Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt
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Effects of salvage logging on biodiversity – Ecological evidence for conservation-oriented management of natural disturbances

Simon Otto Thorn

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Zusammenfassung

Wälder liefern dem Menschen wichtige Ressourcen, wie Nahrung oder Bauholz und beherbergen einen Großteil der terrestrischen Artenvielfalt. In den Wäldern der nördlichen Hemisphäre haben die Intensität und das flächige Ausmaß von natürlichen Störungen, wie Brände, Borkenkäferausbrüche oder Stürme in den letzten Jahrzehnten stark zugenommen. In den ökonomisch wichtigen Fichtenwäldern Europas sind Stürme und begleitende Ausbrüche des Buchdruckers (*Ips typographus*) die Hauptursache solcher Störungen und betreffen durch sturmgeschädigtes Holz jährlich ein Wirtschaftsvolumen von bis zu 16 Milliarden Euro. Um Folgeschäden und Wertverluste des Holzes durch Pilz- und Borkenkäferbefall zu minimieren, werden Sturmschäden von Forstbetrieben schnellstmöglich durch sogenannte „Sanitärhiebe“ aufgearbeitet. Gerade diese Störungen sind jedoch auch die Haupttreiber für eine erhöhte Strukturvielfalt und Biodiversität in Wäldern. Art und Umfang von Sanitärhieben lösen daher heftige Diskussionen zwischen Forstwirtschaft und Naturschutz aus, besonders, wenn es sich um Flächen in Schutzgebieten handelt. Ein detailliertes Verständnis der ökologischen Auswirkungen von Sanitärhieben auf Biodiversität ist daher wichtig, um wissenschaftlich fundierte Naturschutzkonzepte entwickeln zu können. Bisher fehlen vor allem Studien, die untersuchen, welche Arten besonders von Sanitärhieben betroffen sind und welche ökologischen Mechanismen für ihren Rückgang verantwortlich sind.

Im ersten Artikel dieser Dissertation konnte durch eine globale Meta-Analyse gezeigt werden, dass vor allem totholzgebundene (xylobionte) Artengruppen, wie xylobionte Käfer oder Holzpilze, besonders unter Sanitärhieben leiden. Bodenbewohnende Artengruppen, wie Spinnen oder Laufkäfer, profitierten jedoch von Sanitärhieben und der damit verbundenen Auflichtung. Selbst Artengruppen, die keine Veränderung in der Artenzahl aufwiesen, zeigten gravierende Änderungen in der Zusammensetzung ihrer Artengemeinschaften. Der Artenverlust xylobionter Arten war in erster Linie auf einen Verlust der Totholzmenge und nicht auf einen Verlust der Totholzvielfalt zurückzuführen.

Im zweiten Artikel konnte gezeigt werden, dass ein Verlust von Arten nicht nur innerhalb von xylobionten Artengruppen auftreten kann (wie beispielsweise xylobionte Käfer oder Holzpilze), sondern auch innerhalb von Artengruppen, die nicht primär xylobiont sind. Dies verdeutlichte die Reaktion von Nachtfaltergemeinschaften auf Sanitärhiebe nach einem flächigen Ausbruch des Buchdruckers: Obwohl insgesamt nur

eine geringe Veränderung der Artenzahl oder Abundanz festzustellen war, war die Abundanz von Arten mit xylobionten oder Detritus-fressenden Larven signifikant rückläufig. Im Gegensatz dazu konnten Arten, deren Larven sich omnivor oder von krautigen Pflanzen ernähren, von Sanitärhieben profitieren.

Auch Gemeinschaften von Brutvögeln und überwinternden Standvögel wurden von Sanitärhieben nach flächigen Sturmschäden beeinflusst, wie in Artikel III und IV untersucht wurde. Im Vergleich zu unberührten Beständen dominierten hier jedoch die Effekte des Sturmes selbst und nicht die der folgenden Sanitärhiebe. Sowohl auf geräumten (Flächen mit Sanitärhieben) als auch auf ungeräumten Windwurfflächen konnten Vogelarten mit rückläufiger Bestandsentwicklung, wie beispielsweise Bergpieper (*Anthus spinolleta*), nachgewiesen werden. Eine weitere gefährdete Art, der Gartenrotschwanz (*Phoenicurus phoenicurus*), trat nur auf Windwurfflächen ohne Sanitärhiebe auf, die sich durch eine hohe Strukturvielfalt auszeichneten. Neben Wurzeltellern sind kleine Naturverjüngungshorste ein wichtiges Lebensraumelement in von Stürmen beeinträchtigten Wäldern. Diese Verjüngungshorste können überwinternden Vogelarten, wie beispielsweise dem Wintergoldhähnchen (*Regulus regulus*), als Nahrungshabitat dienen.

In Artikel V konnten Veränderungen in den ökologischen Prozessen identifiziert werden, die Artengemeinschaften unter natürlichen Bedingungen strukturieren: Konkurrenz und Umwelteinflüsse. Durch Sanitärhiebe kam es hier je nach Artengruppe zu einer Verschiebung von Umwelteinflüssen hin zu Konkurrenz, oder umgekehrt. Dies bedeutet, dass beispielsweise xylobionte Käferarten aufgrund eines gestiegenen Konkurrenzdrucks um das verbliebene Totholz verloren gehen, wohingegen Holzpilzarten aufgrund stark veränderter Umwelteinflüsse durch Sanitärhiebe verschwinden. Obwohl nicht-xylobionte Arten, wie beispielsweise Vögel oder Gefäßpflanzen, zum Teil deutliche Veränderungen in ihren Artgemeinschaften zeigten, blieben ihre zugrunde liegenden Prozesse von Sanitärhieben unbeeinflusst.

Ein Kompromiss zwischen forstwirtschaftlichen und naturschutzfachlichen Interessen im Umgang mit sturmgefällten Fichten in Schutzgebieten ist häufig die kostenintensive Entrindung der Stämme. Dies verhindert einerseits die Massenvermehrung des Buchdruckers, andererseits verbleibt die Holzbiomasse im lokalen Stoffkreislauf. Im letzten Artikel konnte jedoch durch ein Experiment mit künstlich angelegten Windwürfen gezeigt werden, dass Entrinden die Artenzahl von Holzpilzen, xylobionten Käfern und parasitoiden Hautflüglern drastisch reduzierte. Vergleichend hierzu nahm die Artenzahl dieser Gruppen durch Schlitzen der Rinde nicht ab. Gleichzeitig stellen geschlitzte Stämme kein geeignetes Bruthabitat für den Buchdrucker dar. Maschinelles Schlitzen der Stämme war darüber hinaus mit einem geringeren Zeitaufwand verbunden als maschinelles Entrinden. Für sturmgeworfene Fichten stellt das Rindenschlitzen, im Gegensatz zum Entrinden, sowohl aus ökonomischer als auch aus ökologischer Sicht den besten Kompromiss zwischen Borkenkäferbekämpfung und natürlicher Waldentwicklung dar.

Dem Erhalt der Biodiversität trotz Sanitärhieben können eine Reihe von windwurftypischen Lebensraumelementen, wie beispielsweise aufgeklappte Wurzelteller, Naturverjüngungshorste oder sonnenexponierte Äste, dienen. Ein weiteres wichtiges Schutzinstrument besteht darin, sturmgeworfene Flächen komplett der natürlichen Suksession zu überlassen, um Rückzugsräume für Arten zu schaffen. Die genaue Größe und die räumliche Verteilung dieser Flächen sollten durch zukünftige Forschungsvorhaben ermittelt werden. Da die Ergebnisse aus solchen Forschungsvorhaben möglichweise erst in einigen Jahren zur Verfügung stehen, können geschätzte Flächengrößen auf der Basis bestehender Daten eine mögliche Übergangslösung für Wissenschaft und Praxis darstellen.

Summary

Forests provide important resources such as timber or food to people, while simultaneously harboring large parts of terrestrial biodiversity. The intensity and spatial extend of natural disturbances, such as wildfire, outbreaks of insect pests or windstorms, in forests of the northern hemisphere have increased considerably during the last decades. Windstorms are the dominant disturbance type in spruce-dominated forests of Europe and damage an economic value up to 16 billion euro of wood annually. To preserve damaged timber from an infestation by fungi or beetles, forest managers rapidly intervene into affected stands by post-disturbance salvage logging. Controversially, natural disturbances can enhance biodiversity and structural diversity in forests. Natural disturbances hence create debates between forest managers and conservationists about the appropriate way of salvage logging. Hence, a detailed understanding of the ecological consequences of salvage logging is needed to develop evidence-based conservation concepts for disturbed forests. Particularly studies that quantify the impact of salvage logging on different taxonomic groups and the ecological mechanisms causing such responses are lacking.

In the first article, a global meta-analysis revealed that saproxylic species were most seriously affected by salvage logging, while epigeal groups such as carabids or epigeal spiders benefit from salvage logging and accompanied increase in solar radiation to the ground. Species groups, which displayed little responses in species numbers to salvage logging, can display alterations in assemblage compositions. The extinctions of saproxylic species were predominately caused by the reduction of dead-wood amount, not by the reduction of dead-wood heterogeneity.

The second article demonstrated, that losses of saproxylic species can be present even within a specific species group: Nocturnal moths displayed no overall response in species numbers or abundance to post-beetle salvage logging, but salvage logging significantly decreased the abundance of moth species with detritus feeding or saproxylic larvae. By contrast, omnivorous species that feed on herbaceous plants tend to increase in abundance due to salvage logging.

Article III and IV focused on assemblages of breeding birds and winter residents in storm-felled forests. Here, the windstorm itself had the strongest effect on assemblages compared to vital forest stands. Both, salvaged and unsalvaged areas inhabited threatened bird species such as Water Pipit (*Anthus spinolleta*). A further threatened species, the

Common Redstart (*Phoenicurus phoenicurus*), was found in unsalvaged areas exclusively, whereas its occurrence appeared to depend on high structural diversity and biological legacies such as root plates. A further important biological legacy of storm-felled forests are small groups of natural regenerated trees that act as shelter and foraging habitat for winter resident birds such as the Goldcrest (*Regulus regulus*).

Article V revealed that an extinction of saproxylic species due to post-storm salvage logging was caused by a disruption of natural species assembly mechanisms. For instance, species of saproxylic beetles were extinct because of increasing importance of competitive exclusions, while wood-inhabiting fungi went extinct because of heavily altered environmental conditions by salvage logging. Assembly mechanisms of non-saproxylic groups, such as birds or vascular plants, remained constant despite these groups may display significant changes in their assemblage compositions.

Storm-felled Norway Spruce (*Picea abies*) are commonly debarked as a compromise between forest managers and conservationists. Such debarking prevents a mass outbreak of Spruce Bark Beetle (*Ips typographus*), while woody biomass is retained on-site. However, the experimental creation of windthrows (as described in Article VI) revealed that debarking significantly reduced the species numbers of wood-inhabiting fungi, as well as that of saproxylic beetles and their associated parasitoid wasps. By contrast, bark-scratching achieved similar levels of biodiversity as an untreated control tree, while density of bark beetles was significantly reduced. Furthermore, bark-scratching by device was faster than conventional debarking. Hence, bark-scratching represents the best compromise – ecologically and economically – between pest management and conservation goals compared to debarking.

To conserve biodiversity in post-storm salvage logging operations, a variety of biological legacies, such as root plates, small groups of regenerated trees or sun-exposed dry branches, can be retained. A further major tool is to set-aside unlogged patches of storm-felled trees for natural succession. However, future scientific investigations addressing the amount and spatial distribution of such retention patches in naturally disturbed forests may take decades. Meanwhile estimated sizes of retention patches may act as rules of thumb for forest management and as basis for future research.

1. Introduction

Forests are an important carbon sink and influence the global climate (Valentini et al., 2000; Burton, 2006; Ulyshen, 2014). Furthermore, they provide important resources such as timber, recreation, wood fuel, and food to people (Li et al., 2007; Boucher et al., 2009). However, increasing global population enhanced exploitation of forest ecosystems on different spatial scales (Foley et al., 2005; Gibson et al., 2011). Intensive forest management drastically decreased deadwood amounts (Stokland et al., 2012) and tried to minimize the impact of natural disturbances by windstorms, insect outbreaks, and wildfires (Thom and Seidl, 2015). Nevertheless, the amount of timber volume affected by natural disturbances has increased over the last decades, due to increasing growing stocks and global warming (Kurz et al., 2008; Seidl et al., 2014a). Thus, increasing societal demand for timber compels forest managers to rapidly intervene into affected stands through ‘post-disturbance’ or ‘salvage logging’ to harvest timber before it deteriorates (Lindenmayer et al., 2008). From an ecological point of view, intermediate levels of natural disturbances can enhance structural heterogeneity of forest ecosystems (Sousa, 1984; White and Pickett, 1985) and thus leading to higher biodiversity (i.e., intermediate disturbance hypothesis; Connell, 1978). Furthermore, forest disturbances are often coupled to large resource pulses of dead-wood, which additionally promote biodiversity (Drever et al., 2009).

1.1 Natural disturbances in forest ecosystems

Severe natural disturbances are a fix part of many forest ecosystems worldwide and can appear as ‘stand-replacing’ events that remove all or most of the forest canopy (Swanson et al., 2011; Svoboda et al., 2012). Particularly forests of the boreal and temperate zone are naturally prone to large-scale natural disturbances (Moen et al., 2014).

