133**	**Callidium violaceum**	**0**	**1**
Beetles	**134**	**Calopus serraticornis**	**1**	**3**
Beetles	**135**	**Carpophilus sexpustulatus**	**2**	**0**
Beetles	**136**	**Cerophytum elaterolides**	**0**	**2**
Beetles	**137**	**Cerylon fagi**	**14**	**7**
Beetles	**138**	**Cerylon ferrugineum**	**23**	**15**
Beetles	**139**	**Cerylon histeroides**	**1**	**8**
Beetles	**140**	**Chrysobothris affinis**	**1**	**0**
Beetles	**141**	**Cis bidentatus**	**3**	**1**
Beetles	**142**	**Cis boleti**	**17**	**10**
Beetles	**143**	**Cis castaneus**	**20**	**8**
Beetles	**144**	**Cis dentatus**	**0**	**2**
Beetles	**145**	**Cis festivus**	**2**	**15**
Beetles	**146**	**Cis glabratus**	**2**	**0**
Beetles	**147**	**Cis hispidus**	**8**	**4**
Beetles	**148**	**Cis jacquemartii**	**2**	**0**
Beetles	**149**	**Cis micans**	**7**	**15**
Beetles	**150**	**Cis rugulosus**	**3**	**0**
Beetles	**151**	**Cis submicans**	**0**	**5**
Beetles	**152**	**Clytus arietis**	**1**	**0**
Beetles	**153**	**Colydium elongatum**	**0**	**1**
Beetles	**154**	**Conopalpus brevicollis**	**2**	**0**
Beetles	**155**	**Conopalpus testaceus**	**1**	**5**
Beetles	**156**	**Corticeus unicolor**	**38**	**20**
Beetles	**157**	**Coryphium angusticolle**	**0**	**3**
Beetles	**158**	**Crepidophorus mutilatus**	**0**	**1**
Beetles	**159**	**Cryphalus asperatus**	**10**	**0**
Beetles	**160**	**Cryptolestes duplicatus**	**1**	**0**
Beetles	**161**	**Cryptophagus dorsalis**	**2**	**5**
Beetles	**162**	**Cryptophagus labilis**	**2**	**1**
Beetles	**163**	**Cryptophagus micaceus**	**0**	**9**
Beetles	**164**	**Cychramus luteus**	**42**	**0**
Beetles	**165**	**Cychramus variegatus**	**32**	**12**
Beetles	**166**	**Cyrtanaspis phalerata**	**1**	**0**
Beetles	**167**	**Dacne bipustulata**	**3**	**5**
Beetles	**168**	**Dadobia immersa**	**1**	**0**
Beetles	**169**	**Dasytes aeratus**	**0**	**1**
Beetles	**170**	**Dasytes caeruleus**	**21**	**0**
Beetles	**171**	**Dasytes plumbeus**	**10**	**3**
Beetles	**172**	**Dendrophilus punctatus**	**0**	**1**
Beetles	**173**	**Denticollis linearis**	**21**	**19**
Beetles	**174**	**Denticollis rubens**	**13**	**4**
Beetles	**175**	**Dictyopterus aurora**	**2**	**13**
Beetles	**176**	**Dinaraea aequata**	**1**	**2**
Beetles	**177**	**Diplocoelus fagi**	**2**	**2**

Beetles	**178**	**Dissoleucas niveirostris**	**1**	**3**
Beetles	**179**	**Dorcatoma dresdensis**	**6**	**2**
Beetles	**180**	**Dorcatoma robusta**	**3**	**0**
Beetles	**181**	**Dorcus parallelipipedus**	**7**	**2**
Beetles	**182**	**Dropephylla ioptera**	**0**	**1**
Beetles	**183**	**Dryocoetes autographus**	**1**	**4**
Beetles	**184**	**Dryocoetes villosus**	**1**	**0**
Beetles	**185**	**Dryophilus pusillus**	**0**	**1**
Beetles	**186**	**Echinodera hypocrita**	**1**	**4**
Beetles	**187**	**Elateroides dermestoides**	**34**	**39**
Beetles	**188**	**Enicmus atriceps**	**1**	**0**
Beetles	**189**	**Enicmus brevicornis**	**3**	**2**
Beetles	**190**	**Enicmus fungicola**	**1**	**5**
Beetles	**191**	**Enicmus testaceus**	**0**	**11**
Beetles	**192**	**Ennearthron cornutum**	**6**	**3**
Beetles	**193**	**Epuraea longula**	**1**	**0**
Beetles	**194**	**Epuraea marseuli**	**0**	**4**
Beetles	**195**	**Epuraea neglecta**	**1**	**0**
Beetles	**196**	**Epuraea variegata**	**4**	**2**
Beetles	**197**	**Ernobius abietis**	**2**	**0**
Beetles	**198**	**Ernobius mollis**	**0**	**3**
Beetles	**199**	**Ernoporicus fagi**	**36**	**47**
Beetles	**200**	**Erotides cosnardi**	**1**	**0**
Beetles	**201**	**Eucnemis capucina**	**3**	**1**
Beetles	**202**	**Euglenes oculatus**	**0**	**1**
Beetles	**203**	**Euplectus bescidicus**	**0**	**6**
Beetles	**204**	**Euplectus karsteni**	**6**	**2**
Beetles	**205**	**Euplectus mutator**	**2**	**0**
Beetles	**206**	**Euplectus nanus**	**3**	**2**
Beetles	**207**	**Euryusa castanoptera**	**4**	**3**
Beetles	**208**	**Euryusa optabilis**	**1**	**0**
Beetles	**209**	**Euthiconus conicicollis**	**3**	**0**
Beetles	**210**	**Exocentrus adspersus**	**1**	**0**
Beetles	**211**	**Gabrius splendidulus**	**9**	**15**
Beetles	**212**	**Gastrallus immarginatus**	**1**	**0**
Beetles	**213**	**Glischrochilus quadriguttatus**	**9**	**2**
Beetles	**214**	**Glischrochilus quadripunctatus**	**0**	**1**
Beetles	**215**	**Gnathotrichus materiarius**	**0**	**1**
Beetles	**216**	**Grammoptera ruficornis**	**2**	**0**
Beetles	**217**	**Gyrophaena boleti**	**10**	**1**
Beetles	**218**	**Gyrophaena minima**	**3**	**0**
Beetles	**219**	**Gyrophaena strictula**	**3**	**0**
Beetles	**220**	**Hallomenus binotatus**	**1**	**0**
Beetles	**221**	**Hapalaraea pygmaea**	**2**	**1**
Beetles	**222**	**Hemicoelus costatus**	**61**	**51**
Beetles	**223**	**Hemicoelus fulvicornis**	**0**	**2**
Beetles	**224**	**Hesperus rufipennis**	**1**	**1**
Beetles	**225**	**Hylastes brunneus**	**0**	**1**
Beetles	**226**	**Hylastes cunicularius**	**1**	**3**
Beetles	**227**	**Hylastes opacus**	**1**	**4**
Beetles	**228**	**Hylesinus varius**	**5**	**6**
Beetles	**229**	**Hylis cariniceps**	**2**	**2**
Beetles	**230**	**Hylis foveicollis**	**1**	**2**
Beetles	**231**	**Hylis olexai**	**4**	**1**
Beetles	**232**	**Hylobius abietis**	**1**	**0**
Beetles	**233**	**Hylurgops palliatus**	**35**	**21**
Beetles	**234**	**Hyperisus plumbeum**	**17**	**26**
Beetles	**235**	**Hypnogyra angularis**	**0**	**3**
Beetles	**236**	**Hypoganus inunctus**	**1**	**1**
Beetles	**237**	**Hypopycna rufula**	**0**	**1**
Beetles	**238**	**Ipidia binotata**	**0**	**1**
Beetles	**239**	**Ips cembrae**	**2**	**0**
Beetles	**240**	**Ips typographus**	**0**	**1**
Beetles	**241**	**Ischnoglossa prolixa**	**1**	**0**
Beetles	**242**	**Ischnomera cyanea**	**5**	**0**
Beetles	**243**	**Ischnomera sanguinicollis**	**1**	**0**
Beetles	**244**	**Korynetes caeruleus**	**0**	**2**
Beetles	**245**	**Kyklioacalles roboris**	**0**	**3**
Beetles	**246**	**Laemophloeus kraussi**	**0**	**3**
Beetles	**247**	**Laemophloeus monilis**	**1**	**1**
Beetles	**248**	**Latridius hirtus**	**4**	**2**
Beetles	**249**	**Leiopus nebulosus**	**12**	**2**
Beetles	**250**	**Leptura aethiops**	**1**	**0**
Beetles	**251**	**Leptura quadrifasciata**	**0**	**3**
Beetles	**252**	**Leptusa fumida**	**22**	**7**
Beetles	**253**	**Leptusa pulchella**	**3**	**3**
Beetles	**254**	**Litargus connexus**	**30**	**9**
Beetles	**255**	**Magdalis duplicata**	**2**	**0**
Beetles	**256**	**Magdalis phlegmatica**	**1**	**0**
Beetles	**257**	**Malachius bipustulatus**	**7**	**1**
Beetles	**258**	**Malthinus facialis**	**4**	**1**
Beetles	**259**	**Malthinus fasciatus**	**0**	**1**
Beetles	**260**	**Malthinus flaveolus**	**55**	**23**
Beetles	**261**	**Malthinus seriepunctatus**	**4**	**1**
Beetles	**262**	**Malthodes brevicollis**	**1**	**0**
Beetles	**263**	**Malthodes dispar**	**0**	**4**
Beetles	**264**	**Malthodes guttifer**	**1**	**0**
Beetles	**265**	**Malthodes holdhausi**	**1**	**0**
Beetles	**266**	**Malthodes mysticus**	**3**	**0**
Beetles	**267**	**Malthodes pumilus**	**0**	**10**
Beetles	**268**	**Malthodes spathifer**	**32**	**29**
Beetles	**269**	**Megatoma undata**	**5**	**3**
Beetles	**270**	**Melandrya barbata**	**2**	**3**

Beetles	**271**	**Melandrya caraboides**	**1**	**6**
Beetles	**272**	**Melanotus castanipes**	**31**	**35**
Beetles	**273**	**Melanotus villosus**	**9**	**0**
Beetles	**274**	**Melasis buprestoides**	**16**	**7**
Beetles	**275**	**Mesosa nebulosa**	**0**	**1**
Beetles	**276**	**Micrambe abietis**	**8**	**2**
Beetles	**277**	**Microrhagus lepidus**	**3**	**0**
Beetles	**278**	**Microrhagus pygmaeus**	**8**	**5**
Beetles	**279**	**Microscydmus minimus**	**4**	**0**
Beetles	**280**	**Molorchus minor**	**0**	**1**
Beetles	**281**	**Mordellistena neuwaldeggiana**	**1**	**0**
Beetles	**282**	**Mordellochroa abdominalis**	**4**	**13**
Beetles	**283**	**Mycetina cruciata**	**0**	**3**
Beetles	**284**	**Mycetochara maura**	**7**	**0**
Beetles	**285**	**Mycetophagus atomarius**	**11**	**10**
Beetles	**286**	**Mycetophagus fulvicollis**	**1**	**3**
Beetles	**287**	**Mycetophagus multipunctatus**	**4**	**0**
Beetles	**288**	**Mycetophagus piceus**	**0**	**1**
Beetles	**289**	**Mycetophagus quadriguttatus**	**1**	**2**
Beetles	**290**	**Mycetophagus quadripustulatus**	**1**	**1**
Beetles	**291**	**Nemozoma elongatum**	**4**	**5**
Beetles	**292**	**Neuraphes carinatus**	**0**	**3**
Beetles	**293**	**Neuraphes plicicollis**	**0**	**1**
Beetles	**294**	**Nudobius lentus**	**9**	**5**
Beetles	**295**	**Octotemnus glabriculus**	**10**	**13**
Beetles	**296**	**Oligota granaria**	**0**	**8**
Beetles	**297**	**Orchesia fasciata**	**4**	**2**
Beetles	**298**	**Orchesia minor**	**1**	**1**
Beetles	**299**	**Orchesia undulata**	**18**	**9**
Beetles	**300**	**Orthocis alni**	**4**	**6**
Beetles	**301**	**Orthoperus atomus**	**1**	**0**
Beetles	**302**	**Osphya bipunctata**	**0**	**1**
Beetles	**303**	**Oxymirus cursor**	**2**	**2**
Beetles	**304**	**Pachytodes cerambyciformis**	**3**	**1**
Beetles	**305**	**Paromalus flavicornis**	**6**	**10**
Beetles	**306**	**Phloeocharis subtilissima**	**15**	**2**
Beetles	**307**	**Phloeonomus punctipennis**	**1**	**0**
Beetles	**308**	**Phloeonomus pusillus**	**0**	**1**
Beetles	**309**	**Phloeophagus lignarius**	**4**	**0**
Beetles	**310**	**Phloeopora corticalis**	**1**	**2**
Beetles	**311**	**Phloeopora scribae**	**1**	**0**
Beetles	**312**	**Phloeopora testacea**	**1**	**0**
Beetles	**313**	**Phloiotrya rufipes**	**5**	**4**
Beetles	**314**	**Phyllodrepa melanocephala**	**2**	**1**
Beetles	**315**	**Phymatodes testaceus**	**2**	**1**
Beetles	**316**	**Pissodes piceae**	**1**	**0**