Post-disturbance forest stands are characterized by large amounts of dead wood, increased exposure to sunlight, higher ground wind velocities and more extreme temperatures (Fontaine et al., 2010). Typically, natural disturbances do not remove major proportions of biomass but alter resource availability. For instance, a stand replacing storm event drastically increases the amount of previously limited solar radiation to the forest floor, while tree trunk biomass remains on-site (Peterken, 2008; Shorohova et al., 2009).

Distinct types of natural disturbances create distinct types of biological legacies, such as wildfires create large amounts of standing dead trees (snags); uprooted trees, lying on forest floor are created by severe windstorms; intact understory vegetation can be found after extensive canopy damage by bark beetles (Swanson et al., 2011). Biological legacies are key attributes of early successional stages providing habitat for numerous organisms and enhance long-term stand structural complexity (Müller et al., 2008; Seidl et al., 2014b). Although subject to decomposition, those legacies can persist for many decades, leading to high structural heterogeneity of re-grown forest stands (Donato et al., 2012).

North American forests have experienced increasing wildfire activity, particularly since the mid-1980s, leading to higher large-wildfire frequency, longer wildfire durations, and longer wildfire seasons (Westerling et al., 2006). Simultaneously, large waves of bark-beetle outbreaks caused an unprecedented deforestation of coniferous forests in North America within the last century (Kausrud et al., 2011; Nikiforuk, 2011). The amount of forests affected by natural disturbances in Europe has tripled over the last 40 years (Seidl et al., 2014a), whereas an annual average 35 million m³ wood was damaged by disturbances from 1950 to 2000 (Schelhaas et al., 2003). Outbreaks of the European Spruce Bark Beetle *Ips typographus* (Linnaeus, 1758), damaged an average of 2.9 million m^3 wood annually between 1950 and 2000 in Europe (Schelhaas et al., 2003). Such outbreaks are often facilitated by preceding windstorms, which damaged 18.7 million m^3 of wood (Schelhaas et al., 2003). However, the variation within years is very large, and extraordinary storms, such as occurred in 1990 and 1999 in Europe, caused a damage of 120 and 180 million m³ of wood, respectively (Schelhaas et al., 2003). The combination of windstorms and outbreaks of *I. typographus* is predicted to damage a cumulative amount of 60 million m^3 of wood annually between 2021 and 2030 in Europe (Seidl et al., 2014a).

Climate change and forest change are key factors driving the increasing magnitude and frequency of natural disturbances across Europe (Seidl et al., 2014a). Here, climate change contributes in the same order of magnitude as forest change to increasing disturbances (Seidl et al., 2011). Increasing proportion of mature Norway Spruce (*Picea abies*), increases the probability of a stand-replacing wind-storm event (Thom et al., 2013). Such extensive windstorms are promoted by high mean winter temperatures, high precipitations in spring as well as windstorm damages from previous years that destabilize forest stands (Thom et al., 2013). Outbreaks of bark beetles can be promoted by preceding bark-beetle outbreaks (e.g. temporal autocorrelation) as well as by preceding storm damages (Nagel et al., 2007; Thom et al., 2013; Stadelmann et al., 2014). Likewise preceding windstorms can increase the severity of following wildfires (Kulakowski and Veblen, 2007).

The increase of forest fires during the last decades is promoted by low sums of annual precipitation and high annual mean temperatures (Miller et al., 2009; Seidl et al., 2011) and could be ascribed to land-use changes only to a minor degree (Westerling et al., 2006). Estimated forest damage among all types of disturbances is highest when conducive weather conditions meet increased forest susceptibility (Seidl et al., 2011).

1.2 Effects of natural disturbances on biodiversity

Disturbance is defined as ‘any event, natural or human driven, that causes temporary and localized shifts in demographic rates’ (Mouillot et al., 2013). Disturbances are generally thought to influence species diversity in a positive manner, with highest diversities at intermediate stages of disturbance frequencies, time after disturbance and spatial extend of disturbances (Connell, 1978). Hence, diversity is lowest at extremely high and extremely low levels of disturbance frequencies, e.g. at ecosystem equilibrium stages. However, some ecosystems might be affected often enough by disturbances so that equilibrium is never attained (Connell, 1978).

Early seral stages of forest succession following natural disturbances are species rich and structurally heterogeneous habitats (Bouget and Duelli, 2004; Swanson et al., 2011; Lehnert et al., 2013). Impacts of forest disturbances to biodiversity are closely connected to altered abiotic conditions and often correspond to specific disturbance created legacies (Swanson et al., 2011). For instance, vascular plants can benefit from increased solar radiation after canopy removal by wildfire (Donato et al., 2012) and cavity nesting birds can benefit from increased availability of snags after wildfire (Hutto and Gallo, 2006). Furthermore, burned forest stands in the southern Appalachians had significant higher plant species richness than nearby intact forests (Reilly et al., 2006) and almost twice as many bird species increased as decreased significantly in response to wildfire in the Rocky Mountains (Smucker et al., 2005). However, forest disturbance must not mandatory result in altered species assemblages or abundances if biological legacies, such as extensive soil disturbance, are lacking (Fischer et al., 2015). Also arthropod assemblages can respond to forest disturbance. For instance, Moretti et al. (2004) observed a positive effect of wildfire in the Alps on species richness of carabids, hoverflies, bees and wasps, spiders, true bugs, and lacewings. Negative effects of fire on species numbers or/and abundances were found only for isopods and weevils (Moretti et al., 2004). However, fire-induced changes in assemblage composition of epigeal spiders vanished two years after post-fire development (Moretti et al., 2008). Vice versa, abundances of Northern Flicker (*Colaptes auratus*) and Hairy Woodpecker (*Picoides villosus*) started to respond positively to wildfire from the third year onwards, but not within the first two years (Smucker et al., 2005).

Following bark-beetle outbreaks, species numbers of bees and wasps, lichens, hoverflies, cicadas, vascular plants, spiders and saproxylic beetles increased after a major outbreak in the Bavarian Forest, while those of wood-inhabiting fungi decreased (Beudert et al., 2015). Furthermore, bark-beetle outbreaks benefit red-listed carabids and bird species while the overall number of species in these taxa remained constant (Beudert et al., 2015). The response of biodiversity to bark-beetle outbreaks also depends on the time after the outbreak. While species density of most epigeal taxa remained unaffected by beetle-outbreaks in the Alps, densities of saproxylic beetles that are specialized to fresh dead-wood peaked in early-seral stages of post-disturbance succession (Winter et al., 2015). Consequently, herbs, herbivorous insects and pollinators reached maximum diversities in mid-successional stages (Winter et al., 2015).

Windthrows in the Alps hosted 35–69% more species of insects, reptiles, and small mammals compared to intact forest control plots (Duelli et al., 2002). Particularly dead-wood associated groups, such as saproxylic beetles, can be 30 to 500 times more abundant in windthrows than in adjacent intact forest, whereas species numbers are two up to four times higher in windthrows than in intact forests (Wermelinger et al., 2002). A windstorm in northern Minnesota altered bird communities from canopy-foraging species in mature stands of Black Spruce (*Picea mariana*) towards ground-brush foraging species with a simultaneous increase in overall bird diversity (Lain et al., 2008).

1.3 Management of natural disturbances

Post-disturbance salvage logging has become the most widespread management response to natural disturbances and is often subject to rapid decision making by public authorities (Lindenmayer et al., 2008). The major and most obvious justification for salvage logging is to capture some of the economic value of dead or injured trees that would otherwise be lost (Prestemon et al., 2006). Beside economic purposes, salvage logging has been justified based on further reasons:

Dense, green forests have a high symbolic and identificatory value for people (O'Brien, 2006) and the social conception of nature is closely tied up with ideas of 'equilibrium' and 'nature knowing best' (Zimmerer, 2000). Hence, forest disturbances are commonly perceived as chaos, untidy and catastrophic (Flint et al., 2009), and thought to have limited value for biodiversity (Morissette et al., 2002). In this regard, salvage logging has been justified on the basis that it will contribute to ecological and physical recovery and of naturally disturbed forest (Sessions et al., 2004). Standing dead trees were removed to minimize risks for people working or recreating in burned or beetle-killed areas (Ne'eman et al., 1997).

A second important justification for salvage logging is the reduction of fuels available for subsequent fires (Sessions et al., 2004). Snags, in particular, are a predominant concern as they might generate firebrands (Inbar et al., 1997). Ironically, fuel loads have also been reduced by salvage logging to limit the amount of smoke produced in subsequent prescribed burns of disturbed forests (Achtemeier, 2001). However, post-fire salvage logging can likewise increase the risk of subsequent wildfires (Donato et al., 2006).

Third, disturbance-killed trees are traditionally removed to avoid the establishment of breeding grounds for insect pests and following outbreaks that might kill vital forests nearby (Wermelinger, 2004; Kausrud et al., 2011). Particularly, bark beetle eruptions have intensified socio-economic discussions of how to decrease population densities of insect pests to avoid further spread (Black, 2005; Fettig et al., 2007; Stokstad, 2006). Over the past century, forest management developed a search-and-destroy tradition in which populations of insect pests are reduced by various methods, including prescribed burning, stand thinning, salvage logging, cut-and-leave tactics, electrocuting, and poisoning trap trees (Fettig et al., 2006; Nikiforuk, 2011). Particular storm-affected trees, such as Norway Spruces, are subject to rapid and rigorous salvage logging to limit increasing populations of bark beetles (Eriksson et al., 2005, 2008; Stadelmann et al., 2013, 2014).

Salvage logging typically differs from conventional green tree logging or selective cutting in distinct properties (adapted from Lindenmayer et al., 2008):

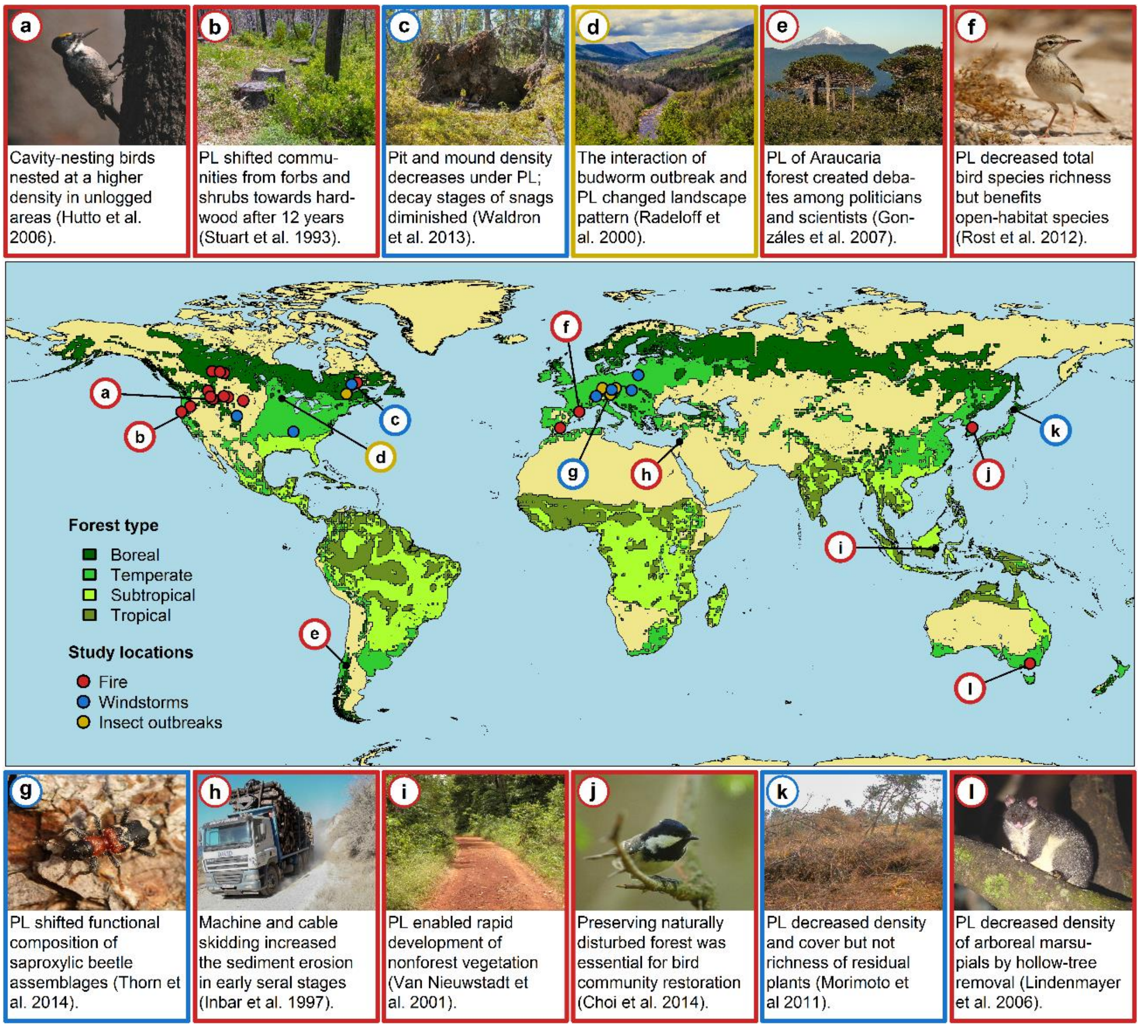
- Salvage logging can be more intense (e.g. removing more trees) on the stand and landscape level than green logging (Schmiegelow et al., 2006).