Beetles	**317**	**Pityogenes bidentatus**	**0**	**4**
Beetles	**318**	**Pityogenes chalcographus**	**9**	**11**
Beetles	**319**	**Pityophthorus pityographus**	**1**	**0**
Beetles	**320**	**Placonotus testaceus**	**3**	**1**
Beetles	**321**	**Placusa depressa**	**1**	**0**
Beetles	**322**	**Placusa tachyporoides**	**1**	**1**
Beetles	**323**	**Platycerus caraboides**	**10**	**32**
Beetles	**324**	**Platycis minutus**	**1**	**0**
Beetles	**325**	**Platydema violacea**	**1**	**0**
Beetles	**326**	**Platyrhinus resinosus**	**6**	**0**
Beetles	**327**	**Platystomos albinus**	**6**	**5**
Beetles	**328**	**Plectophloeus fischeri**	**1**	**0**
Beetles	**329**	**Plegaderus dissectus**	**1**	**0**
Beetles	**330**	**Poecilium pusillum**	**1**	**1**
Beetles	**331**	**Pogonocherus hispidulus**	**1**	**2**
Beetles	**332**	**Pogonocherus hispidus**	**0**	**2**
Beetles	**333**	**Prionocyphon serricornis**	**2**	**1**
Beetles	**334**	**Prionus coriarius**	**1**	**5**
Beetles	**335**	**Ptenidium gressneri**	**6**	**0**
Beetles	**336**	**Ptenidium turgidum**	**6**	**2**
Beetles	**337**	**Pteryngium crenatum**	**1**	**0**
Beetles	**338**	**Pteryx suturalis**	**1**	**0**
Beetles	**339**	**Ptilinus pectinicornis**	**58**	**58**
Beetles	**340**	**Ptinella aptera**	**0**	**1**
Beetles	**341**	**Ptinomorphus imperialis**	**24**	**9**
Beetles	**342**	**Ptinus rufipes**	**0**	**1**
Beetles	**343**	**Pyrochroa coccinea**	**53**	**31**
Beetles	**344**	**Pyropterus nigroruber**	**1**	**1**
Beetles	**345**	**Pyrrhidium sanguineum**	**8**	**1**
Beetles	**346**	**Quedius brevicornis**	**1**	**0**
Beetles	**347**	**Quedius dilatatus**	**1**	**0**
Beetles	**348**	**Quedius maurus**	**1**	**0**
Beetles	**349**	**Quedius microps**	**1**	**1**
Beetles	**350**	**Quedius truncicola**	**1**	**1**
Beetles	**351**	**Quedius xanthopus**	**25**	**89**
Beetles	**352**	**Rabocerus foveolatus**	**1**	**0**
Beetles	**353**	**Rhagium bifasciatum**	**5**	**1**
Beetles	**354**	**Rhagium inquisitor**	**4**	**3**
Beetles	**355**	**Rhagium mordax**	**32**	**41**
Beetles	**356**	**Rhizophagus bipustulatus**	**45**	**28**
Beetles	**357**	**Rhizophagus depressus**	**1**	**2**
Beetles	**358**	**Rhizophagus dispar**	**31**	**11**
Beetles	**359**	**Rhizophagus fenestralis**	**1**	**0**
Beetles	**360**	**Rhizophagus ferrugineus**	**0**	**2**
Beetles	**361**	**Rhizophagus nitidulus**	**11**	**5**
Beetles	**362**	**Rhizophagus perforatus**	**3**	**1**
Beetles	**363**	**Rhyncolus reflexus**	**0**	**1**

Beetles	364	Ropalodontus perforatus	2	0
Beetles	365	Rutpela maculata	10	4
Beetles	366	Salpingus planirostris	19	21
Beetles	367	Salpingus ruficollis	15	21
Beetles	368	Saperda populnea	1	0
Beetles	369	Scaphidium quadrimaculatum	2	5
Beetles	370	Scaphisoma agaricinum	11	5
Beetles	371	Scaphisoma boreale	1	0
Beetles	372	Schizotus pectinicornis	37	38
Beetles	373	Scolytus intricatus	18	8
Beetles	374	Sepedophilus bipunctatus	0	3
Beetles	375	Sepedophilus testaceus	3	3
Beetles	376	Silvanoprus fagi	1	0
Beetles	377	Silvanus bidentatus	0	4
Beetles	378	Silvanus unidentatus	2	1
Beetles	379	Sinodendron cylindricum	30	11
Beetles	380	Sphaeriestes castaneus	1	0
Beetles	381	Stenichnus godarti	4	1
Beetles	382	Stenomax aeneus	1	0
Beetles	383	Stenostola dubia	3	0
Beetles	384	Stenurella melanura	10	8
Beetles	385	Stenurella nigra	1	0
Beetles	386	Stephostethus alternans	31	20
Beetles	387	Stephostethus rugicollis	1	0
Beetles	388	Stereocorynes truncorum	5	4
Beetles	389	Stictoleptura maculicornis	1	0
Beetles	390	Stictoleptura rubra	1	3
Beetles	391	Stictoleptura scutellata	6	2
Beetles	392	Sulcacis fronticornis	2	0
Beetles	393	Sulcacis nitidus	12	2
Beetles	394	Synchita variegata	17	3
Beetles	395	Tachyta nana	6	3
Beetles	396	Taphrorychus bicolor	64	56
Beetles	397	Tetratoma ancora	6	2
Beetles	398	Tetratoma fungorum	5	0
Beetles	399	Tetropium castaneum	1	1
Beetles	400	Thanasimus formicarius	1	4
Beetles	401	Thymalus limbatus	1	1
Beetles	402	Tillus elongatus	24	9
Beetles	403	Tomicus piniperda	5	2
Beetles	404	Tomoxia bucephala	3	1
Beetles	405	Trachodes hispidus	0	3
Beetles	406	Triplax lepida	6	0
Beetles	407	Triplax rufipes	0	8
Beetles	408	Triplax russica	6	0
Beetles	409	Tritoma bipustulata	9	6

Beetles	410	Trypodendron domesticum	91	35
Beetles	411	Trypodendron lineatum	10	1
Beetles	412	Trypodendron signatum	54	55
Beetles	413	Uleiota planatus	21	23
Beetles	414	Variimorda villosa	2	0
Beetles	415	Vincenzellus ruficollis	32	28
Beetles	416	Xestobium rufovillosum	1	0
Beetles	417	Xyleborinus saxesenii	9	9
Beetles	418	Xyleborus monographus	3	2
Beetles	419	Xylosandrus germanus	106	55
Fungi	1	Agaricus silvaticus	1	0
Fungi	2	Agaricus sylvicola	1	8
Fungi	3	Agrocybe praecox	1	0
Fungi	4	Amanita citrina	16	39
Fungi	5	Amanita fulva	1	7
Fungi	6	Amanita phalloides	4	16
Fungi	7	Amanita rubescens	8	36
Fungi	8	Amanita vaginata	2	0
Fungi	11	Antrodiella hoehnelii	6	7
Fungi	16	Bisporella citrina	25	18
Fungi	19	Boletus edulis	7	0
Fungi	20	Boletus erythropus	0	4
Fungi	21	Boletus reticulatus	1	9
Fungi	25	Cantharellus cibarius	0	5
Fungi	26	Cantharellus friesii	0	1
Fungi	27	Clitocybe nebularis	11	11
Fungi	28	Clitocybe odora	4	13
Fungi	31	Cortinarius bolaris	0	16
Fungi	32	Cortinarius caperatus	0	9
Fungi	33	Cortinarius violaceus	1	5
Fungi	34	Craterellus cinereus	0	2
Fungi	35	Craterellus cornucopioides	1	8
Fungi	36	Craterellus tubaeformis	0	10
Fungi	54	Gymnopus confluens	1	6
Fungi	55	Gymnopus dryophilus	3	3
Fungi	56	Gymnopus peronatus	5	26
Fungi	59	Hydnum repandum	6	8
Fungi	60	Hydnum rufescens	0	7
Fungi	68	Infundibulicybe gibba	5	10
Fungi	71	Laccaria amethystina	19	48
Fungi	72	Laccaria laccata	18	23
Fungi	73	Lactarius blennius	15	37
Fungi	74	Lactarius quietus	7	17
Fungi	75	Lactarius subdulcis	26	52
Fungi	79	Lycoperdon perlatum	16	44
Fungi	90	Mycena pura	8	19
Fungi	91	Mycena rosella	44	60

Fungi	96	Paxillus involutus	3	11
Fungi	113	Rhodocollybia butyracea	12	51
Fungi	114	Russula cyanoxantha	7	32
Fungi	115	Russula fellea	5	21
Fungi	116	Russula mairei	10	43
Fungi	117	Russula nigricans	17	43
Fungi	118	Russula ochroleuca	15	40
Fungi	119	Russula rosea	14	32
Fungi	122	Scleroderma areolatum	5	9
Fungi	125	Strobilomyces strobilaceus	5	35
Fungi	126	Suillus grevillei	3	3
Fungi	133	Tricholoma sulphureum	3	15
Fungi	134	Xerocomus badius	7	6
Fungi	**9**	**Annulohypoxylon cohaerens**	**23**	**83**
Fungi	**10**	**Annulohypoxylon multiforme**	**26**	**18**
Fungi	**12**	**Ascodichaena rugosa**	**111**	**141**
Fungi	**13**	**Auricularia auricula-judae**	**0**	**1**
Fungi	**14**	**Auricularia mesenterica**	**0**	**1**
Fungi	**15**	**Biscogniauxia nummularia**	**3**	**29**
Fungi	**17**	**Bjerkandera adusta**	**49**	**27**
Fungi	**18**	**Bjerkandera fumosa**	**3**	**0**
Fungi	**22**	**Bulgaria inquinans**	**2**	**3**
Fungi	**23**	**Calocera cornea**	**19**	**5**
Fungi	**24**	**Calocera viscosa**	**2**	**3**
Fungi	**29**	**Coprinellus micaceus**	**4**	**8**
Fungi	**30**	**Coriolopsis gallica**	**0**	**1**
Fungi	**37**	**Creolophus cirrhatus**	**1**	**0**
Fungi	**38**	**Crepidotus mollis**	**0**	**1**
Fungi	**39**	**Cyathus striatus**	**6**	**8**
Fungi	**40**	**Dacrymyces stillatus**	**8**	**2**
Fungi	**41**	**Daedalea quercina**	**11**	**12**
Fungi	**42**	**Diatrype disciformis**	**78**	**106**
Fungi	**43**	**Diatrype stigma**	**57**	**136**
Fungi	**44**	**Diatrypella favacea**	**13**	**28**
Fungi	**45**	**Eutypa maura**	**0**	**6**
Fungi	**46**	**Eutypa spinosa**	**54**	**92**
Fungi	**47**	**Eutypella quaternata**	**21**	**46**
Fungi	**48**	**Fomes fomentarius**	**90**	**107**
Fungi	**49**	**Fomitopsis pinicola**	**33**	**14**
Fungi	**50**	**Ganoderma applanatum**	**69**	**46**
Fungi	**51**	**Gloeophyllum sepiarium**	**0**	**1**
Fungi	**52**	**Gymnopilus penetrans**	**1**	**1**
Fungi	**53**	**Gymnopilus sapineus**	**0**	**7**
Fungi	**57**	**Hapalopilus rutilans**	**0**	**2**
Fungi	**58**	**Hericium coralloides**	**0**	**2**
Fungi	**61**	**Hygrophoropsis aurantiaca**	**2**	**1**

Fungi	**62**	**Hymenochaete rubiginosa**	**8**	**23**
Fungi	**63**	**Hymenopellis radicata**	**6**	**18**
Fungi	**64**	**Hypholoma capnoides**	**3**	**0**
Fungi	**65**	**Hypholoma fasciculare**	**50**	**57**
Fungi	**66**	**Hypholoma sublateritium**	**12**	**16**
Fungi	**67**	**Hypoxylon fragiforme**	**287**	**116**
Fungi	**69**	**Kretzschmaria deusta**	**125**	**135**
Fungi	**70**	**Kuehneromyces mutabilis**	**18**	**13**
Fungi	**76**	**Laxitextum bicolor**	**4**	**12**
Fungi	**77**	**Lenzites betulinus**	**9**	**7**
Fungi	**78**	**Leptoporus mollis**	**5**	**5**
Fungi	**80**	**Lycoperdon pyriforme**	**6**	**19**
Fungi	**81**	**Marasmius rotula**	**14**	**16**
Fungi	**82**	**Megacollybia platyphylla**	**28**	**36**
Fungi	**83**	**Mensularia nodulosa**	**1**	**28**
Fungi	**84**	**Mensularia radiata**	**1**	**2**
Fungi	**85**	**Meripilus giganteus**	**8**	**5**
Fungi	**86**	**Mucidula mucida**	**6**	**9**
Fungi	**87**	**Mycena crocata**	**8**	**40**
Fungi	**88**	**Mycena galericulata**	**10**	**25**
Fungi	**89**	**Mycena haematopus**	**4**	**24**
Fungi	**92**	**Mycetinis alliaceus**	**39**	**63**
Fungi	**93**	**Nemania serpens**	**34**	**14**
Fungi	**94**	**Oligoporus lacteus**	**0**	**6**
Fungi	**95**	**Panellus stipticus**	**4**	**5**
Fungi	**97**	**Phlebia tremellosa**	**6**	**7**
Fungi	**98**	**Picipes badius**	**22**	**11**
Fungi	**99**	**Pleurotus ostreatus**	**1**	**13**
Fungi	**100**	**Plicaturopsis crispa**	**6**	**4**
Fungi	**101**	**Pluteus cervinus**	**29**	**40**
Fungi	**102**	**Pluteus phlebophorus**	**15**	**13**
Fungi	**103**	**Pluteus umbrosus**	**2**	**1**
Fungi	**104**	**Polyporus brumalis**	**8**	**0**
Fungi	**105**	**Polyporus ciliatus**	**12**	**5**
Fungi	**106**	**Polyporus leptocephalus**	**46**	**14**
Fungi	**107**	**Polyporus tuberaster**	**11**	**6**
Fungi	**108**	**Polyporus varius**	**28**	**1**
Fungi	**109**	**Postia subcaesia**	**7**	**9**
Fungi	**110**	**Psathyrella piluliformis**	**18**	**21**
Fungi	**111**	**Pycnoporellus fulgens**	**2**	**0**
Fungi	**112**	**Ramaria stricta**	**2**	**13**
Fungi	**120**	**Schizophyllum commune**	**24**	**24**
Fungi	**121**	**Schizopora paradoxa**	**13**	**63**
Fungi	**123**	**Stereum hirsutum**	**84**	**92**
Fungi	**124**	**Stereum subtomentosum**	**19**	**29**
Fungi	**127**	**Trametes cinnabarina**	**12**	**3**
Fungi	**128**	**Trametes gibbosa**	**37**	**27**