- Forests may be cut at much younger ages than designated by local management schemes (Radeloff et al., 2000).
- Larger and older trees may be removed if it is not otherwise allowed (Thrower, 2005), such as large Siberian Larches (*Larix sibirica*) in burned forests of Mongolia (Müller et al., 2013).
- Larger amounts of deadwood may be left behind and sometimes burned (Priewasser et al., 2013).
- Areas previously designated as roadless may be roaded to provide access (Karr et al., 2004).
- Particular kinds of trees, stands or areas normally reserved from logging may be logged (Forest et al., 2006). Logging to prevent beetle-outbreaks might occur in protected areas in which logging is usually not allowed (Beudert et al., 2015; Thorn et al., 2014).
- Forest stands may be logged at seasons when it is otherwise not allowed (DellaSala et al., 2006).

In contrast to green logging, salvage logging is conducted in disturbed forests which have already responded to extraordinary environmental conditions, e.g. soils have already been burned and are more vulnerable to soil disturbance by salvage logging machinery (McIver and Starr, 2000; Beschta et al., 2004). Additionally, beetle-killed forest stands have already experienced a reduction of canopy cover and light-sensitive species, such as bryophytes, might suffer from an additional increase in solar radiation due to salvage logging (Jonasova and Prach, 2008). Hence, there is much empirical evidence that salvage logging has profound impacts on ecosystem recovery, biodiversity, and ecological processes (see Lindenmayer et al., 2008 and references therein).

1.4 Ecological consequences of salvage logging

Salvage logging has a variety of impacts on abiotic and biotic components of disturbed forest ecosystems worldwide (Fig. 1). Heavy logging machinery typically increases soil compaction and generates soil disturbances, even to soils that were not affected by the disturbances themselves (Inbar et al., 1997; Morimoto et al., 2011). This impact on forest floor and the simultaneous removal of remaining canopy (e.g., disturbance-killed trees) can result in an increased soil or air temperature (Peterson and Leach, 2008; Fontaine et al., 2010). Not surprisingly, particularly dead-wood habitat features are seriously reduced in their amount (Priewasser et al., 2013) and altered in their distribution of decay stages (Waldron et al., 2013).



a Cavity-nesting birds nested at a higher density in unlogged areas (Hutto et al. 2006).

b PL shifted communities from forbs and shrubs towards hardwood after 12 years (Stuart et al. 1993).

c Pit and mound density decreases under PL; decay stages of snags diminished (Waldron et al. 2013).

d The interaction of budworm outbreak and PL changed landscape pattern (Radeloff et al. 2000).

e PL of Araucaria forest created debates among politicians and scientists (Gonzáles et al. 2007).

f PL decreased total bird species richness but benefits open-habitat species (Rost et al. 2012).

g PL shifted functional composition of saproxylic beetle assemblages (Thorn et al. 2014).

h Machine and cable skidding increased the sediment erosion in early seral stages (Inbar et al. 1997).

i PL enabled rapid development of nonforest vegetation (Van Nieuwstadt et al. 2001).

j Preserving naturally disturbed forest was essential for bird community restoration (Choi et al. 2014).

k PL decreased density and cover but not richness of residual plants (Morimoto et al 2011).

l PL decreased density of arboreal marsupials by hollow-tree removal (Lindenmayer et al. 2006).

Figure 1: Post-disturbance salvage logging (PL) is commonly applied and leads to changes in abiotic and biotic components of various forest ecosystems worldwide (as highlighted by the studies illustrated in panels a-l). Study locations also highlight major study sites that contributed data to the meta-analysis presented in this thesis (Article I).

Positive effects of natural disturbances to forest biota strongly depend on disturbance-created biological legacies (see chapter 1.2). Controversially, salvage logging typically alters or removes those legacies. For instance, salvage logging after windstorm removes the storm-created pit and mount system, leading to homogenized structures, altered microsite diversity, and altered assemblages of vascular plants (Waldron et al., 2013, 2014). Further, salvage logging after wildfire can reduce overall snag abundance and snag diameter (Russell et al., 2006), leading to a decrease in cavity-nesting birds, including rare woodpecker species (Hutto and Gallo, 2006; Koivula and Schmiegelow, 2007).

Salvage logging affects a majority of taxa in different directions (Fig. 2). Not surprisingly, the extensive removal of dead-wood resources by post-disturbance salvage logging leads to a loss of species depending on such resources, such as saproxylic beetles (Cobb et al., 2011; Norvez et al., 2013; Thorn et al., 2014). An additional number of taxa indirectly suffers from the removal of dead-wood habitat features, such as cavity-dependent mammals (Lindenmayer and Ough, 2006), cavity-nesting birds (Hutto and Gallo, 2006; Saab et al., 2007; Nappi and Drapeau, 2009) or epigeal bryophytes that depend on the shade provided by beetle-killed canopy (Jonasova and Prach, 2008).

Salvage logging, however, must not mandatory result in a decrease of species numbers. For instance, post-fire salvage logging did not decrease the number of vascular plants species but altered assemblage composition (Stuart et al., 1993). Such changes in assemblage compositions are often mediated by the rapid establishment of non-forest (i.e., ‘ruderal’) plant species in salvage logged areas (Van Nieuwstadt et al., 2001). Furthermore, salvage logging can reduce the cover of bryophytes, while it simultaneously increases the cover of pioneer species such as Aspen (*Populus tremuloides*) (Macdonald, 2007). Birds, as well as vascular plants, generally display little negative responses to salvage logging in species numbers, whereas their assemblage compositions may change (Castro et al., 2010; Zmihorski, 2010; Choi et al., 2014). While typical forest species, such as woodpeckers, might disappear in salvage-logged areas, such areas can inhabit typical open-land bird species, such as grouses or pipits (Radeloff et al., 2000; Rost et al., 2012).

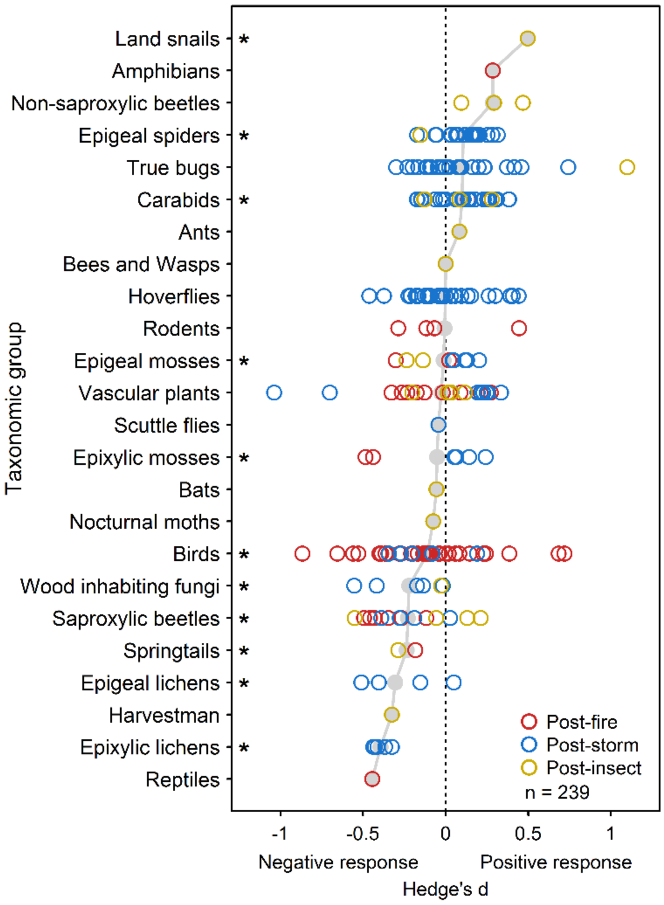


Figure 2: Estimated response of Hedge's d based on 239 individual comparisons of logged and unlogged naturally disturbed forests. Increased species numbers by salvage logging indicated by positive Hedge's d, whereas negative values indicate decreasing species numbers. Asterisks on the left indicate significant responses based on multilevel mixed effect models. Grey dots and line represent mean effect sizes in each taxonomic group for illustrative purposes.

Finally, the removal of remaining, disturbance-affected canopy might benefit epigeal species groups such as carabids (Phillips et al., 2006; Cobb et al., 2007) or epigeal spiders (Ziesche and Roth, 2008) that benefit from increased solar radiation to the forest floor. However, even those taxonomic groups that benefit from salvage logging can display changes in assemblage composition. For instance, salvage logging increases the abundance of open-habitat carabids, while the abundance of common forest-dwelling carabids decreases simultaneously (Koivula and Spence, 2006).

1.5 The management dilemma

Society has increasingly valued forests more than simply as sources of fuel wood and timber, such as for the provision of important ecosystem services like the supply of drinking water, recreation or as hosts for high levels of biodiversity (Aerts and Honnay, 2011). Hence, forest management decisions, including actions of post-disturbance salvage logging, based on multiple criteria, in turn are influenced by multiple stakeholders, and hence often represent a mixture of economic and ecological goals. Furthermore, ecological goals might depend on the maintenance of a specific habitat (e.g., salvage logging and replanting of a specific forest type (Morimoto et al., 2011)) or on the conservation of a specific species (Lee et al., 2013). Due to the large economic values affected by large-scale natural disturbances, their management has led to serious debates among policy makers and forest managers on the one hand and ecologists and forest conservationists on the other hand (Donato et al., 2006; Stokstad, 2006). Conflicts often emerge because broadly applicable prescriptions, such as available for scattered locales in Quebec, eastern Canada (Nappi et al., 2011) and Victoria, south-eastern Australia (Franklin et al., 2000), are still lacking, despite there have been attempts to summarize current knowledge (McIver and Starr, 2000; Lindenmayer and Noss, 200). Furthermore, distinct species groups may respond differently (Fig. 2), additionally increasing uncertainty among natural resource managers, policy-makers and conservationists on how to manage natural disturbances (Zmihorski and Durska, 2011). For instance, the loss of saproxylic beetles due to salvage logging might be a justification for a ‘benign-neglect strategy’ (i.e., allowing natural disturbances without any human intervention), while the positive effects on some declining open-land bird species might support the removal of disturbance affected trees (Rost et al., 2013).

The debate on how to manage large areas of natural disturbed forests is particularly intense in protected areas, legally demanded to prevent pest outbreaks by salvage logging, whereas whose primary objective should be the conservation of biodiversity (Müller et al., 2008; Spinelli et al., 2013; Beudert et al., 2015). A sustainable management of natural disturbances should ideally address both the socioeconomic needs of human communities and biodiversity conservation (Moen et al., 2014).

To obtain a compromise between reduction of insect pests and conservation targets, mechanical bark treatments, such as debarking, have been widely promoted as an on-site method that accounts for conservation targets as woody biomass is retained (Wermelinger, 2004). Despite major scientific efforts to increase the efficiency in reducing insect pests (see Wermelinger, 2004; Fettig et al., 2007; Kausrud et al., 2011 and references therein), potential collateral damage of debarking to non-target biodiversity has been largely ignored. Today, debarking of storm-felled trees, particularly Norway Spruces, is commonly applied in conventionally managed forests (e.g., in remote mountains, where timber is debarked on-site to reduce insect pests) as well as in protected areas, which are legally mandated to reduce insect pests (Connor and Wilkinson, 1983; Juha and Turcani, 2008; Haack and Petrice, 2009).

1.6 Knowledge gaps

Norway Spruce is the most widespread and the economically most important tree species in Europe (Brus et al., 2011). Due to conventional forest management, the growing stock of mature spruce forests has been increased during the past century owing (Schelhaas et al., 2003). Nevertheless, mature spruce stands are naturally prone to large-scale natural disturbances such as windstorms (Ulanova, 2000; Shorohova et al., 2009; Thom et al., 2013). Hence, stands of Norway Spruce have become the most common post-disturbance logged forest type in Central Europe and can reach wood volumes of more than 100 m^3 within a single year if extraordinary large storm events take place (Schelhaas et al., 2003).

Despite their major economic importance, studies that investigate the effects of post-storm salvage logging are relatively scarce. Previous studies have been conducted in storm-felled forests dominated by Pine (*Picea sylvestris*) (Zmihorski, 2010; Zmihorski and Durska, 2011) and in sub-boreal forests in northeastern Minnesota (Gandhi et al., 2008). Furthermore, previous studies predominantly focused on taxonomic groups that typically display little response to salvage logging, such as birds (Lain et al., 2008; Zmihorski, 2010) or vascular plants (Lain et al., 2008; Peterson and Leach, 2008). Yet, studies that investigate the effects of post-storm salvage logging on saproxylic taxa (e.g., those taxa most heavily affected by salvage logging) are lacking. However, salvage logging of storm-felled spruce stands is daily fare in the majority of European forest and can be assumed to be even more widespread in near future (Seidl et al., 2014b). Thus, a detailed ecological understanding of the effects of salvage logging on biodiversity of multiple taxa is needed to identify possible impacts, conservation targets and ultimately provide management recommendations to conserve post-disturbance biodiversity. Furthermore, some species groups, such as nocturnal moths, have been ignored by preceding research despite their high species diversity in temperate forests.

From an ecological perspective, salvage logging represents a dramatic reduction of dead-wood resources. The ‘more-individuals hypothesis’ predicts that increasing availability of chemical energy (e.g. dead wood resources) will result in more individuals and ultimately in higher species numbers (Storch et al., 2005; Clarke and Gaston, 2006).

Vice versa, the ‘habitat-heterogeneity hypothesis’ predicts that increasing niche diversity within a given habitat promote higher species numbers (e.g. higher species numbers per number of individuals; i.e. “species richness”) (MacArthur and MacArthur, 1961; Gotelli and Colwell, 2001; Kostylev et al., 2005). Which of these basic ecological principles might best explain changes in species numbers due to salvage logging remains unclear, particularly since existing studies predominantly focus on measures of taxonomic diversity instead of functional or phylogenetic diversity (Cadotte et al., 2012). However, conservation strategies for disturbed forests may focus on retaining a certain amount of disturbance-created dead-wood or a certain level of dead-wood heterogeneity. It is crucial to understand the mechanisms that might be responsible for species losses to develop basal management recommendations and point out future research directions.

1.7 Main objectives

The main objective of the present thesis is to improve our understanding on the effects of salvage logging to assemblages of species and ecological processes. In particular, this thesis focuses on the effects of salvage logging to overall species abundances and species densities as well as abundances and densities of specific guilds or functional guilds. In contrast to existing studies, this thesis further investigates the effects of salvage logging to trait-based and phylogenetic dissimilarities among assemblages.

Management recommendations are developed on multi-taxa approaches to support a sustainable forest management. The spatial extend of the present thesis ranges from a global meta-analysis of published literature on the effects of salvage logging up to detailed case studies in the temperate montane forest ecosystem Bavarian Forest National Park. Finally, this thesis aims to embed the management of storm-felled spruce forests to an extended framework of managing natural disturbed forests around the world.

The specific sub-goals of this thesis are:

1. Point out current gaps in knowledge in the effects of salvage logging to biodiversity after windstorms, insect outbreaks, and wildfire around the globe; reveal evidence for ecological processes that cause shifts in species assemblages by salvage logging (Article I).

2. Determine changes in overall species numbers and abundances as well as changes in specific larval feeding guilds of nocturnal moths between salvaged and unsalvaged forests following an outbreak of European Spruce Bark Beetle (Article II).

3. Identify changes in overall species numbers and abundances as well as changes in specific nesting-, foraging- and migration strategies of forest-dwelling bird assemblages; identify habitat factors that determine the presence of resident bird species in logged- and unlogged windthrows as well as in intact, mature spruce stands (Article III and IV).

4. Disentangle if species losses of saproxylic taxa by salvage logging after a major windstorm can be addressed either to resource loss itself or to competitive exclusions among remaining resources (Article V).

5. Quantify the effects of different mechanical bark treatments of storm-felled trees in an experimental approach to develop a trade-of between bark beetle management and nature conservation aspects in post-storm salvage logging (Article VI).

2. Methods

The present thesis consists of distinct sub-goals that incorporate several distinct field methods, data processing and data analyses. The following section provides a brief overview of underlying experimental designs and methods of data analyses.

2.1 Literature review

An extensive literature search was conducted to provide a quantitative basis for the meta-analysis incorporated in this thesis (Article I). Therefore, I followed guidelines for systematic literature reviews to compile comparisons of species numbers between salvaged and unsalvaged disturbance affected forests (Pullin and Stewart, 2006). The databases of Web of Science, Scopus and Google Scholar were screened on May 5th 2014 by using the simplified search strings [salvage logging OR post$disturbance* OR salvaging] and [forest$ OR vegetation OR disturbance OR ecosystem]. From this body of literature (> 1500 articles), I retained 457 field-based studies based on the title and abstract. I excluded modelling studies and restricted studies to those providing standardized comparisons between post-disturbance salvage logged plots (over 75 % of trees affected by natural disturbances) und paired unsalvaged control plots. Control plots were of equivalent size and had the same sampling effort during the same study period as salvage-logged plots. Studies were further restricted to those investigating fully salvage logged plots (no retention approaches; 100 % of disturbance affected trees removed) and without any initial plantings in salvaged areas. Studies that sampled in forests undergoing multiple types of disturbances were excluded.

I extracted mean species number and standard deviation per plot from published text and tables, or from figures using PLOT DIGITIZER 2.6.2. (http://plotdigitizer.sourceforge.net/). Furthermore, I compiled information on the disturbance agent and the time since disturbance and subsequent salvage logging to be included as covariates in subsequent statistical analysis. Studies using the same set of field plots were identified and nested in subsequent statistical analysis. Finally, I frequently contacted study authors to clarify their results and/or to provide original species-by-plot matrices that underlie the published papers.

2.2 Study designs and species surveys

2.2.1 Study area

This thesis presents analyses and results from three different field surveys and experimental designs (note that Article I was based on literature data and not on field surveys). All those studies were conducted in the Bavarian Forest National Park, encompassing an area of 242 km² in south-eastern Germany (49.0777° N, 13.3030° E). The National Park covers a vertical range of approximately 800 m (650 – 1,453 m a.s.l.) and inhabits montane as well as subalpine areas. Annual precipitation ranges from 1,300 to 1,800 mm, and annual mean air temperature ranges from 3.0 to 4.0°C (Bässler et al., 2010). Ninety-eight percent of the Bavarian Forest National Park is covered by forest (Bässler et al., 2010). Norway Spruce dominates high mountain forest stands above 1,100 m a.s.l. with low proportions of Silver Fir (*Abies alba*) and European Beech (*Fagus sylvatica*). The dominant species of plants in the herb layer are Hairy Reed Grass (*Calamagrostis villosa*) and Blueberry (*Vaccinium myrtillus*).

Within the last three decades, *I. typographus* extensively infested forest stands at a maximum of 800 ha in one year (Müller et al., 2008). Owing to a benign-neglect strategy in the core zones of the national park, these infested stands remained unsalvaged, while infested stands in the management zones were salvage logged. This combination of salvage logging and benign neglect strategy after beetle outbreaks has led to a mosaic of salvaged, unsalvaged and vital mature spruce stands in the Bavarian Forest National Park.

On January 16, 2007, an area of approximately 1,000 ha of spruce forest was felled with various intensity by the windstorm ‘Kyrill’, ranging from single trees to entire stands covering several hundreds of hectares (Fink et al., 2009). From a total affected amount of about 160,000 m^3, 50,000 m^3 are concentrated on four larger windthrow areas (~300 m^3 ha^{-1}). These centers were partially excluded from the overall salvage logging operation, while salvage logging in that area removed about 255 m^3 ha^{-1} and was completed in late summer 2007 (Thorn et al., 2014). Unsalvaged stands are characterized by dead-wood amounts of about 300 m³ ha^{-1} and an initial natural regeneration of Norway Spruce and European Beech. In contrast, salvaged stands visually appear similar to clear-cuts, but with more dead wood from logging residuals (stumps and branches) at about 50 m³ ha^{-1} (Thorn et al., 2014).

2.2.2 Experimental designs

For Article II, I used the established plot network of the ‘BIOKLIM-Project’ (Bässler et al., 2009) to investigate the effects of salvage logging after bark-beetle outbreaks on nocturnal moths. Here, I selected 32 plots across an elevational range from 666 to 1,327 m a.s.l. representing four distinct forest stand types, namely i) stands killed by *I. typographus* and subsequently salvage logged, ii) unsalvaged beetle-killed stands, iii) single-layered vital spruce stands and iv) multi-layered vital spruce stands. For details and photos of all plot types, see Mehr et al. (2012). The minimum distance between two plots of the same forest type was 800 m, whereas the largest distance between two plots was 30 km. Salvage logged stands were killed by *I. typographus* and subsequently salvage logged between two and eight years before the study took place (Müller et al., 2008).

Articles III, IV and V investigated the effects of post-storm salvage logging to multiple taxa in a stratified observational study. Therefore, 44 plots were established in forest stands felled by windstorm Kyrill in Janurary 2007. 22 plots were experimentally salvage logged, while 22 were left as unlogged control plots. 22 additional plots were established in vital, mature spruce stands for bird surveys presented in Article III and Article IV. During salvage logging operations the main trunk was removed, while branches were cut off and remained on the forest floor. The shortest distance between two plots was 50 m, and the largest distance between plots was 6,500 m.

For Article VI natural storm damage was simulated by pulling down and uprooting three mature spruce trees with steel cables and winches attached to tractors in April 2013. Each experimental windthrow persisted of one uprooted tree as a control and two trees that were cut off the root plates and branches. All trees had similar physical attributes. Six plots were established in stands with high canopy closure (i.e., shady conditions) and six plots were established at forest edges without canopy cover (i.e., sunny conditions). The minimum distance between each pair of open- and closed stand plot was 200 m.

2.2.3 Sampling of nocturnal moths

Nocturnal moths (Article II) were trapped using light traps consisting of a 12 V, 15 W super-actinic ultraviolet light tube mounted above a plastic funnel. Trapped specimens were collected in a plastic container at the bottom of the trap and killed by chloroform (Müller et al., 2012). Light traps were placed in the centre of the plot, since they may attract moths within a radius of up to 50 m (Truxa and Fiedler, 2012). Hence, light traps within the centre of each five-hectare-plot should optimally reflect the structure of the surrounding forest stands. Light traps were set up for seven consecutive nights on each plot throughout the whole vegetation period from early May (shortly after snow melt) to mid-September in 2009, comprising a total of 224 individual trap nights, to acquire full assemblages of nocturnal moths. Sampling was only conducted within a maximum of ten consecutive days (since a maximum of ten traps could be set per night) and only in frostless nights with low wind speeds. Trapped specimens of micro-moths and macro-moths were identified by H. Hacker, if necessary by examining genital preparations. For references and species lists of moths recorded in Bavaria, see Hacker and Müller (2006). Trapped specimens were aggregated from seven trap nights to the plot level for further analysis. In total, 15,504 specimens of macro-moths were trapped, representing 291 species and 137 species of micro-moths (2,713 specimens). For a detailed analysis, each moth species was assigned to one of six larval feeding guilds according to Hacker and Müller (2006): ‘herbs and grasses’, ‘detritus’, ‘trees and shrubs’, ‘moss’, ‘omnivores’ and ‘saproxylic’.

2.2.4 Biodiversity surveys in ‘Kyrill’ windthrows

To monitor the effects of post-storm salvage logging on each plot, standardized species surveys started in summer 2007 and lasted for seven years up to 2014, but not all taxonomic groups were surveyed each year due to personal and financial constraints (Articles III–IV). Surveys focused on four saproxylic species groups, namely wood-inhabiting fungi, saproxylic beetles, epixylic bryophytes and epixylic lichens as well as four non-saproxylic species groups, namely vascular plants, birds, epigeal bryophytes and epigeal lichens. Classification of saproxylic and non-saproxylic species groups follows the definition given by Alexander (2008), which is that saproxylic organisms are species which are involved in or dependent on the process of fungal decay of wood, or on the products of that decay, and which are associated with living as well as dead trees.

Saproxylic beetles were trapped by flight interception traps placed in the center of each plot, which reflect the emerging beetle fauna of surrounding dead wood (Sverdrup-Thygeson et al., 2009). Each trap consisted of a crossed pair of transparent plastic shields (40 × 60 cm) and contained 3.0% copper-vitriol solution to preserve trapped specimens, as described by Hyvärinen et al. (2006). Flight interception traps were exposed during the entire growing season between May after the snow melted until September over four consecutive years from 2008 to 2011. Traps were emptied monthly. All sampled beetles were identified to the species level according to Freude et al. (1963–1984) but only saproxylic beetles (according to Schmidl and Bußler, 2004) were considered in subsequent analysis.

Vascular plants, epigeal bryophytes and epigeal lichens were surveyed from 2007 until 2011. Therefore, relevees of 200m² size were established around the plot centroid (Bässler et al., 2012). Within each relevee all species of vascular plants, bryophytes and lichens were recorded and abundance was estimated in percentage of ground cover.

Wood-inhabiting, epixylic bryophytes and epixylic lichens were recorded on the same five randomly selected dead-wood objects around each plot center from 2007 until 2011 (Bässler et al., 2012). Fruiting-bodies of wood-inhabiting fungi were assessed visually on a standardized surface and abundance was estimated according to bark surface covered by fruiting-bodies in three classes (<1%, 1–10%, > 10%). Species of wood-inhabiting fungi were identified either in the field or, especially for cryptic species of corticoid-like fungi, in the laboratory (Eriksson and Ryvarden, 1987; Ryvarden and Gilbertson, 1993; Knudsen and Vesterhold, 2008).

Birds were surveyed by standardized census counts at the center of each plot, five times per year from mid-March to mid-June in 2010, 2012 and 2014. In Central Europe, five visits per plot and year ensures the detection of early resident breeding birds as well as late-arriving long-distance migrants (Südbeck et al., 2005). Furthermore, winter residents were sampled once per month from November 2013 to February 2014. On each plot, all bird individuals seen and/or heard within a fixed radius of 50 m around the plot centroid and during a time period of five minutes were recorded (Hutto et al., 1986; Moning and Müller, 2008). Bird censuses were only performed on days without rain, with low wind speed, and clear or slightly overcast sky (Bibby et al., 2000). Note that bird surveys were also conducted in vital forest stands for Articles III and IV. All biodiversity data were aggregated to the plot level within each year for subsequent statistical analysis. In total, 349 saproxylic species and 152 non-saproxylic species were recorded during the entire study period.