Fungi	**129**	**Trametes hirsuta**	**22**	**13**
Fungi	**130**	**Trametes ochracea**	**24**	**2**
Fungi	**131**	**Trametes versicolor**	**49**	**68**
Fungi	**132**	**Trichaptum abietinum**	**7**	**8**
Fungi	**135**	**Xylaria hypoxylon**	**33**	**63**
Birds	1	Accipiter gentilis	2	0
Birds	2	Accipiter nisus	0	4
Birds	3	Aegithalos caudatus	5	4
Birds	4	Anthus trivialis	1	0
Birds	5	Buteo	9	0
Birds	6	Coccothraustes coccothraustes	71	19
Birds	7	Columba palumbus	41	29
Birds	8	Corvus corax	1	2
Birds	9	Corvus corone	1	0
Birds	10	Cuculus canorus	10	1
Birds	11	Erithacus rubecula	116	170
Birds	12	Fringilla coelebs	274	221
Birds	13	Garrulus glandarius	58	43
Birds	14	Oriolus oriolus	10	1
Birds	15	Pernis apivorus	1	0
Birds	16	Phylloscopus collybita	41	19
Birds	17	Phylloscopus sibilatrix	19	18
Birds	18	Phylloscopus trochilus	5	1
Birds	19	Prunella modularis	3	1
Birds	20	Regulus ignicapillus	14	7
Birds	21	Regulus regulus	4	1
Birds	22	Strix aluco	9	3
Birds	23	Sylvia atricapilla	43	49
Birds	24	Sylvia borin	1	1
Birds	25	Troglodytes troglodytes	71	106
Birds	26	Turdus merula	69	99
Birds	27	Turdus philomelos	82	37
Birds	28	Turdus pilaris	1	8
Birds	29	Turdus viscivorus	14	5
Birds	**30**	**Certhia brachydactyla**	**9**	**2**
Birds	**31**	**Certhia familiaris**	**91**	**42**
Birds	**32**	**Columba oenas**	**41**	**13**
Birds	**33**	**Dendrocopos major**	**134**	**127**
Birds	**34**	**Dendrocopos medius**	**28**	**5**
Birds	**35**	**Dendrocopos minor**	**3**	**0**
Birds	**36**	**Dryocopus martius**	**8**	**0**
Birds	**37**	**Ficedula albicollis**	**13**	**13**
Birds	**38**	**Ficedula hypoleuca**	**38**	**21**
Birds	**39**	**Ficedula parva**	**2**	**0**
Birds	**40**	**Parus ater**	**40**	**4**
Birds	**41**	**Parus caeruleus**	**108**	**112**
Birds	**42**	**Parus cristatus**	**0**	**5**
Birds	**43**	**Parus major**	**214**	**283**
Birds	**44**	**Parus montanus**	**1**	**0**
Birds	**45**	**Phoenicurus phoenicurus**	**0**	**8**
Birds	**46**	**Picus canus**	**1**	**0**
Birds	**47**	**Picus viridis**	**5**	**1**
Birds	**48**	**Poecile palustris**	**114**	**19**
Birds	**49**	**Sitta europaea**	**262**	**143**
Birds	**50**	**Sturnus vulgaris**	**7**	**4**
Plants	1	Abies alba	0.5	0.5
Plants	2	Acer platanoides	6.5	19
Plants	3	Acer pseudoplatanus	11	51
Plants	4	Aesculus hippocastanum	0	0.5
Plants	5	Agrostis capillaris	1	0
Plants	6	Ajuga reptans	5	7.5
Plants	7	Alliaria petiolata	3.5	5
Plants	8	Alnus glutinosa	0	1
Plants	9	Anemone nemorosa	12	109
Plants	10	Anthoxanthum odoratum	0	2.5
Plants	11	Athyrium filix-femina	12.5	8.5
Plants	12	Betula pendula	0.5	1.5
Plants	13	Brachypodium sylvaticum	2	3.5
Plants	14	Calamagrostis arundinacea	3.5	2.5
Plants	15	Calamagrostis epigejos	9.5	16
Plants	16	Cardamine bulbifera	10.5	104.5
Plants	17	Cardamine flexuosa	0	13
Plants	18	Cardamine hirsuta	3	0
Plants	19	Cardamine impatiens	0	0.5
Plants	20	Cardamine pratensis	0	4.5
Plants	21	Carex brizoides	152	581
Plants	22	Carex digitata	1	0
Plants	23	Carex echinata	0	2.5
Plants	24	Carex lepidocarpa	3	0
Plants	25	Carex leporina	2.5	2.5
Plants	26	Carex pallescens	0	2
Plants	27	Carex pilulifera	10.5	26
Plants	28	Carex remota	59.5	63.5
Plants	29	Carex sylvatica	11	93.5
Plants	30	Carpinus betulus	5.5	102
Plants	31	Circaea alpina	0	0.5
Plants	32	Circaea lutetiana	5.5	22
Plants	33	Convallaria majalis	0.5	0
Plants	34	Cystopteris fragilis	7.5	9.5
Plants	35	Dactylis glomerata	6.5	0
Plants	36	Deschampsia cespitosa	4	32

Plants	37	Deschampsia flexuosa	4.5	33.5
Plants	38	Dryopteris carthusiana	21	27
Plants	39	Dryopteris dilatata	0	15
Plants	40	Dryopteris filix-mas	11	6.5
Plants	41	Epilobium angustifolium	3	6.5
Plants	42	Epilobium montanum	0	1
Plants	43	Equisetum sylvaticum	0.5	2.5
Plants	44	Fagus sylvatica	253	309.5
Plants	45	Festuca gigantea	1.5	1
Plants	46	Festuca pratensis	0.5	0
Plants	47	Ficaria verna	0	2.5
Plants	48	Fragaria vesca	1	3.5
Plants	49	Fraxinus excelsior	3.5	13
Plants	50	Galeopsis pubescens	1.5	0
Plants	51	Galeopsis tetrahit	13.5	14
Plants	52	Galium album	2	0
Plants	53	Galium aparine	1.5	2.5
Plants	54	Galium odoratum	1	33
Plants	55	Galium rotundifolium	0	0.5
Plants	56	Galium sylvaticum	1	0
Plants	57	Geranium robertianum	1	5.5
Plants	58	Geum urbanum	1	0
Plants	59	Glechoma hederacea	1	0
Plants	60	Glyceria fluitans	0.5	0
Plants	61	Gymnocarpium dryopteris	7.5	15
Plants	62	Holcus lanatus	1	10
Plants	63	Holcus mollis	2.5	10
Plants	64	Hypericum hirsutum	0.5	0
Plants	65	Hypericum pulchrum	2	0
Plants	66	Impatiens noli-tangere	12	22.5
Plants	67	Impatiens parviflora	7	19
Plants	68	Juncus effusus	13.5	29
Plants	69	Lactuca muralis	2.5	1
Plants	70	Lapsana communis	0	3.5
Plants	71	Larix decidua	1	2.5
Plants	72	Lathyrus linifolius	0.5	0
Plants	73	Lathyrus sylvestris	0.5	0
Plants	74	Luzula luzuloides	37.5	145.5
Plants	75	Luzula sylvatica	2	0
Plants	76	Melampyrum nemorosum	0.5	0
Plants	77	Melampyrum pratense	0.5	0
Plants	78	Melica nutans	0.5	1
Plants	79	Melica uniflora	64.5	91.5
Plants	80	Mercurialis perennis	0.5	0
Plants	81	Milium effusum	53.5	68
Plants	82	Moehringia trinervia	10.5	7.5
Plants	83	Oxalis acetosella	11	48.5
Plants	84	Persicaria dubia	0	3
Plants	85	Persicaria hydropiper	0	0.5
Plants	86	Picea abies	5.5	8.5
Plants	87	Pinus sylvestris	2.5	2
Plants	88	Poa nemoralis	15.5	41.5
Plants	89	Polygonatum verticillatum	0.5	5
Plants	90	Populus tremula	0.5	0
Plants	91	Prunus avium	2	1.5
Plants	92	Prunus padus	0	11
Plants	93	Pseudotsuga menziesii	1	0.5
Plants	94	Quercus petraea	32	99.5
Plants	95	Ranunculus lanuginosus	0	1
Plants	96	Ranunculus repens	0.5	2.5
Plants	97	Rubus caesius	1.5	0
Plants	98	Rubus fruticosus	0	120
Plants	99	Rubus idaeus	0	19.5
Plants	100	Sambucus nigra	4.5	5
Plants	101	Sambucus racemosa	0	8.5
Plants	102	Scrophularia nodosa	4.5	6.5
Plants	103	Sorbus aucuparia	3.5	12
Plants	104	Sorbus torminalis	0.5	176
Plants	105	Stachys sylvatica	4	7.5
Plants	106	Stellaria holostea	0	16
Plants	107	Taraxacum officinale	1	1.5
Plants	108	Tilia platyphyllos	0.5	0
Plants	109	Trifolium pratense	0.5	0
Plants	110	Urtica dioica	7.5	24.5
Plants	111	Vaccinium myrtillus	0.5	31.5
Plants	112	Veronica montana	1	3.5
Plants	113	Veronica officinalis	3	0
Plants	114	Vicia parviflora	0.5	0
Plants	115	Vicia sepium	1	12
Plants	116	Viola reichenbachiana	1	5
Plants	117	Viola riviniana	0	3.5
Bugs	1	Acalypta parvula	1	0
Bugs	2	Acanthosoma haemorrhoidale	1	1
Bugs	3	Aelia acuminata	10	13
Bugs	4	Anthocoris confusus	39	6
Bugs	7	Arma custos	1	0
Bugs	8	Blepharidopterus angulatus	1	0
Bugs	9	Brachycarenus tigrinus	1	1
Bugs	10	Campyloneura virgula	3	4
Bugs	11	Carpocoris fuscispinus	9	14
Bugs	12	Carpocoris purpuripennis	4	0
Bugs	13	Coreus marginatus	3	0
Bugs	14	Corizus hyoscyami	1	2
Bugs	15	Cyllecoris histrionius	2	0

Bugs	16	Deraeocoris lutescens	40	87
Bugs	17	Deraeocoris trifasciatus	1	0
Bugs	18	Dolycoris baccarum	49	37
Bugs	19	Drymus ryei	6	0
Bugs	20	Dryophilocoris flavoquadrimaculatus	1	2
Bugs	21	Elasmostethus interstinctus	1	1
Bugs	22	Elasmucha fieberi	1	1
Bugs	23	Elasmucha grisea	5	0
Bugs	24	Eurydema oleracea	3	1
Bugs	25	Eurygaster testudinaria	1	1
Bugs	26	Harpocera thoracica	15	17
Bugs	27	Himacerus apterus	0	0
Bugs	28	Kleidocerys resedae	33	23
Bugs	29	Liocoris tripustulatus	1	2
Bugs	30	Loricula elegantula	3	3
Bugs	31	Loricula pselaphiformis	1	1
Bugs	32	Lygus punctatus	1	0
Bugs	33	Megalonotus chiragra	8	0
Bugs	34	Miris striatus	0	0
Bugs	35	Nabis pseudoferus	9	20
Bugs	36	Orius minutus	13	2
Bugs	37	Orius vicinus	1	0
Bugs	38	Palomena prasina	42	39
Bugs	39	Palomena viridissima	2	0
Bugs	40	Pentatoma rufipes	9	8
Bugs	41	Peribalus vernalis	1	0
Bugs	42	Phoenicocoris obscurellus	1	0
Bugs	43	Phylus melanocephalus	1	1
Bugs	44	Phytocoris dimidiatus	1	2
Bugs	45	Phytocoris longipennis	1	0
Bugs	46	Phytocoris reuteri	1	0
Bugs	47	Phytocoris tiliae	2	0
Bugs	48	Piesma maculatum	1	0
Bugs	49	Piezodorus lituratus	3	5
Bugs	50	Pinthaeus sanguinipes	6	1
Bugs	51	Psallus mollis	6	1
Bugs	52	Psallus perrisi	2	1
Bugs	53	Psallus varians	416	63
Bugs	54	Rhabdomiris striatellus	3	4
Bugs	55	Scolopostethus grandis	2	0
Bugs	56	Sphragisticus nebulosus	1	0
Bugs	57	Stenodema laevigata	12	22
Bugs	58	Trapezonotus arenarius	1	0
Bugs	59	Troilus luridus	13	4
Bugs	60	Amphiareus obscuriceps	0	1
Bugs	61	Carpocoris purpureipennis	0	6

Bugs	62	Ceraleptus gracilicornis	0	2
Bugs	63	Ceraleptus lividus	0	1
Bugs	64	Closterotomus biclavatus	0	2
Bugs	65	Coriomeris denticulatus	0	1
Bugs	66	Cymus claviculus	0	1
Bugs	67	Cymus glandicolor	0	1
Bugs	68	Cymus melanocephalus	0	1
Bugs	69	Drymus ryeii	0	1
Bugs	70	Empicoris vagabundus	0	1
Bugs	71	Eremocoris plebejus	0	1
Bugs	72	Eurydema ornata	0	1
Bugs	73	Gerris lacustris	0	1
Bugs	74	Lygus pratensis	0	19
Bugs	75	Lygus rugulipennis	0	2
Bugs	76	Orius majusculus	0	1
Bugs	77	Peribalus strictus	0	3
Bugs	78	Physatocheila harwoodi	0	1
Bugs	79	Psallus salicis	0	1
Bugs	80	Rhopalus parumpunctatus	0	3
Bugs	81	Rhyparochromus vulgaris	0	1
Bugs	82	Syromastus rhombeus	0	1
Bugs	83	Taphropeltus contractus	0	1
Bugs	84	Temnostethus pusillus	0	1
Bugs	85	Thyreocoris scarabaeoides	0	2
Bugs	86	Trapezonotus dispar	0	2
Bugs	87	Tropistethus holosericus	0	1
Bugs	**88**	**Aradus conspicuus**	**2**	**3**
Bugs	**89**	**Aradus depressus**	**1**	**0**

Appendix F: Boosting models - variable calculation and discussion on boosting

Harvesting intensity and natural mortality

The harvesting intensity and natural mortality are defined as basal area of trees deceased between the inventories by harvest or naturally. These values were calculated from the DBH [cm] of those trees that were classified dead in the following inventory. The DBH was multiplied with 0.01 to convert the value from cm to m (F-Eq. 1).

(F-Eq. 1) $\text{DBH [m]} = \text{DBH} * 0.01$

From this value the basal area g (in m^2) was calculated (F-Eq. 2).

(F-Eq. 2) $g = \pi * (\text{DBH [m]}^2 / 4)$

To calculate the variables harvesting intensity and natural mortality as used in the models, we separated trees measured on the 500 m^2 (DBH $\geq$ 30 cm) and on the 125 m^2 (DBH $\leq$ 30 cm) circle and extrapolated them to one hectare, as described in the main methods part. The sum of the extrapolated basal area of these trees was taken as explanatory variables for the model (F-Eq. 3).

(F-Eq. 3) $$\text{Harvesting intensity/natural mortality } [m^2\ ha^{-1}] = (g_{\text{DBH} \geq 30}\ [m^2] * 20) + (g_{\text{DBH} < 30}\ [m^2] * 80)$$

Living stand volume

Sum of the volume of all living trees in all strata. To calculate the volume of the living stand we excluded all trees that were classified as dead. The living stand volume was then calculated as the sum of the volume [$m^3\ ha^{-1}$] of all living trees in all strata (height > 0.2 m).