2.2.5 Insect sampling in artificial windthrows

Experimental windthrows were created, to compare the effects of complete debarking and bark-scratching on the abundance of *I. typographus* as well as on species densities of wood-inhabiting fungi, saproxylic beetles and parasitoid wasps (Article VI). After the initial creation of artificial windthrows, one tree per plot was debarked, using a debarking device mounted on conventional chainsaw and one tree was bark-scratched by bark-scratching devices mounted on conventional chainsaws or by a light weighted chainsaw itself. Bark-scratching consisted of regular scratches that disrupt phloem every 3 cm. Furthermore, the amount of time needed to complete debarking and bark-scratching was recorded on 15 separate trees per treatment (debarking device, bark-scratching device, bark-scratching by chainsaw), resulting in 45 additional experimental trees independent of the main experimental design. The amount of time, standardized by tree volume, was used as surrogate for economic costs in subsequent analysis.

Assemblages of saproxylic beetles and parasitoid wasps were trapped from June 2013 until September 2013 and from April 2014 until September 2014 with stem emergence traps mounted on all 36 experimental trees. Emergence traps were filled with 90% ethanol to preserve species material for barcoding (Wikars et al., 2005; Brin et al., 2011). Saproxylic beetles were identified to the species level according to Freude et al. (1963–1984) and parasitoid wasps were identified by DNA-barcoding (Hebert et al., 2003). Furthermore, fruiting-bodies of wood-inhabiting fungi, wood wasp emergence holes and holes made by foraging woodpeckers were counted on the complete trunk surface. The abundance of wood-inhabiting fungi was estimated in three classes, according to the bark surface covered (<1%, 1–10%, > 10%). Species of wood-inhabiting fungi were identified either in the field or, especially for cryptic species of corticoid-like fungi, in the laboratory (Eriksson and Ryvarden, 1987; Ryvarden and Gilbertson, 1993; Knudsen and Vesterhold, 2008). Data of all surveyed species groups were accumulated on the trunk level for subsequent analysis.

2.3 Characterization of species dissimilarities

Several analytical approaches presented in this thesis are based on species assignments to a specific guild (such as larval feeding guilds of nocturnal moths in Article II) or on a quantification of mean dissimilarities within species assemblages. Consequently, species pairwise dissimilarities within assemblages need to be characterized either by morphological, ecological or evolutionary differences among each other’s. The following section provides a brief overview on species traits and phylogenies used in this thesis. Data processing and analyses were conducted with the free statistical software ‘R’ and respective add-on packages (www.r-project.org).

2.3.1 Species traits

Species traits determine a species performance in a given environment (Petchey and Gaston, 2006). For instance, plant species that produce many, light-weighted seeds might be more successful in recolonizing post-disturbance logged areas than plants producing less, heavy seeds. Traits were compiled for all study taxa investigated in this thesis and are based on published studies (see Table 1 for full list). Species-by-species distance matrices (Gower distance, accounting for categorical and continuous variables; Gower, 1971) for subsequent analysis were calculated using the function ‘daisy’ from the ‘cluster’ package.

Table 1: List of species traits and corresponding data sources used in the present thesis. Species groups are in alphabetical order.

Species group	Functional traits	Reference
Birds	Weight (g), clutch size, nest position (cavity, ground, canopy, shrub), migrating (yes/no), main component of diet (plant, vertebrates, invertebrates), foraging focus (ground, vegetation, trunk, aerial)	Glutz von Blotzheim and Bauer (1985)
Bryophytes	Plant height (mm), light value, moisture value, temperature value, mean spore diameter (mm), life strategy (colonistic, perennials, short-lived shuttles, long-lived shuttles), stem (ascending, procumbent, erect), life form (turf, welft, cushion patch)	Dierßen (2001), Ellenberg and Leuschner (2001)
Lichens	Ascomata area (mm²), spore volume (mm³), presence of spore septation (yes/no), presence of prothallus (yes/no), presence of vegetative growth forms (yes/no), presence of conidia (yes/no), presence of secondary compounds (yes/no), thallus form (leprose, immersed, emersed, foliose, fruticose), spore pigmentation (yes/no), presence of asexual isidia/soredia (yes/no), photobiont partner trebouxioid (yes/no)	Bässler et al. (2015)
Saproxylic beetles	Body size (mm), feeding strategy (detritivorous, predatory, xylophagous, mycetophagous), flower visitor (yes/no), decay niche position, diameter niche position, canopy niche position, host tree (coniferous/ broadleaved and feeding guild (fungi, wood/bark, cavities)	Gossner et al. (2013), Thorn et al. (2014), Seibold et al. (2015a)
Vascular plants	Plant height (mm), leaf form (ratio length/width), specific leaf area, seed weight (g), leaf anatomy (scleromorphic, mesomorphic, helomorphic, hygromorphic, succulent), dispersal strategy (enemochorous, zoochorous, autochorous), perennial (yes/no), woodiness (yes/no), propagation predominantly vegetative (yes/no)	Poschlod et al. (2003), Kleyer et al. (2008)
Wood-inhabiting fungi	Basidiome size (mm), Spore volume (mm), Spore shape (ratio volume/spore size), Crustose cystidia (yes/no), Galertic consistence (yes/no), Asexual reproduction (yes/no), hypha type (monomitic, dimitic, trimitic), host (gymnosperm, angiosperm), lifestyle (saprotrophic, ectomycorrhiza), Spore surface ornamented (yes/no), basidiome shape (pileate, resupinate, stipitate), polyphagous (yes/no)	Bässler et al. (2014, 2015)

2.3.2 Phylogenies of study taxa

Besides traits, species dissimilarities can be determined by evolutionary distances (i.e., patristic distances between two species in a phylogenetic tree). Therefore, ultrametric phylogenetic trees (i.e., branch lengths correspond to evolutionary time) were compiled for all study taxa. Ultrametric trees do not make assumptions about the differential rates of evolution of individual genes (Whitfeld et al., 2012). Phylogenetic trees for birds (Hackett et al., 2008), lichens (Bässler et al., 2015), saproxylic beetles (Seibold et al., 2015a) and wood-inhabiting fungi (Hibbett et al., 2007; Bässler et al., 2014) were compiled by expanding respective existing phylogenetic backbones. Phylogenetic trees for bryophytes and vascular plants were constructed via a data-assembly pipeline in R language that mines nuclear and mitochondrial sequences of the study taxa from the nucleotide repository at GenBank (‘megaptera’ package). The data pipeline was also used to mine sequences of species that were missing in existing phylogenetic backbones. Tree topology and branch lengths were modelled in a maximum-likelihood framework (Stamatakis, 2014). The phylogenetic tree for bird species were created using the webpage of www.birdtree.org, based on the backbone provided by Hackett et al. (2008). 4,000 bootstrap trees for study bird species were mined from the repositories at ‘BirdTree’ and afterwards were condensed into one fully dated consensus tree using TreeAnnotator 1.8.2 (Drummond and Rambaut, 2007). Species-by-species distance matrices based on phylogenetic trees were calculated using the function ‘cophenetic’ from the ‘stats’ package.

2.4 Statistical methods

All statistical analysis presented in this thesis were performed with the free statistical software ‘R’ (www.r-project.org). The two most central statistical analyses used in all articles of this thesis are outlined below.

2.4.1 Null models

Null models are a widespread analytical technique in community ecology. For instance, they are used to simulate the influence of invading species, randomly drawn from a regional species pool (Li et al., 2015) or to compare body-size based assembly of observed tropical ant communities to simulated communities (Fayle et al., 2015). Null models provide a standardized effect size that quantifies the difference between observed patterns of co-occurrence against the expected levels of co-occurrence when species are randomly drawn from a given set of species (Gotelli, 2000).

Null models have become increasingly relevant to reveal the mechanisms that assemble species into communities (Pausas and Verdú, 2010). Therefore, null models are used to compare observed mean pairwise distance of species assemblages (based on a trait- or phylogenetic species-by-species distance matrix) per sampling unit against artificial assemblages build of randomly selected species from the regional species pool (Webb et al., 2002; Emerson and Gillespie, 2008). Resulting standardized effect size values > 0 indicate that observed mean pairwise distance is higher than expected by chance (i.e., 'over-dispersion', species are more dissimilar than expected) and values < 0 indicate that observed mean pairwise distance is lower than expected by chance (i.e., 'clustered', species are less dissimilar than expected; Pausas and Verdú, 2010). These mechanisms, are thought to be dominated by environmental filtering, where abiotic constraints enable co-occurrence of similar species (clustering) or competitive exclusion, that select for species that are dissimilar (over-dispersion; Cavender-Bares et al., 2009). Analytical approaches based on either trait-based or phylogenetic dissimilarities have been increasingly criticized since they implicit assumptions that lack broad empirical evidence (see Mayfield and Levine, 2010; HilleRisLambers et al., 2011; Gerhold et al., 2015 and references therein). To overcome such deficiencies, Cadotte et al. (2013) proposed to take trait convergence and divergence into account by combining trait-based and phylogenetic distance matrices.

I combined trait-based distance matrix stepwise with the phylogenetic distance matrix by a weighting parameter (a) using the function 'funct.phylo.dist' from the 'pez' package. When $a = 0$, the mixed distance matrix only includes trait-based distances, and when $a = 1$, the mixed distance matrix only includes phylogenetic distances. At intermediate values of a, both trait-based and phylogenetic distances contribute to the resulting mixed distance matrix. This procedure was repeated for 40 pre-selected a-values between zero and one to maximize model quality according to the highest adjusted R^2 in subsequent linear models (Cadotte et al., 2013). In this thesis, assembly mechanisms were best explained (highest adjusted R^2) when using intermediate values of a, meaning that both trait-based and phylogenetic distances contribute to quantify dissimilarities among species.

2.4.2 Linear models

Different types of linear models represent a central analytical tool of this thesis. Statistical analysis were mainly conducted by means of linear-mixed effect models that allow a variety of model settings, depending on the type and structure of the data. Linear-mixed effect models were fitted by means of function ‘lmer’, respectively ‘glmer’ from the ‘lme4’ package (Bolker et al., 2009).

To model species numbers per plot in dependence of salvage logging (salvaged/ unsalvaged) as fixed factor, I repeatedly used linear mixed-effects with Poisson-error distribution. By contrast, standardized effect sizes of null models were modelled assuming Gaussian-error distribution. Observation specific random effects where included in order to account for possible Poisson-overdispersion (Elston et al., 2001) and plot identity was included identity as random factor to account for repeated measurements on each and the same plot among several study years (pseudo-replication). The species numbers or abundances within specific guilds, such as nest positions, were modelled by including the overall species numbers or abundances as an additional ‘offset’ term to the model formula. This enables to untangle shifts in species numbers or abundances in specific guilds from overall changes in species numbers or abundances.

A major challenge in analysing data from observational field study is to account for temporal or spatial autocorrelation (Dormann et al., 2013). Thus, I included the distance-weighted auto-covariate of neighboring plots as fixed effect to the model formula to account for possible spatial autocorrelation of neighboring plots (function 'autocov_dist' from 'spdep' package; Augustin et al. 1996). Furthermore, if data of more than one year were analyzed, temporal autocorrelation was addressed by including the year as ordered fixed effect to the model. Finally, I implemented simultaneous inference procedures with adjustment of p-values for multiple comparisons among different years and/or salvage logging (salvaged/ unsalvaged). This was done by means of the function ‘glht’ from the ‘multcomp’ package (Hothorn et al., 2008).

3. Manuscript overview

The present thesis contains five published articles and one article currently under review, for which the original abstracts, the publication status and the individual author contributions are provided below.

Within the disciplines of natural disturbances, ecology and nature conservation, a number of twelve additional articles were published or accepted in peer-reviewed journals during the time span of the thesis. Further nine articles were published or accepted in non-peer-reviewed journals. All articles are listed in Appendix B.

Article I

Impacts of salvage logging on biodiversity – a global meta-analysis

Simon Thorn, Claus Bässler, Roland Brandl, Philip J. Burton, Rebecca Cahall, John L. Campbell, Jorge Castro, Chang-Yong Choi, Tyler Cobb, Daniel C. Donato, Ewa Durska, Joseph B. Fontaine, Sylvie Gauthier, Christian Hebert, Torsten Hothorn, Richard Hutto, Eun-Jae Lee, Alex B. Leverkus, David B. Lindenmayer, Martin K. Obrist, Joseph Rost, Sebastian Seibold, Rupert Seidl, Dominik Thom, Kaysandra Waldron, Beat Wermelinger, Maria-Barbara Winter, Michal Zmihorski, Jörg Müller

In prep

The amount of forest impacted by natural disturbances has increased in recent decades and will further increase due to ongoing climate change. A commonly applied management response is to remove affected trees (post-disturbance or salvage logging), a practice increasingly criticised because of its impacts on biodiversity. Our global meta-analysis of 24 taxonomic groups revealed that post-disturbance logging significantly reduces dead wood-dependent groups and induces species turnover. This effect is mainly due to a reduction in the amount of dead wood. We conclude that after major disturbances, forest management should encourage the retention of affected trees.

ST developed the idea, conducted the literature search, analysed the data and wrote the first draft of the manuscript. All other authors contributed significantly to revisions.