Stand age

Mean age of all trees in the top layer. To calculate the stand age, we selected only trees from the top layer as classified in the inventory. From the trees of the top layer we calculated a mean age of all trees older than 0 years.

Percentage broadleaf trees

Percent basal area of broadleaf trees in the top layer. To calculate the percentage broadleaf trees, we selected only trees from the top layer from the trees of the top layer we calculated a sum of all values for the basal area separating between broadleaf and coniferous tree species. The percentage of broadleaf was calculated as the sum of the basal area per hectare of all broadleaf divided by the total basal area (F-Eq. 3).

$$\text{Percentage broadleaf} = (\text{basal area broadleaf trees } [m^2\ ha^{-1}]) / (\text{basal area broadleaf trees } [m^2\ ha^{-1}] + \text{basal area coniferous trees } [m^2\ ha^{-1}]) * 100 \qquad \textit{(F-Eq. 3)}$$

Number of tree species

Number of tree species in the top layer. To count the number of trees we selected only trees from the top layer and counted all trees which had a basal area > 0.

Presence of spruce and presence of pine

For the variables presence of spruce and presence of pine the variable was set to 1 when the basal area was greater than zero, i.e. when a tree of the respective species was present.

Slope, forest nature reserve, Gauss-Krueger coordinates and management districts

These data were used as original values from the regular inventory data base. For each plot, the slope, whether it was located in a forest nature reserve (1 = in nature reserve, 0 = in managed stands), and the spatial position (Gauss-Krueger coordinates) were noted. Besides that, we defined the management districts (1-3), which are managed by a different forester using a map provided by the Bavarian State Forestry.

Component wise gradient boosting

Component-wise gradient boosting (Hofner, Mayr et al. 2014, Mayr, Binder et al. 2014) is a machine learning method for optimizing prediction accuracy and for obtaining statistical model estimates via gradient descent techniques. A key feature of the method is that it carries out variable selection during the fitting process without relying on heuristic techniques such as stepwise variable selection. Model optimization proceeds by fitting each covariate separately and several times to the negative gradient of a suitable loss function (which can be seen as pseudo residuals). Only the best fitting covariates are added to the final model. The optimal number of so-called boosting iterations is determined by 25-fold subsampling (Mayr, Hofner et al. 2012). Subsampling is a cross validation technique where the dataset is split into test and training datasets each of size n/2. The training dataset is used to fit the model, while the test data is used to evaluate this model and to find the optimal number of boosting iterations, which minimizes the empirical risk on the test dataset.

Literature Appendix F:

Hofner, B., A. Mayr, N. Robinzonov and M. Schmid (2014). "Model-based boosting in R: a hands-on tutorial using the R package mboost." Computational Statistics **29**(1-2): 3-35.

Mayr, A., H. Binder, O. Gefeller and M. Schmid (2014). "The Evolution of Boosting Algorithms - From Machine Learning to Statistical Modelling." Methods of Information in Medicine **53**(6): 419-427.

Mayr, A., B. Hofner and M. Schmid (2012). "The importance of knowing when to stop. A sequential stopping rule for component-wise gradient boosting." Methods of Information in Medicine **51**(2): 178-186.

Table F1: Correlation coefficients of Pearson correlation between all variables used in the boosting model.

	Growing stock	Percentage broadleaf trees	Presence of spruce	Presence of pine	Number of tree species	Stand age	Slope	Harvesting intensity	Natural mortality	Management district	Forest nature reserve
Growing stock	1	0.1197	0.0124	0.0653	0.0521	0.3708	0.0959	0.0418	-0.2399	0.1040	0.0799
Percentage broadleaf trees	0.1197	1	-0.5222	-0.4415	-0.1527	0.3752	0.0786	-0.0617	-0.1952	0.0138	0.0808
Presence of spruce	0.0124	-0.5222	1	0.0977	0.3161	-0.2810	-0.0582	0.0149	0.0964	0.0148	-0.0134
Presence of pine	0.0653	-0.4415	0.0977	1	0.4118	-0.0736	-0.0444	0.0944	-0.0171	0.0269	-0.1027
Number of tree species	0.0521	-0.1527	0.3161	0.4118	1	-0.2248	-0.0424	-0.0424	-0.1490	0.0011	-0.0747
Stand age	0.3708	0.3752	-0.2810	-0.0736	-0.2248	1	0.1281	0.0498	-0.0600	0.0924	0.1195
Slope	0.0959	0.0786	-0.0582	-0.0444	-0.0424	0.1281	1	0.0380	-0.0315	-0.0009	-0.0281
Harvesting intensity	0.0418	-0.0617	0.0149	0.0944	-0.0424	0.0498	0.0380	1	-0.1308	-0.0227	-0.1000
Natural mortality	-0.2399	-0.1952	0.0964	-0.0171	-0.1490	-0.0600	-0.0315	-0.1308	1	0.0281	0.0283
Management district	0.1040	0.0138	0.0148	0.0269	0.0011	0.0924	-0.0009	-0.0227	0.0281	1	-0.0745
Forest nature reserve	0.0799	0.0808	-0.0134	-0.1027	-0.0747	0.1195	-0.0281	-0.1000	0.0283	-0.0745	1

Appendix G: Correlation coefficients of the three variables used in the generalized linear model for the analysis of the biodiversity

Table G1: Correlation coefficients for all correlations of the variables with each other, calculated for all variables and the subset in Reserves and Production forests.

Plots	Variable 1	Variable 2	Correlation coefficient
All	deadwood	canopy change	-0.1888325
Reserve	deadwood	canopy change	-0.4390615
Production forest	deadwood	canopy change	-0.1121515
All	deadwood	change habitat trees	-0.06720719
Reserve	deadwood	change habitat trees	-0.04035848
Production forest	deadwood	change habitat trees	-0.09384509
All	canopy change	change habitat trees	0.09384199
Reserve	canopy change	change habitat trees	0.01805346
Production forest	canopy change	change habitat trees	0.127703

Appendix H: Biodiversity in reserves und Model with reserves

Table H1: Results of the generalized linear model given as t- and p-values, with the different diversities as dependent, the canopy change, deadwood change and change in habitat trees as independent variables and the location within reserves or production forests as interaction term. Significant results are indicated in bold.

Dependent variable	Reserve		Canopy change				Change cavity bearing trees				Deadwood change			
			Production forest		Reserve		Production forest		Reserve		Production forest		Reserve	
	t	p	t	p	t	p	t	p	t	p	t	p	t	p
Multidiversity	1204	0.23	-0.07	0.94	-0.01	1	0.27	0.78	-0.56	0.58	**3141**	**0.003**	**2487**	**0.02**
Multidiversity saproxylic	1153	0.25	1325	0.19	1523	0.13	**2117**	**0.04**	0.83	0.41	**4893**	**< 0.001**	**3850**	**0.0003**
Multidiversity non-saproxylic	0.89	0.38	-0.65	0.52	-0.59	0.56	-0.41	0.69	-0.08	0.94	0.82	0.42	0.23	0.82
Species number beetles	0.38	0.7	0.34	0.74	-0.31	0.76	0.55	0.59	-1358	0.18	**2935**	**0.005**	**2009**	**0. 05**
Species number beetles saproxylic	0.98	0.33	0.44	0.66	0.97	0.33	0.51	0.61	-0.11	0.91	**3072**	**0.003**	**3041**	**0.003**
Species number beetles non-saproxylic	0.37	0.72	-0.22	0.83	0.12	0.91	0.39	0.7	-0.37	0.71	1	0.32	-0.69	0.49
Species number fungi	1641	0.11	0.94	0.35	**2005**	**0.05**	0.33	0.74	0.41	0.68	**4258**	**< 0.001**	**2669**	**0.01**
Species number fungi saproxylic	1945	0.06	0.44	0.66	**2115**	**0.04**	1134	0.26	0.8	0.43	**6065**	**< 0.0001**	**3255**	**0.002**
Species number fungi non-saproxylic	0.3	0.77	0.74	0.46	0.92	0.36	-0.66	0.51	-0.71	0.48	-0.3	0.77	0.41	0.68
Species number birds	0.96	0.34	-0.31	0.76	-1866	0.06	0.99	0.32	0.94	0.35	0.82	0.41	-0.62	0.53
Species number birds saproxylic	0.06	0.95	0.49	0.63	0.14	0.89	0.92	0.36	-0.08	0.93	0.15	0.88	0.66	0.51
Species number birds non-saproxylic	1398	0.16	-0.91	0.36	**-2783**	**0.01**	0.5	0.62	1488	0.14	1115	0.26	-1606	0.11
Species number plants	0.25	0.8	-1605	0.11	1287	0.2	-1301	0.2	-0.29	0.77	0.4	0.69	1587	0.12
Species number bugs	0.28	0.78	-0.33	0.74	-0.3	0.77	-0.12	0.9	0.02	0.98	0.27	0.78	1040	0.3
Species number bugs non-saproxylic	0.19	0.85	-0.26	0.79	-0.35	0.73	-0.15	0.88	0.07	0.95	0.16	0.87	1	0.32

Appendix I: List of traits

Table I1: List of traits used in the assembly analysis, their type, value, the result of the vifstep analysis (package usdm), the value for the phylogenetic signal (K, D) calculated with phylosignal for numeric traits (package picante) and pyhlo.d for binary traits (package caper) and the source of the phylogeny. Traits with a value > 10 in the vifstep analysis were excluded. 1) calculated with (π/4)*d^2, d=mean of width and length of the basidiome (sporocarp, i.e. fruiting body); 2) Calculated using a PCA of the log-scale mean length and width of the spores, using the scores of the axes correlated with the width – with lower value more elongated the spores; 3) Same approach as for the spore shape using the scores of the axis correlated with the length – with higher value indicating larger volume; 4) Completely adhering to the substrate, covering the substrate; 5) e.g. spiky surface.

	Trait	Type	Min	Mean	Max	VIF	Phyl. Signal		Phylogeny
Saproxylic beetles	Body size [cm]	numeric	0.7	5.07	31.5	1.33	K:	0.92	(Seibold, Brandl et al. 2015)
	Feeding strategy mycetophagous	binary	0	0.33	1	2.45	D:	-0.64	
	Feeding strategy detritivorous	binary	0	0.06	1	1.08	D:	-0.78	
	Feeding strategy xylophagous	binary	0	0.41	1	2.37	D:	-0.74	
	Feeding strategy predatory	binary	0	0.39	1	3.01	D:	-0.75	
Saproxylic fungi	Basidiome size [cm] 1)	numeric	3.14	8,566.79	196,349.54	1.10	K:	0.19	Compiled with megaptera package
	Spore shape 2)	numeric	-0.71	-0.07	0.67	1.26	K:	0.48	
	Spore volume 3)	numeric	-0.23	0.02	0.38	1.91	K:	0.56	
	Resupinate 4) basidiomes	binary	0	0.29	1	1.85	D:	0.08	
	Spore surface ornamented 5)	binary	0	0.06	1	1.08	D:	-0.23	
	Asexual reproduction	binary	0	0.18	1	2.51	D:	-1.18	
	Galertic consistence	binary	0	0.08	1	1.26	D:	-0.63	
	Presence of skeletal hyphae	binary	0	0.27	1	1.60	D:	-0.63	
	Crustose cystidia and or setae	binary	0	0.07	1	1.32	D:	-0.08	
	Perennial basidiomes	binary	0	0.08	1	1.54	D:	-0.09	
Birds	Weight [g]	numeric	5.5	163.98	1,300	3.85	K:	0.88	(Hackett, Kimball et al. 2008)
	Life span [years]	numeric	3.5	11.69	29	3.10	K:	0.43	
	Clutch size [number of eggs]	numeric	1	6.06	19	2.64	K:	0.64	
	Migrating	binary	0	0.55	1	1.49	D:	-0.66	
	Nocturnal	binary	0	0.02	1	2.41	D:	-0.06	
	Diet plant	binary	0	0.33	1	1.20	D:	-0.49	
	Diet vertebrates	binary	0	0.16	1	3.59	D:	-1.25	
	Diet invertebrates	binary	0	0.86	1	1.41	D:	-0.15	
Plants	Plant height [cm]	numeric	0.08	5.30	65	3.11	K:	1.29	Compiled with megaptera package
	Specific leaf area	numeric	5.35	28.03	64.85	1.64	K:	0.18	
	Seed weight [g]	numeric	0.01	136.09	12,976	1.18	K:	0.31	
	Leaf anatomy helomorphic	binary	0	0.16	1	1.39	D:	0.55	
	Leaf anatomy scleromorphic	binary	0	0.11	1	1.53	D:	0.69	
	Leaf anatomy mesomorphic	binary	0	0.75	1	1.80	D:	0.43	
	Leaf anatomy hygromorphic	binary	0	0.44	1	1.59	D:	0.31	
	Anemochorous	binary	0	0.41	1	1.39	D:	0.16	

Autochorous	binary	0	0.50	1	1.32	D:	0.26
Zoochorous	binary	0	0.82	1	1.34	D:	-0.03
Woodyness	binary	0	0.23	1	3.62	D:	-0.47
Propagation predominantly vegetative	binary	0	0.06	1	1.12	D:	0.85
Perennial	binary	0	0.13	1	1.34	D:	0.31

Literature Appendix I:

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K. L. Han, J. Harshman, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, F. H. Sheldon, D. W. Steadman, C. C. Witt and T. Yuri (2008). "A phylogenomic study of birds reveals their evolutionary history." Science **320**(5884): 1763-1768.

Seibold, S., R. Brandl, J. Buse, T. Hothorn, J. Schmidl, S. Thorn and J. Muller (2015). "Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe." Conservation Biology **29**(2): 382-390.

Appendix J: Deadwood amounts

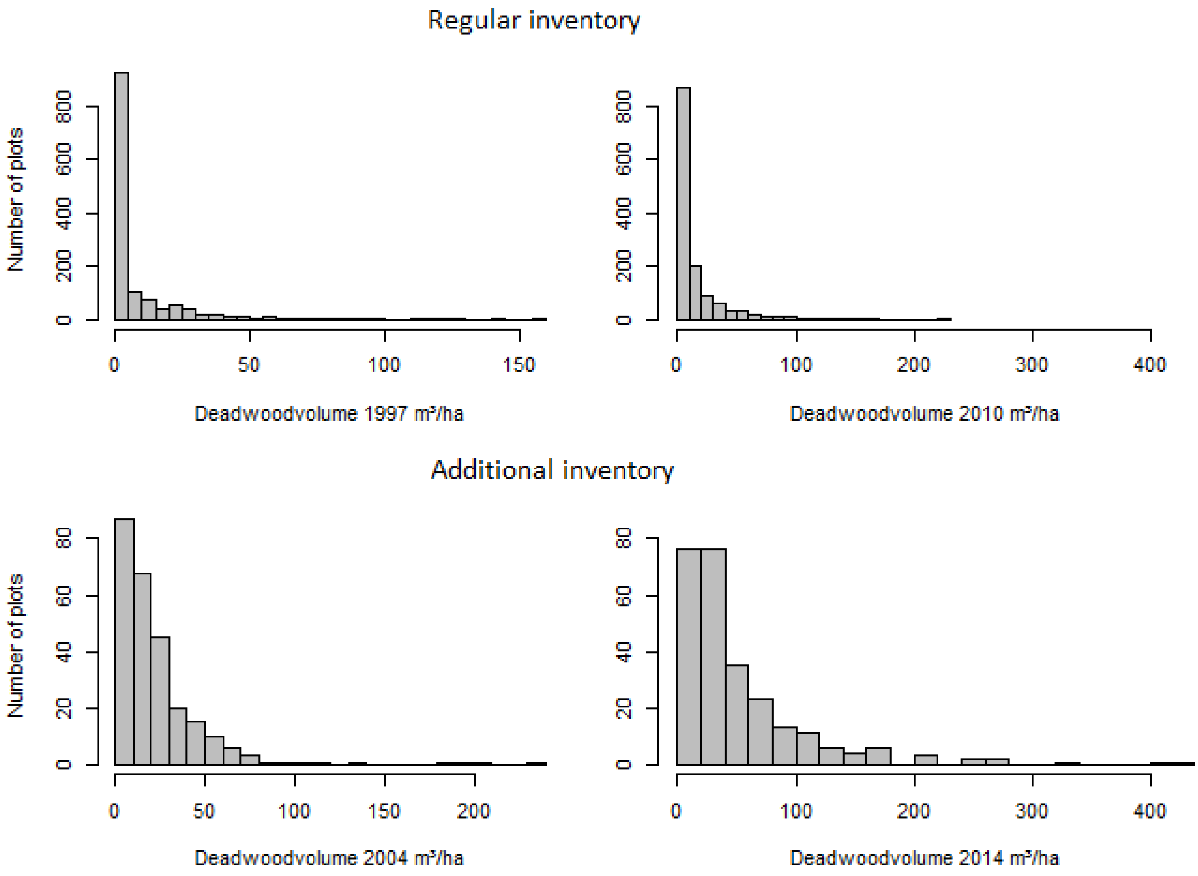

Figure J1: Histogram of deadwood amounts in all four study years. The top diagrams show the repeated regular inventory from 1997 and 2010. The bottom diagrams show the repeated additional inventory from 2004 and 2014. The y-axis displays the number of plots with the respective deadwood amount. In the additional inventory in 2014 one plot with an extreme volume of 2772.273 m^{3} ha^{-1} was deleted to make the plots comparable. Note that the y-axes are differently scaled for the inventories and the x-axes for every year.

If we consider plots in production forests and reserves separately we found that deadwood amounts in forest nature reserves before the implementation of the strategy were 22.3 ± 5 m^{3} ha^{-1} in 1997 (N = 63), and therefore higher than in managed forests which had an amount of 8 ± 0.5 m^{3} ha^{-1} (N = 1282, t = 5.969, p-value <0.0001). While deadwood amounts in managed plots increased significantly by about 61 percent to 12.9 ± 0.6 m^{3} ha^{-1} in 2010 (N = 1282, V = 121180, p <0.0001), the increase in forest nature reserves to 26.5 ± 5.6 m^{3} ha^{-1} was not significant (N = 63, V = 428, p = 0.9793). The difference in deadwood amounts is significant

Appendix K: Results of the living stand inventory

Table K1: values of harvesting intensity and natural mortality of the regular forest inventory. Mean and standard error, such as the test statistics (V) and the p-value (p) of the Wilcoxon Signed-Rank Test are given for the five main tree species in both years. Significant results are indicated in bold

Harvesting intensity [m² ha^{-1}]				
	1997	2010		
	Mean ± SE	Mean ± SE	V	p
Beech	1.84 ± 0.09	2.47 ± 0.10	**107880**	**9.74E-07**
Spruce	0.44 ± 0.05	0.84 ± 0.09	**8334.5**	**1.47E-03**
Pine	0.70 ± 0.05	0.92 ± 0.07	**24852**	**0.004324**
Oak	0.21 ± 0.02	0.64 ± 0.06	**6316.5**	**3.92E-11**
Hornbeam	0.13 ± 0.02	0.15 ± 0.02	3073.5	0.9203
Natural mortality [m² ha^{-1}]				
Beech	1.00 ± 0.09	0.20 ± 0.03	**33968**	**< 2.2e-16**
Spruce	1.62 ± 0.15	0.25 ± 0.04	**29202**	**< 2.2e-16**
Pine	0.33 ± 0.04	0.13 ± 0.02	**7740**	**3.52E-03**
Oak	0.19 ± 0.03	0.09 ± 0.02	**3426.5**	**0.0009014**
Hornbeam	0.03 ± 0.01	0.03 ± 0.01	535.5	0.6404

Table K2: Basal area (m² ha^{-1}) of different tree species in both inventory years and the development of the basal area.

Tree species	Scientific name	1997	2010	Development
Beech	Fagus sylvatica	16186	18578	2391.8
Oak	Quercus spp.	6258.9	6599.2	340.3
Spruce	Picea abies	4373.5	3823	-550.5
Pine	Pinus sylvestris	3782.3	3446.5	-335.8
Hornbeam	Carpinus betulus	2133.8	2530.7	396.9
Larch	Larix decidua	1163.5	1328.5	165
Sycamore	Acer pseudoplatanus	459.7	633	173.3
Birch	Betula spp.	341.6	402.8	61.2
Douglas fir	Pseudotsuga menziesii	310.3	507.5	197.2
Ash	Fraxinus excelsior	212	231.3	19.3
Black alder	Alnus glutinosa	211.9	305.4	93.5
Lime	Tilia spp.	204	290.3	86.3
Aspen	Populus tremula.	136.7	232.2	95.5
Fir	Abies alba	85.5	95.1	9.6
Poplar	Popoulus spp.	70	67.6	-2.4
Rowan	Sorbus aucuparia	58.7	85.2	26.5
Cherry	Prunus spp.	56.6	77.3	20.7
Willow	Salix spec	45	61.1	16.1
Elm	Ulmus spp.	36.6	46.8	10.2
Red Oak	Quercus rubra	33.4	44.8	11.4
Field maple	Acer campestre	30.4	43.6	13.2
European black pine	Pinus nigra	28.4	28.1	-0.3

White alder	Alnus incana	20.7	22.2	1.5
Checkers tree	Sorbus torminalis	19.4	33.5	14.1
Norway maple	Acer platanoides	13.6	13.7	0.1
Japanese larch	Larix kaempferi	13.3	10.4	-2.9
Chestnut	Aesculus hippocastanum	2.7	2.9	0.2

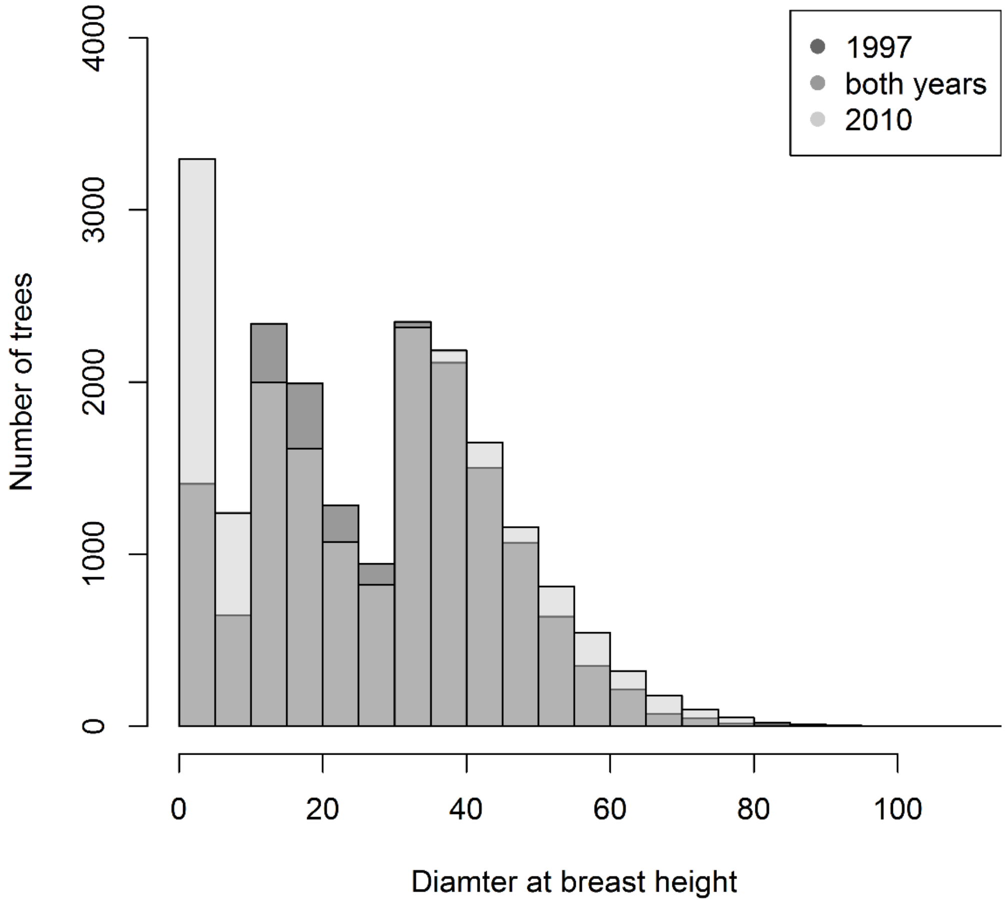

Figure K1: Diameter at breast height of single living trees in the regular inventory of both years. Bars with light grey on top indicate higher numbers of trees in 2010 and with dark grey on top higher numbers of trees in 1997.

Appendix L: Results of the component wise gradient boosting

Table L1: Range of the effect size and selection frequency for all explanatory variables from the three models.

	Range of effect size						Selection frequency		
	1997		2010		change		1997	2010	change
	Min	Max	Min	Max	Min	Max			
Number of tree species	0	0	-0.13	0.26	0	0	0	0.06	0
Growing stock	-0.06	0.08	0	0	0	0	0.06	0	0
Percentage broadleaf trees	-0.08	0.02	-0.24	0.05	0	0	0.04	0.06	0
Presence of spruce	0	0	-0.02	0.10	0	0	0	0.04	0
Presence of pine	0	0	0	0	0	0	0	0	0
Stand age	-0.44	0.40	-0.73	0.23	-0.12	0.07	0.21	0.09	0.15
Natural mortality	-0.36	1.22	-0.24	2.36	0.26	2.36	0.16	0.12	0.27
Harvesting intensity	-0.02	0.07	-0.12	0.12	-0.05	0.41	0.03	0.05	0.13
Forest nature reserve	-0.02	0.29	0	0	0	0	0.01	0	0
Management district	-0.02	0.01	0	0	0	0	0.04	0	0
Slope	-0.03	0.43	-0.05	0.27	0	0	0.04	0.05	0
Gauss-Krueger coordinates	-0.42	0.32	-0.6	0.45	0.12	0.25	0.40	0.54	0.45

Appendix M: Deadwood profile split into management

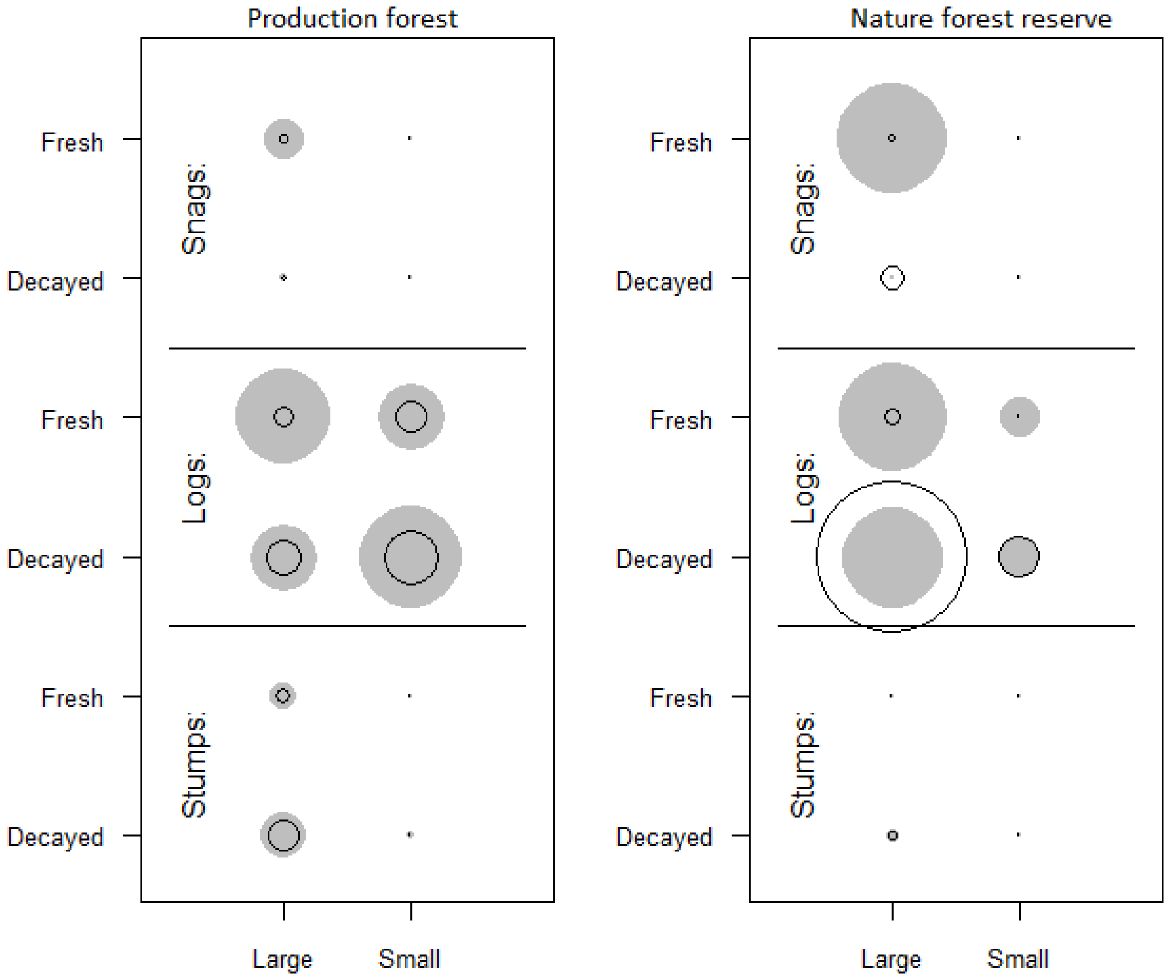

Figure M1: Deadwood profile in production forest and reserves. The x-axis displays the object size (large > 30 cm diameter, small < 30 cm diameter), the y-axis displays the decay stages (fresh: decay stage 1 and 2, decayed: decay stage 3 and 4). The fields separated by horizontal lines display the volume of stumps, logs and snags separately. The size of the circles and rings display the deadwood volume for each category. The grey circles display the amount in 2014 and the black rings the volume in 2004.