Article II

Guild-specific responses of forest Lepidoptera highlight conservation-oriented forest management – implications from conifer-dominated forests

Simon Thorn, Hermann H. Hacker, Sebastian Seibold, Hans Jehl, Claus Bässler, Jörg Müller

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http://www.sciencedirect.com/science/article/pii/S0378112714006136

The loss of biodiversity in forest ecosystems has led to a discussion on conservation-oriented forest management, particularly in intensively managed coniferous forest of the northern hemisphere. Two conservation-oriented management strategies, namely advancement of multi-layered forests stands and benign neglect of naturally disturbed stands, are currently being promoted over conventional management strategies of single-layered stands and salvage logging after natural disturbances. However, the effect of these conservation-oriented strategies on nocturnal Lepidoptera has not yet been assessed, despite the high contribution of this order to biodiversity. Here we used full assemblage data of forest-dwelling micro-moths and macro-moths to compare species densities and relative abundance of moths of the larval feeding guilds in single-layered and multi-layered stands, and in naturally disturbed salvaged or unsalvaged stands. We demonstrate that forest moth assemblages are sensitive to conservation-oriented forest management strategies. The relative abundance of moths of the saproxylic and detritus-feeding larval guilds was higher in naturally disturbed unsalvaged stands and in multi-layered stands, whereas that of moths of the moss-feeding larval guild was lower in multi-layered stands. These results corroborate the benefit of a benign-neglect strategy in the management of naturally disturbed stands in conserving saproxylic and detritus-feeding moths and in using natural disturbance to guide the enhancement of stand complexity. Our results demonstrate both the power of functional approaches to reveal slight changes in species communities

and the importance of including micro-moths (a frequently disregarded group) in studies aimed at developing management implications for forest managers.

ST and JM developed the idea. JM and CB designed the experiment. HHH determined species. ST analysed the data and wrote the first draft of the manuscript. All other authors contributed significantly to revisions.

Article III

Response of bird assemblages to windstorm and salvage logging – Insights from analysis of functional guild and indicator species

Simon Thorn, Sinja A.B. Werner, Jürgen Wohlfahrt, Claus Bässler, Sebastian Seibold, Petra Quillfeldt, Jörg Müller

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http://www.sciencedirect.com/science/article/pii/S1470160X15003660

Natural disturbances, such as fire, windstorms and insect outbreaks, are important drivers of biodiversity in forest ecosystems, but at the same time cause large economic losses. Among the natural disturbances in Europe, windstorms cause the highest economic loss. After such storms, damaged forest stands are commonly salvage logged to restore economic value. However, such interventions could affect species assemblages of various taxonomic groups, including breeding birds. Despite these potential effects, investigations of the impacts of post-storm logging are largely lacking. We thus investigated assemblages of breeding birds in 21 logged and 21 unlogged windstorm-disturbed forest plots and 18 undisturbed, control forest plots using fixed-radius point-stop counts three, five and seven years after a windstorm within the Bavarian Forest National Park as part of the European Long-Term Ecosystem Research Network. We recorded 2100 bird individuals of 55 bird species. Bird assemblages were predominantly altered by the consequences of the windstorm and affected only to a minor degree by subsequent logging of storm-felled trees. Nevertheless, bird species richness was significantly reduced by post-storm logging within the first season. In general, the windstorm led to a shift in bird assemblage composition from typical forest species towards open- and shrub-land species. Assemblages of logged and unlogged disturbed plots consisted mainly of long-distance migrants and ground-foraging bird species, whereas assemblages of undisturbed control plots consisted of resident species that forage within vegetation. Both unlogged and logged storm-felled coniferous forest stands were inhabited by endangered or declining bird species, such as Water Pipit (*Anthus spinoletta*) on logged plots and Eurasian Redstart (*Phoenicurus phoenicurus*) on unlogged plots. Indicator species analyses suggested that species of

unlogged storm disturbed plots depended on storm-created legacies, such as pits and snags, for foraging and nesting. Hence, we recommend reducing post-storm logging of these legacies to support species restricted to unlogged disturbed forest. To increase the diversity of breeding birds on the landscape scale, diverse logged and unlogged post-disturbance stands should be provided, which could be gained by a partial benign neglect strategy of storm disturbed forest stands

ST and JM developed the idea. ST, JW, SABW collected the data. JM and CB designed the experiment. ST analysed the data and wrote the first draft of the manuscript. All other authors contributed significantly to revisions.

Article IV

Natural regeneration determines wintering bird presence in wind-damaged coniferous forest stands independent of post-disturbance logging

Sinja A.B. Werner*, Jörg Müller, Marco Heurich, Simon Thorn*

*Those authors contributed equally.

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http://www.nrcresearchpress.com/doi/abs/10.1139/cjfr-2014-0501

Natural disturbances in European production forests are undesired from an economic perspective but are important drivers of biodiversity. The removal of damaged timber to restore economic value is accompanied by negative effects on various species groups, particularly breeding bird communities, and can hinder natural regeneration. However, little is known about the effect of postdisturbance logging on bird assemblages in winter when temperatures are low and food resources are unpredictable. We conducted fixed-radius point counts of wintering birds in forest stands logged or unlogged after windthrows and in mature forest stands to test our predictions that bird species densities and abundances (i) are lower in postdisturbance logged stands and (ii) depend on the amount of natural regeneration, (iii) which differs between logged and unlogged stands. Our generalized linear mixed model did not support the expected differences in bird abundance or species densities between postdisturbance logged and unlogged stands but indicated that mature forest stands harbor the highest bird abundances and species densities. The number of regenerated coniferous trees significantly positively affected wintering bird abundances in both postdisturbance logged and unlogged stands. Hence, the number of coniferous trees appears to be a main predictor of wintering bird presence.

ST and SABW developed the idea, analysed the data and wrote the first draft of the manuscript. SABW collected the data. All other authors contributed significantly to revisions.

Article V

Changes in the dominant assembly mechanism drive species loss caused by declining resources

Simon Thorn, Claus Bässler, Markus Bernhardt-Römermann, Marc Cadotte, Christoph Heibl, Hanno Schäfer, Sebastian Seibold, Jörg Müller

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The species–energy hypothesis predicts that more productive areas support higher species richness. Conversely, when resources are reduced, species richness is reduced. Empirical tests of whether extinctions are predominantly caused by environmental constraints or competitive exclusion are lacking. We experimentally reduced dead wood to c. 15% of the initial amount after a major windstorm and examined changes in assembly mechanisms by combining trait-based and evolutionary species dissimilarities of eight taxonomic groups, differing in their dependence on dead wood (saproxylic/non-saproxylic). Species richness and assembly mechanisms of non-saproxylic taxa remained largely unaffected by removal of dead wood. By contrast, extinctions of saproxylic species were caused by reversing the predominant assembly mechanisms (e.g. increasing importance of competitive exclusion for communities assembled through environmental filtering or vice versa). We found no evidence for an intensification of the predominant assembly mechanism (e.g. competitive exclusion becoming stronger in a competitively structured community).

JM and CB designed the study. JM, CB and ST collected the data. MBR, HS, CH, ST, SS, JM and CB compiled functional traits and phylogenetic trees. ST analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

Article VI

Bark-scratching of storm-felled trees preserves biodiversity at lower economic costs compared to debarking

Simon Thorn, Claus Bässler, Heinz Bußler, David B. Lindenmayer, Stefan Schmidt, Sebastian Seibold, Beate Wende, Jörg Müller

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http://www.sciencedirect.com/science/article/pii/S037811271500777X

The simultaneous control of insect pests and compliance of conservation targets in conifer-dominated forests has intensified public debate about adequate post-disturbance management, particularly in protected areas. Hence, mechanical bark treatments, such as debarking, of disturbance-affected trees have been widely promoted as an on-site method of pest control that accounts for conservation targets because woody biomass is retained. However, the effects of debarking to non-target biodiversity remain unclear. We analyzed data from a two-and-a-half-year field survey of wood-inhabiting fungi, saproxylic beetles and parasitoid wasps in twelve artificial windthrows, created by pulling down mature Norway spruce trees (*Picea abies*) with winches. Each experimental windthrow comprising one control tree, one completely debarked tree and one bark-scratched tree. Insects were sampled using stem emergence traps. Fruiting bodies of wood-inhabiting fungi, number of wood wasp emergence holes, and number of holes made by foraging woodpeckers were assessed by visual counts. We recorded the amount of time needed to complete debarking by machine, bark-scratching by machine and bark-scratching by chainsaw each on 15 separate trees independent of the main experimental design to estimate the economic costs of mechanical bark treatments.

Our results revealed that both debarking and bark-scratching significantly decreased numbers of the emerging target pest *I. typographus* to in median 4% (debarked) and 11% (scratched bark) of the number of individuals emerging from untreated control trees. Compared to control trees, debarking significantly reduced the species density of wood-inhabiting fungi, saproxylic beetles, and parasitoid wasps. By contrast, bark-scratching did not reduce the overall species density of wood-inhabiting fungi, saproxylic beetles or

parasitoid wasps. The time needed for bark-scratching by machine was significantly lower than debarking, whereas bark-scratching by chainsaw needed a similar amount of time as conventional debarking. However, bark-scratching did have some negative effects in common with debarking, such as the significant reduction of wood wasps emergence holes and the reduction of holes made by foraging woodpeckers. Hence, bark-scratching of downed trees, like debarking, might affect higher trophic levels of biodiversity and should be applied only if pest management is urgently needed. We urge policy makers and natural resource managers to rapidly shift current pest management towards new techniques of bark-scratching, particularly in protected areas. Such a shift in post-disturbance pest-control will foster ecosystem integrity at lower economic cost compared to debarking.

ST and JM developed the idea and the experimental design. ST collected the data. ST, CB, StS and HB determined species. ST analysed the data and wrote the first draft of the manuscript. All other authors contributed significantly to revisions.

4. Discussion

The main objective of this thesis was to improve our knowledge on the ecological effects of salvage logging, particularly in stands of Norway Spruce, which have become the most common post-storm salvage logged forest type in Central Europe (Schelhaas et al., 2003). Dead-wood dependent species have been identified as most affected by post-storm salvage logging, while some ground-dwelling arthropods may benefit from salvage logging (Article I and II). However, even groups that show little or no response in species numbers can display extensive species turnovers in assemblages such as the invasion of open-land bird species at the simultaneous loss of woodpecker species. Assemblage turnovers and species extinctions are closely connected to the loss of specific storm-created legacies, such as root plates that provide foraging grounds for breeding birds or clusters of natural regeneration that can provide shelter and food to winter resident birds (Article III and IV). The loss of dead-wood dependent species is caused by a reversal of the predominant assembly mechanisms (e.g. increasing importance of competitive exclusion for communities assembled through environmental filtering or vice versa) and not by an intensification (e.g. competitive exclusion becoming stronger in a competitively structured community). Consequently, species may get extinct because of the loss of dead-wood resources itself or by an increasing competition among remaining resources (Article V). Furthermore, saproxylic species numbers are also drastically reduced by conventional debarking, that aims on retaining dead-wood biomass on-site while populations of *I. typographus* decreased as well. As the best compromise between pest management and benign neglect strategy in protected areas, mechanical bark-scratching of storm-felled spruce may be applied to sustain significant portions of saproxylic biodiversity, while reducing the abundance of pest bark beetle *I. typographus* to 10 % of an untreated control tree. Additionally, bark-scratching by device was significant faster and hence cheaper than debarking. Such compromises represent an important puzzle piece in developing a toolbox for future management of natural disturbances, which incorporate management tools for distinct societal demands (Article VI).

Today, the majority (> 95%) of scientific studies addressing salvage logging (whereas the present thesis is no exception) are conducted within less than 10 years after natural disturbances. Nevertheless, there is scientific evidence that the effects of post-fire logging on breeding bird assemblages can last for up to 20 years (Hobson et al., 1999) or even for up to 200 years in case of arboreal marsupials in Australia (Lindenmayer and Franklin, 1997; Lindenmayer and Ough, 2006). Furthermore, the overwhelming majority of studies focus on measures of species taxonomic diversity, rather than on phylogenetic diversity or ecosystem functioning (Gamfeldt et al., 2013; Leverkus et al., 2012, 2015). At that point, the present thesis has significantly improved our knowledge on the effects of salvage logging by linking taxonomic diversity to measures of phylogenetic and trait-based dissimilarities among assemblages. In detail, guild-specific responses of nocturnal moths and birds revealed that species depending on disturbance-created legacies were most affected by salvage logging. By combining trait-based and phylogenetic species-by-species distances, this thesis further demonstrated that salvage logging reverses natural assembly processes. Finally, the experimental creation of natural windthrows allowed testing the effects of mechanical bark treatments at standardized environmental conditions to develop the best compromise between conservation goals and economic needs.

Studies investigating the effects of salvage logging still face two major methodological problems. First, forest disturbance itself can have major influences on forest biota (see chapter 1.2). Subsequent salvage logging may have only little additional impacts that might be overvalued by study designs without vital forest stands as an undisturbed control. Indeed, the present thesis aimed to overcome these difficulties at least partially by surveying bird species in different seasons (e.g., Article III and IV) in vital spruce stands simultaneously.

Second, observational studies that investigate the effects of post-disturbance salvage logging predominantly use measures of species activity densities, such as point counts of breeding birds or flight interception traps, rather than real estimates of population sizes (Wikars et al., 2005; Sverdrup-Thygeson et al., 2009). Furthermore, activity patterns of arthropods can depend on habitat type (Riecken and Raths, 1996), habitat sizes (Holland et al., 2005) or season (Chiari et al., 2013). Despite several methodological attempts to standardize recorded species numbers, e.g. for sampling effort (Chao et al., 2009; Colwell et al., 2012) or detection probability (Reidy et al., 2011), responses of species activity densities might poorly reflect the response of populations. However, stem emergence traps, as used in experimental windthrows in this thesis, represent species numbers observed within a specific area (e.g., species density) and are independent of species activities (Gotelli and Colwell, 2001).

4.1 Effects of salvage logging to biodiversity

Post-disturbance salvage logging removes the majority of disturbance-created biological legacies, which in turn results in major losses and alterations of disturbance associated biodiversity (Lindenmayer and Franklin, 1997; Nappi and Drapeau, 2009). Post-disturbance forests inhabit large volumes of deadwood with high structural diversity (Swanson et al., 2011). Not surprisingly, salvage logging most seriously affects saproxylic species groups. Moreover, losses of dead-wood dependent species can be present within taxonomic groups that displayed no response in overall species numbers as well. Among others, this thesis revealed that abundance of saproxylic and detritus-feeding moth species decreased by salvage logging with a simultaneous increase of abundance of herb- and grass-feeding moths. However, the amount of dead-wood following post-storm salvage logging can reach more than 70 m^3 ha^{-1} (Priewasser et al., 2013), which is significantly higher than the critical threshold of 30–40 m^3 dead-wood in boreal coniferous forests, as recommended by Müller and Bütler (2010). Indeed, branches, stumps and logging residuals remain on site, but are rapidly overgrown by ground vegetation. The resulting shift in microclimatic conditions then additionally modifies resource quality, leading to extinction of saproxylic beetles depending on sun-exposed, dry branches (Thorn et al., 2014).

This thesis provides strong evidence that extinction of saproxylic taxa under dead-wood reduction is caused by a reversal of the predominant assembly mechanisms, e.g. increasing over-dispersion to clustered communities and increasing clustering to over-dispersed communities, and not by an intensification of the pre-existing assembly mechanism. Interestingly, all saproxylic taxa investigated in the present thesis assembled through environmental filtering, with the exception of wood-inhabiting fungi. Extinctions of wood-inhabiting fungi species were explained by an increasing importance of environmental filtering, in contrast to all remaining saproxylic groups. In contrast to all other investigated saproxylic groups, wood-inhabiting fungi heavily exploit dead-wood resources from within and start competing among dead-wood resources quickly (Fukami et al., 2010). By contrast, epixylic lichens are autotrophic and depend on dead-wood predominantly as a growing substrate. These fundamental differences in the life style of wood-inhabiting fungi compared to other saproxylic groups may account for important differences in the assembly mechanisms and resulting mechanisms causing species extinctions (Bässler et al., 2015).

4.2 Conservation oriented management of natural disturbances

Besides protected areas and intensive wood productions, ecologically sustainable managed forests cover a majority (85%) of global forested areas (Lindenmayer et al., 2012). Within the overwhelming majority of these forests, natural disturbances are conventionally salvage logged without any set-aside approaches since economic goals play a major role in forest management decisions. For instance, storm-felled spruces can easily exceed an economic value of more than 30,000 € ha^{-1}. Nevertheless, conventional salvage logging is not in consensus with the primary objectives of ecologically sustainable managed forests, given its major impacts to biodiversity (Lindenmayer et al., 2008). Hence, an implementation of sustainable disturbance management to the main management goals of ecologically sustainable managed forests is urgently needed to meet global goals of sustainability and economy alike (Fischer et al., 2007). The main management goals of natural disturbed forests can vary from i) conventional managed forest, where all timber is completely salvage logged in order to retain economic values to ii) remote mountain areas or buffer zones of protected areas where salvage logging is primarily applied to reduce populations of insect pests to iii) central parts of national parks and protected areas, where absolutely no salvage logging takes place. However, such an implementation is a time consuming and cost intensive procedure that may take several years. Nevertheless, local forest managers can retain storm-created legacies in the short run. Some feasible management recommendations to retain disturbance-created legacies in storm-felled forests among different main management goals are (Fig. 3):

- ❖ <u>Root plates</u> of storm-felled trees can be kept uprooted to maintain pits and mounds, which increase habitat heterogeneity and represent important biological legacies for breeding birds (Article III). Likewise, increasing habitat heterogeneity enhance the diversity of vascular plants (Kooch et al., 2012) and moist patches provided beneath root plates of storm-felled trees, can act as important refuges for moist-adapted arthropod species in open areas (Toivanen et al., 2014).
- ❖ The present thesis suggests that mechanical <u>bark-scratching</u> represents a good compromise between the reduction of pest species *I. typographus* on the one hand and preservation of non-target biodiversity on the other hand. Such

compromise might be applied in buffer zones of national parks or remote mountain areas, were woody biomass should be retained on-site (Article VI).

- Cable yarding or helicopter logging can avoid soil disturbance, increasing erosion and damage to natural regeneration and assemblages of herbaceous plants and shrubs (Waldron et al. 2013, Priewasser et al., 2013). Both animal and machine harvesting perform well in salvage logging at low removal intensities in Mediterranean Pine forests, while animal harvesting is more expensive. However, profit may not be as large as to become a major driver in a national park, since visitors may represent a main factor promoting the use of animal harvesting. Hence, in some cases animal harvesting might represent a valuable alternative to machine harvesting (Spinelli et al., 2013).
- Snags and storm-felled trees of low economic value still represent important biological legacies and can be retained (Hutto, 2006). Sun-exposed dry branches, a characteristic biological legacy in storm-felled forests, may be retained by preserving branches at unchipped tree crowns (Thorn et al., 2014). A further removal of logging residuals or stump extraction following post-storm salvage logging may additionally decrease biodiversity (Lassauce et al., 2012).
- The present thesis revealed that the impacts of salvage logging to biodiversity were predominantly caused by a reduction of dead-wood amount (according to the more individuals hypothesis) and only to a minor degree to a reduction of dead-wood heterogeneity (according to the habitat-heterogeneity hypothesis). Hence, strategies for the conservation of biodiversity in salvage logging on a landscape scale may likewise focus on a certain amount of natural disturbed forest to be retained (Article I). Taxa which are negatively affected by post-disturbance logging can be simply supported by set-aside approaches (Nappi et al., 2011).

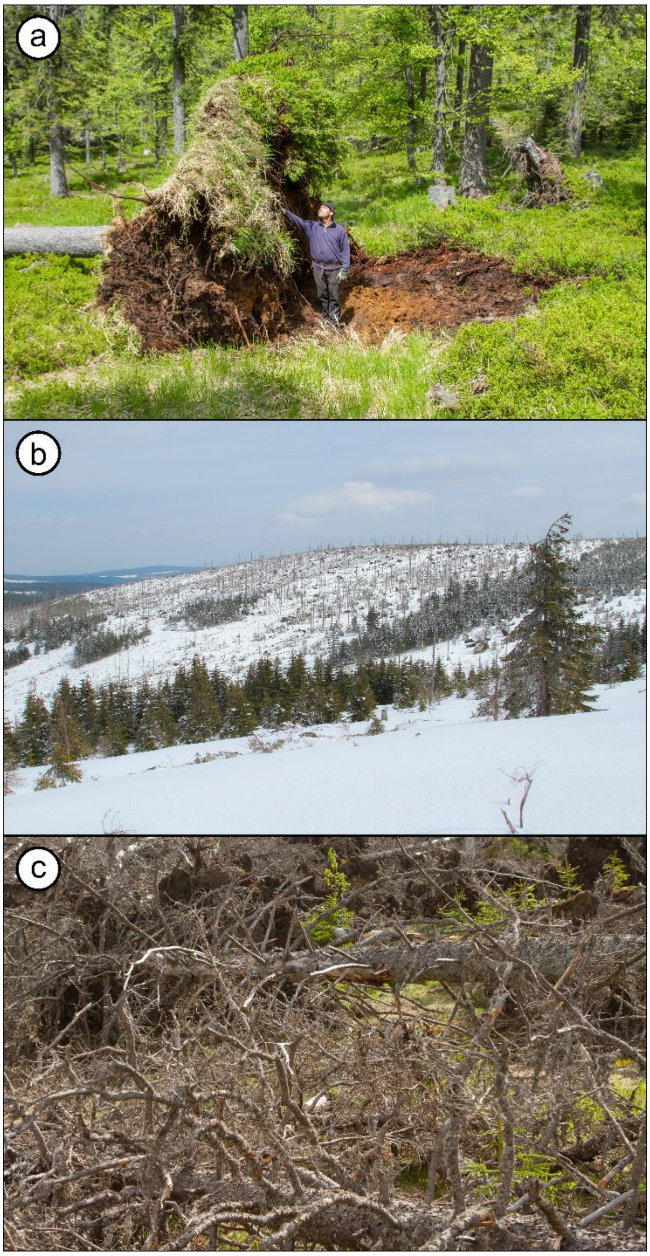

Figure 3: Typical biological legacies of storm-felled forests which can be retained in post-disturbance salvage logging operations: a) uprooted root plates may act as refuge for moist-adapted arthropods; b) natural regeneration in storm-felled forests representing important habitat features for foliage-gleaning winter resident birds; and c) sun-exposed, dry branches of storm-felled trees are habitat for specialized saproxylic beetles.

The number of retained biological legacies will be most effective for conservation of legacy-associated taxa if it covers the full range of ecological and microhabitat conditions, e.g. wide range of diameter, to support a broad set of taxa (e.g., Hutto 2006). Preservation of storm-created biological legacies is applicable in all types of forest ecosystems around the world to foster the resilience of species assemblages and habitat structure (Seidl et al., 2014b), even where the effects of post-disturbance logging are not known in detail but decision-making is already under way (González and Veblen, 2007).

Natural disturbances and forest management compete for timber. Thus, the wood amount created by natural disturbances may be implemented a priori in annual harvesting plans to adjust overall logging rates (Schmiegelow et al., 2006). Furthermore, in areas were salvage logging should be applied, retention approaches may follow a raw and feasible prioritization to sustain disturbed forests at least partially. For instance, areas with very sensitive soils, near water bodies, high conservation interest, steep slopes, or operational constraints, such as areas with difficult accessibility, may be excluded a priori from overall logging operations to act as refuges for disturbance dependent species (Nappi et al., 2011). Indeed, such a combination of salvage logged and unlogged areas enhance biodiversity at the landscape level significantly more than a single treatment (Duelli et al., 2002).

4.3 Future directions

Despite the emulation of natural disturbances to forest management plans has already been promoted as a paradigm to guide conservation efforts (Angelstam, 1998), salvage logging without any set-aside approaches is still widespread (Schmiegelow et al., 2006).

To support declining forest biota and likewise preserve overall forest sustainability within an ongoing forest management, conservationists and ecologists developed various types of green tree retention approaches (Gustafsson et al., 2010, 2012). Such approaches are based on ‘the long-term retention of structures (vital and dead trees) at the time of harvest to achieve a significant level of continuity in forest structure that promotes the maintenance of biodiversity and ecological functions’ (e.g., Lindenmayer et al., 2012). This approach was primarily developed in clear-cut forests, but is now increasingly applied to various logging schemes (Fedrowitz et al., 2014; Mori and Kitagawa, 2014). Retention approaches, as those developed for green-tree logging (Gustafsson et al., 2012), are sparsely available for post-disturbance logging (but see Nappi et al., 2011), despite frequency and extend of natural disturbances will further increase (Seidl et al., 2014). As a result, conservationists increasingly demand for retention approaches in post-disturbance logging that address the needs of early successional species (Nappi et al., 2011). The present thesis confirmed that retention approaches in salvage logging could help to preserve biodiversity.

Today, benign-neglect approaches in disturbed forests of the northern hemisphere are extremely rare, resulting in extensive salvage logging operations. Hence, the most urgent step to preserve biodiversity in salvage logging operations are evidence based suggestions on minimum areas to be retained to preserve a certain amount of biodiversity. Such evidence-based recommendations for minimum areas do not exist so far but can guide decision-making toward post-disturbance retention areas. Using the 199 original species-by-plot matrices (Article I) and corresponding taxonomically individual plot sizes and seamless sample-size based extrapolation (Chao and Jost, 2012), I estimated the minimum unsalvaged disturbance area required to maintain 95% of local species richness of unlogged disturbance forests (Fig. 4). This approach revealed a coarse and wide range of area sizes to be retained ranging from less than one hectare to more than 500 ha, depending on the respective disturbance regime. Across all studied taxa and disturbance types a median value of 16 ha was required to conserve 95% of the species richness of an otherwise post-disturbance salvage logged area. Disturbance regime specific analyses (Fig. 4 b-d) revealed a clear tendency to larger requirements for retention areas in burned forests.