Appendix N: Deadwood characteristics additional inventory

Table N1: Deadwood volume of objects in the additional inventory: Volume [$m^3\ ha^{-1}$], standard error of both years of record and results of the Wilcoxon signed rank test of the comparison of both years. Deadwood objects are separated into different object classes, decay stages and tree species. Significant results are indicated in bold.

		2004		2014		Wilcoxon test	
		Volume	Standard error	Volume	Standard error	V	p
Total		24.6	2	67.9	11.3	**4851**	**< 0.0001**
Production forest		18.9	1.1	49.1	3.8	**2505**	**< 0.0001**
Forest nature reserve		49.4	8	150.3	57.4	**312**	**< 0.01**
Object classes	snags	2.6	0.4	7.5	1.3	**3090**	**< 0.001**
	logs	17.5	1.7	51	11.2	**7453**	**< 0.0001**
	stumps resulting from harvest	4	0.2	6	0.2	**5405**	**< 0.0001**
Decay stages	1	0.69	0.2	6.9	1	**1402**	**< 0.0001**
	2	3.3	0.4	17.3	2	**5579**	**< 0.0001**
	3	11.04	1.3	12.9	1	**14151**	**< 0.05**
	4	3.4	0.6	7.7	0.6	**4674**	**< 0.0001**
Tree species deadwood	Beech	14.8	1.7	49.7	11.2	**5955**	**< 0.0001**
	Other broadleaf (aspen, maple, birch, ash, cherry, elm)	0.2	0.1	2.7	1.6	**227**	**< 0.0001**
	Oak	1.4	0.2	1.9	0.4	5571	> 0.1
	Hornbeam	0.3	0.1	0.6	0.2	528	> 0.05
	Fir	0.1	0.1	0.2	0.1	0	> 0.1
	Spruce	0.6	0.2	2.7	1	309	> 0.1
	Pine	0.9	0.2	2	0.5	1453	> 0.1
	Larch	0.3	0.1	0.9	0.3	295	> 0.1

Table N2: Number of deadwood of objects in different decay stages of the additional inventory: Mean number per hectare and standard error. Results of the Wilcoxon signed rank test of the comparison of both years. Significant results are indicated in bold.

		2004		2014		Wilcoxon test	
		Number	Standard error	Number	Standard error	V	p
	Total	2074	7	327	10.7	**2150**	**< 0.0001**
Object classes	snags	3.9	0.4	7.3	0.8	**1794.5**	**< 0.0001**
	logs	64.9	3.6	151.4	7.7	**2234.5**	**< 0.0001**
	stumps resulting from harvest	133.9	5.6	171.6	7.4	**5935.5**	**< 0.0001**

Table N3: Deadwood volume of objects in the subset of the additional inventory: Volume [$m^3\ ha^{-1}$], standard error of both years of record and results of the Wilcoxon signed rank test of the comparison of both years. Deadwood objects are separated into different object classes, decay stages and tree species. Significant results are indicated in bold.

	2004		2014		Wilcoxon test	
	Volume	Standard error	Volume	Standard error	V	p
Total	39.2	5.9	122.5	41.2	**494**	**< 0.0001**
Production forest	18.8	2.4	54.6	8.2	**109**	**< 0.0001**
Forest nature reserve	69.6	12.4	251.2	114.3	**75**	**0.03**

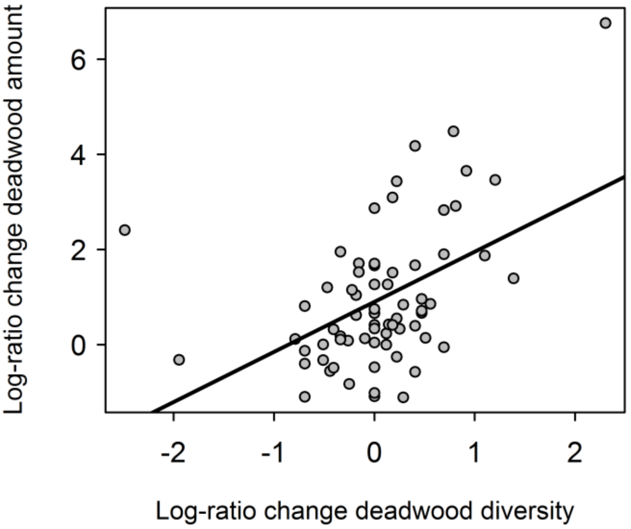

Figure N1: relationship between log transformed ration of change in deadwood amount and diversity, the t-test shows a significance relationship: (t = 5.72, p < 0.0001).

Appendix O: Deadwood characteristics regular inventory

Table O1: Deadwood volumes of objects in different decay stages, object classes and tree species in the regular inventory: Volume [m³ ha^{-1}], standard error of both years of record and results of the Wilcoxon signed rank test of the comparison of both years. Significant results are indicated in bold.

		1997		2010		Wilcoxon test	
		Volume	Standard error	Volume	Standard error	V	p
Object classes	snags	2.6	0.3	3.7	0.4	**3090**	**< 0.001**
	logs	6	0.4	9.9	0.5	**108980**	**< 0.0001**
Decay stages	1	1.1	0.2	1.2	0.2	6699	> 0.1
	2	7	0.5	9.9	0.6	**125060**	**< 0.0001**
	3	0.6	0.1	2.4	0.2	**10668**	**< 0.0001**
Tree species deadwood	Broadleaf	3.18	0.3	5.8	0.4	**42588**	**< 0.0001**
	Oak	1.9	0.3	1.9	0.24	14791	0.889
	Coniferous	3.6	0.3	5.6	0.5	**40560**	**< 0.0001**

Appendix P: Habitat trees split into management

Table P1: Number of habitat trees dataset 2 in both inventories. Mean number per plot and results of a linear model with the nature forest reserve as factor. Separated in plots in production forests (N=214) and nature forest reserves (N=49). Significant results are indicated in bold.

	Inventory	Production forest		Nature forest reserve		Linear model	
		Number	Standard error	Number	Standard error	t	p
Stem rot	2004	8.90	0.77	9.95	1.88	0.57	0.5699
	2014	0.70	0.17	0.82	0.49	0.27	0.7866
Large woodpecker holes	2004	0.65	0.17	3.16	0.87	4.58	< **0.0001**
	2014	0.77	0.22	0.66	0.29	-0.22	0.8255
Medium woodpecker holes	2004	2.90	0.49	10.41	2.57	4.72	< **0.0001**
	2014	4.53	0.55	11.79	2.36	4.51	< **0.0001**
Small woodpecker holes	2004	0.53	0.12	4.03	1.05	6.29	< **0.0001**
	2014	0.77	0.11	0.66	0.24	0.66	0.5072
Fungi brackets	2004	0.28	0.11	1.02	0.53	2.15	**0.0324**
	2014	0.23	0.10	0.61	0.35	1.39	0.1651
Mould filled cavities	2004	0.77	0.17	5.97	1.23	7.59	< **0.0001**
	2014	1.45	0.30	4.39	0.91	3.86	**0.0001**
Nesting boxes	2004	0.40	0.13	0.41	0.22	0.04	0.9698
	2014	0.32	0.09	0.46	0.29	0.64	0.5250
Natural cavities	2004	0.68	0.20	3.57	1.18	4.16	< **0.0001**
	2014	1.20	0.23	4.64	1.18	4.63	< **0.0001**

Appendix Q: Taxa in reserves before and after the implementation

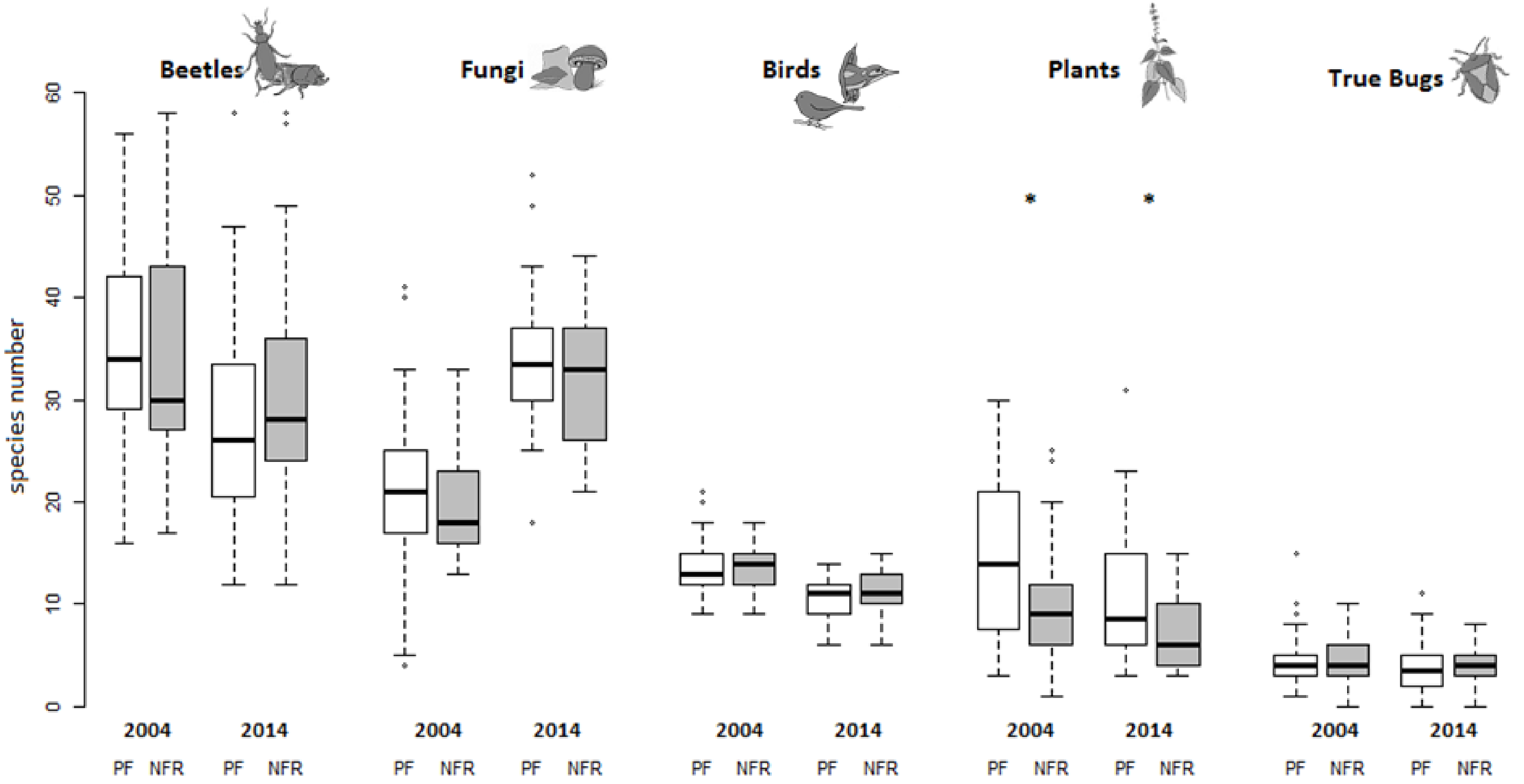

Figure Q1: Species numbers of the five examined groups within the two sampling years (2004 and 2014) and within production forest (PF: white boxes) and within nature forest reserves (NFR: gray boxes). Significant results ($p < 0.05$) are marked with a star.

Appendix R: Rarefaction curves for q = 1 and q = 2 for all examined taxonomic groups

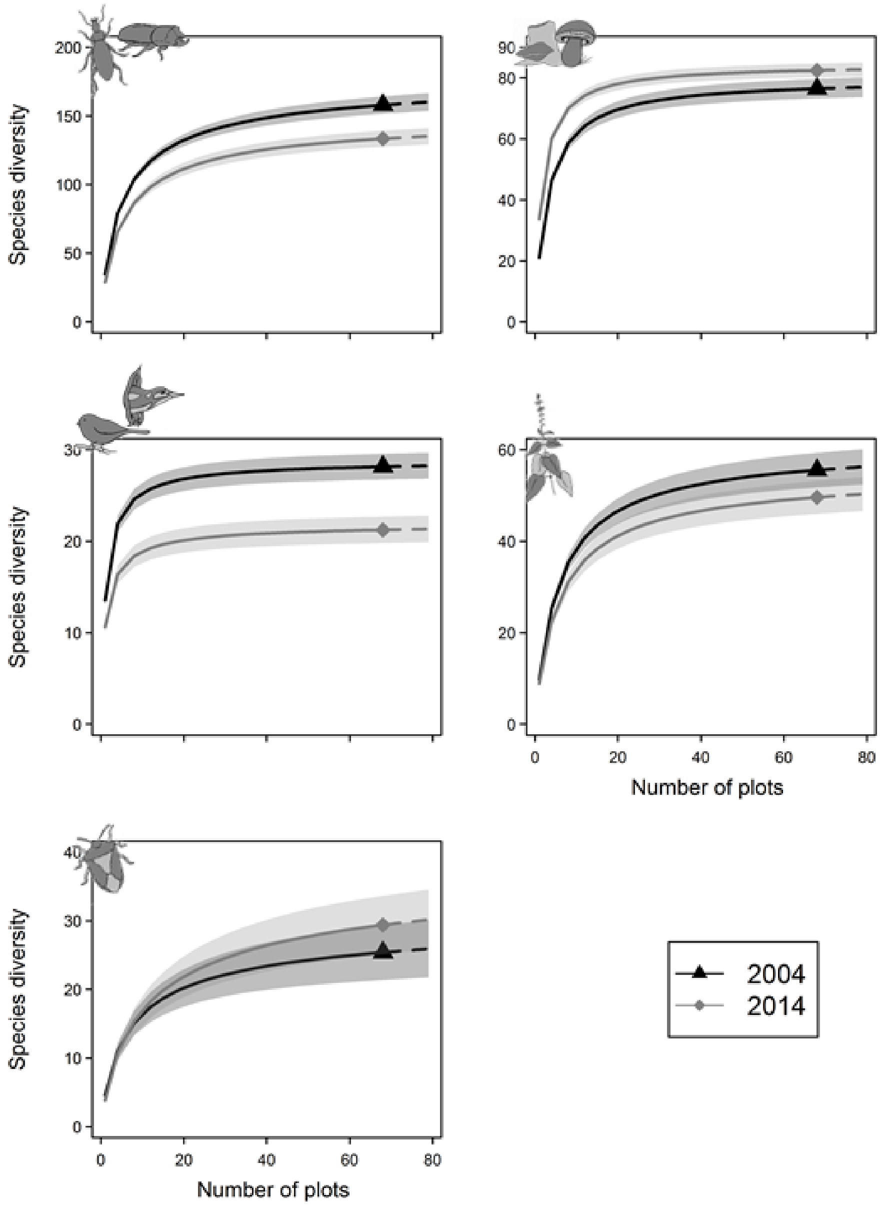

Figure R1: Rarefaction curves for beetles (top left), fungi (top right), birds (middle left), plants (middle right) and true bugs (lower left) of q=1. Species diversity in 2004 with a black line and the confidence interval in dark gray, species diversity in 2014 with a gray line and the confidence interval indicated in light gray.

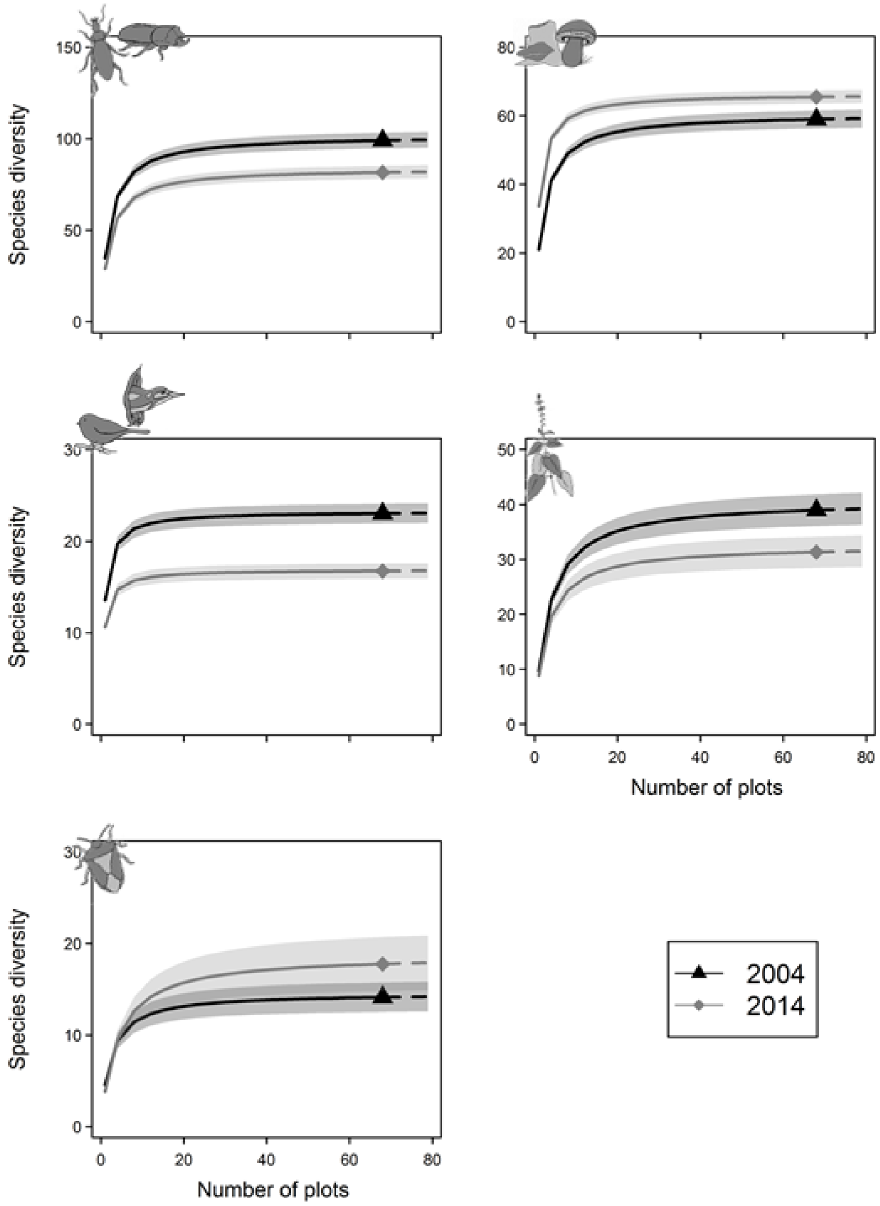

Figure R2: Rarefaction curves for beetles (top left), fungi (top right), birds (middle left), plants (middle right) and true bugs (lower left) of q=2. Species diversity in 2004 with a black line and the confidence interval in dark gray, species diversity in 2014 with a gray line and the confidence interval indicated in light gray.

Appendix S: Results of the generalized linear models of the species numbers of the five examined taxonomic groups.

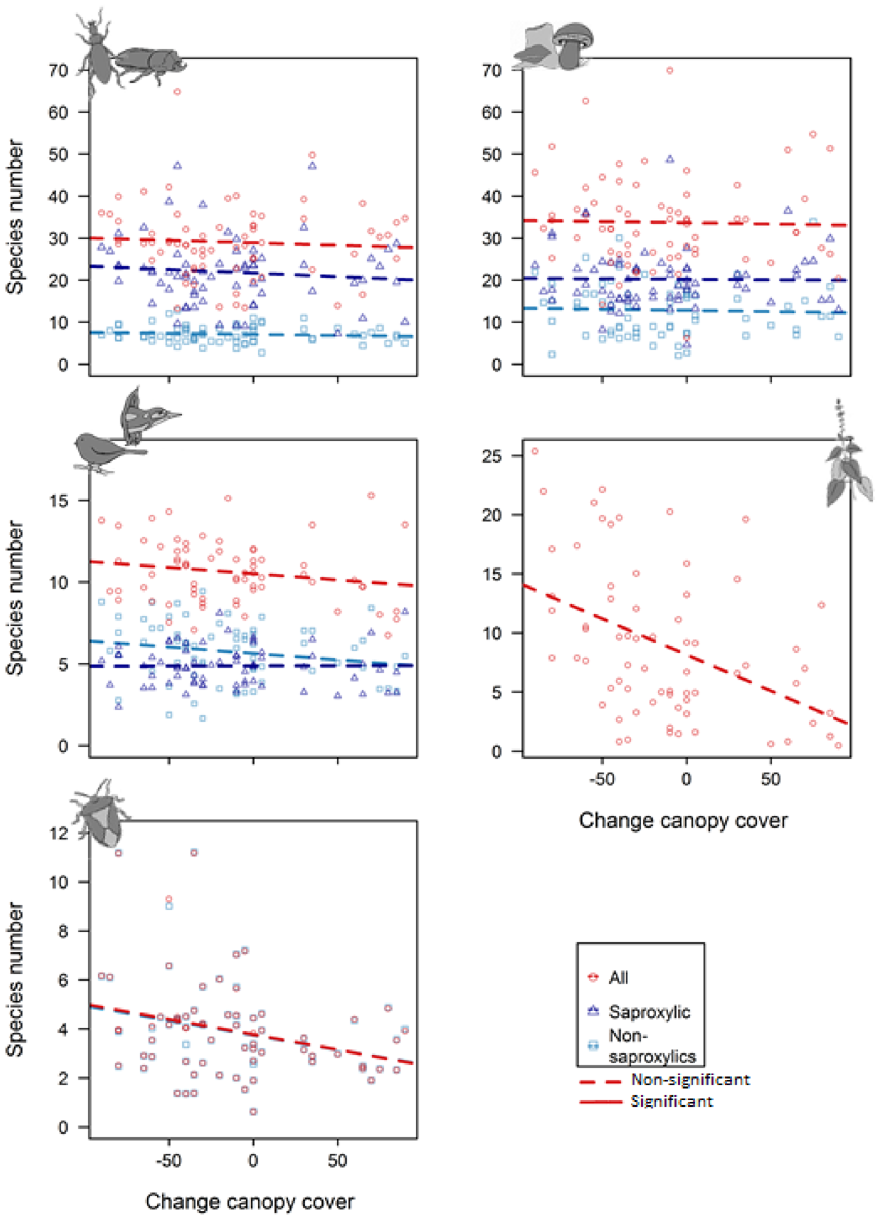

Figure S1: Results of the generalized linear model with the species numbers of the five taxonomic groups and the saproxylic and non-saproxylics species separate as dependent variables and the log-transformed ratio of deadwood change, the difference in canopy cover between the years and the log-transformed ratio of the change in the number of cavity bearing trees as predictor variables and the diversity before the implementation of the strategy as offset variables. The x-axis displays the change in canopy cover.

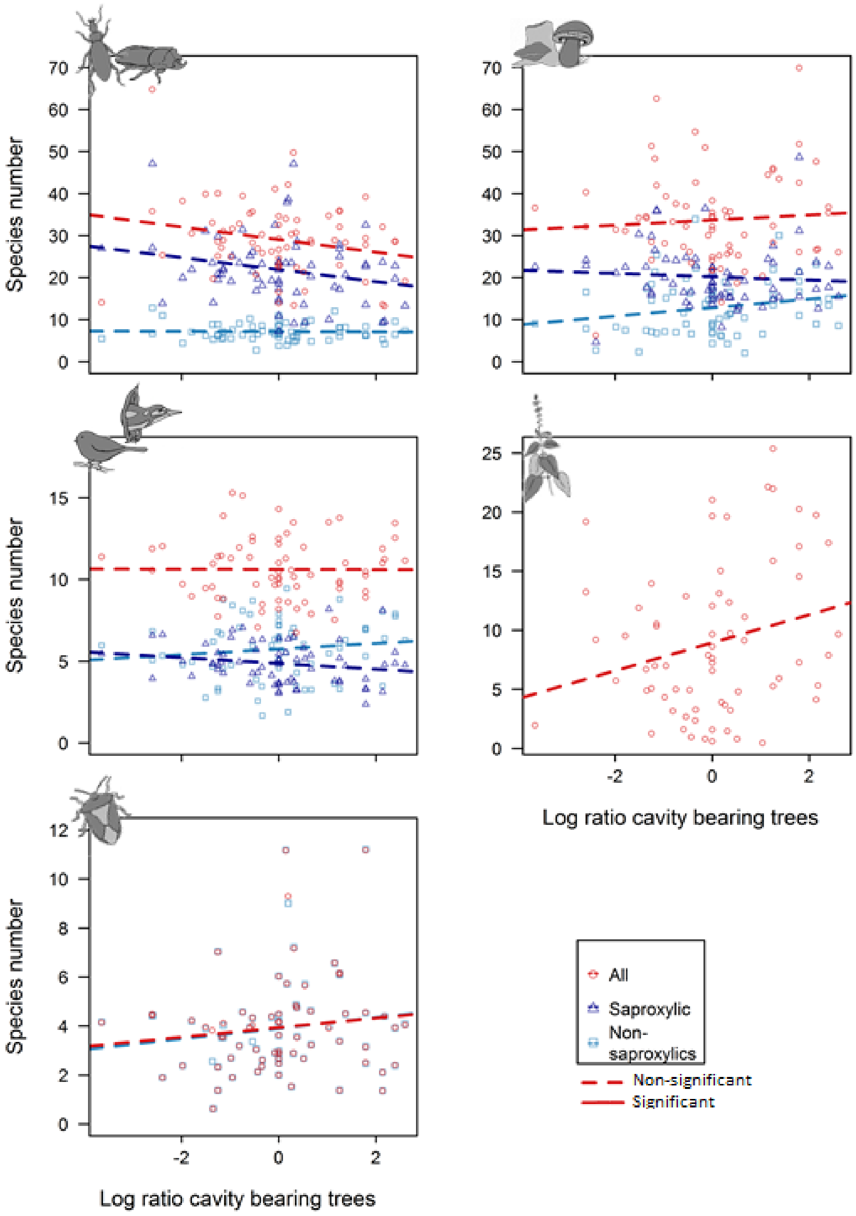

Figure S2: Results of the generalized linear model with the species numbers of the five taxonomic groups and the saproxylic and non-saproxylics species separate as dependent variables and the log-transformed ratio of deadwood change, the difference in canopy cover between the years and the log-transformed ratio of the change in the number of cavity bearing trees as predictor variables and the diversity before the implementation of the strategy as offset variables. The x-axis displays the change in the number of cavity bearing trees.