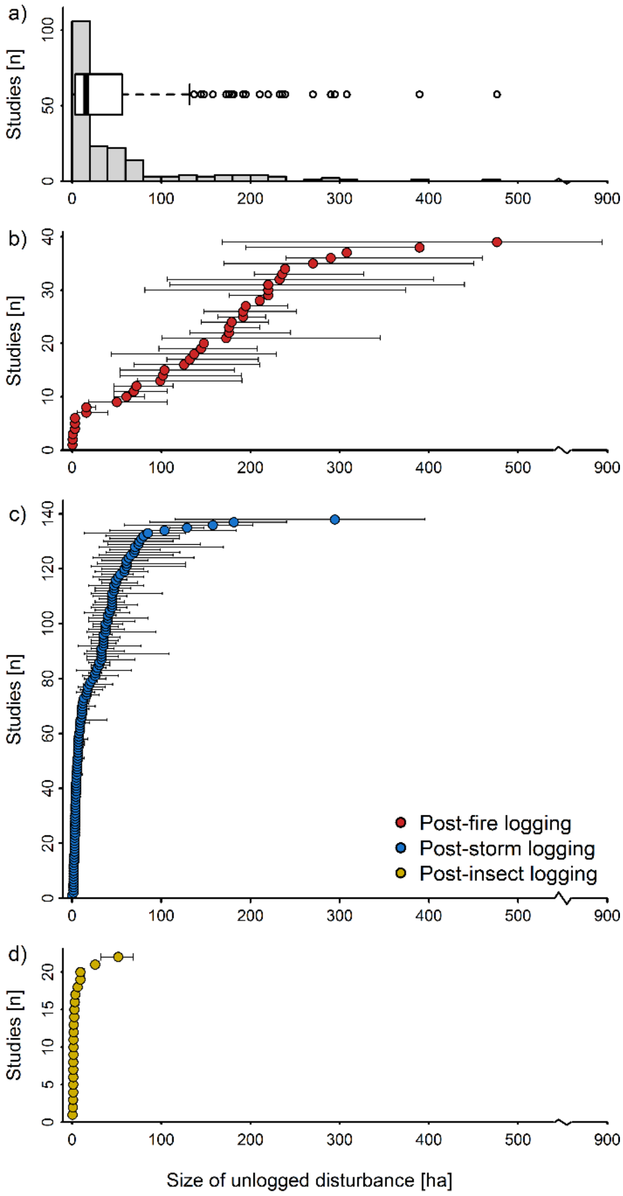

Figure 4: Estimated mean size (ha) as well as upper and lower confidence intervals of unlogged natural disturbed forest that is needed to support 95 % of local species richness, based on seamless sample-size based extrapolation (Chao and Jost, 2012). Analyzed jointly (a), data suggests a median of 16 ha of disturbed forest to be left unsalvaged. Note that values vary significantly with disturbance regime (b-d).

These findings are certainly biased by an uneven distribution of available studies across taxonomic groups, but also reflect the spatial extent of the respective disturbance regimes and study areas. It is important to note that this analysis is based on estimated areas, does not correspond to viable populations of a specific species, and should hence be treated with caution. Furthermore, the estimated area strongly depends on disturbance type and investigated species group. From an ecological point of view, the meta-community concept can provide a theoretical framework for understanding and investigating both the extend and the spatial distribution of retention patches (reviewed in Leibold et al., 2004). Here, all individuals of a specific species within a patch of unlogged disturbed forest represent a population, which is linked by dispersal to other patches, together forming a meta-population (Hanski, 1998). Consequently, the suitable area and spatial distribution of retention patches strongly depend on the dispersal ability and the home range of a given species of conservation interest (Leibold et al., 2004). However, Fahrig (2013) proposed to replace size and isolation of habitat patches in the ongoing SLOSS debate (**S**ingle **L**arge **O**r **S**everal **S**mall) by a single variable ‘habitat amount’, which corresponds to the total amount of habitat on a landscape scale. Such a simplified view may additionally guide forest management and future research plans by explicitly focusing on the retention of as much patches of 16 ha as possible, irrespective of their spatial distribution.

Research plans for investigating dead-wood retention approaches should focus on the same questions that remain to be addressed in common green tree retention: namely, to identify an adequate amount (and spatiotemporal distribution) of areas to set-aside (e.g., Gustafsson et al. 2012). Nevertheless, a size of 16 ha might act as rule of thumb for managing natural disturbances and – even more important – as origin for future research programs that determine suitable sizes of retention patches in salvage logging operations in detailed.

Experiments are the most rigorous form of ecological research and allow researchers to untangle the effects of different determinants on species assemblages and ecosystem processes. In contrast to observational studies, experimental designs can help to untangle the influence of factors, which are correlated under natural conditions, such as dead-wood amount and dead-wood heterogeneity (Seibold et al., 2015b). However, the experimental creation of post-disturbance forest remains a challenging task, owing to high costs and difficulties in technical realization (Lindenmayer et al., 2010). Nevertheless, prescribed burning has been established as a fix discipline in ecological research (Greene et al., 2006; Hyvärinen et al., 2009; Ryan et al., 2013), while experimental creations of windthrows remain scarce (but see Cooper-Ellis et al., 1999). Experimental creation of large windthrows might be used to untangle the effects of disturbance and salvage logging in comparison to vital forest stands as well as to determine suitable sizes of retention patches in salvage logging. However, forest experiments on a landscape scale, such as for instance the EMEND (Ecosystem Management by Emulating Natural Disturbance) experiment in eastern Canada (Work et al., 2010), remain extremely challenging in densely populated and intense managed forest landscapes of central Europe.

A major challenge for natural resource managers and scientists is that the incidence of stand-replacing natural disturbances remains spatially and temporally unpredictable, an inherent uncertainty that needs to be addressed in forest research and management plans. Hence, such contingency plans are less controversial when jointly developed with (and confirmed by) stakeholders, scientists and natural resource managers before the next disturbance occurs (Lindenmayer et al., 2010). The prior implementation of sampling grids and pre-disturbance monitoring programs – which provide useful information even if and where the forest is not disturbed – can provide a stronger framework for evaluating natural disturbances and management options than post-hoc comparisons.

4.4 Conclusions

The preservation of early-successional (post-disturbance) forest communities frequently evokes disagreement between conservationists and natural resource managers. However, the removal of disturbance-affected trees is the business as usual in the majority of managed forests of the northern hemisphere. The results of this thesis indicate that species associated with dead-wood legacies (which are often also associated with mature forest and hence targeted by conservation efforts) show strongest declines in species numbers after post-disturbance logging. To obtain some economic return while retaining those taxa, I recommend an expansion of the green-tree retention approach to storm-felled forests and a preservation of storm-created legacies, such as root plates or sun-exposed dry branches. Researcher should identify minimum levels of retention patches, particularly through well-planned and detailed long-term experiments.

Post-disturbance logging is often applied to avoid outbreaks of pest species only, such as the European Spruce Bark Beetle. Here, selective bark treatments, such as mechanical bark scratching, can drastically reduce population densities of the pest species but maintain large parts of non-target biodiversity. Mechanical bark-treatments represent a valuable compromise between targets of pest management and biodiversity conservation. Such compromises may help to combine the complex socio-economic needs that society imposes on the management of natural disturbed forest. Nevertheless, mechanical bark treatments, technical devices as well as conservation guidelines in general might refined by upcoming research efforts, particularly in the light of increasing natural disturbances in near future. Detailed future scientific investigations on the amount and spatial distribution of retention patches in naturally disturbed forests may take decades. Meanwhile estimated sizes of retention patches may act as rules of thumb for forest management and as basis for future research.

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Appendix A – Curriculum Vitae

Personal data

Simon Otto Thorn
Birth: 14.02.1988 in Darmstadt, Germany
Privat address: Hardenbergstraße 12, 95444 Bayreuth
Email: simon@thornonline.de
Telephone: +49-151-22900426

Education

2013 – 2016 PhD student at Technical University of Munich in cooperation with Bavarian Forest National Park

2010 – 2012 Master of Science Biology at Justus-Liebig-University Giessen

Thesis: “Collateral damage beyond species – How post-windthrow salvage logging alters the functional composition of saproxylic beetles assemblages“
Grade: 0.8 (with distinction)

2007 – 2010 Bachelor of Science Biology at Justus-Liebig-University Giessen

Thesis: “GIS-based habitat model for the little owl (*Athene noctua*) in Hessen”
Grade: 2.1 (good)

1998 – 2007 Abitur at Wilhelm-von-Oranien-Schule Dillenburg
Grade: 2.1 (good)

Work experience

Sep 2014	Project on Scopoli's Shearwater (*Calonectris diomedea*) in Linosa Island, Mediterranean Sea
May 2014 – Dec 2014	Member of research staff at Bavarian Forest National Park, Germany
Jan 2013 – Mar 2013	DFG-project on breeding ecology of the Wilson's storm petrel (*Oceanites oceanicus*) and the Black-bellied storm petrel (*Fregetta tropica*) at King-George Island, Antarctic Peninsula
Aug 2010 – Sep 2012	Under-/graduate scientific assistant at Justus Liebig University Giessen, Chair of Animal Ecology
Apr 2010 – today	Qualification as state-approved bird-ringer and ongoing cooperation in distinct scientific bird banding projects
Sep 2009 – today	Freelance consultant for birds, bats, dragonflies, damselflies and grasshoppers
May 2006 – today	Municipal commissioner for the protection of birds by order of the "Ornithological state institute for Hesse, Rhineland-Palatinate and the Saarland"

Grants

2015	Lecture grant by the German academic exchange service
2014	Research Grant by the German Ornithologists' Society
2014	Research Grant by the German Ornithologists' Society (cooperation)
2013	PhD Scholarship by the German Environmental Foundation

Reviewer for

Forest Ecology and Management, Journal of Ornithology, Journal of Applied Ecology, Basic and Applied Ecology, European Journal of Forest Research, PlosOne

Appendix B – Publication list

List of peer-reviewed articles published during the time span of this thesis.

Accepted / Online first

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., **Thorn**, S., Ulyshen, M. & J. Müller (online first). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. **Journal of Applied Ecology**.

2016

Thorn, S., Bässler, C., Bussler, H., Lindenmayer, D.B., Schmidt, S., Seibold, S., Wende, B. & J. Müller (2016). Bark-scratching of storm-felled trees preserves biodiversity at lower economic costs compared to debarking. **Forest Ecology and Management**, 364, 10-16.

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S. & J. Müller (2016). Changes in the dominant assembly mechanism drives species loss caused by declining resources. **Ecology Letters**, 19(2), 163-170.

Müller, J., **Thorn**, S, Baier, R., Talebi, S.K., Barimani, H.V., Seibold, S., Ulyshen M.U. & M.M. Gossner (2016). Protecting the forests while allowing removal of damaged trees may ecologically degrade the Hyrcanian beech forests of Iran. **Conservation Letters**, 9(2), 106-113.

Thorn, S., Werner, S. A. B., Wohlfahrt, J., Bässler, C., Seibold, S., Quillfeldt, P. & J. Müller (2016). Response of bird assemblages to windstorm and salvage logging – Insights from analyses of functional guild and indicator species. **Ecological Indicators**, 65, 142-148.

Bässler, C., Müller, J., Cadotte, M.W., Heibl, C., Bradtka, J.H., **Thorn**, S. & H. Halbwachs (2016). Functional response of lignicolous fungal guilds to bark beetle deforestation. **Ecological Indicators**, 65, 149-160.

Heikkala, O., Seibold, S., Koivula, M., Martikainen, P., Müller, J., **Thorn**, S. & J. Kouki (2016). Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. **Forest Ecology and Management**, 359, 51-59.

Mader. V., Birkhofer, K., Fiedler, D., **Thorn**, S., Wolters, V. & E. Diehl (2016). Land use at different spatial scales alters the functional role of web-building spiders in arthropod food webs. **Agriculture, Ecosystems & Environment** 219, 152-162.

Thorn, C.J., Bissinger, K., **Thorn** S. & F.X. Bogner (2016). "Trees live on soil and sunshine!"-Coexistence of Scientific and Alternative Conception of Tree Assimilation. **PlosOne**, 11(1), e0147802.

2015

Thorn, S., Hacker, H. H., Seibold, S., Jehl, H., Bässler, C., & J. Müller. (2015). Guild-specific responses of forest Lepidoptera highlight conservation oriented forest management - implications from conifer-dominated forests. **Forest Ecology and Management** 337, 41-47.

Thorn, S., Müller, J., Bässler, C., Gminder, A., Brandl, R. & C. Heibl. (2015). Host abundance, durability, basidiome form and phylogenetic isolation determine fungivore species richness. **Biological Journal of the Linnean Society** 114, 699-708.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., **Thorn**, S. & J. Müller (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. **Conservation Biology**, 29, 382–390.

Werner*, S.A.B., Müller, J., Heurich, M. & S. **Thorn*** (2015). Natural regeneration determines wintering bird presence in wind-damaged coniferous forest stands independent of post-disturbance logging. Canadian Journal of Forest Research 45(9), 1232-1237. * These authors contributed equally.

Beudert, B., Bässler, C., **Thorn**, S., Noss, R., Schröder, B., Dieffenbach-Fries, H., Foullois, N. & J. Müller (2015). Bark beetles increase biodiversity while maintaining drinking water quality. **Conservation Letters** 8, 272-281.

Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., **Thorn**, S., Ulyshen, M.D. & J. Müller (2015). Experimental studies of dead-wood biodiversity - A review identifying global gaps in knowledge. **Biological Conservation**, 191, 139-149.

2014

Thorn, S., Bässler, C., Gottschalk, T., Hothorn, T., Bußler, H., Raffa, K., & J. Müller (2014). New insights into the consequences of post-windthrow salvage logging revealed by functional structure of saproxylic beetles assemblages. **Plos One** 9, e101757.

Seibold, S., Bässler, C., Baldrian, P., **Thorn**, S., Müller, J. & M. M. Gossner (2014). Wood resource and not fungi attract early-successional saproxylic species of Heteroptera - an experimental approach. **Insect Conservation and Diversity**, 7, 533–542.

Articles in non-peer-reviewed journals

Gelpke, C., Stübing S. & **Thorn**, S. (accepted). Aktuelle Ergebnisse zu Raumnutzung, Zugwegen und Bruterfolg hessischer Rotmilane anhand von Telemetrie-Untersuchungen. Vogel und Umwelt.

Müller, J., Seibold, S. & **Thorn**, S. (2014). Fledermausforschung im Nationalpark Bayerischer Wald. AFZ-Der Wald, 9, 29–30.

Müller, J., Seibold, S., Werner, S. & **Thorn**, S. (2014). Die Rückkehr des Habichtskauzes in den Bayerischen Wald. Der Falke, Sonderheft, 47–49.

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