Appendix T: Models of weighted mean traits

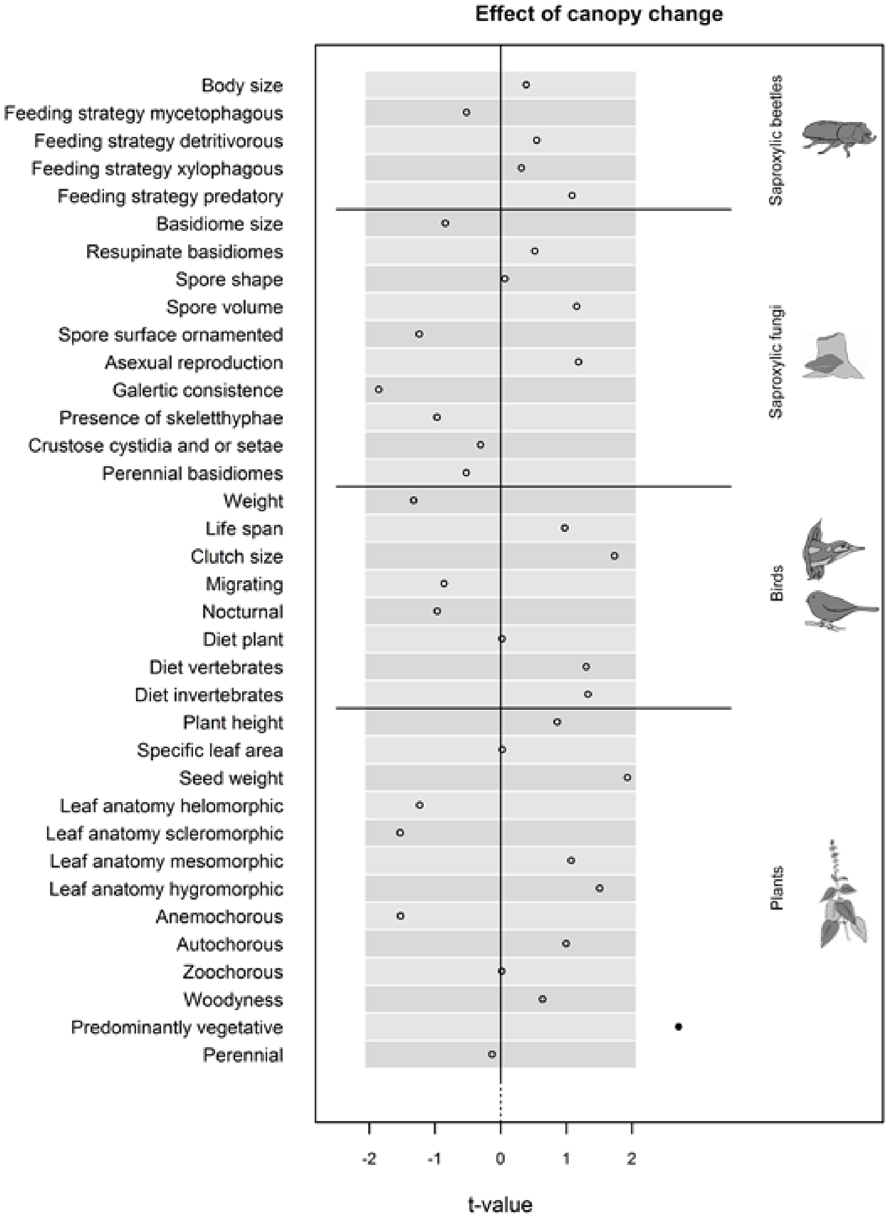

Figure T1: Results of linear model with the mean weighted traits in 2014 as dependent variable and the log ratio of deadwood volume, the change in canopy cover and the weighted mean of traits in 2004 as independent variables. The x-axis shows the t-value of the change in canopy cover. The gray bar marks the significance level: black points are significant, circles are not significant. The horizontal lines mark to which taxonomic group the trait belongs.

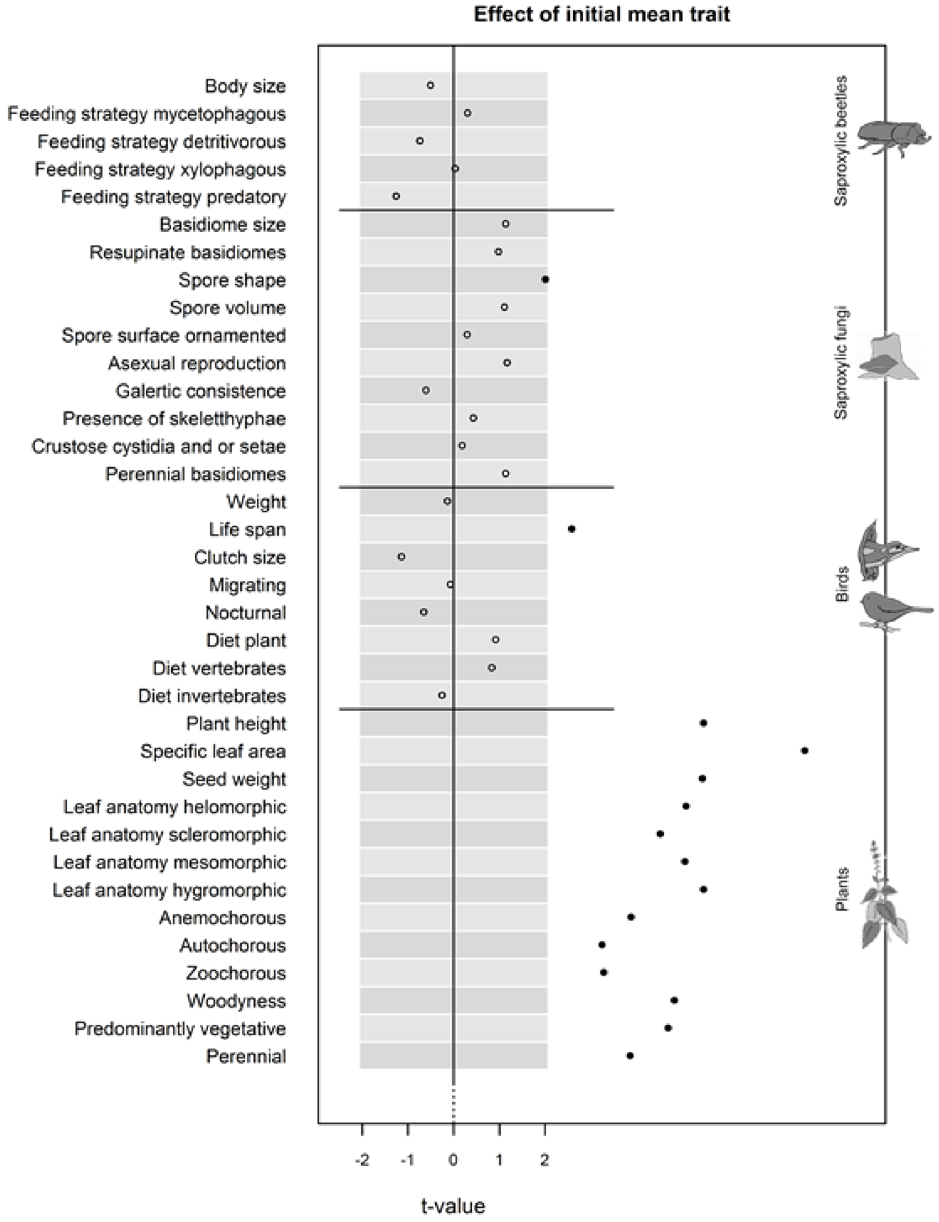

Figure T2: Results of linear model with the mean weighted traits in 2014 as dependent variable and the log ratio of deadwood volume, the change in canopy cover and the weighted mean of traits in 2004 as independent variables. The x-axis shows the t-value of the previous mean trait. The gray bar marks the significance level: black points are significant, circles are not significant. The horizontal lines mark to which taxonomic group the trait belongs.

Appendix U: Results of the optimal linear model with the standardized effect size of the mean pairwise functional-phylogenetic distance for the difference in canopy cover and the previous assembly

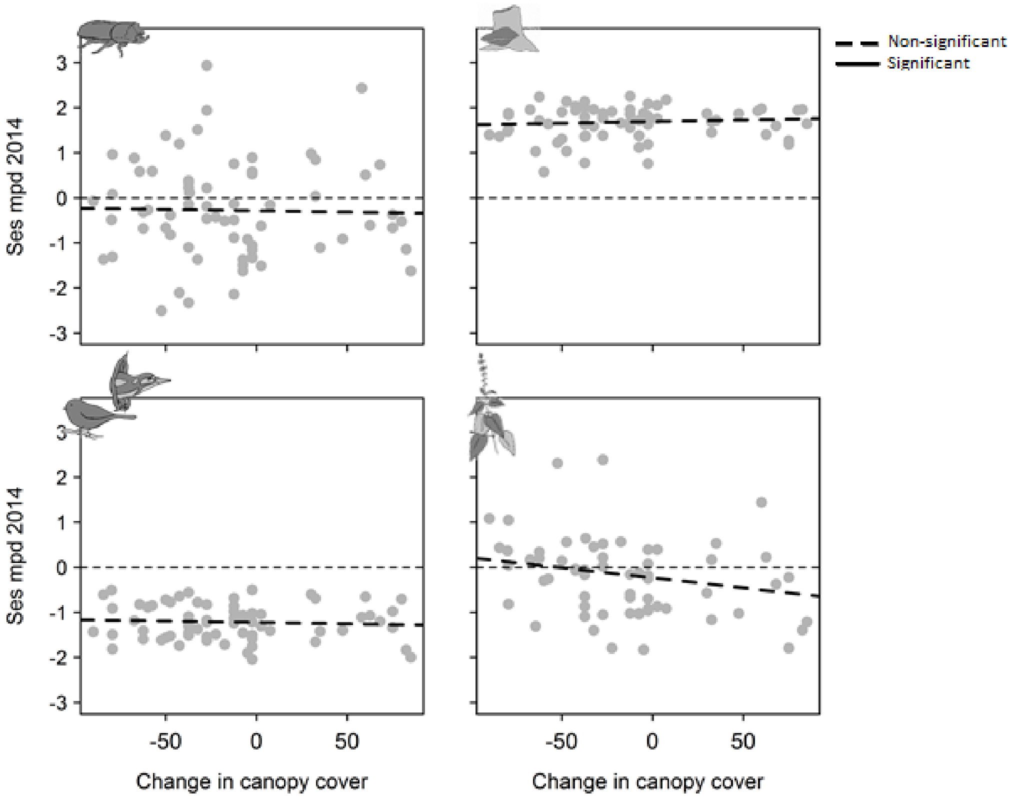

Figure U1: Results of the optimal linear model for the relationship of the standardized effect size of the mean pairwise phylogenetic-functional distance (ses mpd) for all examined five taxonomic groups with the change in canopy cover. Top left: saproxylic beetles, top right: saproxylic fungi, bottom left: birds, bottom right: plants.

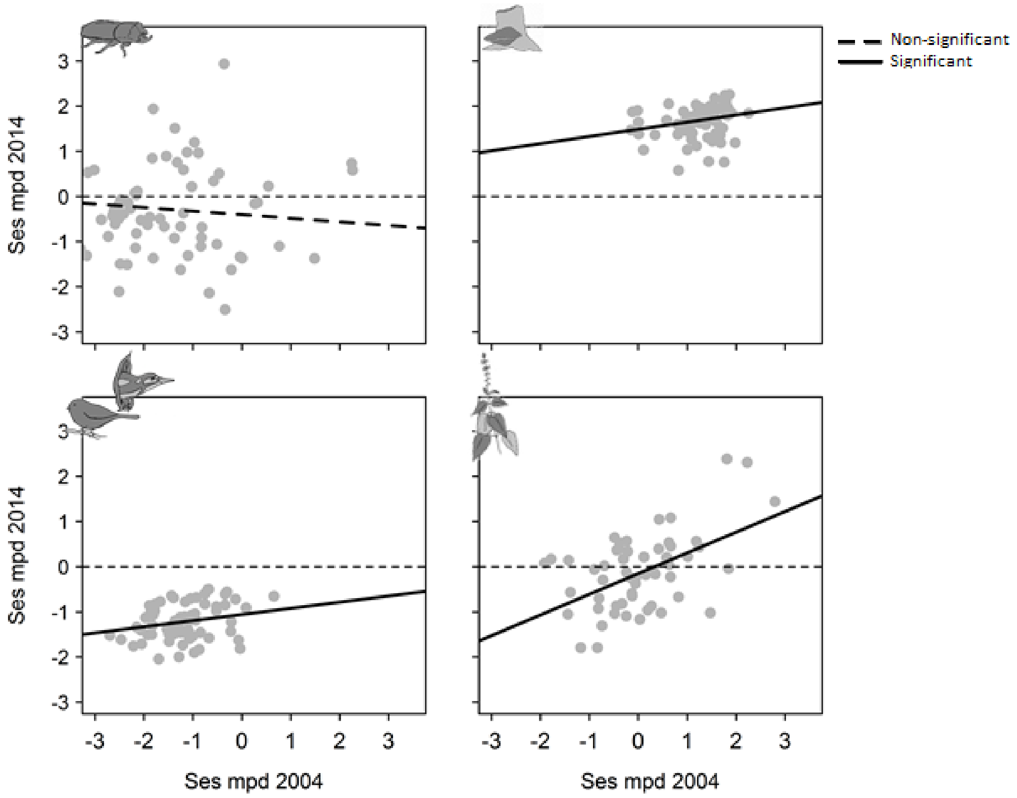

Figure U2: Results of the optimal linear model for the relationship of the standardized effect size of the mean pairwise phylogenetic-functional distance (ses mpd) for all examined five taxonomic groups with the previous standardized effect size of the mean pairwise phylogenetic-functional distance. Top left: saproxylic beetles, top right: saproxylic fungi, bottom left: birds, bottom right: plants.

Appendix V: Results of the optimal linear model for the standardized effect size of the mean pairwise functional-phylogenetic distance testing the effect of deadwood diversity

To identify if the deadwood amount or diversity was the driving factor for the changes in species assembly, although they are strongly correlated (Appendix N, Figure N1) we compared linear type 1 models with the function anova (package base) to see which variable explains more variance. The idea behind this is that if we use a type 1 model, these calculate the variance explained by the single variables in a specific, given order. By interchanging the variables of deadwood amount and deadwood diversity we can see how much variance is explained by the single variables. For example: if the deadwood amount is defined as the first variable and it explains variance but the diversity, as second variable does not explain variance, this indicates a stronger effect of the deadwood amount. If then, in the basically same model the diversity is assigned as first variable and does explain variance but the deadwood amount does not explain any variance the F-values of both models can be compared to identify which variable explains more variance. However, if both variables explain variance if the deadwood diversity is assigned as first variable this indicates that the diversity only explains a small amount of variance additionally to the deadwood amount.

Table V1: results of the above described linear models with the standardized effect size of the mean pairwise functional-phylogenetic distance (ses mpd) and the change in deadwood amount, deadwood diversity (as log ratio), the canopy cover and the standardized effect size in the previous inventory.

Dependent variable	first variable of deadwood change	cover change		deadwood change		ses mpd previous		deadwood diversity change	
		F	p	F	p	F	p	F	p
Saproxylic beetles	amount	0.25	0.62	20.47	**0.00003**	0.09	0.77	0.87	0.35
Saproxylic beetles	diversity	0.25	0.62	12.49	**0.001**	0.09	0.77	8.85	**0.004**
Birds	amount	0.20	0.66	1.50	0.23	4.54	**0.04**	0.35	0.56
Birds	diversity	0.20	0.66	0.63	0.43	4.54	**0.04**	1.21	0.27
Saproxylic fungi	amount	0.48	0.49	1.54	0.22	19.59	**0.0001**	0.04	0.84
Saproxylic fungi	diversity	0.48	0.49	1.42	0.24	19.59	**0.0001**	0.17	0.68
Plants	amount	4.17	0.05	0.16	0.69	4.91	**0.03**	0.06	0.80
Plants	diversity	4.17	0.05	0.21	0.65	4.91	**0.03**	0.01	0.92